

Systematics and Evolution of the Family Chrysopidae (Neuroptera),  
with an Emphasis on their Morphology

By  
© 2018

Laura C.V. Breitzkreuz  
M.Sc. Humboldt Universität zu Berlin, 2012  
B.Sc., Freie Universität Berlin, 2009

Submitted to the graduate degree program in Ecology and Evolutionary Biology and the  
Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for  
the degree of Doctor of Philosophy.

---

Chair: Michael S. Engel

---

Mark Holder

---

Kirsten Jensen

---

Bruce Lieberman

---

Erik Lundquist

Date Defended: 24 April 2018

The dissertation committee for Laura C.V. Breitkreuz certifies that this is  
the approved version of the following dissertation:

**Systematics and Evolution of the Family Chrysopidae (Neuroptera),  
with an Emphasis on their Morphology**

---

Chair: Michael. S. Engel

Date Approved: 24 April 2018



## Abstract

Chrysopidae, commonly known as ‘green lacewings,’ are worldwide-distributed insects that are integral to sustainable agricultural practices, acting as important biological control agents. With approximately 1,400 species segregated in 80 genera, the green lacewings comprise one of the largest groups in the order Neuroptera, rivaling the antlions (Myrmeleontidae). The group is widely studied not only for their agricultural benefits, but also as models for cryptic or sympatric speciation, complex communication systems, and peculiar behaviors linked to specific anatomical traits. As such, the group has attracted much attention and previous studies have attempted to resolve relationships within the family, but for varying reasons these studies have had their limitations.

In the present dissertation, phylogenetic relationships among the major lineages of green lacewings are reconstructed with the inclusion of a variety of data sources. A detailed morphological data set, based on diverse sampling is the core of this work, and was combined with molecular data including seven loci and mitogenomic data, in order to infer a comprehensive phylogeny of the family Chrysopidae. We provide the results of several phylogenetic analyses, primarily using Bayesian inference, covering the entire family as well as detailed analyses of the subfamilies and tribes. Divergence times of the major groups in Chrysopidae were estimated, and the evolution of several morphological characters is investigated. On the basis of the resulting phylogenetic hypotheses, we provide a revised classification of the subfamilies, tribes, genera, and subgenera of Chrysopidae. The dissertation has a strong focus on morphology, and the basis for the combined data phylogeny was a revision of the homology statements of all external and genitalic characters of Chrysopidae. As an exemplar for the family, we here describe the

morphological characters of *Chrysopa oculata* Say, and provide a revised ontology for the family.

The wings of Chrysopidae are unique among lacewings given the high amount of vein fusion. This trait is further investigated and set into a comparative morphological framework in Neuropteroida.

## **Acknowledgements**

First and foremost, I would like to thank my advisor Michael Engel. I feel extremely honored to have gotten the chance to be his student. The amount of resources he provides are enormous, and his investment in the well-being of his students has been imperative for my time at the University of Kansas. Talking for hours about insects in general, taxonomy, systematics, and the semantics of biology and philosophy has broadened my scientific horizon, and I will miss it dearly. I am certain that I would have left this degree with half the skills if it wasn't for him and his dedication to share his knowledge. Secondly, I want to thank my second (unofficial) supervisor, Shaun Winterton, who complimented Michael's advisory perfectly. The time I spent in his lab at the CDFA, Sacramento, was extremely beneficial for my research and I also thoroughly enjoyed the time at the CDFA, and in his lab. I am truly grateful to have had these two wonderful scientists and people as my mentors over the past five years.

Thank you to the members of my doctoral committee. Bruce Lieberman, who introduced me (and an entire discussion group) to the ideas of macroevolution. Mark Holder, who had to spend endless hours helping me to figure out script errors in RevBayes. Kirsten Jensen, who, through kind conversations, helped me focus my time and energy in the right directions for my dissertation, such as not dwelling in ancestral character state reconstructions for fairly uninteresting characters. Eric Lundquist who was a very kind external committee member.

I would like to thank the NSF for funding the project on the phylogeny of Chrysopidae, KU for providing me with a first year scholarship, and several GRA and GTA appointments, and

the KU Entomology Endowment, for awarding me several summer support scholarships and travel rewards.

I want to thank Michael Ohl, from the Berlin Natural History Museum, for introducing me to the academic world of entomology at the age of 14, by showing me that there is a scientific approach to simply “liking bugs”. He has been a mentor ever since, and I am grateful for his guidance throughout my career, especially in my Bachelors and Masters degree in his lab.

A thank to my many collaborators on this project. To the late Norm Penny, who graciously invited me to the Calacademy in my first year and shared all his wisdom on chrysopid morphology and systematics with me. To Kady Tauber, who has been a tremendous resource and was eager to talk about Chrysopids and especially their larvae with me. The incredible detail and thoroughness in her body of work has been a role model for my studies of Chrysopidae. As well as to her late husband, Maurice Tauber, whom I had the honor of meeting at the beginning of my Dissertation. Both are incredible researchers, and had a great impact in the field of Chrysopidae. To John Oswald, whose outstanding online bibliography and species catalog (Lacewing Digital Library) simplified this project by about 5 years. To Horst and Ulrike Aspöck, for their advice and kind interest in my research.

Thank you to the curators who lent me specimens: Norm Penny at the Calacademy, Ben Price (British Museum of Natural History), the entomology division at the Paris Natural History Museum, Harald Bruckner at the Vienna Natural History Museum, and Lukas Kirschey at the Berlin Natural History Museum .

Thank you to the KU Ecology and Evolutionary Biology Department, the faculty, the helpful administration staff, and the people of the Entomology Department at KU, especially Jennifer Thomas and Zach Falin.

Thank you to my Sacramento lab: Ivonne Garzón, who has helped me greatly with the molecular phylogenetics, and Jessica Gillung, who helped me with more theoretical phylogenetics and debugging RevBayes scripts, and both for being great friends in Sacramento.

My time in Lawrence would have been not nearly as good without my many wonderful friends here. Thank you to the EEB GSO people for providing such a friendly environment. Thank you to my non-biology friends Shannon O'Shea and Stephanie Crawford, for making me feel at home in Kansas. I especially want to thank my PSB/Entomo-Crew including Marianna Simoes, Stephen Baca, Mabel Alvarado, Jennifer Girón, and Manu Toussaint. Thank you to all of you for your great friendship. We have had incredibly great times here and our reunions will be epic. Stephen, thank you for your kindness and care, as well as your help over the last five years. Mabel, my one and only lab mate, thank you for going through all of this together with me.

Thank you to my three best friends, who have supported me in so many ways. Katrina Mayer, with whom I grew up together, and we surprisingly both ended up as biologists. Lukas Kirschey, whom is one of my favorite people to talk to, and who has gone with me through our bachelors and masters degree. And Marianna Simões, who has become my family in a small town in Kansas, and has been extraordinarily important for the success of my dissertation. Thank you for these last few years, as a bestie, roomie and sister, and for being the biggest reason why I loved it here so much. You are, indeed, better than mascara.

And at last, but not least, I would like to thank my family. To my mom, Sabine Moeck-Breitkreuz, and dad, Christoph Breitkreuz, whose strength, love, nourishment for critical thinking, and interest in science has provided me with all I needed. Thank you for supporting my university career, financially and emotionally. Thank you for providing a ten year old with “scientific equipment” to study and document ant colonies, and for disregarding some teachers strongly

voiced opinions on her not being smart enough for high school. And especially, thank you for being so proud of me. Thank you to my wonderful sister, Merle Breitzkreuz, who gets me, is very good at putting things into (for me) new perspectives, and whom I admire greatly. Thank you to my boyfriend Stefan Erler, who has helped me incredibly much these last two years, foremost by keeping me sane. Thank you for spending way too many vacation days in Kansas, for being so interested in a field that was new to you, and especially for your love. Long distance while writing a dissertation is not easy, but worth every bit for you. Thank you to my grandparents (Horst and Christa Moeck) for creating a large and especially loving family environment, with a wonderful motto of “hier MUSS jeder machen was er will” (everybody HAS to do what they want here). And finally thank you to my aunts, uncles, and all cousins from the Moeck- and Breitzkreuz-family. Throughout my eleven years in the university I felt extremely loved and supported, and very much enjoyed your interest in my work.



*Chrysopa oculata* Say

*“How so small an insect, reared from infancy upon cleanly diet of the juices of just-killed animals, spending its resting period in a “glistening, white cocoon, which looks like a large seed-pearl,” and deriving nourishment as an adult from cleanly sources, can develop so disagreeable a stench is indeed a wonder”*

— Weed, 1897

# Table of Contents

<b>Introduction</b> .....	1
References.....	7

## CHAPTER 1: A Phylogeny of Chrysopidae Inferred from Morphological and Molecular Data

<b>Introduction</b> .....	12
<b>Material and methods</b> .....	19
Taxon sampling.....	19
Morphological character list.....	21
Analyses.....	40
Output.....	43
<b>Results</b> .....	45
Bayesian analyses.....	45
Analysis 1: molecular data.....	45
Analysis 2: morphological data.....	48
Analysis 3: combined data, Chrysopidae I.....	50
Analysis 4: combined data, Chrysopidae II.....	52
Analysis 5: combined data, Apochrysinæ.....	53
Analysis 6: combined data, Nothochrysinæ.....	55
Analysis 7: combined data, Belonopterygini and Leucochrysinini.....	57
Analysis 8: combined data, Ankylopterygini and <i>Nineta</i> -group.....	62
Analysis 9: combined data, Chrysopini.....	65



Analysis 10 and 11: combined data, Chrysopidae divergence times .....	66
Maximum Likelihood analysis.....	70
Analysis 12: combined data, Chrysopidae .....	70
Parsimony analyses .....	72
Analysis 13: morphological data, Chrysopidae.....	72
Analysis 14: combined data, Chrysopidae .....	72
<b>Discussion</b> .....	76
Analyses .....	76
Relationships of Chrysopidae and character evolution.....	77
The family Chrysopidae .....	77
Relationships between subfamilies – Apochrysinæ, Nothochrysinæ, and Chrysopinæ .....	79
Relationships within Apochrysinæ.....	93
Relationships within Nothochrysinæ.....	94
Relationships between the tribes of Chrysopinæ.....	96
Age of Chrysopidae.....	114
<b>Conclusion</b> .....	116
<b>References</b> .....	117
Supplementary Material.....	126

## CHAPTER 2: Generic Revision of Chrysopidae (Neuroptera)

<b>Introduction</b> .....	134
<b>Material and Methods</b> .....	139
<b>Key of to the genera of Chrysopidae</b> .....	140
<b>Classification of Chrysopidae</b> .....	161

Family Chrysopidae Scheider 1851 .....	161
Subfamily <b>Apochrysinæ</b> Handlirsch 1908 .....	162
Genus <i>Apochrysa</i> Schneider 1851 .....	163
Genus <i>Domenechus</i> Navás 1913 .....	168
Genus <i>Joguina</i> Navás 1912 .....	172
Genus <i>Loyola</i> Navás 1913 .....	175
Genus <i>Nobilinus</i> Navás 1913 .....	179
Subfamily <b>Nothochrysinæ</b> Navás 1910 .....	182
Genus <i>Asthenochrysa</i> Adams and Penny 1992 .....	183
Genus <i>Dictyochrysa</i> Esben-Petersen 1917 .....	186
Genus <i>Hypochrysa</i> Hagen 1866 .....	190
Genus <i>Kimochrysa</i> Tjeder 1966 .....	194
Genus <i>Leptochrysa</i> Adams and Penny 1992 .....	197
Genus <i>Nothochrysa</i> McLachlan 1868 .....	200
Genus <i>Pamochrysa</i> Tjeder 1966 .....	204
Genus <i>Pimachrysa</i> Adams 1956 .....	208
Genus <i>Triplochrysa</i> Kimmins 1952 .....	212
Subfamily <b>Chrysopinae</b> Schneider 1815 .....	215
Tribe <b>Ankylopterygini</b> Navás 1910 .....	216
Genus <i>Ankylopteryx</i> Brauer 1864 .....	217
Genus <i>Chrysopidia</i> Navás 1910 .....	221
Subgenus <i>Chrysopidia</i> Navás 1910 .....	222
Subgenus <i>Chrysotropia</i> Navás 1911 .....	225
Genus <i>Nineta</i> Navás 1912 .....	229

Subgenus <i>Nineta</i> Navás 1912.....	229
Subgenus <i>Tumeochrysa</i> Needham 1909 <b>stat. nov.</b> .....	233
Genus <i>Parankylopteryx</i> Tjeder 1966.....	237
Genus <i>Retipenna</i> Brooks 1986.....	241
Genus <i>Semachrysa</i> Brooks 1938.....	245
Genus <i>Signochrysa</i> Brooks and Barnard 1990.....	249
Tribe <b>Belonopterygini</b> Navás 1913 .....	253
Genus <i>Abachrysa</i> Banks 1938.....	254
Genus <i>Belonopteryx</i> Gerstaecker 1863 .....	258
Genus <i>Calochrysa</i> Banks 1943.....	262
Genus <i>Chrysacanthia</i> Lacroix 1923.....	266
Genus <i>Chrysaloyisia</i> Navás 1928.....	270
Genus <i>Dysochrysa</i> Tjeder 1966.....	273
Genus <i>Evanochrysa</i> Brooks and Barnard 1990.....	277
Genus <i>Italochrysa</i> Principi 1946.....	281
Genus <i>Nacarina</i> Navás 1915.....	286
Genus <i>Nesochrysa</i> Navás 1910 .....	291
Genus <i>Nodochrysa</i> Banks 1938.....	295
Genus <i>Oyochrysa</i> Brooks 1984 .....	299
Genus <i>Stigmachrysa</i> Navás 1925.....	303
Genus <i>Turnerochrysa</i> Kimmins 1935.....	307
Genus <i>Vieira</i> Navás 1913.....	310
Tribe <b>Chrysopini</b> Schneider 1851 .....	314
Genus <i>Anachrysa</i> Hölzel 1973 <b>stat. nov.</b> .....	315

Genus <i>Anomalochrysa</i> McLachlan 1883 .....	318
Genus <i>Apertochrysa</i> Tjeder 1966.....	323
Genus <i>Atlantochrysa</i> Hölzel 1970.....	329
Genus <i>Austrochrysa</i> Esben-Petersen 1928.....	333
Genus <i>Borniochrysa</i> Navás 1928.....	337
Genus <i>Brinckochrysa</i> Tjeder 1966.....	341
Genus <i>Ceraeochrysa</i> Adams 1982 .....	345
Genus <i>Ceratochrysa</i> Tjeder 1966.....	350
Genus <i>Chrysemosa</i> Brooks & Barnard, 1990.....	354
Genus <i>Chrysocerca</i> Weele 1909 .....	358
Genus <i>Chrysopa</i> Leach 1815.....	362
Genus <i>Chrysoperla</i> Steinmann 1964.....	367
Genus <i>Chrysopodes</i> Navás 1913 .....	371
Subgenus <i>Chrysopodes</i> Navás 1913.....	372
Subgenus <i>Neosuarius</i> Adams and Penny 1987 .....	376
Genus <i>Crassochochrysa</i> Hölzel 1990 .....	380
Genus <i>Cunctochrysa</i> Hölzel 1970.....	383
Genus <i>Eremochrysa</i> Banks 1903 .....	387
Subgenus <i>Chrysopiella</i> Banks 1911 .....	388
Subgenus <i>Eremochrysa</i> Banks 1903 .....	391
Genus <i>Glenochrysa</i> Esben-Petersen 1920.....	395
Genus <i>Himalochrysa</i> Hölzel 1973 .....	400
Genus <i>Kostka</i> Navás 1913 .....	404
Genus <i>Kymachrysa</i> Tauber and Garland 2014.....	407

Genus <i>Mallada</i> Navás 1925.....	411
Genus <i>Meleoma</i> Fitch 1855.....	415
Genus <i>Nipponochrysa</i> Tsukaguchi 1995 .....	420
Genus <i>Parachrysoptera</i> Brooks and Barnard 1990 .....	423
Genus <i>Peyerimhoffina</i> Lacroix 1920.....	427
Genus <i>Plesiochrysa</i> Adams 1982.....	431
Genus <i>Rexa</i> Navás 1920.....	435
Genus <i>Suaris</i> Navás 1914 .....	439
Genus <i>Titanochrysa</i> Sosa and de Freitas 2012.....	444
Genus <i>Ungla</i> Navás 1914.....	448
Genus <i>Yumachrysa</i> Banks 1950.....	453
Tribe <b>Leucochrysinini</b> Adams 1978.....	457
Genus <i>Berchmansus</i> Navás 1913.....	458
Genus <i>Cacarulla</i> Navás 1910.....	461
Genus <i>Gonzaga</i> Navás 1913.....	465
Genus <i>Leucochrysa</i> McLachlan 1868.....	469
Genus <i>Neula</i> Navás 1917 .....	473
Genus <i>Nodita</i> Navás 1916 <b>res. stat.</b> .....	475
Genus <i>Nuvol</i> Navás 1916 .....	479
Genus <i>Santocellus</i> Tauber et al. 2008 .....	482
Tribe <b>Nothancylini</b> Garzón et al in rev.....	485
Genus <i>Nothancylla</i> Navás 1910 .....	486
Genera incertae sedis .....	490
Genus <i>Sinochrysa</i> Yang 1992 .....	490

Genus <i>Tibetochrysa</i> Yang et al. 1988.....	491
Genus <i>Yunchrysopa</i> Yang and Wang 1994.....	491
<b>Conclusion</b> .....	492
<b>References</b> .....	493

**CHAPTER 3: Morphology of *Chrysopa oculata* as an exemplar for the family Chrysopidae (Neuroptera)**

<b>Introduction</b> .....	515
<b>Material and Methods</b> .....	523
<b>Morphology</b> .....	525
General appearance .....	525
Head .....	525
General shape .....	525
Antenna.....	528
Frons .....	529
Gena.....	530
Vertex .....	531
Clypeus .....	531
Labrum.....	534
Mandible.....	534
Maxilla.....	534
Labium.....	535
Eyes .....	536
Thorax .....	537

Thoracic body .....	538
Legs .....	544
Wings.....	548
Forewing .....	552
Hind wing.....	556
Abdomen .....	558
External sclerites.....	558
Genitalia.....	560
Female genitalia .....	560
Male genitalia.....	562
<b>Glossary</b> .....	568
<b>Conclusion</b> .....	578
<b>References</b> .....	579

## CHAPTER 4: Wing Tracheation in Chrysopidae and Other Neuropterida (Insecta):

### A Resolution of the Confusion about Vein Fusion

Abstract .....	587
Introduction.....	588
Wings .....	593
Wing Venation of Chrysopidae.....	598
Material and Methods .....	600
Results.....	601
Lineages of Neuropterida.....	602
Order Megaloptera .....	602

Order Raphidioptera.....	605
Order Neuroptera.....	605
Superfamily Myrmeleontoidea.....	605
Family Psychopsidae.....	605
Family Nymphidae.....	607
Family Nemopteridae.....	609
Family Ascalaphidae.....	611
Family Myrmeleontidae.....	613
Superfamily Ithonoidea.....	614
Family Ithonidae.....	614
Superfamily Coniopterygoidea.....	617
Family Coniopterygidae.....	617
Superfamily Osmyloidea.....	618
Family Osmylidae.....	618
Family Sisyridae.....	620
Family Nevrorthidae.....	623
Superfamily Dilaroidea.....	623
Family Dilaridae.....	623
Superfamily Mantispoidea.....	626
Family Berothidae.....	626
Family Rhachiberothidae.....	626
Family Mantispidae.....	628
Superfamily Chrysopoidea.....	630
Family Hemerobiidae.....	630



Family Chrysopidae .....	632
Subfamily Nothochrysinæ.....	635
Subfamily Apochrysinæ.....	637
Discussion .....	639
The Controversy of ‘MA’ .....	644
References.....	647

# Table of Figures

## CHAPTER 1

<b>Figure 1.1.</b> Comparison of differing phylogenetic hypotheses proposed for Chrysopidae since 1998.....	13
<b>Figure 1.2.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from molecular data of Chrysopidae; analysis 1.....	47
<b>Figure 1.3.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological data of Chrysopidae; analysis 2 .....	49
<b>Figure 1.4.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, including only species for which molecular data was available; analysis 3 .....	51
<b>Figure 1.5.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae; analysis 4 .....	53
<b>Figure 1.6.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Apochrysinæ; analysis 5 .....	55
<b>Figure 1.7.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Nothochrysinæ; analysis 6 .....	57
<b>Figure 1.8.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Belonopterygini and Leucochrysinini; analysis 7 .....	59

<b>Figure 1.9.</b> 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Ankylopterygini; analysis 8 .....	61
<b>Figure 1.10.</b> : 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopini; analysis 9.....	64
<b>Figure 1.11.</b> 50 % Majority rule consensus tree of the node-dated Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, with strict date settings; analysis 10 .....	68
<b>Figure 1.12.</b> 50 % Majority rule consensus tree of the node-dated Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, with relaxed date settings; analysis 11 .....	69
<b>Figure 1.13.</b> Maximum likelihood inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae; analysis 12. ....	71
<b>Figure 1.14.</b> 50 % Majority rule consensus tree of the parsimony phylogenetic hypotheses from morphological data of Chrysopidae; analysis 13.....	73
<b>Figure 1.15.</b> 50 % Majority rule consensus tree of the parsimony phylogenetic hypotheses from morphological and molecular data of Chrysopidae; analysis 14 .....	74
<b>Figure 1.16.</b> Photomicrographs of fore- and hind wing, in dorsal view. ....	79
<b>Figure 1.17.</b> Photomicrographs of fore- and hind wing, in dorsal view. ....	81
<b>Figure 1.18.</b> Photomicrograph of fore- and hind wing of <i>Borniochrysa squamosa</i> , in dorsal view, including character states (refer to list of characters). ....	83

<b>Figure 1.19.</b> Photomicrographs of flagella, lateral view, curved lines indicate the base of the flagellar setae, and black arrows indicate the tip of the flagellar setae.....	86
<b>Figure 1.20.</b> <i>mamp1</i> character states traced on the BI tree inferred from combined data (analysis 4). .....	88
<b>Figure 1.21.</b> Photomicrographs of tarsi.....	90
<b>Figure 22.</b> Tibial spurs character states traced on the BI tree inferred from combined data (analysis 4), each formula summarizes number of tibial spurs on the pro-, meso-, and metathoracic leg.....	92
<b>Figure 1.23.</b> Photomicrographs of the meso- and metanotum, dorsal view.....	95
<b>Figure 1.24.</b> Parameres character states traced on the BI tree inferred from combined data (analysis 4). .....	99
<b>Figure 1.25.</b> ra-rp crossveins presence or absence basal to basal most RP branch traced on the BI tree inferred from combined data (analysis 4), including photomicrographs of the respective character states; bRP (basal most RP branch). .....	106
<b>Figure 1.26.</b> Tignum absence and presencetraced on the BI tree inferred from combined data (analysis 4), including scematic drawing of male terminalia, tignum orange. ....	108
 <u>CHAPTER 2</u>	
<b>Figure 2.1.</b> Illustrations relevant to the key to genera.....	160
<b>Figure 2.2.</b> Illustrations of <i>Apochrysa</i> .....	168
<b>Figure 2.3.</b> <i>Domenechus mirifica</i> (Gerstaecker), head, frontal view, photomicrograph.....	172
<b>Figure 2.4.</b> <i>Nobilinius albardae</i> (McLachlan), head, frontal view, photomicrograph.....	182

<b>Figure 2.5.</b> Illustrations of <i>Dictyochrysa peterseni</i> Kimmins .....	190
<b>Figure 2.6.</b> Illustrations of <i>Hypochrysa elegans</i> (Burmeister).....	194
<b>Figure 2.7.</b> Illustrations of <i>Nothochrysa</i> . .....	204
<b>Figure 2.8.</b> Illustrations of <i>Pamochrysa stellata</i> Tjeder.....	208
<b>Figure 2.9.</b> <i>Pimachrysa nigra</i> Adams, head, frontal view, photomicrograph.....	212
<b>Figure 2.10.</b> Illustrations of <i>Ankylopteryx sp.</i> .....	221
<b>Figure 2.11.</b> Illustrations of <i>Chrysopidia (Chrysotropia)</i> .....	229
<b>Figure 2.12.</b> Illustrations of <i>Nineta</i> .....	233
<b>Figure 2.13.</b> Illustrations of <i>Parankylopteryx</i> .....	241
<b>Figure 2.14.</b> Illustrations of <i>Retipenna</i> .....	245
<b>Figure 2.15.</b> Illustrations of <i>Semachrysa matsumurae</i> (Okomoto).....	249
<b>Figure 2.16.</b> Illustrations of <i>Signochrysa sp.</i> .....	253
<b>Figure 2.17.</b> <i>Abachrysa eureka</i> (Banks), male genitalia, lateral and dorsal view, schematic line drawing. ....	258
<b>Figure 2.18.</b> <i>Belonopteryx arteriosa</i> Gerstaecker, male genitalia, lateral and dorsal view, schematic line drawing. ....	262
<b>Figure 2.19.</b> Illustrations of <i>Calochrysa extranea</i> (Esben-Petersen).....	266
<b>Figure 2.20.</b> Illustrations of <i>Chrysacanthia hainana</i> (Yang and Yang) .....	270
<b>Figure 2.21.</b> Illustrations of <i>Chrysaloisia somalica</i> Navás.....	273
<b>Figure 2.22.</b> Illustrations of <i>Dysochrysa furcata</i> Tjeder.....	277

<b>Figure 2.23.</b> Illustrations of <i>Evanochrysa infecta</i> (Newman).....	281
<b>Figure 2.24.</b> Illustrations of <i>Italochrysa</i> .....	286
<b>Figure 2.25.</b> <i>Nacarina megaptera</i> (Navás), head, frontal view, photomicrograph.....	291
<b>Figure 2.26.</b> Illustrations of <i>Nesochrysa macrostigma</i> (Gerstaecker) .....	295
<b>Figure 2.27.</b> Illustrations of <i>Nodochrysa necrota</i> (Banks).....	299
<b>Figure 2.28.</b> Illustrations of <i>Oyochrysa ancora</i> Brooks.....	303
<b>Figure 2.29.</b> Illustrations of <i>Stigmachrysa</i> .....	307
<b>Figure 2.30.</b> Illustrations of <i>Vieira elegans</i> (Guerin).....	314
<b>Figure 2.31.</b> Illustrations of <i>Anomalochrysa hepatica</i> McLachlan.....	323
<b>Figure 2.32.</b> Illustrations of <i>Apertochrysa</i> .....	329
<b>Figure 2.33.</b> Illustrations of <i>Atlantochrysa atlantica</i> (McLachlan). .....	333
<b>Figure 2.34.</b> Illustrations of <i>Austrochrysa abnormis</i> (Albarda).....	337
<b>Figure 2.35.</b> Illustrations of <i>Borniochrysa squamosa</i> (Tjeder).....	341
<b>Figure 2.36.</b> Illustrations of <i>Brinckochrysa</i> .....	345
<b>Figure 2.37.</b> Illustrations of <i>Ceraeochrysa cincta</i> (Schneider).....	350
<b>Figure 2.38.</b> Illustrations of <i>Ceratochrysa ceratina</i> (Navás). .....	354
<b>Figure 2.39.</b> Illustrations of <i>Chrysemosa</i> .....	358
<b>Figure 2.40.</b> <i>Chrysocerca formosa</i> (Okamoto), male genitalia, lateral and dorsal view, schematic line drawing. ....	362

<b>Figure 2.41.</b> <i>Chrysoperla carnea</i> (Stephens), male genitalia, lateral and dorsal view, schematic line drawing. ....	371
<b>Figure 2.42.</b> Illustrations of <i>Chrysopodes (Chrysopodes) limbata</i> (Navás) .....	376
<b>Figure 2.43.</b> Illustrations of <i>Crassochrysa aculeata</i> (Tjeder).....	383
<b>Figure 2.44.</b> Illustrations of <i>Cunctochrysa albolineata</i> Killington.....	387
<b>Figure 2.45.</b> <i>Eremochrysa (Chrysopiella)</i> sp., head, frontal view, photomicrograph. ....	391
<b>Figure 2.46.</b> Illustrations of <i>Eremochrysa (Eremochrysa)</i> .....	395
<b>Figure 2.47.</b> Illustrations of <i>Glenochrysa</i> .....	400
<b>Figure 2.48.</b> Illustrations of <i>Kostka nacaratus</i> Navás.....	407
<b>Figure 2.49.</b> <i>Mallada basalis</i> (Walker), male genitalia, lateral and dorsal view, schematic line drawing. ....	415
<b>Figure 2.50.</b> Illustrations of <i>Meleoma</i> .....	420
<b>Figure 2.51.</b> Illustrations of <i>Parachrysopiella</i> .....	427
<b>Figure 2.52.</b> Illustrations of <i>Peyerimhoffina gracilis</i> (Schneider) .....	431
<b>Figure 2.53.</b> <i>Plesiochrysa</i> sp., male genitalia, lateral and dorsal view, schematic line drawing. ....	435
<b>Figure 2.54.</b> Illustrations of <i>Rexa raddai</i> (Hölzel).....	439
<b>Figure 2.55.</b> <i>Suarius alisteri</i> (Navás), male genitalia, lateral and dorsal view, schematic line drawing. ....	444
<b>Figure 2.56.</b> <i>Titanochrysa chloros</i> (Freitas and Penny), head, frontal view, photomicrograph. ....	448

<b>Figure 2.57.</b> <i>Ungla argentina</i> (Navás), head, frontal view, photomicrograph. ....	453
<b>Figure 2.58.</b> Illustrations of <i>Yumachrysa</i> .....	457
<b>Figure 2.59.</b> <i>Cacarulla maculipennis</i> (Banks), head, frontal view, photomicrograph. ....	464
<b>Figure 2.60.</b> Illustrations of <i>Gonzaga nigriceps</i> (McLachlan).....	469
<b>Figure 2.61.</b> Illustrations of <i>Nothancyla verreauxi</i> Navás .....	489

### CHAPTER 3

<b>Figure 3.1.</b> Habitus of <i>Chrysopa oculata</i> .....	516
<b>Figure 3.2.</b> <i>Chrysopa oculata</i> , immature states, photomicrographs .....	519
<b>Figure 3.3.</b> <i>Chrysopa oculata</i> , head .....	527
<b>Figure 3.4.</b> <i>Chrysopa oculata</i> , head details.....	529
<b>Figure 3.5.</b> <i>Chrysopa oculata</i> , head appendages, line drawings.....	534
<b>Figure 3.6.</b> <i>Chrysopa oculata</i> , thorax, dorsal view .....	538
<b>Figure 3.7.</b> <i>Chrysopa oculata</i> , thorax, with fore- and hind wing removed, lateral view .....	540
<b>Figure 3.8.</b> <i>Chrysopa oculata</i> , thorax, lateral view, simplified schematic line drawing .....	542
<b>Figure 3.9.</b> <i>Chrysopa oculata</i> , legs .....	545
<b>Figure 3.10.</b> <i>Chrysopa oculata</i> , wingbase.....	550
<b>Figure 3.11.</b> <i>Chrysopa oculata</i> , fore- and hind wing, line drawing, venation based on tracheation pattern .....	552
<b>Figure 3.12.</b> Wing details.....	556
<b>Figure 3.13.</b> <i>Chrysopa oculata</i> , male abdomen, line drawing, lateral view .....	558



**Figure 3.14.** *Chrysopa oculata*, female genitalia ..... 562

**Figure 3.15.** *Chrysopa oculata*, male terminalia ..... 564

**Figure 3.16.** *Chrysopa oculata*, male genitalia ..... 568

#### CHAPTER 4

**Figure 4.1.** Photomicrograph and line drawing of *Chrysopa nigricornis* Burmeister show detail of *mamp1* (first intermedial cell, indicated by asterisk) and surrounding area, illustrating the dissimilarity between apparent and actual venation, ventral view. .... 592

**Figure 4.2.** Line drawings of forewings and hind wings of Megaloptera and Raphidioptera ... 604

**Figure 4.3.** Line drawings of forewing and hind wing of *Psychopsis insolens* McLachlan (Psychopsidae) ..... 607

**Figure 4.4.** Line drawings of forewing and hind wing of *Myiodactylus osmyloides* Brauer (Nymphidae) ..... 609

**Figure 4.5.** Line drawings of undetermined nemopterine genus (forewing) and *Nemoptera sinuata* Olivier (hind wing) (Nemopteridae) ..... 611

**Figure 4.6.** Line drawings of forewings and hind wings of an antlion and owlfly ..... 613

**Figure 4.7.** Line drawings of forewings and hind wings of a moth lacewing and dustywing ... 616

**Figure 4.8.** Photomicrograph (above) and line drawing (below) of the proximal radial and medial sector of the hind wing of *Ithone fulva* Tillyard (Ithonidae), showing the elongate 1rp-m (sigmoid vein) in ventral view ..... 617

**Figure 4.9.** Line drawings of forewing and hind wing of *Oedosmylus* sp. (Osmylidae) ..... 620

<b>Figure 4.10.</b> Line drawings of forewings and hind wings of a spongillafly and aquatic lacewing .....	622
<b>Figure 4.11.</b> Line drawings of forewings and hind wings of a pleasing lacewing and a beaded lacewing .....	625
<b>Figure 4.12.</b> Line drawings of forewings and hind wings of a thorny lacewing and a mantispid lacewing .....	628
<b>Figure 4.13.</b> Photomicrograph and line drawing of the wing base of <i>Plega</i> sp. (Mantispidae), showing the basal fusion of R and M, ventral view.....	630
<b>Figure 4.14.</b> Forewings and hind wings of brown lacewings (Hemerobiidae) .....	631
<b>Figure 4.15.</b> Line drawings of forewings and hind wings of green lacewings (Chrysopidae) ..	636
<b>Figure 4.16.</b> Line drawing <i>Cryptochrysa chloros</i> Freitas and Penny (Chrysopidae: Chrysopinae) .....	638
<b>Figure 4.17.</b> Line drawings of the variation of mamp1 (first intermedial cell) in Chrysopidae.. ..	639
<b>Figure 4.18.</b> Photomicrograph and line drawing of the wing base of <i>Nothochrysa californica</i> Banks (Chrysopidae: Nothochrysinae), showing that R and M are not fused, ventral view .....	640
<b>Figure 4.19.</b> Photomicrograph and line drawing of the wing base of <i>Apochrysa</i> sp. (Chrysopidae: Apochrysinae), showing that R and M are not fused, ventral view.....	642

**Figure 4.20.** Photomicrograph and line drawing of the wing base of *Chrysopa nigricornis* Burmeister (Chrysopidae: Chrysopinae), showing the tympanal organ and the associated basal fusion of R and M..... 643

## Introduction

When sitting outside on a warm Midwestern summer evening, some of the first visitors are little, green, delicate insects that are drawn to the porch light. These comparatively simple looking, flimsy flyers are merely representatives of the almost 1,400 species of Chrysopidae worldwide. They are often mistaken as a single species, given their hidden morphological diversity – exteriorly, about 70% of chrysopids are simply green, with hyaline wings, and an intricate venation pattern. These characteristics have given chrysopids the name ‘green lacewings’. But their true diversity lies within the interior genitalic characters. Apart from our typical chrysopid, occurring in temperate regions, there are numerous intricate species in the tropics, varying in size, coloration, venation pattern and behavior (fig. 1). Chrysopids have intriguing larval stages, which – in contrast to the delicate adult – are effective predators, sucking fluids out of soft-bodied insects, and can camouflage themselves with animal and plant debris (Tauber et al. 2014). The adults of some genera communicate through substrate-borne vibration for courtship (e.g. *Chrysoperla* Steinmann), and emit a diverse array of semiochemicals for the attraction of conspecifics or repulsion of predators (Henry 1984). Due to a powerful foul smell released by many common chrysopids (e.g., all *Chrysopa* Leach) when handled, they have been dubbed ‘stink-flies’ in the USA. Worldwide Chrysopidae are fairly diverse in terms of species richness, morphology, and biology, but often overlooked – except for the few agriculturally important species. This introduction gives a short overview of Chrysopidae and their biology, whereas we will go into further detail of the systematics and morphology in the specific chapter introductions.

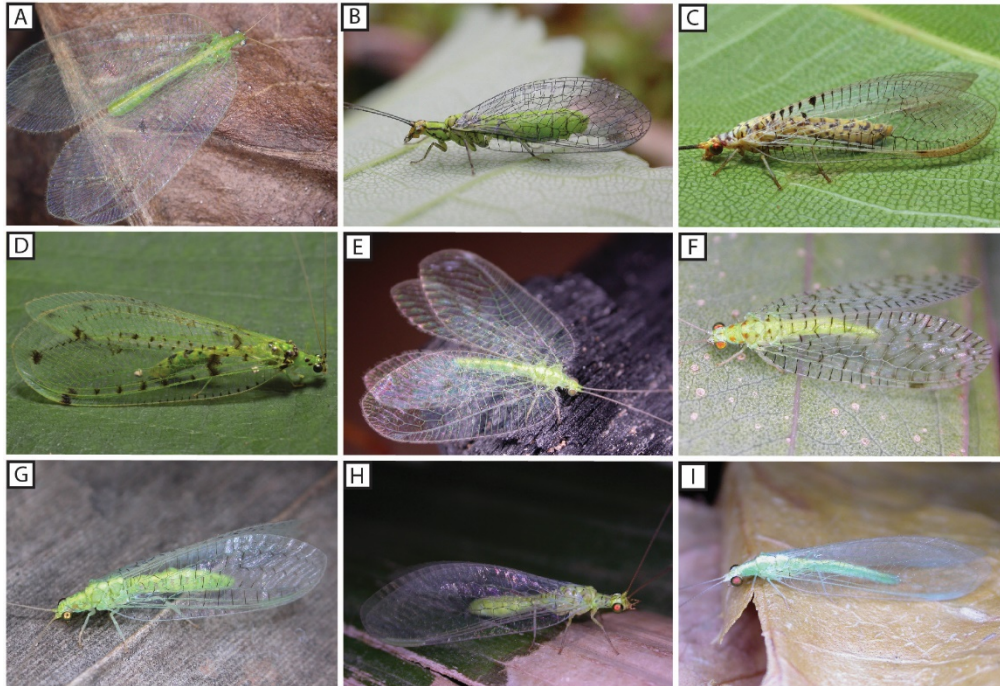


Figure 1: Examples of Chrysopidae, habitus photographs of living individuals. A. *Apochrysa lutea* (Walker). B. *Hypochrysa elegans* (Burmeister). C. *Dysochrysa* sp. D. *Cacarulla maculipennis* (Banks). E. *Ankylopteryx rieki* New. F. *Glenochrysa opposite* (McLachlan). G. *Mallada traviata* (Banks). H. *Plesiochrysa ramburi* (Schneider). I. *Chrysoperla congrua* (Walker). Image sources: A and E-I taken by Shaun Winterton, with the authors permission; B taken by Gilles San Marin, accessed through Wikimedia Commons under the creative commons license; C and D taken by L. Breitkreuz.

The family Chrysopidae is part of the order Neuroptera (lacewings), which includes the familiar ant-lions (Myrmeleontidae), as well as lesser known families, such as Hemerobiidae (brown lacewings), Ascalaphidae (owlflies), and Ithonidae (moth or giant lacewings) (Engel et al. 2018). Neuropterida (which include Neuroptera, Megaloptera, and Raphidioptera) are sister to Coleoptera + Strepsiptera (Misof et al. 2014), the beetles and twisty wings. Relationships within Neuroptera are still hotly debated, with several different hypotheses proposed over the last decade (e.g., Haring and Aspöck 2004, Winterton et al. 2017). The most recent phylogenetic analysis used anchored hybrid enrichment data to infer relationships within the lineage (Winterton et al. 2017). Chrysopidae, which has long been treated as sister to Hemerobiidae, was recovered as sister to Myrmeleontoidea, and not closely related to the former in that study. The age of crown-group

Chrysopidae was estimated around 130 million years, which sets the first green lacewings in the Early Cretaceous (see chapter 1). The question about the true sister group of Chrysopidae is still not completely resolved, and further complicated by the long ghost lineages in the stem of the family.

One of their most intriguing aspects is the biology of Chrysopidae. Their life cycle is divided into three larval states, the pupa, and the adult. The adults of the majority of species feed on honeydew or pollen (Principi and Canard 1984) and are active through the night hours, being most commonly out during twilight. Different forms of courtship have been demonstrated for Chrysopidae, involving primarily olfactory and tactile senses. The males of several species emit semiochemicals to attract females, but the mechanisms as well as the specific chemicals are barely known or understood (Aldrich et al. 2009). As an example, males of several members of *Ankylopteryx* Brauer have been found in chemical traps, especially attracted to methyl eugenol (Breitkreuz et al. 2015). The secretions of the males in only five genera have been analyzed, but show great diversity and specificity (e.g., Aldrich et al. 2009). The component leading to the negative odor of many green lacewings is not part of the sexual attraction, but rather a defense mechanism against predators. Skatole is emitted through prothoracic or abdominal glands and, as one of the chemicals that gives the bad odor to feces, is quite effective in repulsing the threat (Aldrich 2009).

A second – and very well studied – behavior is the production of mating songs in some genera (best documented in *Chrysoperla*). These songs are not acoustic, but substrate-borne surface vibrations. To transfer a vibration pattern to the substrate (most commonly a leaf), the male jerks his abdomen in a high frequency and the female can detect species-specific vibration patterns through tactile sensory organs (e.g., Henry 1979, 1984, Henry et al. 1999). On the basis of

differences in these courtship songs, several species have been described, which are morphologically indistinguishable (e.g., Henry et al. 2014), and some could not be recovered as monophyletic in molecular analyses (Henry et al. 2013).

After copulation, the female lays her eggs on leaves or branches, usually close to potential prey for the larvae (Duelli 1984, New 1989). The eggs are ovate, and, apart from a few exceptions (e.g., *Anomalochrysa* McLachlan), stalked. This has been interpreted as a defense against predators, especially ants. The eggs are either laid in clusters, spirals, or singular and spread out. The first instar hatches from the egg (usually after about a week) and immediately starts preying on small, soft-bodied insects (Canard and Principi 1984). The type of prey varies among chrysopid taxa, but the most common insects are aphids, hence the fact that larvae are commonly used in biological pest control in agriculture (McEwen et al. 2007). The eggs of species of *Chrysoperla* and less frequently *Chrysopa* can be purchased in immense quantities to be released in orchards or crops. The larvae have elongate, scythe-shaped mandibles and maxilla forming a tube with a sharp tip, to pierce their prey, inject salivary enzymes, and suck the digested juices. There are two main strategies among chrysopid larvae, regarding their way of approaching prey (Tauber et al. 2014). They are either naked, often elongate and capable of moving comparatively fast, therefore 'hunting' their aphid prey, or they camouflage themselves, giving them the ability to slowly approach their prey while staying hidden. Larvae of debris-carrying taxa use numerous kinds of animal and plant material to disguise their body, varying from plant fibers, and small sticks to the carcasses of their prey, or combinations, with some species even stacking tiny snail shells, between the long setae on their back (e.g., *Leucochrysa* McLachlan, see Tauber et al. 2013). The origin of this behavior is still debated, because it is present in many taxa in the family, but is equally as common as the non-debris-carrying life style. The larvae of one group of Chrysopidae

(Belonopterygini) have been shown to be associated with ant nests, preying on ant larvae, where the naked and completely white chrysopid larvae live amongst their prey and are treated as one of the ant larvae by the adults (Weber 1942, Principi 1946). After several weeks, the third instar spins a round, silken cocoon, out of which the prepupa will hatch (Principi and Canard 1984). Contrary to most insects, Chrysopidae have a mobile prepupa, which walks from the cocoon to a spot where the adult can eclose. The life span of the adults is dependent on the taxon and distribution, but most chrysopids in the temperate regions are active between mid-Spring and Fall.

The 1399 species of Chrysopidae are divided into three subfamilies, five tribes, and 79 genera (Oswald 2018), with three species that currently cannot be placed into a higher taxon. The subfamilies Apochrysinæ and Nothochrysinæ are minute, in regards to diversity, next to the vast Chrysopinæ, with more than 95% of the species.

Apochrysinæ are a solely tropical subfamily with most of their diversity in South East Asia, and few species in the Afrotropics and Neotropics. The 24 species of these large-winged chrysopids are divided into five genera (Oswald 2018). The members retained numerous plesiomorphies, but are nonetheless derived, especially regarding the wing venation. The strongly reticulated vein pattern, as well as the absence of a fossil record for the subfamily, lead prior researchers to believe that Apochrysinæ were the most recently diverged chrysopids. The results of the most recent phylogenetic analyses, however, indicate that it is more likely that the current representatives of Apochrysinæ are highly derived members of an otherwise ancient lineage and sister to all other Chrysopidae.

Nothochrysinæ are a similarly small taxon, with only 27 species in nine genera (Oswald 2018), but are rather small to medium-sized lacewings, with stout bodies and comparatively reduced wing venation. They occur world-wide, but are somewhat more common in temperate



regions. Due to the simple pattern of venation of many genera, their brown color and stout bodies, they have long been thought to be the most plesiomorphic lineage of Chrysopidae. Many similarities to the wings of certain fossil chrysopids, as well as the presumed resemblance to Hemerobiidae were considered as support for this notion. However, the belief that nothochrysines are the oldest of the family has not been corroborated by recent studies, particularly given the fact that Hemerobiidae are likely not sister to Chrysopidae and that phylogenetic analyses have placed Nothochrysininae in a more derived position as sister to Chrysopinae.

Chrysopinae are by far the largest of the three subfamilies, with 1,345 species in 62 genera (Oswald 2018), and further divided into five tribes: Ankylopterygini, Belonopterygini, Chrysopini, Leucochrysinini, and Nothancylini. Members are distributed world-wide and all share the presence of a tympanal organ on the forewing, with which they are able to detect high frequency wave lengths. This organ was shown to be involved in a bat-avoidance behavior, where bat echolocation sounds induce a dropping reaction mid-flight (Miller 1984). It has been hypothesized that the presence of this character played a role in the evolutionary radiation of Chrysopinae, but the evidence needs further exploration. The monotypic tribe Nothancylini is sister to all other Chrysopinae, which is composed of two monophyletic groups: Belonopterygini + Leucochrysinini, and Ankylopterygini + Chrysopini.

On the basis of phylogenies, we can make predictions about the evolution the taxa, of certain morphological traits, behaviors, or correlations between them. However, in order to be able to answer specific questions we must first demonstrate the monophyly of taxa under study, and the validity of morphological homology statements. By combining molecular and morphological data to recover chrysopid relationships we are able to study character evolution in a traditionally challenging family, known to exhibit with numerous homoplastic traits.

The present dissertation is aimed at investigating chrysopid evolution from multiple angles with a strong focus on morphological diversity. Chapter 1 will discuss the results of our comprehensive phylogenetic analyses, through which we inferred relationships from combined molecular and morphological data. We investigate genus-level relationships and discuss morphological characters that serve as synapomorphies for taxa at various hierarchical levels. Chapter 2 provides a generic revision of the family, based on the results of the recovered phylogenetic relationships that are presented in chapter 1. Detailed descriptions are given for all currently recognized genera, as well as illustrations, diagnoses, remarks and a key to the genera. Chapter 3 provides an in-depth discussion and illustration of all external morphological and genitalic characters of a single chrysopid representative, serving as a proxy for the family. The common lacewing *Chrysopa oculata* Say is used to reexamine homology statements and give an ontology of chrysopid morphology. Chapter 4 is a comparative morphological analysis of the wing venation in the families of Neuropterida. Vein homologies are discussed on the basis of tracheation and illustrations as well as synapomorphies regarding vein fusions are provided for each family.

This dissertation serves as the basis for future studies exploring the evolution of lacewings, and their intriguing biology, morphology, biogeography, and lengthy history, tying into the investigation of specific taxa with great agricultural significance. Understanding the phylogenetic history of Chrysopidae integrates into the study of evolutionary patterns and processes, such as illuminating the diversification of one of the subfamilies over its relatives. Ultimately, we aim to describe the striking diversity of Chrysopidae, which is hidden to most observers, when seeing the typical little green lacewing at the porch, and hope to shed light on this comparatively small, but nonetheless interesting insect lineage.

## References

- Aldrich, J.R., Le, T.C., Zhang, Q.H., Torres, J., Winterton, S. L., Han, B., Miller, G.L. and K.R. Chauhan. 2009. Prothoracic gland semiochemicals of green lacewings. *Journal of Chemical Ecology* 35(10): 1181.
- Breitkreuz, L.C., Winterton, S. L., and M.S. Engel. 2015. Revision of the green lacewing subgenus *Ankylopteryx* (*Sencera*) (Neuroptera, Chrysopidae). *ZooKeys* 543: 111–127.
- Canard, M., and M.M. Principi. 1984. Development of Chrysopidae. Pp. 57–75 in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Duelli, P. 1984. Oviposition. Pp. 129–133 in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Haring, E., and U. Aspöck. 2004. Phylogeny of the Neuropterida: a first molecular approach. *Systematic Entomology* 29(3): 415–430.
- Henry, C.S. 1984. The sexual behavior of green lacewings. Pp. 101–110 in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Henry, C.S. 1979. Acoustical communication during courtship and mating in the green lacewing *Chrysopa carnea* (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America* 72:68–79.
- Henry, C. S., Brooks, S. J., Johnson, J. B., Mochizuki, A., and P. Duelli. 2014. A new cryptic species of the *Chrysoperla carnea* group (Neuroptera: Chrysopidae) from western Asia: parallel speciation without ecological adaptation. *Systematic Entomology* 39:380–393.

- Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., and A.Mochizuki. 2013. Obligatory duetting behaviour in the *Chrysoperla carnea*-group of cryptic species (Neuroptera: Chrysopidae): its role in shaping evolutionary history. *Biological Reviews* 88(4): 787–808.
- Henry, C. S., Wells, M. L. M., and C.M. Simon. 1999. Convergent evolution of courtship songs among cryptic species of the carnea group of green lacewings (Neuroptera: Chrysopidae: Chrysoperla). *Evolution* 53:1165–1179.
- McEwen, P. K., New, T. R. and Whittington, A. E. (Eds.). 2007. *Lacewings in the crop environment*. Cambridge University Press.
- Miller, L.A. 1984. Hearing in green lacewings and their responses to the cries of bats. Pp. 134–149 in in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., and O. Niehuis. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346(6210): 763–767.
- New, T. R. 1989. *Handbuch der Zoologie, Band/Volume IV Arthropoda: Insecta, Planipennia: lacewings*. Walter de Gruyter, Berlin, New York.
- Oswald, J. D. 2018. *Neuropterida Species of the World. Version 5.0*. <http://lacewing.tamu.edu/SpeciesCatalog/Main>. Last accessed on April 08 2018.
- Principi, M. M. 1946. Contributi allo studio dei Neurotteri italiani. IV. *Nothochrysa italica* Rossi. *Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna*. 15: 85–102.

- Principi, M.M., and M. Canard. 1984. Feeding habits. Pp. 76–92 in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Tauber, C. A., Sosa, F., Albuquerque, G. S., and M. J. Tauber. 2013. Adults and larvae of two *Leucochrysa* (*Leucochrysa*) species (Neuroptera, Chrysopidae): descriptions, biological notes, and relationships. *Zootaxa* 3750: 101–129.
- Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2014. Debris-carrying in larval Chrysopidae: unraveling its evolutionary history. *Annals of the Entomological Society of America* 107(2): 295–314.
- Weber, N. A. 1942. A neuropterous myrmecophile, *Nadiva valida* Erichs. *Psyche* 49: 1–3.
- Weed, C. M. 1897. The golden-eye or lace-wing fly. *American Naturalist* 31: 500–502.
- Winterton, S. L., Lemmon, A.R., Gillung, J.P., Garzon, I.J., Badano, D., Bakkes, D.K., Breitkreuz, L., Engel, M.S., Lemmon, E.M., Liu, X., and R.J. Machado. 2017. Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology*. DOI: 10.1111/syen.12278, pp. 25.

# Chapter 1

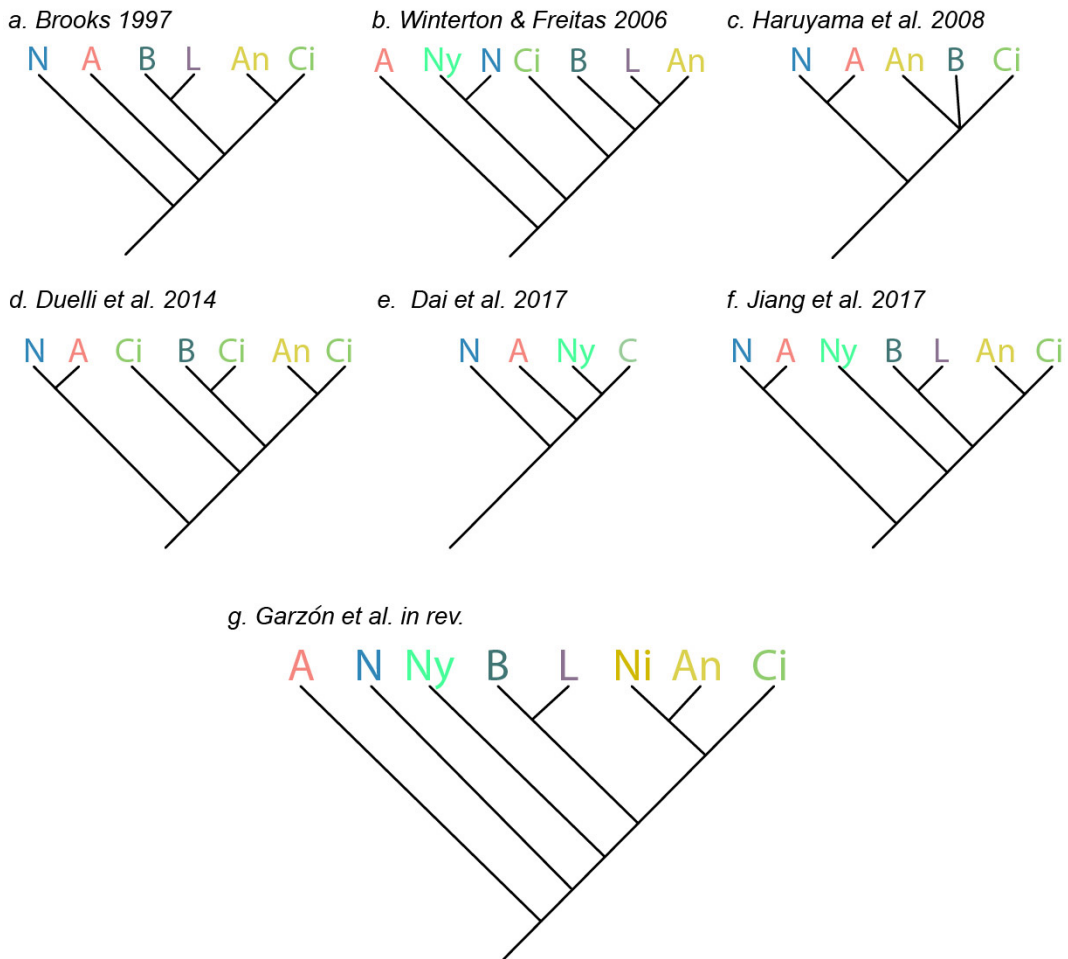
## A Phylogeny of Chrysopidae Inferred from Morphological and Molecular Data

## Introduction

The neuropteran family Chrysopidae is a small group of cosmopolitan lacewings, and the modern representatives are placed in three subfamilies – Apochrysinæ, Nothochrysinæ, and Chrysopinæ (New 1989, Brooks and Barnard 1990). The latter is further divided into five tribes – Ankylopterygini, Belonopterygini, Chrysopini, Leucochrysinini (see Brooks and Barnard 1990), and Nothancylini (see Garzón et al. in rev.). There are about 1,400 species of Chrysopidae (Oswald 2018). The adults of most species are small, green and delicate lacewings, especially within the subfamily Chrysopinæ. Apochrysinæ have the largest wing spans within Chrysopidae, including an intricate wing pattern, whereas Nothochrysinæ seem to have reduced wing venation and often sturdier bodies. The larvae are predacious and often used in agriculture, to control pests biologically (Ridgway and Murphy 1984, McEwen et al. 2007). A revised phylogenetic hypothesis of this important group is a significant stepping stone to understanding their biology, such as the larval debris carrying behavior that occurs throughout the family (Tauber et al. 2014), and many more traits.

The understanding of relationships within Chrysopidae and the family's position in Neuroptera has been the subject of many studies during the last 20 years (e.g., Brooks and Barnard 1990, Brooks 1997, Winterton and Freitas 2006, Haruyama et al. 2008, Duelli et al. 2014, Dai et al. 2017, Jiang et al. 2017, Garzón et al. in rev). Especially the rise of molecular phylogenetics allowed to shed light on the frequently misinterpreted relationships in the group that were not recoverable through morphology alone. Since their first description, Chrysopidae were considered the sister group of Hemerobiidae (brown lacewings) (Haring and Aspöck 2004, Beutel et al. 2010, Winterton et al. 2010, Wang 2016), a relationship that that was supported by few morphological characters, especially from the larvae (New 1989), such as a campodeiform body shape, a similar

head shape, and the presence of trumpet-like empodia on the pretarsus in at least the first instar (Engel et al. 2018). Recent phylogenetic analyses of all Neuroptera, based on molecular data, have challenged the close relationship of these two families (Winterton et al. 2017). In this analysis, Hemerobiidae are recovered fairly “low” in the tree and Chrysopidae are sister to Myrmeleontoidea, but currently there are no known morphological features to support this relationship.



**Figure 2.** Comparison of differing phylogenetic hypotheses proposed within Chrysopidae since 1998. A: Apochrysinæ; N: Nothochrysinæ; C: Chrysopidae; Ni: *Nineta*-group; Ny: *Nothancylla*; B: Belonopterygini; L: Leucochrysinini; An: Ankylopterygini; Ci: Chrysopini.

Traditionally, Chrysopidae have been grouped in three subfamilies (Brooks and Barnard 1990): Apochrysinæ with ca. 25 species in five genera, Nothochrysinæ with ca. 27 species in nine



genera, and the by far most diverse Chrysopinae with slightly more than 1000 species in 88 genera (Oswald 2018). Within Chrysopinae there are five currently recognized tribes. Nothancylini has only recently been erected (Garzón et al. in rev) for the monotypic genus *Nothancylla* Navás, as sister to all other Chrysopinae, but traditionally the subfamily only included Ankylopterygini, Belonopterygini, Chrysopini, and Leucochrysinini (Brooks and Barnard 1990). The relationships between these tribes was uncertain, and several hypotheses (fig. 1) have been proposed over the last 30 years (Brooks and Barnard 1990, Brooks 1997, Winterton and Freitas 2006, Haruyama et al. 2008, Duelli et al. 2014, Dai et al. 2017, Jiang et al. 2017, Garzón et al. in rev). The first phylogenetic hypothesis of Chrysopidae was conducted by Brooks and Barnard (1990) as part of their monograph on chrysopid genera, but their morphological matrix did not result in a resolved tree and they, instead, presented a hypothesis based on their personal observations. They presumed Nothochrysininae as sister to Apochrysininae + Chrysopinae and within the subfamily Chrysopinae, Belonopterygini was sister to a polyphyly between Ankylopterygini, Chrysopini, and Leucochrysinini. Brooks (1997) presented the first phylogeny in a cladistic framework, which is the only phylogenetic work on higher-level Chrysopidae that included morphological data to date. Between 2006 and 2017 several phylogenetic studies on Chrysopidae based on molecular data were conducted: Winterton and Freitas (2006) analyzed three genes (*COI*, *CAD*, and *16S*) and found Apochrysininae as sister to all other Chrysopidae, *Nothancylla* as sister to Nothochrysininae, and Chrysopini sister to Belonopterygini + (Ankylopterygini + Leucochrysinini). Both Haruyama et al. (2008) and Duelli et al. (2014) used the three genes *wg*, *PepCK*, and *ATPase*, but obtained somewhat different results regarding the relationships within Chrysopidae, but recovered Apochrysininae + Nothochrysininae as sister to Chrysopinae, but neither included *Nothancylla*. Dai et al. (2017) and Jiang et al. (2017) analyzed mitogenomes of five and nine species, respectively.

Whereas Dai et al. (2017) found a sister group relationship of Nothochrysinæ and Apochrysinæ, Jiang et al. (2017) recovered Apochrysinæ as sister to Nothochrysinæ + Chrysopinæ. *Nothancyla* is the sister to all Chrysopinæ in both analyses, and not as previously assumed part of Apochrysinæ or Nothochrysinæ. The most recent phylogenetic analysis was conducted by Garzón et al. (in rev.), combining all previously published molecular data to a super-matrix in order to infer the relationships of Chrysopidae at the generic level. This large molecular dataset is the basis, excluding the morphological data presented herein, of the present phylogenetic analyses. In their phylogeny (Garzon et al. in rev.), Apochrysinæ are sister to Nothochrysinæ + Chrysopinæ, *Nothancyla* is sister to all other Chrysopinæ, Belonopterygini + Leucochrysinini are sister to a clade in which Ankylopterygini renders Chrysopini paraphyletic, by resulting as sister to the *Nineta*-group.

Several studies have focused on specific lower-level chrysopid taxa in a phylogenetic framework. Winterton and Brooks (2002) analyzed the subfamily Apochrysinæ and presented a classification based on the phylogeny inferred from morphological data. As a result, they synonymized numerous genera in the subfamily which had been established on the basis of often rare, morphologically distinct species. The South American chrysopine genus *Ceraeochrysa* Adams was subjected to a parsimony analysis based on morphological data, including most species of the genus (De Freitas et al. 2009). The Holarctic species *Chrysoperla carnea* (Stephens) and its related cryptic species were analyzed multiple times using small sets of molecular data (Henry and Wells 2004, Henry et al. 2013) to reveal their interrelationships as well as the phylogenetic implications of substrate-borne vibrational courtship song patterns in the species. A phylogenetic analysis of molecular data including representatives of all subfamilies and tribes of Chrysopidae conducted by Duelli et al. (2014) was focused on the placement of the monotypic genus

*Atlantochrysa* Hölzel, which emerged as sister to *Cunctochrysa* Hölzel + *Meleoma* Fitch. The most recent phylogenetic study of a chrysopid genus is the comprehensive analysis of *Apertochrysa* Tjeder based on molecular data (Mochizuki 2017). The genus was found to be polyphyletic, arising in three distinct lineages of Chrysopini.

Apart of the now confidently placed *Nothancyra*, Brooks and Barnard (1990) mentioned several genera for which possible sister groups were difficult to determine based on morphological characters alone, and none of these have been included in phylogenetic analyses. The most curious of these genera are *Kostka* Navás, *Nuvol* Navás, *Neula* Navás, *Berchmansus* Navás, *Belonopteryx* Gerstaecker, *Himalochrysa* Hölzel, and *Austrochrysa* Esben-Petersen, many of which are rare and/or monotypic. Some more recently described genera that also lack detailed placement are *Santocellus* Tauber et al., *Kymachrysa* Tauber and Garland, and *Titanochrysa* Sosa and de Freitas. Many of these genera have either strongly derived morphologies or exhibit characters of apparently distantly related taxa, presumably through convergence.

The morphology of Chrysopidae is complicated, and many characters used for generic and specific determinations are highly plastic across higher-level taxa. Because of this, it is challenging to infer higher-level relationships from morphological datasets alone, especially in a large analysis (as shown in the present results and in Brooks and Barnard [1990], and Brooks [1997]). That said, there are numerous morphological characters that are of significance in determining taxa in Chrysopidae and that have undergone fascinating character evolution throughout the lineages, found mainly in the genitalia and wing venation (see chapter 2). As in most insects, the male genitalia have evolved into highly diverse structures, which can differ greatly in form, size, and composition. The homology statements of the male genitalia in Neuroptera were revised by Aspöck and Aspöck (2008), but there is a great diversity in form and composition within

Chrysopidae that could not be included due to the large scope of their study on all Neuroptera. For a detailed description of the genitalic structures in Chrysopidae see chapter 3. The male genitalia of all Chrysopidae have a gonarcus and a mediuncus as the minimal set of genitalic sclerites. The gonarcus is a sclerite composed of a median arch that can be expanded in various ways, and a lateral arm on each side, that can vary especially in width, as well as the presence and form of ventral attachments (entoprocessi). The mediuncus is a medial attachment of the gonarcus, which can be basally fused to the median arch of the gonarcus or completely detached and far removed, including all intermediate states. It varies greatly in width and general form, including different processes such as hooks, forks, lobes, or setae.

The parameres are possibly the genitalic character that has undergone most transitions. It is present in most neuropteran families (except most Myrmeleontoidea and few other families, such as Sisyridae), and exhibiting numerous variations in form and size (Aspöck and Aspöck 2008). Hitherto, two kinds of ventrally positioned (in regard to the gonarcus complex) sclerites were recognized in Chrysopidae: the parameres in most Belonopterygini (fig 23 A–C), and the gonapsis in several lineages of Chrysopini (fig. 24 D–J). Parameres are usually long and paired, rarely medially fused, whereas the gonapsis can vary greatly in size but is medially fused, forming a single sclerite in most cases. We here discuss the homology of these two structures, given their position in the male terminalia. In some lineages of Chrysopini there is an additional sclerite present in the male genitalia. The tignum is a thin and arched sclerite positioned dorsal to the gonarcus that does not vary in form. This structure is unique among Neuroptera and is present in only three lineages of Chrysopini.

Besides the male genitalia, wing venation characters have been a focus for taxon diagnoses, due to their vast morphological diversity. Fusions of veins in specific positions or the amount of

fusion in a vein can be deterministic for higher-level taxa within Neuropterida (see chapter 4) and especially in Chrysopidae, where the wing veins are subject to ample fusion. Characters such as the composition of the pseudomedia (PsM) and pseudocubitus (PsC), the form of the *im* cell as well as the fusion of radius posterior (RP) and media anterior (MA) in the hind wing are informative at higher taxonomic levels. Some of these fore wing-venation characters discussed here are traditionally used for generic and specific descriptions, but others have never before been discussed, such as hind wing vein fusion and leg characters.

With the inclusion of a broad character and taxon sampling, we here focus on the combined phylogenetic analysis of molecular and morphological data, in the first analysis of this kind for Chrysopidae. In the study of phylogenetics we are aiming for comprehensive scopes including the maximal possible data input and as such the addition of morphological data is an additional source of information to the molecular data (Lee and Palci 2015). The inclusion of morphological data can illuminate relationships that are not well supported or resolved in hypotheses inferred from molecular data, given that the phylogenetic signal of the morphological data is high enough. However, morphology can also often further confuse relationships based on molecular data. This might be because the signal of the molecular data is not strong enough to withstand alternative signal from the morphology, or because the amount of homoplasy is too great in the morphological data set. We included as much morphological data as possible but were limited due to the large amounts of missing data in both the molecular and to some degree, the morphological dataset, which often lead to uncertainty in the analyses. The addition of morphological data also allows the placement of terminal taxa for which no molecular data could be sampled, resulting in a more comprehensive phylogenetic hypothesis that includes even rare taxa.

Here we present our revised phylogeny of Chrysopidae, based on a large combined data

set including morphological and molecular data. The monophyly of all subfamilies and most tribes is confirmed and Chrysopini several clades are identified. We discuss the newly resolved relationships within Chrysopidae, with a special regard to character evolution along the lineages of the family. We present several phylogenetic trees at different taxonomic levels and discuss the characters that support clades as well as the transformations underlying these relationships. The resulting trees of each conducted analysis are presented and illustrated, and the relationships of all taxonomic groups to the generic level are individually discussed.

## Material and methods

### Taxon sampling

The **molecular data** (S1\_table 1) was generated in collaboration with S. Winterton and I. Garzón from the CDFA (California Department of Food and Agriculture, Sacramento, CA), and used as it was aligned for a manuscript focusing on DNA sequence data and chrysopid relationships (Garzón et al. in rev). No additional sequence data were added to the molecular data set, but all of the data were reanalyzed. Some taxa were excluded for the more detailed analyses due to the large amount of missing data. The data include seven loci (16S rDNA, cytochrome oxidase 1 (COI), CPSase region of carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD), wingless (WG), phosphoenolpyruvate carboxykinase (PepCk), sodium/potassium ATPase alpha subunit (ATPase), and 18S) and for some taxa a mitogenome was present. The sequences were either extracted from alcohol material (by I. G., S. W., and a few by L. B.) or taken from GeneBank (for citations see supplemental material S1\_table 1) (refer to Garzón et al. in rev for methods).

The **morphological data** was gathered from pinned specimens and few specimens

preserved in alcohol from the following institutions: British Museum of Natural History, London, United Kingdom (BMNH); California Academy of Sciences, San Francisco, CA, USA (CAS); California Department for Food and Agriculture, Sacramento, CA, USA (CDFA); Museum für Naturkunde Berlin, Germany (ZMNB); Muséum National d'Histoire Naturelle, Paris, France (MHNM); Naturhistorisches Museum Wien, Austria (NHMW); and Snow Entomological Museum, University of Kansas, Lawrence, KS, USA (SEMC). Data for some rare species were added on the basis of the original descriptions and subsequent literature. We were able to include 63 of the 88 currently recognized chrysopid genera in the final analysis, the largest data set to date. A total of 84 genera were examined or sufficient data was gathered from the literature and habitus photographs of specimens of the BMNH (taken by L. B.) and photos provided by C. Martens from the University of São Paulo and Lukas Kirschey from the ZMNB, but not all specimens could be included in the final phylogenetic analyses. Whenever possible, we included multiple species of more speciose genera to sample the morphological diversity. Specimens were examined with a Nikon SMZ 1500 stereomicroscope. Male and female genitalia were cleared in 10% KOH, stained with Chlorazol black and stored in glycerin. The matrix was compiled in Mesquite Version 3.4 (Maddison and Maddison 2018) and had a total of 177 terminal taxa (including 15 fossil taxa and 12 outgroup taxa) and 165 characters. After several trial analyses it was reduced to an optimal taxa (see table 1) and character set for each analysis (see table 2). Many characters were not phylogenetically informative (either too plastic throughout the ingroup or present only in single terminal taxa), and many taxa were not possible to securely place into the topology, due to the lack of data. In the final analyses the morphological character matrix included 87 discrete characters (binary and multistate present, all weighted equally) and varied in number of taxa, depending on the target taxon (see table 2). These characters and their states are defined below (see list of

characters). The matrices were exported from Mesquite in simplified nexus or NONA format, depending on the program used for the analysis.

Morphological and molecular data was **concatenated** for MrBayes (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) and PAUP\* (Swofford 2003) in a text editor, and kept separate for IQ-TREE (Nguyen et al. 2014). They were analyzed separately as well as combined, with a focus on a comprehensive tree inference including both types of data.

The following genera were analyzed (all with only morphological data), but could not be included in any of the final analyses presented here, because they lead to large polytomies. Belonopterygini and Leucochrysinini: *Berchmansus*, *Chrysacanthia* Lacroix, *Chrysaloisia* Navás, *Dysochrysa* Tjeder, *Nesochrysa* Navás, *Nodochrysa* Banks, and *Turnerochrysa* Kimmins. The leucochrysinine genera *Nuvol*, *Santocellus* were recovered in several different positions in Chrysopinae. Chrysopinae not in Belonopterygini and Leucochrysinini: *Austrochrysa*, *Chrysocerca* Weele, *Himalochrysa*, *Kymachrysa* Tauber and Garland, *Rexa* Navás, and *Titanochrysa*.

## Morphological character list

The following list describes all characters (87) used, and character states and includes short discussions on the occurrence in Chrysopidae. The numbers of the characters and their states are used throughout the discussion (e.g., 1:0 meaning body color is green, or 2:3 meaning that there are 6 flagellar setal rings present on the flagellum). The list is organized from anterior to posterior of the specimen. (Morphological character matrix see supplemental material 2).

## Head

**1. Body color:** [0] green; [1] yellow; [2] brown. The majority of Chrysopidae are light



green in color, while there are Nothochrysinæ, Belonopterygini, and members of the *Eremochrysa*-group with a light brown or yellow body color.

**2. Number of flagellar setal rings:** [0] 3; [1] 4; [2] 5; [3] 6; [4] 2. Apochrysinæ have five rings, Nothochrysinæ five or six rings, and Chrysopinæ have four rings, except for *Nothancylla* with five rings. This character is the only character that unambiguously identifies Chrysopinæ sensu stricto. Flagellar setal rings of two or three in number are only present in outgroup taxa.

**3. Flagellar setae relative to flagellomere:** [0] shorter than width of flagellomere; [1] as long or longer than width of flagellomere. In most Chrysopidae, the flagellar setae are longer than the width of the flagellomere, but there are numerous groups in all subfamilies and most tribes, that have short setae. This is a character that, in combination with others, has been used to define Belonopterygini, but we show that it can be found in many more, and not closely related, taxa.

**4. Flagellomere dimensions:** [0] as long as wide or shorter; [1] at least 1.5 times longer than wide. In most Chrysopidae the flagellomeres are longer than wide. Short flagellomeres are present in Belonopterygini, but there are a few exceptions in Chrysopini that also have shorter than wide flagellomeres, and a few taxa in Belonopterygini with flagellomeres slightly longer than wide.

**5. Antenna length:** [0] longer than forewing; [1] shorter than or about equal in length to forewing. The antenna is usually shorter than the extent of the forewing. All Apochrysinæ, some Leucochrysinæ and very few Belonopterygini and Chrysopini have longer antennae.

**6. Setae on vertex:** [0] absent; [1] present and long (longer than flagellar setae); [2] present and short (shorter than flagellar setae). The setae on the vertex are absent in most Chrysopidae, especially Chrysopinæ. They are dense and either long or short in most of the outgroup taxa, short

in most Nothochrysinæ, and either short or long in Apochrysinæ. There are several groups in Chrysopinae that have very short and sparse setae present.

## **Thorax**

**7. Metascutum frontomedially:** [0] simple; [1] expanded. In Nothochrysinæ the metascutum is medially slightly expanded towards the front, leading to a small rounded bulge. This feature is only present in Nothochrysinæ and could be observed in all examined specimens.

## **Wings**

**8. Humeral vein:** [0] absent; [1] present. The humeral vein is absent in all Chrysopidae, but present in many other Neuroptera (see chapter 4).

**9. Costal area basally:** [0] narrow (costa diverges from the subcosta in an angle of 45° or less, within the first three costal crossveins); [1] broad (costa diverges from the subcosta in an angle exceeding 45°, within the first three costal crossveins). The costal area of Apochrysinæ and some Ankylopterygini is basally broad, which is not the case in all other Chrysopidae, although some taxa in Chrysopini have a somewhat subbasally expanded costal area. In Apochrysinæ and Ankylopterygini this expansion originates in the first costal cell, where the costa diverges from the subcosta at a steep angle, contrary to the more gradual expansion in some Chrysopini, in which the costa diverges from the subcosta at a much less steep angle (usually not exceeding 45°).

**10. Maximal number of c-sc before 1sc-r:** [0] 4; [1] 5; [2] 3; [3] more than 5.

**11. Costal crossvein configuration:** [0] all simple, undivided; [1] partially forked. There are forked veins present in many outgroup taxa, most Apochrysinæ, *Nothancyla*, and some Leucochrysinini, but usually Chrysopidae have simple and undivided costal crossveins.

**12. Costal field apically:** [0] narrow (crossveins shorter than the space between two

crossveins); [1] broad (crossveins longer than the space between two crossveins). The costal field is wide at the pterostigma in Apochrysinæ and some outgroup taxa, and in most Chrysopidae it is much more narrow than basal to the pterostigma.

**13. 1sc-r position (basal subcostal crossvein - bsx):** [0] apically on wing (bsx absent); [1] strongly proximal on wing (bsx present). The bsx is absent in Apochrysinæ and *Nothancyla*, but present in Nothochrysinæ and Chrysopinæ. It can be slightly further apically positioned in some nothochrysinæ taxa.

**14. Subcosta approximating wing margin:** [0] basal to pterostigma; [1] apical to pterostigma. In many Nothochrysinæ, the costa and subcosta seem almost fused basal to the pterostigma, which is never the case in Apochrysinæ and Chrysopinæ.

**15. Subcosta at base:** [0] simple, not inflated; [1] inflated (occupying about half of the subcostal space). The subcosta of Apochrysinæ is inflated basally, but simple or not as extensive in Nothochrysinæ and Chrysopinæ.

**16. Distance between Sc and R:** [0] close; [1] widely separated. This character is of questionable value given its subjective nature, and will be excluded in future analyses. It had very little effect on the analysis, because it simply underlines Apochrysinæ, which is well supported by many other characters.

**17. Number of sc-r at forewing pterostigma:** [0] 0–2; [1] 3–7; [2] 8 or more.

**18. Number of sc-r at hind wing pterostigma:** [0] 0–2; [1] 3–7; [2] 8 or more.

**19. Tympanal organ:** [0] absent; [1] present. The tympanum is present in all Chrysopinæ, including *Nothancyla*, and absent in Apochrysinæ and Nothochrysinæ. It is a distinctive structure, with a basally inflated R and the fusion of M, making it easy to detect. Brooks and Barnard (1990)

and Winterton and Brooks (2002) state that Apochrysinæ have an elongate tympanal organ, but after extensive study we cannot confirm its presence in this subfamily.

**20. Gradates in RA:** [0] absent; [1] present. In some Apochrysinæ and few Leucochrysinæ crossveins between the ra-rp crossveins are present, leading to the formation of a gradate series within the RA field.

**21. Number of gradate series in forewing:** [0] absent; [1] 1; [2] 2; [3] 3; [4] 4; [5] more than 4. Although two gradate series are the most common state in Chrysopidae, there are different numbers possible in all subfamilies. Gradates are defined as crossveins between the RP branches, and are usually divided into inner and outer gradates.

**22. Number of gradate series hind wing:** [0] absent; [1] 1; [2] 2; [3] 3; [4] 4; [5] more than 4. See character 21.

**23. Form of gradate series with respect to each other:** [0] divergent; [1] parallel; [2] diffuse. The two (or more) gradate series are most often parallel to each other, but can be divergent whereby the inner gradates diverge towards the anterior wing margin apically, or irregularly arranged where numerous gradates are present and they do not form one or more prominent lines.

**24. Number outer versus inner gradates:** [0] outer more than inner (+/-2); [1] inner more than outer (+/-2); [2] approx. same in each (+/- 1). In most Chrysopidae there are about as many crossveins in the outer as inner gradates, but in this can vary, where the inner gradates are reduced or basally extended and therefore more numerous, as in many Apochrysinæ and Leucochrysinæ.

**25. Basal extension of inner gradate series:** [0] absent; [1] present. In many Apochrysinæ and Leucochrysinæ, as well as few other taxa, the inner gradates are extended basally, and parallel to PsM. We counted the inner gradates as basally extended when the

basalmost crossvein of the inner gradates was basal to the third to last cell between PsM and PsC.

**26. Basal inner gradate:** [0] not meeting Psm; [1] meeting Psm.

**27. M and R vein at base:** [0] separated; [1] fused. These two veins are fused in all Chrysopinae including *Nothancyla* and close, but still separated in Apochrysiniae and Nothochrysiniae.

**28. 1r-m originating from:** [0] RP; [1] RA. This crossvein originates from RP in the vast majority of Chrysopidae, with the exception of Apochrysiniae that are not in the genus *Apochrysa* and few genera in Chrysopinae, such as *Berchmansus* and *Vieira*.

**29. 1rp-m position:** [0] at *im*; [1] in *im* cell; [2] on *im* distal vein; [3] distal to *im* cell; [4] basal to *im*; [5] on basal vein. In most Chrysopidae the crossvein rp-m meets M at the *im* cell (therefore the crossvein is 1rp-ma), but it can be in a different position in some genera for which it is often diagnostic (e.g., *Chrysoperla*, where it usually is distal to the *im* cell).

**30. PsM continuous:** [0] with inner gradates; [1] with outer gradates; [2] in between. The PsM is continuous with the outer gradates in Apochrysiniae and Chrysopinae, and with the inner gradates in Nothochrysiniae, although the absence of a well-defined PsM in a few genera can obscure this character in the latter.

**31. PsM-PsC distance:** [0] close (distance between PsM and PsC less than the space between two psm-psc crossveins); [1] widely separated (distance between PsM and PsC as wide or wider than the space between two psm-psc crossveins).

**32. Number of psc-psm in forewing:** [0] 0–9; [1] 10–14; [2] 15 or more. The number of crossveins between PsC and PsM is higher in the large and strongly reticulate wings of Apochrysiniae relative to those in most other Chrysopidae, although there are some exceptions

(e.g., *Tumeochrysa*; some species of *Nineta*; some Belonopterygini, especially species of *Italochrysa* and Leucochrysinini), although never to the extent of apochrysin wings.

**33. Number of psc-psm in hind wing:** [0] 0–9; [1] 10–14; [2] 15 or more.

**34. *im* cell (*mamp1*):** [0] triangular with crossvein; [1] rectangular with crossvein; [2] triangular without crossvein; [3] absent, *mamp1* regular; [4] more than four corners. The *im* cell (= irregular *mamp1*) is diagnostic for higher taxa in Chrysopidae. Apochrysininae lack the *im* cell, and their *mamp1* is a regular cell between PsM and PsC. Nothochrysininae have a triangular *im* with a crossvein, a quadrangular *im* with a crossvein or rarely an irregularly shaped *im* with more than four corners. Chrysopinae have a triangular *im*, without a crossvein, leading to a somewhat ovate shape, or a quadrangular *im* with a crossvein.

**35. PsM maximum number of overlapping veins:** [0] 0; [1] 2.

**36. PsC maximum number of overlapping veins:** [0] 0; [1] 2; [2] 3; [3] 4 or more.

**37. MA-MP first meeting:** [0] not meeting; [1] on psm; [2] on psc. This character further defines the *mamp1*. State 0 can only be found in some nothochrysinines where there is no fusion in the PsC between MA and MP, state 1 is present in all Chrysopinae with a triangular *im* cell without a crossvein, and state 2 is present in any other kind where MA and MP are fused in PsC.

**38. MA-CuA fusion in PsC:** [0] absent; [1] present.

**39. MP-CuA fusion in PsC:** [0] absent; [1] present.

**40. Distal vein of m2:** [0] meeting distal vein of *c1*; [1] apical of distal vein of *c1*; [2] basal to distal vein of *c1*.

**41. 2m-cu originating from:** [0] M; [1] MP. The second crossvein between M and Cu originates from MP in most Chrysopidae, meaning that it diverges from MP at the *im* cell. It

originates basal to the split of MA and MP in all Apochrysinæ, many Nothochrysinæ, and outgroup taxa.

**42. *c1* length:** [0] longer than *c2*; [1] same length or shorter than *c2*; [2] more than 3x shorter than *c2*. The cell *c1* (first cubital cell) is often much longer than *c2* in Belonopterygini.

**43. 1A:** [0] simple, not forked; [1] forked. The first anal vein (1A) is usually forked in Chrysopinae but can be simple in Apochrysinæ and Nothochrysinæ.

**44. Anal lobe form:** [0] simple; [1] with elongate pointed lobe. The anal lobe in the forewing of Chrysopidae is reduced, except in Nothochrysinæ where it is pointed and often bears long setae.

**45. Jugal lobe form:** [0] reduced; [1] well-defined. The jugal lobe in the hind wing of Chrysopidae is reduced, except in Nothochrysinæ where it is pointed and often bears long setae.

**46. M terminals at posterior margin:** [0] singular; [1] forked. Usually each medial branch has two terminals that meet the posterior margin (with a few exceptions where the branch terminals are simple), and the two terminals can originate from the PsC (state 0) or a single vein can originate from PsC and then split anterior to the posterior wing margin, forming a forked terminal (state 1)

**47. Number of CuA terminals:** [0] 2; [1] 3; [2] 4; [3] 5; [4] more than 5. CuA has four terminals meeting the posterior wing margin in most Chrysopidae.

**48. Fusion present up to:** [0] absent; [1] half; [2] 2/3s; [3] 3/4s. The fusion of veins in the PsM and especially PsC are usually present up to about two thirds of the wing length, but can be less extensive in Nothochrysinæ or extend up to over three quarters of the wing length in Apochrysinæ.

**49. Termination of veins:** [0] arched; [1] forming angled edges. In primitive-looking

chrysopid wings, extinct members of Chrysopidae, and many outgroup taxa the termination of the longitudinal branches are forked and arched before they meet the posterior wing margin, but in most Chrysopidae these terminations split off a PsC (including fused veins) or are forked with crossveins between the terminals, leading to angulate edges.

**50. Hind wing RP1 and MA:** [0] separated; [1] fused. The first RP branch and MA are fused for one or two abscissae in most Chrysopidae, but can be connected through a crossvein in rare exceptions.

**51. RP1 in hind wing:** [0] at *mamp1*; [1] apical to *mamp1*. The position of the first RP branch is apical to the *mamp1* cell in most Chrysopidae, but at *mamp1* in the majority of Belonopterygini.

**52. CuA in hind wing:** [0] unmodified; [1] extending anteriorly to MA at *dcc*; [2] in between (CuA up, MA down). In all modern Chrysopidae CuA merges with PsC at the level of MP and not, as in the forewing, at the level of CuA. This is never the case in other Neuroptera, and can only rarely be found in fossil taxa of Chrysopidae.

**53. Number of ra-rp anterior to RP1 in hind wing:** [0] 0; [1] 1; [2] 2 or more. Most Apochrysinæ and Nothochrysinæ, as well as outgroup taxa, have at least one ra-rp crossvein before the origin of the first RP branch in the hind wing, whereas it is usually absent in Chrysopinae, with the exception of most Ankylopterygini sensu stricto.

**54. Costal field with many straight veinlets after pterostigma:** [0] absent; [1] present.

## Legs

**55. Pretarsal claws:** [0] dilated; [1] simple. This character is highly homoplastic in Chrysopidae.



**56. Number of long setae medioapically on tarsomere V:** [0] 0; [1] 2; [2] 4. There are no prominent setae present in Nothochrysinæ; some Apochrysinæ, *Nothancyla*, and *Kostka* have four equally long setae, and all other Chrysopinæ have two medial setae that are prominent amongst the smaller surrounding setae.

**57. Tarsus color:** [0] pale; [1] dark; [2] only tarsomere V dark.

**58. Protibial spur:** [0] absent; [1] 1; [2] 2; [3] more than 2. The protibial spur is absent in all Chrysopidae, except for some Nothochrysinæ and most general of the *Eremochrysa*-group, where more than two are present. One or two protibial spurs are only present in outgroup taxa.

**59. Mesotibial spur:** [0] absent; [1] 1; [2] 2; [3] more than 2. The mesotibial spur is absent in all Apochrysinæ and Ankylopterygini and very few Chrysopini and Nothochrysinæ. There is one spur present in the majority of Chrysopinæ and *Nothochrysa*, two in some Nothochrysinæ and most outgroup taxa and more than two in some Nothochrysinæ and all members of the *Eremochrysa*-group.

**60. Metatibial spur:** [0] absent; [1] 1; [2] 2; [3] more than 2. The metatibial spur is absent in all Apochrysinæ and Ankylopterygini and very few Chrysopini and Nothochrysinæ. There is one spur present in the majority of Chrysopinæ and *Nothochrysa*, two in some Nothochrysinæ and most outgroup taxa, and more than two in some Nothochrysinæ and all members of the *Eremochrysa*-group.

## **Abdomen**

**61. Microtholi on male abdomen (♂):** [0] absent; [1] present. Although there are some clades where microtholi are present more than in others (e.g., Belonopterygini or *Chrysopa*-group), this character is spread throughout Chrysopinæ and Nothochrysinæ.

**62. Praegenitale in female terminalia** (♀): [0] absent; [1] present. The identity of the praegenitale in the female terminalia is in need of revision. Traditionally it is present only in Belonopterygini, but there are several chrysopine genera that have additional sclerotized structures at the apex of sternum VII, which should be further investigated (see also chapter 3).

### **Male genitalia**

**63. Ventral apodeme** (♂): [0] without projections; [1] with dorsal projections; [2] with basal expansion; [3] with extra plate. The ventral apodeme is simple in most Chrysopidae, but can have a dorsally pointing projection or tip in some Chrysopini (e.g., *Chrysopa*), and can be basally extended past the base of the dorsal apodeme in *Kymachrysa*.

**64. Tergum IX and ectoproct** (♂): [0] fused; [1] separated. The ninth tergum and ectoproct are fused in most Chrysopidae, but can rarely be separated in all subfamilies, most commonly in Apochrysininae.

**65. Dorsal apodeme** (♂): [0] without projections; [1] with ventral projection. The dorsal apodeme is simple in most Chrysopidae, but can rarely have a ventrally pointing projection or tip in Nothochrysininae and Chrysopinae.

**66. Ectoproct** (♂): [0] normal; [1] strongly exerted; [2] ventral lobe or horn; [3] cone-like lobe pointing apically apical projections (small in comp to rest of ectoproct). The ectoproct of the male terminalia is usually rounded but can be expanded in different forms throughout Chrysopidae.

**67. Dorsal invagination of ectoprocts** (♂): [0] shallow; [1] deep. Most Chrysopidae have a shallow invagination dorsally between the ectoprocts of each side, but it can be deeper in some genera, especially where the ectoprocts are apically expanded.

**68. Sternum VIII + IX** (♂): [0] fused; [1] not fused. Sternum eight and nine are usually

fused in Chrysopidae, and rarely separated in exceptions within all subfamilies. Where microtholi are present it is possible to determine the line of fusion, because there usually are no microtholi present on the ninth sternum.

**69. Sternum VIII + IX projection (♂):** [0] simple; [1] with dorsal projecting horn or lobe; [2] with cone-like invagination for dorsal structure space; [3] strong apical expansion with setae; [4] sclerotized lobes apically; [5] three sharp tips apically; [6] three lobes apically with setae/cristae; [7] slightly elongate (simple but, longer than tergum); [8] two-pointed lobes with thick setae; [9] ventral apical lip. The fused eighth and ninth sternum can be shaped variously, but is simple and rounded in most Chrysopidae.

**70. Strong spines on apical sternum VIII+IX (♂):** [0] absent; [1] present. In some Chrysopinae (e.g., *Eremochrysa*, *Nineta*, and *Chrysotropia*) thick setae can be present on the apical tip of sternum VIII IX (not the same as gonocristae).

**71. Tignum (♂):** [0] absent; [1] present. The presence of a tignum, which is an additional thin arched sclerite dorsal to the gonarcus, is unique to Chrysopini and possibly *Nothancylla*. Within Chrysopini, only a few groups have this character.

**72. Gonarcus medially (♂):** [0] fused, median arch sclerotized; [1] separated, but connected by membranous, non-sclerotized median arch. The gonarcus is medially fused in most Chrysopidae, but it can be separated and only connected with a loose membrane in few Apochrysinæ, Ankylopterygini s. l., and we found it in one species of *Meleoma* and *Titanochrysa*.

**73. Gonarcus medial expansion (♂):** [0] normal (thin); [1] completely expanded (median plate); [2] forward projecting medially; [3] forward projecting 2 horns; [4] forward pointing lobes. The gonarcus is medially not expanded in most Chrysopidae, but can have numerous variations,

which can be genus specific, although there is some homoplasy present in this character, which might be partially resolved when further studying the details of it.

**74. Gonarcus lateral arms (♂):** [0] thin or slightly broadened; [1] evenly expanded to a broad flat surface; [2] strongly expanded to ear-like structure; [3] thin towards medial arch and apically with large flat expansion.

**75. Number of attachments on gonarcus (♂):** [0] 0; [1] 1; [2] 2. There is usually one attachment on the gonarcus (=entoprocessus), in some taxa the gonarcus is simple and there is no attachment and in few taxa there is one longer attachment (entoprocessus) and an additional smaller one.

**76. Position of gonarcus attachments (entoprocessi) (♂):** [0] at arch; [1] medially; [2] at end of lateral arm. The entoprocessus is attached to the gonarcus where the lateral arm fade into the medial arch, or medially on the lateral arm in most Chrysopidae, and can rarely be at the tip of the lateral arm (mostly in outgroup)

**77. Form of gonarcus attachment (entoprocessi) (♂):** [0] short (shorter than width of gonarcus at the point of attachment); [1] long (longer than width of gonarcus); [2] arching (both entoprocessi connecting); [3] long and with extra additional on the entoprocessus, often articulating. The form of the entoprocessus is simple and varies in length in most Chrysopidae, but can be arching (both entoprocessi medially connected) or with additional structures present.

**78. Position of gonarcus complex (♂):** [0] normal (lateral arms pointing ventroapically); [1] rotated >100. The gonarcus complex (gonarcus, entoprocessus and mediuncus) is usually oriented with the median arch of the gonarcus pointing towards the apex of the abdomen, the lateral arms pointing towards the base of the abdomen and the mediuncus and entoprocessus attaching

ventrally. In most Belonopterygini, the gonarcus complex is rotated when not in copula, where the median arch is pointing ventrally and the base of the abdomen.

**79. Position of mediuncus** (♂): [0] closely attached (with thin membranous connection); [1] apparently detached. The mediuncus can be closely attached to the median arch of the gonarcus (formerly termed arcessus), with a clearly visible membranous connection, or far removed (formerly termed pseudopenis). We scored the former two as one state because many intermediate states exist in which the mediuncus is not closely connected, but by thick membrane or where the mediuncus is close but connected by a thin barely visible membrane.

**80. Mediuncus** (♂): [0] elongate, thin; [1] short, triangle (+- as long as broad); [2] long, with lateral expansion; [3] very short (shorter than long). The mediuncus varies greatly in form and is usually small and triangular (formerly termed arcessus) in Apochrysinæ and some Nothochrysinæ, often elaborate and about as long as the lateral arms of the gonarcus in most Chrysopinae and some Nothochrysinæ, thin and elongate (formerly termed pseudopenis) in many Ankylopterygini and some Chrysopini, and in few exceptions have a short broadened mediuncus.

**81. Parameres** (♂): [0] absent; [1] present. The parameres are present in many groups of Chrysopinae (see discussion), but can never be found in Apochrysinæ and Ankylopterygini and rarely in Nothochrysinæ. We scored the presence of parameres as well as the gonapsis under this character, according to the suggested homology of these two structures (see chapter 3).

**82. Parameres medially** (♂): [0] completely fused (single structure); [1] separated, but connected by membrane. The parameres are usually medially fused in Chrysopini, with few exceptions, and medially separated, forming a paired structure in Belonopterygini (with the exception of the medially fused large parameres of *Nesochrysa*), and a few Leucochrysinini.

**83. Parameres opening** (♂): [0] towards apex; [1] towards base; [2] no opening. If the parameres are not completely fused, the paired apices can point towards the apex of the abdomen, with a fusion at the basal part of the parameres, or they can be pointing towards the base of the abdomen, with the fusion at the apical part of the parameres, which is less common.

**84. Parameres position** (♂): [0] ventral; [1] close to mediuncus. The parameres are usually positioned in the area of the sternum, distinctively ventral of the gonarcus complex, but can rarely be closely positioned to the lateral arms of the gonarcus or lateral to the mediuncus in a few Belonopterygini.

**85. Parameres size** (♂): [0] shorter than gonarcus; [1] as long or longer than gonarcus. In many Belonopterygini the parameres are much longer than the lateral arm of the gonarcus, and often pointing out of the apex of the abdomen. In the few cases of parameres that we found in Leucochrysinini (e.g., *Leucochrysa insularis*), they were very small. In Chrysopini the parameres are usually shorter than the lateral arm of the gonarcus, but can be elongate in some taxa (e.g., *Eremochrysa* or *Ceraeochrysa*)

**86. Gonosetae** (♂): [0] absent; [1] sparse (under ten); [2] abundant (10 or more); [3] on gonarcus arch. The presence of gonosetae, which are usually positioned on the gonosaccus, posterior or lateral to the mediuncus, occurs throughout Chrysopidae, but in various degrees from absent to abundant. The only group in which over 10 gonosetae can be present is Chrysopini. Gonosetae on the gonarcus are only present in outgroup taxa.

**87. Gonocristae** (♂): [0] absent; [1] present in one patch apically on sternum; [2] present in 2 patches; [3] present on ectoproct apically. Gonocristae are small and numerous present sharply pointed serrations of the membrane, that, when present are usually present at the apex of sternum VIII + IX or more rarely on the ectoproct. The cristae point towards the base of the

abdomen.

Table 1: Species included in the final analyses. A: ingroup (family Chrysopidae; B: outgroup taxa including their respective family. Abbreviations: Anky: Ankylopterygini; Apo: Apochrysinæ; Belo: Belonopterygini; Chrni: Chrysopini; Chry: Chrysopinae; Leuco: Leucochrysinæ; Notho: Nothochrysinæ.

Genus name	Species name	Subfamily	Tribe	morph.	mol.
<b>A: Ingroup (family Chrysopidae)</b>					
<i>(Nineta) Nineta</i>	<i>flava</i>	Chry	Chrni	x	
<i>(Nineta) Nineta</i>	<i>gravida</i>	Chry	Chrni	x	
<i>(Nineta) Nineta</i>	<i>itoi</i>	Chry	Chrni	x	x
<i>(Nineta) Nineta</i>	<i>pallida</i>	Chry	Chrni	x	x
<i>Abachrysa</i>	<i>eureka</i>	Chry	Belo	x	x
<i>Anachrysa</i>	<i>elegans</i>	Chry	Chrni	x	
<i>Ankylopteryx</i>	<i>alluauri</i>	Chry	Anky	x	x
<i>Ankylopteryx</i>	<i>gracilis</i> + sp.	Chry	Anky	x	x
<i>Ankylopteryx</i>	<i>rieki</i>	Chry	Anky	x	
<i>Ankylopteryx</i>	sp.	Chry	Anky		x
<i>Ankylopteryx</i>	<i>anomala</i>	Chry	Anky	x	x
<i>Ankylopteryx</i>	<i>anomala</i>	Chry	Anky		x
<i>Anomalochrysa</i>	<i>hepatica</i>	Chry	Chrni	x	x
<i>Apertochrysa (=Pseudomallada)</i>	<i>crassinervis</i>	Chry	Chrni	x	
<i>Apertochrysa (=Pseudomallada)</i>	<i>edwardsi</i> + <i>eurydera</i>	Chry	Chrni	x	x
<i>Apochrysa</i>	<i>leptala</i>	Apo		x	x
<i>Apochrysa</i>	<i>lutea</i>	Apo		x	x
<i>Apochrysa</i>	<i>matsumurae</i>	Apo		x	x
<i>Apochrysa</i>	<i>montrouzieri</i>	Apo		x	x
<i>Asthenochrysa</i>	<i>viridula</i>	Notho		x	x
<i>Atlantochrysa</i>	<i>aylantica</i>	Chry	Chrni	x	x

<i>Austrochrysa</i>	<i>apoana</i>	Chry	Chrni	x	
<i>Belonopteryx</i>	<i>arteriosa</i>	Chry	Belo	x	
<i>Borniochrysa</i>	<i>squamosa</i>	Chry	Chrni	x	x
<i>Brinckochrysa</i>	<i>stenoptera</i>	Chry	Chrni	x	
<i>Brinckochrysa</i>	<i>turkanensis</i>	Chry	Chrni	x	x
<i>Cacarulla</i>	<i>maculipennis</i>	Chry	Leuc	x	x
<i>Calochrysa</i>	<i>extranea</i>	Chry	Belo	x	x
<i>Ceraeochrysa</i>	<i>caligata</i>	Chry	Chrni	x	x
<i>Ceraeochrysa</i>	<i>dislepis</i>	Chry	Chrni	x	x
<i>Ceratochrysa</i>	<i>ceratina</i>	Chry	Chrni	x	
<i>Chrysacanthia</i>	<i>iwo</i>	Chry	Belo	x	
<i>Chrysemosa</i>	<i>jeanelli</i>	Chry	Chrni	x	x
<i>Chrysemosa</i>	<i>simillima</i>	Chry	Chrni	x	
<i>Chrysemosa</i>	<i>umbralis</i>	Chry	Chrni	x	x
<i>Chrysopa</i>	<i>excepta</i>	Chry	Chrni	x	x
<i>Chrysopa</i>	<i>nigricornis</i>	Chry	Chrni	x	
<i>Chrysopa</i>	<i>oculata</i>	Chry	Chrni	x	
<i>Chrysopa</i>	<i>pallens + perla</i>	Chry	Chrni	x	x
<i>Chrysoperla</i>	<i>carnea</i>	Chry	Chrni	x	
<i>Chrysoperla</i>	<i>externa</i>	Chry	Chrni	x	x
<i>Chrysoperla</i>	<i>rufilabris</i>	Chry	Chrni	x	
<i>Chrysoperla</i>	<i>nipponensis + furcifera</i>	Chry	Chrni	x	x
<i>Chrysopidia (Chrysopidia)</i>	<i>nigrata</i>	Chry	Chrni	x	
<i>Chrysopidia (Chrysotropia)</i>	<i>ciliata</i>	Chry	Chrni	x	x
<i>Chrysopidia (Chrysotropia)</i>	<i>obliqua</i>	Chry	Chrni	x	
<i>Chrysopodes (Chrysopodes)</i>	<i>divisa</i>	Chry	Chrni	x	x
<i>Chrysopodes (Chrysopodes)</i>	<i>spinellus</i>	Chry	Chrni	x	x
<i>Chrysopodes (Neosuarius)</i>	<i>krugii</i>	Chry	Chrni	x	
<i>Cunctochrysa</i>	<i>baetica</i>	Chry	Chrni	x	x
<i>Dictyochrysa</i>	<i>peterseni</i>	Notho		x	x
<i>Domenechus</i>	<i>mirifica</i>	Apo		x	
<i>Dysochrysa</i>	<i>furcata</i>	Chry	Belo	x	
<i>Eremochrysa (Chrysopiella)</i>	<i>pallida</i>	Chry	Chrni	x	x



<i>Eremochrysa (Eremochrysa)</i>	<i>fraterna</i>	Chry	Chrni	x	
<i>Eremochrysa (Eremochrysa)</i>	<i>hageni</i>	Chry	Chrni	x	x
<i>Eremochrysa (Eremochrysa)</i>	<i>punctinerva</i>	Chry	Chrni	x	
<i>Evanochrysa</i>	<i>evanescens</i>	Chry	Belo	x	x
<i>Furcochrysa</i>	<i>allata</i>	Chry	Chrni	x	
<i>Glenochrysa</i>	<i>conradina</i>	Chry	Chrni	x	x
<i>Glenochrysa</i>	<i>opposita</i>	Chry	Chrni	x	x
<i>Glenochrysa</i>	<i>splendida</i>	Chry	Chrni	x	x
<i>Gonzaga</i>	<i>nigriceps</i>	Chry	Leuc	x	x
<i>Hypochrysa</i>	<i>elegans</i>	Notho		x	x
<i>Hypochrysa</i>	<i>nobilis</i>	Notho		x	
<i>Italochrysa</i>	<i>fascialis</i>	Chry	Belo	x	
<i>Italochrysa</i>	<i>japonica</i>	Chry	Belo	x	x
<i>Italochrysa</i>	<i>peringueyi</i>	Chry	Belo	x	x
<i>Italochrysa</i>	<i>insignis + italica</i>	Chry	Belo	x	x
<i>Joguina</i>	<i>constellata</i>	Apo		x	
<i>Kimochrysa</i>	<i>africana + impar</i>	Notho		x	x
<i>Kostka</i>	<i>nacaratus</i>	Chry	Chrni	x	x
<i>Leptochrysa</i>	<i>prisca</i>	Notho		x	
<i>Leucochrysa (Leucochrysa)</i>	<i>nr. nigrilabris</i>	Chry	Leuc	x	
<i>Leucochrysa (Leucochrysa)</i>	<i>pretiosa</i>	Chry	Leuc	x	x
<i>Leucochrysa (Nodita)</i>	<i>americana</i>	Chry	Leuc	x	x
<i>Leucochrysa (Nodita)</i>	<i>cruentata</i>	Chry	Leuc	x	x
<i>Leucochrysa (Nodita)</i>	<i>marquezi</i>	Chry	Leuc	x	x
<i>Leucochrysa (Nodita)</i>	<i>robusta</i>	Chry	Leuc	x	x
<i>Loyola</i>	<i>atlanticus</i>	Apo		x	
<i>Loyola</i>	<i>coesus</i>	Apo		x	
<i>Mallada</i>	<i>signata</i>	Chry	Chrni	x	x
<i>Mallada</i>	<i>tripunctata</i>	Chry	Chrni	x	x
<i>Meleoma</i>	<i>emucta + arizonensis</i>	Chry	Chrni	x	x
<i>Nacarina</i>	sp.	Chry	Belo		x
<i>Nineta (Tumeochrysa)</i>	spp.	Chry	Chrni	x	x
<i>Nipponochrysa</i>	<i>moriutii</i>	Chry	Chrni	x	x

<i>Nobilinius</i>	<i>albardae</i>	Apo		x	
<i>Nothancyla</i>	<i>verreauxi</i>	Chry		x	x
<i>Nothochrysa</i>	spp.	Notho		x	
<i>Nothochrysa</i>	<i>californica</i> + <i>fuviceps</i>	Notho		x	x
<i>Oyochrysa</i>	<i>ancorra</i>	Chry	Belo	x	
<i>Pamochrysa</i>	<i>stellata</i>	Notho		x	
<i>Parachrysoptera</i>	<i>argentina</i>	Chry	Chrni	x	x
<i>Parachrysoptera</i>	<i>pallidicornis</i>	Chry	Chrni	x	x
<i>Parankylopteryx</i>	sp.	Chry	Anky		x
<i>Parankylopteryx</i>	<i>multipunctata</i> + sp.	Chry	Anky	x	x
<i>Peyerimhoffina</i>	<i>gracilis</i>	Chry	Chrni	x	x
<i>Pimachrysa</i>	<i>nigra</i>	Notho		x	x
<i>Plesiochrysa</i>	<i>atalotis</i>	Chry	Chrni	x	x
<i>Plesiochrysa</i>	<i>ramburi</i>	Chry	Chrni	x	x
<i>Pseudomallada</i>	<i>luctosa</i>	Chry	Chrni	x	x
<i>Pseudomallada</i>	<i>prasinus</i> + <i>marianus</i>	Chry	Chrni	x	x
<i>Pseudomallada</i>	<i>tactus</i>	Chry	Chrni	x	x
<i>Retipenna</i>	<i>hasegawai</i>	Chry	Anky	x	x
<i>Retipenna</i>	<i>notata</i>	Chry	Anky	x	
<i>Retipenna</i>	<i>variegata</i>	Chry	Anky	x	x
<i>Semachrysa</i>	<i>matsumurae</i>	Chry	Anky	x	x
<i>Signochrysa</i>	<i>caliptera</i>	Chry	Anky	x	
<i>Signochrysa</i>	<i>ornatissima</i>	Chry	Anky	x	x
<i>Stigmachrysa</i>	<i>cladostigma</i>	Chry	Belo	x	x
<i>Suarius</i>	sp. + <i>walsinghami</i>	Chry	Chrni	x	x
<i>Triplochrysa</i>	<i>pallida</i>	Notho		x	
<i>Ungla</i>	<i>ivancruzi</i>	Chry	Chrni	x	x
<i>Vieira</i>	<i>elegans</i>	Chry	Leuc	x	x
<i>Yumachrysa</i>	<i>apache</i>	Chry	Chrni	x	x
<i>Yumachrysa</i>	<i>clarives</i>	Chry	Chrni	x	
<b>B: Outgroup</b>		Family:			
<i>Conchopterella</i>	<i>stangei</i>	Hemerobiidae		x	x
<i>Drepanopteryx</i>	<i>phalaenoides</i>	Hemerobiidae			x

<i>Fontecilla</i>	<i>graphicus</i>	Ithonidae		x
<i>Ithone</i>	<i>fulva</i>	Ithonidae	x	x
<i>Micromus</i>	sp. + <i>linearis</i>	Hemerobiidae		x
<i>Myiodactylus</i>	<i>osmyloides</i>	Nymphidae	x	
<i>Notiobiella</i>	<i>viridis</i>	Hemerobiidae	x	
<i>Osmylops</i>	<i>ectoarticulatus</i>	Osmylidae	x	
<i>Psychopsis</i>	<i>gracilis</i>	Psychopsidae	x	

## Analyses

The **parsimony** analyses were conducted with the desktop version of PAUP\* v4.0a (Swofford 2003) and TNT v1.1. (Goloboff et al. 2008). To analyze the morphological data, we conducted a new technology search in TNT, initially increasing the memory, with 10,000 random trees to hold (initial addseq. = 500, ratchet = 1000 iterations, drift = 100 cycles, and tree fusing = 100 cycles). From the resulting parsimony trees we constructed a 50% majority rule consensus tree. The combined data set was analyzed in PAUP\*, because TNT had problems reading the different data types. The heuristic search was conducted using the default settings, and with 10000 maximal trees in hold, and a 50% majority rule consensus tree was calculated.

**Maximum Likelihood** analyses of the combined data were run in IQ-TREE v1.5.6 (Nguyen et al. 2014). The dataset was partitioned *a priori* as in other analyses, with the morphological matrix treated as a single data subset and the molecular matrix partitioned by gene. Substitution models for each data subset were selected using the IQ-TREE default model search algorithm ModelFinder (Kalyaanamoorthy et al. 2017, “-m MFP” command) via the edge-linked partition model (Chernomor 2016, “-spp” option), in which all partitioned subsets share the same underlying branch lengths, but are allowed their own independent evolutionary rates. Nodal support of the ML tree was assessed by 1,000 ultrafast bootstrap replicates (Minh et al. 2013,

Hoang et al. 2018, “-bb 1000” command), and the bootstrap values were mapped on the most likely tree. An ultrafast bootstrap value (UFB) of 95 is considered the threshold for high support of a given node (Minh et al. 2013, Hoang et al. 2018).

Most analyses shown here were conducted under a **Bayesian** framework in MrBayes v3.2.6 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003). We conducted tree inference based on morphological, molecular, and combined data in MrBayes. To identify the best partition scheme and substitution models for the molecular data, we ran PartitionFinder v2.1.1. (Lanfear et al. 2012) on CIPRES (Miller et al. 2010) resulting in 21 separate partitions, for all of which the GTR+I+ $\gamma$  model was suggested, except for one with the K80+I+ $\gamma$  model. The morphological data was analyzed under the MK model, leading to a total of 22 partitions and three different models in the concatenated data set. Due to the large dimensions of the data set we ran all analyses via the online platform CIPRES. In some analyses we constrained the topology by forcing monophyly (subfamilial or tribal level) or included a starting tree, based on previous results. Based on the topology resulting from analyses 1, 3, and 4, we conducted (stepwise) analyses, ranging from the inclusion of all available terminal taxa and morphological characters (not shown), to subsets tailored to the target taxon. The generations of the analyses were set between 10 and 100 million, based on the size of the data set. In most runs a stoprule at 0.01 (SDSF) was employed, which is the suggested threshold for convergence between runs. It was lifted in some analyses to achieve higher ESS values. Trees and probability values were sampled every 1,000 generations. The results of a selection of the analyses with the best resolved trees and highest support values are shown here. The criteria for evaluating the confidence in a phylogenetic hypotheses were (1) the resolution in the consensus tree, and whether the runs converged and were mixing well, measured by (2) the standard deviation split frequencies (SDSF) of under the standard value 0.01, and (3)

the effective sample size (ESS) values of the average log normal likelihood (LnL), log normal probability (LnPr), and tree length (TL) to assess whether the entire tree landscape was searched thoroughly enough (larger values imply a better sampling of the posterior distribution, values over 100, or better 200 are suggested). The minimum SDSF value, and the ESS values of the combined trace files of the two runs are reported for every analysis. These criteria were assessed in Figtree (v. 1.4.3) (tree topology), Notepad++ (SDSF values) and Tracer v1.6.0 (Rambaut et al. 2018) (ESS values). Posterior probabilities (PP) of the nodes are reported in the tree figures and the Results section.

The node-dated **divergence-time analysis** was conducted in MrBayes under the fossilized birth-death model (FBD) (Heath et al. 2013) following the tutorial by Zhang (2017). The relaxed clock model IGR (implemented gamma rate) (Lepage et al. 2007) was applied to allow for relative changes of the clock rate along the branches. We analyzed the combined data set with the same general parameters and models as in the non-time tree analyses. The calibration points were given with an offset exponential distribution of the minimum and maximum time of the fossil. The monophyly of the subfamilies and tribes was constrained due to the much more time intense analyses. We also conducted a tip based analysis, but because the fossils are often only preserved wings, there was not enough information to recover a resolved tree, and many of these fossils are placed in the stem and not crown group. Seven fossils were used as markers for the node dated analysis, and we conducted two analyses with differently strict maximum ages for the fossils. We based the ages of the fossils on the minimum age of the Lagerstätte in which it was found and the maximum age of the Lagerstätte (strict) or the minimum age of the next Lagerstätte with chrysopid fossils present, in which the species of interest was absent (relaxed), according to a commonly used method (Briggs and Fortey 2005). We included seven fossils as calibration points: the root

age was based on the oldest ithonid fossil *Mesopolystoechus apicalis* Martynov (strict and relaxed: 201–230 MA), *Mesypochrysa magna* Makarkin was used as the oldest definitive member of crown Chrysopidae (strict and relaxed: 126–131 Ma), *Okanaganochrysa coltsunae* Makarkin and Archibald was putatively used as a stem to Apochrysinæ (strict: 52.9–100 MA; relaxed: 52.9–100 MA), *Asiachrysa tadushiella* Makarkin was used as the oldest crown Nothochrysinæ (strict: 43.4–52.9 MA; relaxed: 43.4–100 MA), and *Paleochrysa monteliensis* Séméria and Nel was used as the oldest member of Chrysopidae (strict: 33.9–37.9 MA; relaxed: 33.9–66 MA). *Hypochrysa hercyniensis* Schlüter (strict: 3.6–2.6 MA; relaxed: 3.6–5.3 MA) was placed in its genus, as well as *Nothochrysa praeclara* Statz (strict: 23–20.4 MA; relaxed: 23–56 MA), respectively.

## Output

Line drawings were produced in Adobe Illustrator CC 2017. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and then assembled in Adobe Photoshop and Illustrator CC2017. A total of 14 analyses were conducted (see table 2) including eleven BI, one ML and two parsimony analyses. A selection of morphological characters was traced on the resulting tree of analysis 4, using the “trace character history” function to reconstruct parsimony ancestral states in Mesquite. The output statistics of all analyses were viewed in Tracer, to evaluate the validity of the results. Trees were visualized and arranged in Figtree (v. 1.4.3), exported in PDF format and edited in Adobe Illustrator CC 2017. We here describe the results, including the support values and resulting topologies of each analysis and then discuss the relationships within Chrysopidae by taxon.

Table 2: conducted analyses, including the framework used, the input, and the statistical support values to assess convergence. Low ESS values are indicated by a \*. SDSF values of 0.01 indicate that a stoprule (str) was implied to terminate the analysis after reaching the value 0.01.

analysis #	type	program	ingroup	ingroup taxa	data type	SDSF	ESS LnL	ESS LnPr	ESS TL
1	BI	MrBayes	Chrysopidae	79	molecular	>0.01	2049	84*	83*
2	BI	MrBayes	Chrysopidae	86	morphological	0.0085	4222	3418	3186
3	BI	MrBayes	Chrysopidae	78	combined	0.01 (str)	2480	111*	96*
4	BI	MrBayes	Chrysopidae	100	combined	0.01 (str)	2971	110*	109*
5	BI	MrBayes	Apochrysinæ	9	combined	0.0057	5582	267	1723
6	BI	MrBayes	Nothochrysinæ	11	combined	0.0082	2211	1660	1083
7	BI	MrBayes	Belonopterygini + Leucochrysinini	17	combined				
8	BI	MrBayes	Ankylopterygini	22	combined	0.01 (str)	1003	622	427
9	BI	MrBayes	Chrysopini	53	combined	0.00978	3133	392	390
10	BI (time)	MrBayes	Chrysopidae	79	combined	0.01 (str)	41*	8*	49*
11	BI (time)	MrBayes	Chrysopidae	79	combined	0.01 (str)	3993	10*	200
12	ML	IQ TREE	Chrysopidae	91	combined				
13	parsimony	PAUP*	Chrysopidae	91	combined				
14	parsimony	TNT	Chrysopidae	91	morphological				

## Results

### Bayesian analyses

#### Analysis 1: molecular data (fig. 2)

Analysis 1 includes multiple representatives of all subfamilies and tribes of Chrysopidae, and all terminal taxa for which molecular data was available – a total of 84 terminal taxa (79 ingroup). The topology was not constrained, and no starting tree was provided. The data set from Garzón et al. (*in review*) was reanalyzed. The analysis did not reach an average standard deviation of split frequencies (SDSF) of 0.01 after 100 million generations and was automatically terminated due to a time limit on CIPRES. The effective sample size (ESS) values were not high enough to consider this analysis truly converged (LnL: 1029, LnPr: 84, TL: 83), with low numbers in the posterior probabilities and tree length.

The monophyly of Chrysopidae was confirmed in this analysis (as in all other analyses), with a posterior probability of 1 (PP=1). All three subfamilies are monophyletic with high nodal support (Apochrysinæ PP= 1, Nothochrysinæ PP= 0.99, Chrysopinæ sensu lato (including *Nothancylla*) PP= 0.99, Chrysopinæ sensu stricto (without *Nothancylla*) PP= 0.99), and Apochrysinæ was found as sister to Nothochrysinæ + Chrysopinæ. *Nothancylla* was recovered as sister to all other Chrysopinæ, and not as hitherto classified within Apochrysinæ (this possibility has been discussed previously in Dai et al. 2017, Jiang et al. 2017, and Garzón et al. in rev). The tribes within Chrysopidae could only partially be recovered, as discussed in the taxon specific analyses below. Belonopterygini and Leucochrysinini form a monophyletic group which is sister to all other Chrysopinæ sensu stricto. Ankylopterygini is monophyletic but rendered Chrysopini paraphyletic, due to a sister-group relationship with the *Nineta*-group (now included in Ankylopterygini, see discussion). Chrysopini as currently recognized is split into the *Nineta*-group



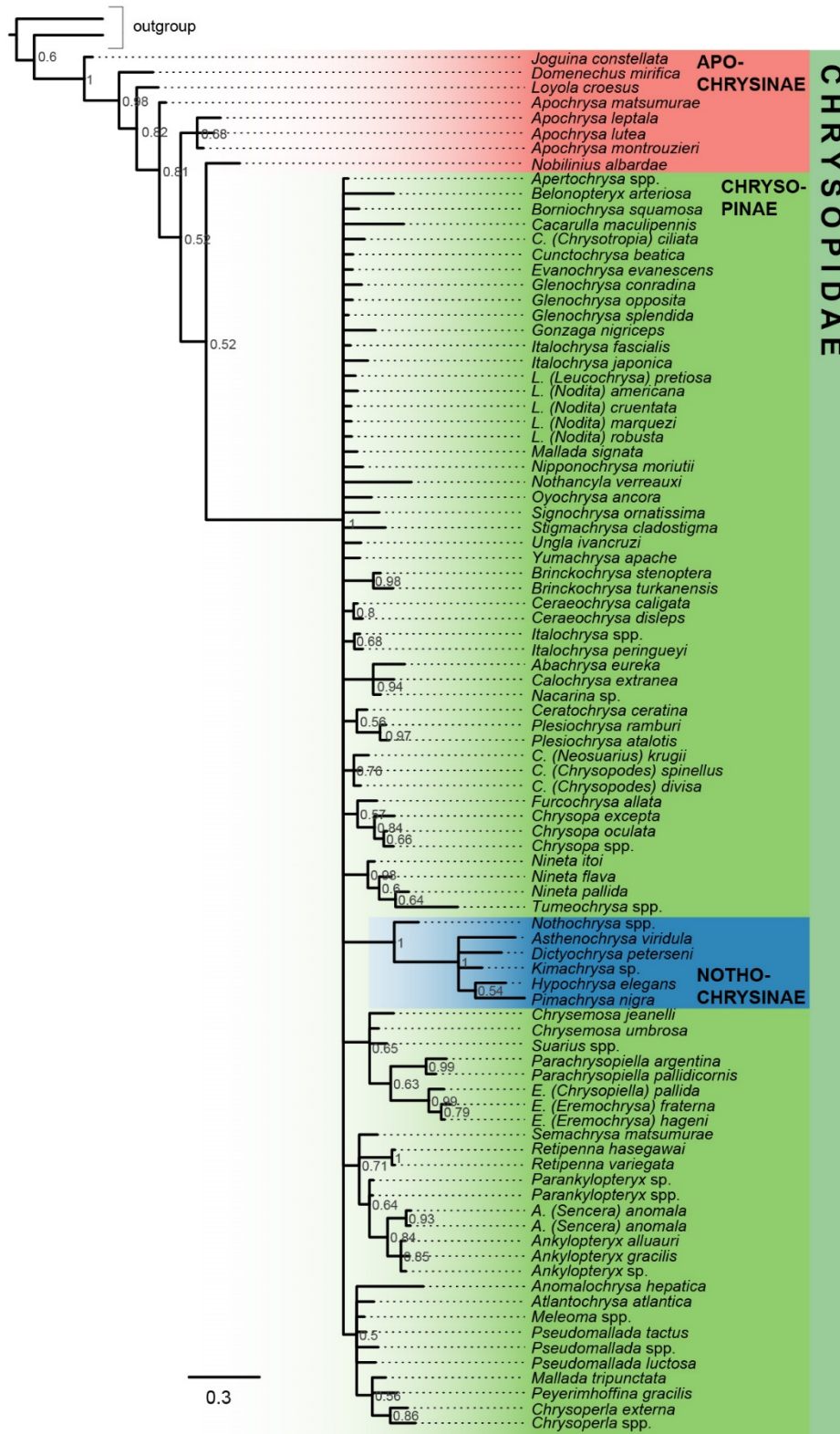
and the remainder of the tribe, including five larger clades, which will be described in detail below (*Chrysopodes*-, *Eremochrysa*-, *Chrysoperla*-, *Meleoma*-, and *Chrysopa*-groups).



## Analysis 2: morphological data (fig. 3)

Analysis 2 includes multiple representatives of all subfamilies and tribes of Chrysopidae for which morphological data was available, leading to a somewhat different set of outgroup taxa. A total of 91 terminal taxa (86 ingroup) were included in the analysis. We analyzed the morphological data set in a parsimony (see below) and Bayesian framework, and both resulting phylogenetic hypotheses are poorly resolved. The Bayesian analysis reached an average SDSF of 0.01 after 2 hours and ca. 13.5 million generations, but was continued for 5 hours (a total of 35 million generations) (minimum SDSF: 0.0085). The ESS values were high enough to consider this analysis converged (LnL: 4222, LnPr: 3418, TL: 3186).

As shown in the tree in figure 3, Chrysopidae are monophyletic, but there is a polytomy between Apochrysininae and several chrysopine branches, a large polytomy including most chrysopine taxa, and few monophyletic groups within Chrysopinae. The results of the morphological analyses show that molecular data is essential for resolving the phylogeny of Chrysopidae at the generic level.



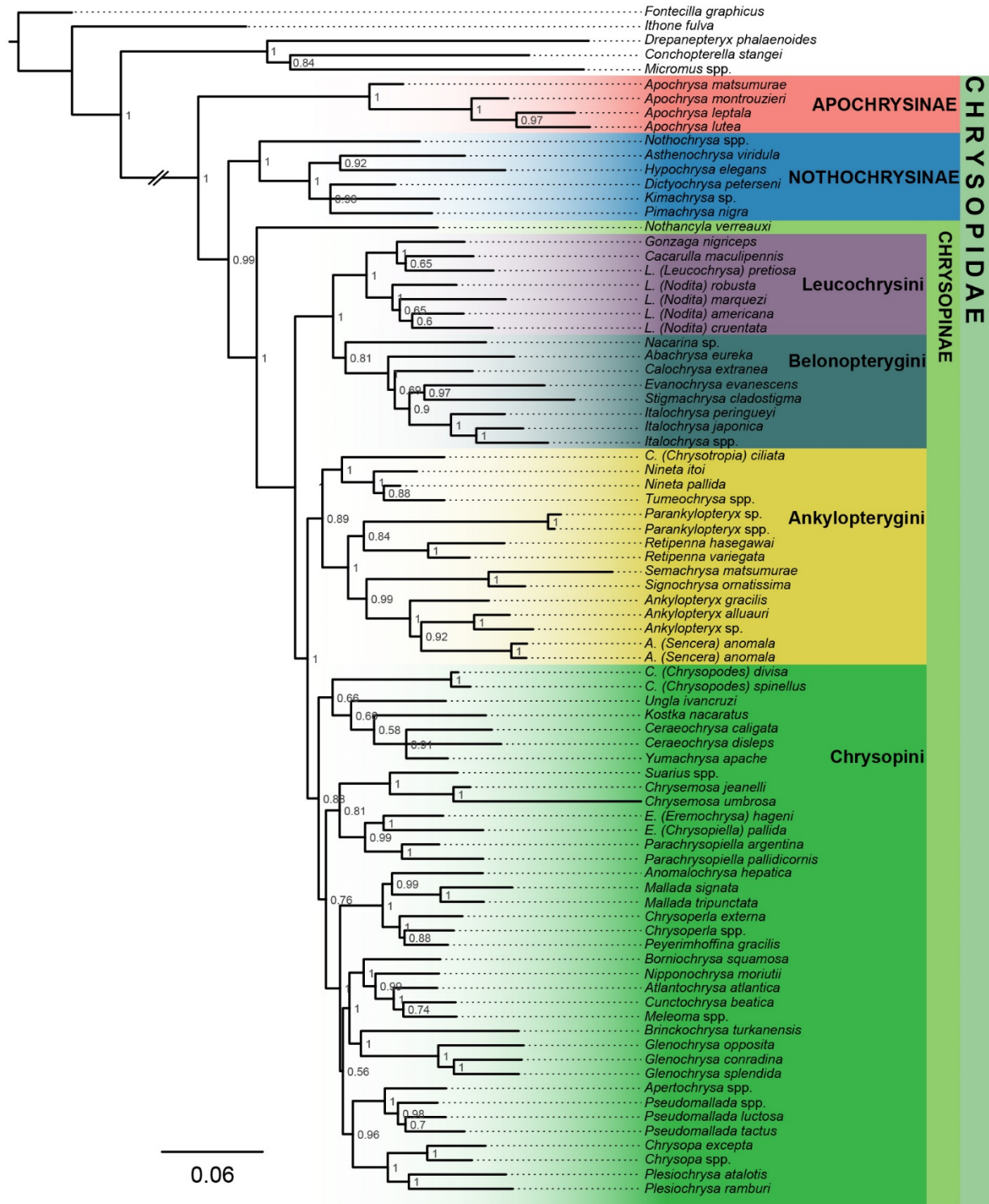
**Figure 4.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological data of Chrysopidae; analysis 2. Posterior probabilities (PP) indicated on nodes.

### Analysis 3: combined data, Chrysopidae I (fig. 4)

Analysis 3 includes multiple representatives of all subfamilies and tribes of Chrysopidae, and all terminal taxa for which molecular data was available—a total of 83 terminal taxa (78 ingroup taxa). Morphological data were available for all ingroup and most outgroup taxa, but some taxa were not available for examination and the data had to be gathered from the literature, often resulting in incomplete character coding. The topology was not constrained, and no starting tree was provided. The analysis reached an average standard deviation of split frequencies (SDSF) of 0.01 after 47 hours and ca. 22 million generations and was automatically terminated after reaching this given stop value. The ESS values were high enough to consider this analysis converged (LnL: 2971, LnPr: 110, TL: 109), although the LnPr and TL values are comparatively low. Further analyses without the automatic termination after reaching the specified stop value of 0.01 were conducted in order to reach higher ESS values, but did not yield significant improvement regarding these numbers.

The relationships recovered in this analysis are almost the same as in the tree of analysis 1 (inferred from molecular data alone), but we had to exclude the genus *Vieira* in order to receive resolution within Belonopterygini + Leucochrysinini. There are minor differences in support values of clades and in the relationships between some genera. The enigmatic genus *Kostka* was found as a member of the *Chrysopodes*-group in this analysis and in the *Eremochrysa*-group in the tree of analysis 1.

The tree of analysis 3, which includes only the taxa for which molecular data were available, with the addition of morphological data, was the basis for the following trees in which more taxa with only morphological data present were included. Some nodes within the tribes were better resolved here than in the individual analyses where more taxa were included.



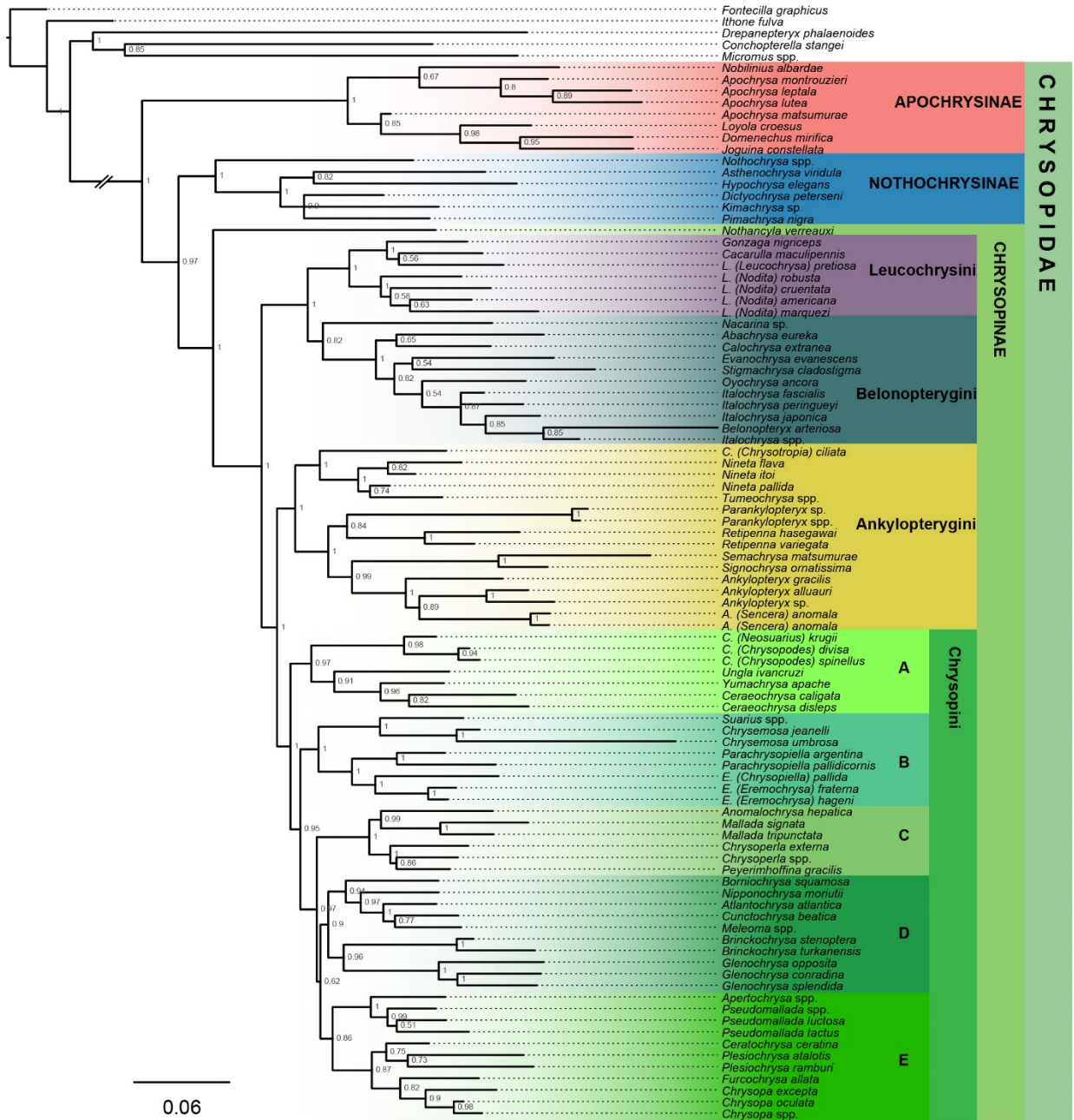
**Figure 5.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, including only species for which molecular data were available; analysis 3. Posterior probabilities (PP) indicated on nodes.



#### Analysis 4: combined data, Chrysopidae II (fig. 5)

Analysis 4 includes multiple representatives of all subfamilies and tribes of Chrysopidae, aiming for a high diversity within the clades, but does not include all terminal taxa that were available. This reduction was done to get a converging tree, which was not possible when all terminal taxa were included in the analyses, due to the lack of molecular data in many species. The analysis included 95 terminal taxa (90 ingroup taxa), of which 84 had both molecular and morphological data present and 9 taxa with only morphological data. The topology was not constrained, and no starting tree was provided. The analysis reached an average SDSF of 0.01 after 69 hours and ca. 23 million generations and was automatically terminated after reaching this given stop value. The ESS values were not high enough to consider this analysis truly converged (LnL: 2480, LnPr: 111, TL: 96), with medium and low numbers in the posterior probabilities and tree length. Although this analysis did not converge (regarding LnPr and TL) we are presenting the resulting consensus tree, because the topology remained unchanged throughout multiple analyses. Further analyses without the automatic termination after reaching the specified stop value of 0.01 were conducted in order to reach higher ESS values, but did not yield significant improvement regarding these numbers.

The results of this analysis with more taxa included (tree of analysis 4) resulted in the same general topology the tree of analysis 3. A few additional species are included, and all place within their respective subfamilies or tribes, which will be further discussed in the sections of the more detailed analyses. *Kostka* and *Vieira* were excluded from the analysis, because the inclusion resulted in significantly lower support and less resolution.



**Figure 6.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae; analysis 4. Posterior probabilities (PP) indicated on nodes.

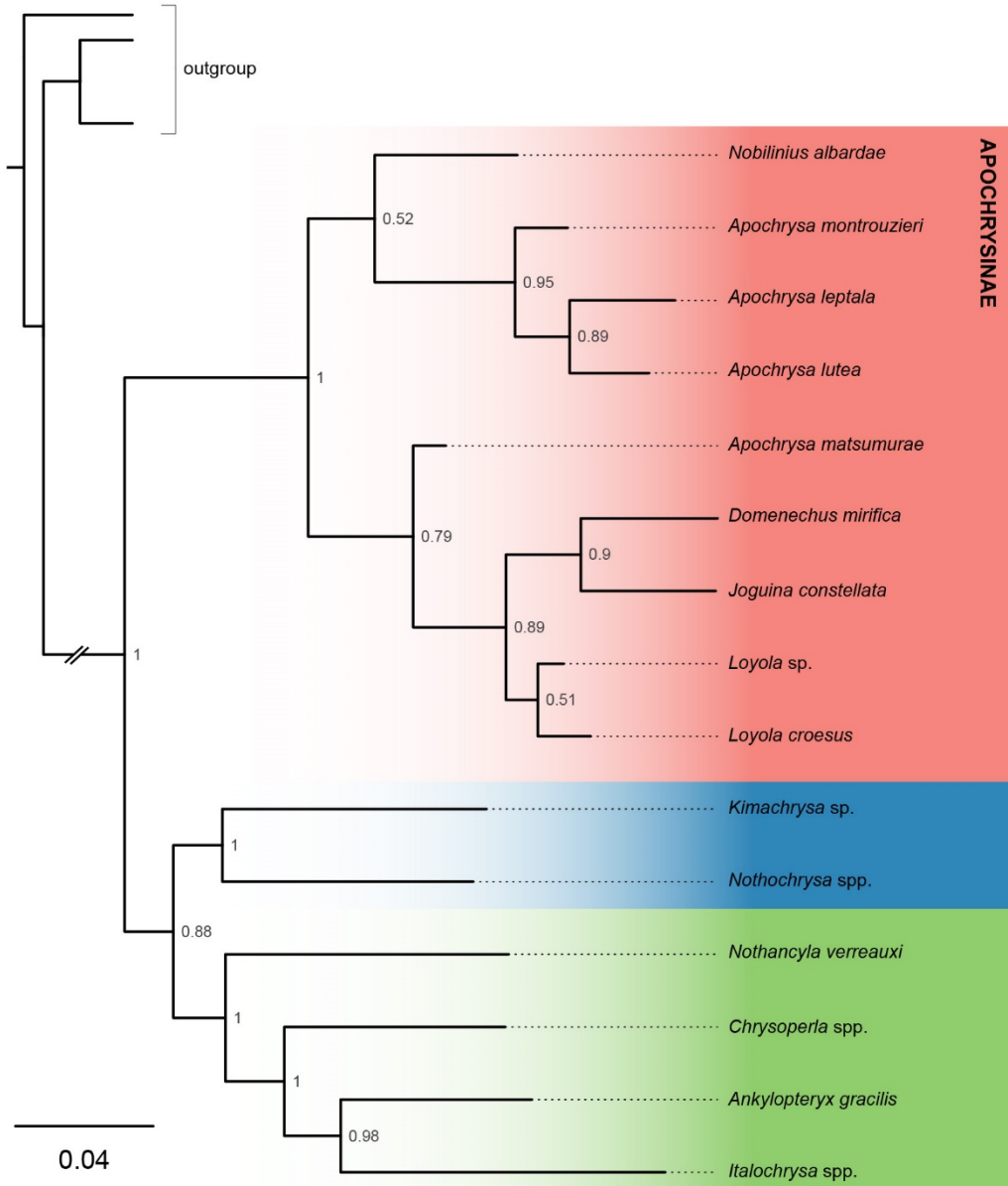
Analysis 5: combined data, Apochrysinae (fig. 6)

Analysis 5 included at least one representative of all subfamilies and tribes of Chrysopidae, and all species that were available for the subfamily Apochrysinae—a total of 21 terminal taxa (16



ingroup taxa), of which 16 had both molecular and morphological data present and 5 taxa (all within Apochrysinæ) with only morphological data. Species of all five genera of Chrysopidae were sampled. The topology was not constrained, and no starting tree was provided. The analysis reached an average SDSF of 0.01 after about 45 minutes and ca. 2.9 million generations but was continued for 3 hours (a total of 12 million generations) to reach higher ESS values (minimum SDSF: 0.0057). The ESS values were high enough to consider this analysis converged (LnL: 5585, LnPr: 267, TL: 1723), although the LnPr value is comparatively low.

The tree of analysis 5 shows two clades in Apochrysinæ, one consisting of three species of *Apochrysa* and *Nobilinius*, and the other of one species of *Apochrysa*, and the genera *Domenechus*, *Joguina*, and *Loyola*. The support values of both are low (PP= 0.52 and PP=0.79). We conducted a second analysis of Apochrysinæ (not shown here) including a single additional wing-venation character and received an altered phylogenetic hypothesis, where *Nobilinius* resulted as sister to the second clade, but also with low posterior probability.



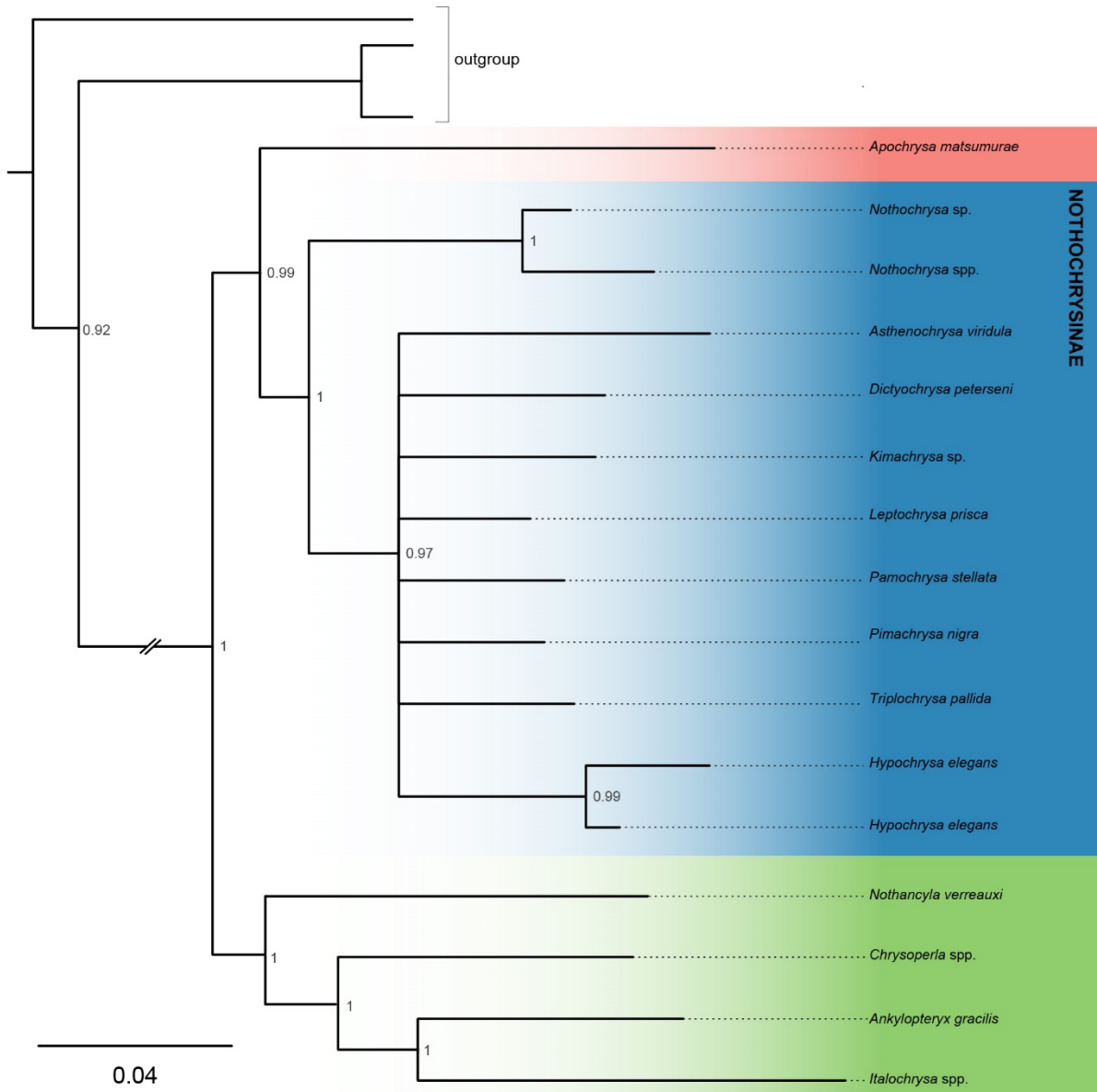
**Figure 7.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Apochrysinæ; analysis 5. Posterior probabilities (PP) indicated on nodes.

Analysis 6: combined data, Nothochrysinæ (fig. 7)

Analysis 6 included at least one representative of all subfamilies and tribes of Chrysopidae, and all species that were available for the subfamily Nothochrysinæ – a total of 21 terminal taxa (16 ingroup taxa), of which 16 had both molecular and morphological data present and 5 taxa (all

within Nothochrysinæ) with only morphological data. The topology was not constrained, and no starting tree was provided. The analysis reached an average SDSF of 0.01 after about 50 minutes and ca. 2.2 million generations but was continued for 1 hour (a total of 5 million generations) to reach higher ESS values (minimum SDSF: 0.0082). The ESS values were high enough to consider this analysis converged (LnL: 2211, LnPr: 1660, TL: 1083).

Nothochrysinæ are the subfamily with the least resolved phylogeny. Some nodes within Nothochrysinæ are resolved in analyses 1, 3, and 4, but the addition of species with no molecular data present leads to lower resolution. The large polytomy in the 50% majority rule tree (tree of analysis 6) contains all included nothochrysinæ taxa, except for the genus *Nothochrysa*. Possible relationships within the subfamily will be discussed further below.



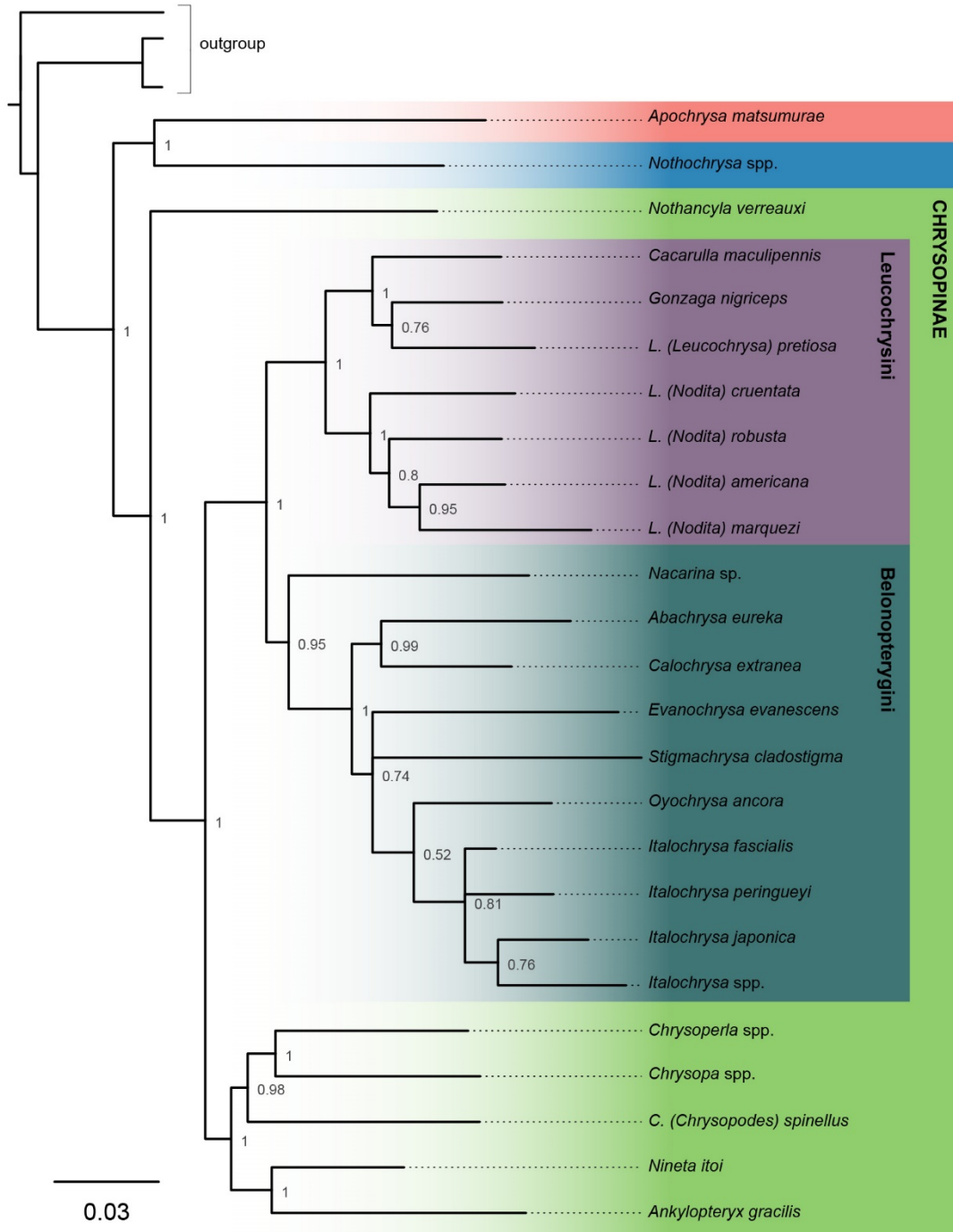
**Figure 8.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Nothochrysoinae; analysis 6. Posterior probabilities (PP) indicated on nodes.

Analysis 7: combined data, Belonopterygini and Leucochrysinini (fig. 8)

Analysis 7 included at least one representative of all subfamilies and tribes of Chrysopidae, and is focusing on species from the tribes Belonopterygini and Leucochrysinini—a total of 30 terminal taxa (25 ingroup taxa), of which 28 had both molecular and morphological data present

and only 2 taxa (both within Belonopterygini) with only morphological data. Analyses with more terminal taxa, which did not have molecular data, resulted in large polytomies (not shown). The topology was not constrained, and no starting tree was provided. The analysis reached an average SDSF of 0.01 after about 3 hours and ca. 5.2 million generations and was automatically terminated after reaching this given stop value. The ESS values were high enough to consider this analysis converged (LnL: 2949, LnPr: 329, TL: 319), although LnPr and TL values are comparatively low.

The tribes Belonopterygini and Leucochrysinini were recovered as sister taxa with high support (PP= 1). The monophyly of both tribes is highly supported (Leucochrysinini PP= 1, Belonopterygini PP= 0.95) in analysis 7, where rogue taxa were excluded. Leucochrysinini is divided into two clades, one composed of *Nodita* (PP= 1), and one of *Leucochrysa*, *Gonzaga*, and *Cacarulla* (PP= 1). The addition of any other leucochrysinine genera, which only had morphological data available, resulted in the formation of large polytomies including leucochrysinine and belonopterygine taxa. *Leucochrysa* and *Nodita* are currently treated as subgenera of *Leucochrysa*, but do not resolve as sister taxa in the analysis, calling for a reclassification (see chapter 2) in which either *Gonzaga* and *Cacarulla* are demoted to subgeneric level, or elevating *Leucochrysa* s. str. and *Nodita* to generic rank, as originally described. The South American *Nacarina* are sister to all other Belonopterygini. *Calochrysa* and *Abachrysa* form a monophyletic group (PP= 0.99) and are sister to a clade including *Evanochrysa*, *Stigmachrysa*, *Oyochrysa*, and *Italochrysa* (PP=0.74). The relationships within the latter clade are poorly supported and it is expected that the inclusion of further species of the highly diverse *Italochrysa* would severely change these relationships.



**Figure 9.** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Belonopterygini and Leucochrysinini; analysis 7. Posterior probabilities (PP) indicated on nodes.

We examined many genera that were of special interest to place in the phylogeny of Chrysopidae and are representatives of Belonopterygini or Leucochrysini, but were not able to include them in this analysis due to the lack of molecular data and their rather puzzling morphology. These are: *Nuvol*, *Santocellus*, *Chrysacanthia*, *Chrysaloisia*, *Dysochrysa*, *Nesochrysa*, and *Turnerochrysa*. We attempted to place them with only morphological data, but the inclusion of a single one of these rogue taxa resulted in a constant drop in resolution, often with difficulties to even place them into one of the four tribes of Chrysopinae. Further investigation of these genera is needed to place them correctly, including a more detailed study of their morphology and ideally including larval characters (which were not examined for this analysis) and sequence data.



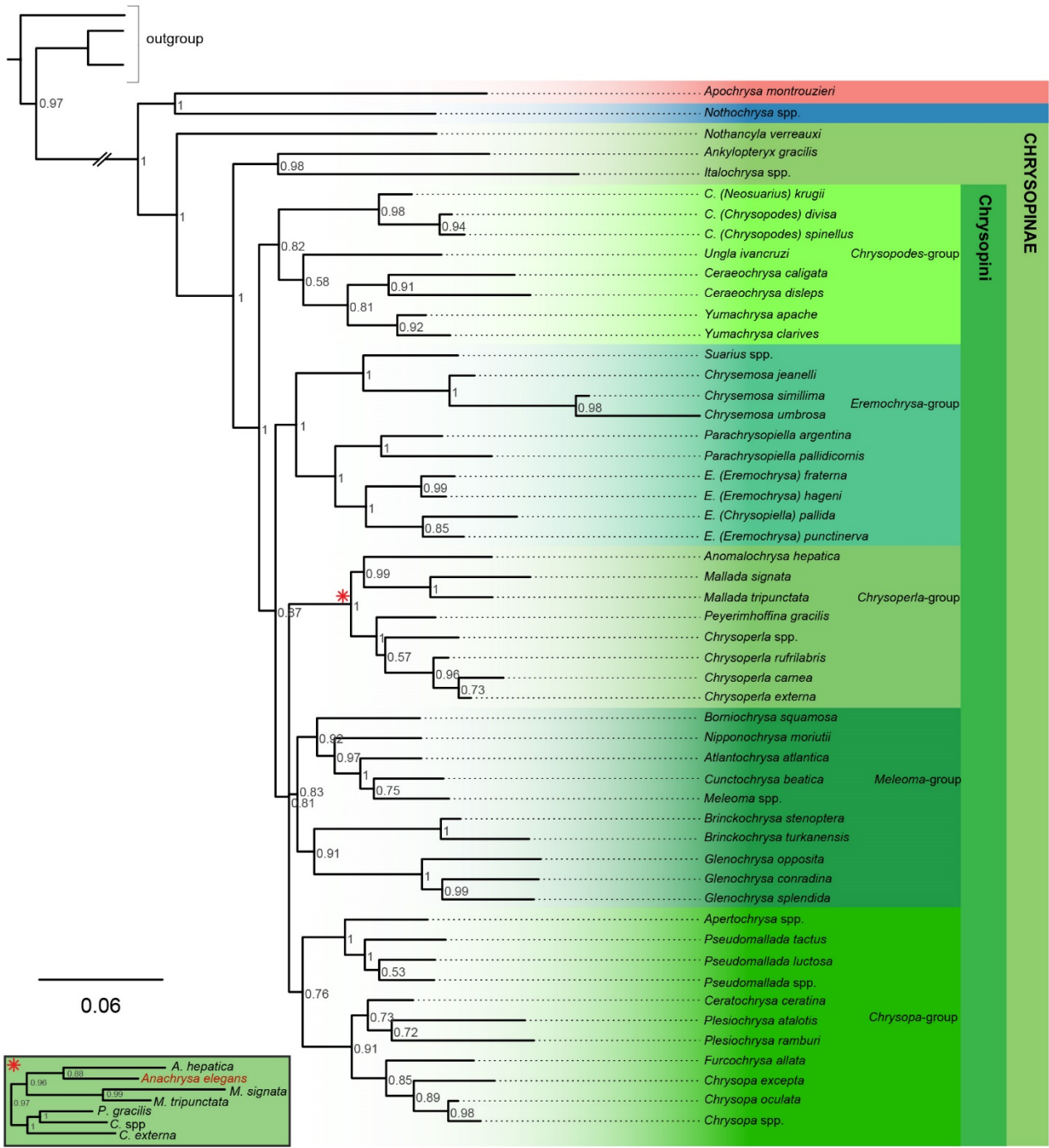


Analysis 8: combined data, Ankylopterygini and *Nineta*-group (fig. 9)

Analysis 8 included at least one representative of all subfamilies and tribes of Chrysopidae, and is focusing on species from the tribe Ankylopterygini and the *Nineta*-group. These two clades were discovered as sisters in all larger scale analyses conducted in this study (see trees of analyses 1, 3, and 4), as well as in analyses with substantial molecular data sets (Duelli et al. 2014, Garzón in rev.). Our analysis included 32 terminal taxa (27 ingroup taxa), of which 26 had both molecular and morphological data present and 6 taxa (all within Ankylopterygini and the *Nineta*-group) with only morphological data. The topology was constrained by forcing the monophyly of Ankylopterygini + *Nineta*-group (the monophyly of the two groups themselves was not forced). The clade was strongly supported in larger scale analyses, but without this constrain *Parankylopteryx* resulted outside of the clade, which was never the case in analyses that included larger sample sizes of other subfamilies and tribes. No starting tree was provided. The analysis reached an average SDSF of 0.01 after about 1.5 hours and ca. 2.4 million generations and was automatically terminated after reaching this given stop value. The ESS values were high enough to consider this analysis converged (LnL: 1003, LnPr: 622, TL: 427).

The tribe Ankylopterygini was found to be monophyletic, with high support (PP= 1), but within Chrysopini. A well supported clade (PP= 1) composed of the Chrysopini-genera *Nineta*, *Chrysopidia* (*Chrysotropia*), and *Tumeochrysa* resulted as sister to Ankylopterygini with high support (PP= 1). Within this clade, *Chrysopidia* is sister to *Nineta* + *Tumeochrysa*, and the latter renders *Nineta* paraphyletic, although with low nodal support (PP= 0.52). The genus *Chrysopidia* currently includes three subgenera—*Chrysopidia*, *Chrysotropia* and *Anachrysa*. For the subgenus *Anachrysa* no molecular data was present, and it has morphological characters, that could place the taxon either within the *Nineta*-group, or more likely deeper nested in Chrysopini. This

conflicting morphology resulted in the formation of polytomies in higher nodes of Chrysopinae in all analyses that included *Anachrysa* (see also discussion of Chrysopini genera below, analysis 9, figure 10). The tribe Ankylopterygini, as it was recognized hitherto, is divided into two sister clades, one including *Retipenna* and *Parankylopteryx* ( $p= 0.69$ ), and one including *Semachrysa*, *Signochrysa*, and *Ankylopteryx* (PP= 0.83). *Parankylopteryx*, which is currently recognized as a subgenus of *Ankylopteryx*, was not recovered in such a relationship but rather as sister to *Retipenna*. The second subgenus of *Ankylopteryx* is the monotypic *Sencera* and fell within the subgenus *Ankylopteryx* with high support (PP= 1).



**Figure 11:** 50 % Majority rule consensus tree of the Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopini; analysis 9. Posterior probabilities (PP) indicated on nodes. Result of additional analysis with *Anachrysa elegans* included shown in box, red asterisk indicated position of clade.

Analysis 9: combined data, Chrysopini (fig. 10)

Analysis 9 included at least one representative of all subfamilies and tribes of Chrysopidae, and focuses on species from the tribe Chrysopini (without the *Nineta*-group)—a total of 58 terminal taxa (53 ingroup taxa), of which 49 had both molecular and morphological data present and 9 taxa (all within Chrysopini) with only morphological data. Analyses with additional terminal taxa, which did not have molecular data, resulted in large polytomies. The topology was not constrained, and no starting tree was provided. The analysis reached an average SDSF of 0.01 after about 2 hours and ca. 6.6 million generations but was continued for 20 hours (a total of 20 million generations) to reach higher ESS values (minimum SDSF: 0.0098). The ESS values were high enough to consider this analysis converged (LnL: 3133, LnPr: 392, TL: 390), although LnPr and TL values are comparatively low.

The monophyly of Chrysopini without the *Nineta*-group is highly supported (PP= 1). The tribe is well resolved except for one node including three clades. The *Chrysopodes*-group is a well-supported clade (PP= 0.82) comprised of *Chrysopodes* (*Chrysopodes*), *Chrysopodes* (*Neosuarius*), *Ungla*, *Yumachrysa*, and *Ceraeochrysa*, which are all Neotropical or Nearctic genera. The two subgenera *Chrysopodes* and *Neosuarius* placed as sister-groups, but the latter had only a single representative in the analysis. The *Chrysopodes*-group is sister to a clade including all other Chrysopini (PP= 0.92). The second clade (PP= 1) within Chrysopini is the *Eremochrysa*-group, which includes *Suarius*, *Chrysemosa*, *Eremochrysa* (*Eremochrysa*), *Eremochrysa* (*Parachrysopiella*), and *Eremochrysa* (*Chrysopiella*). All subgenera of *Eremochrysa* occur in the Neotropic or Nearctic, whereas the sister genera *Suarius* and *Chrysemosa* occur in the Palearctic or Afrotropical Regions. The relationships between the three most derived clades of Chrysopini (*Chrysoperla*-, *Meleoma*-, and *Chrysopa*-group) could not be resolved in this analysis and resulted

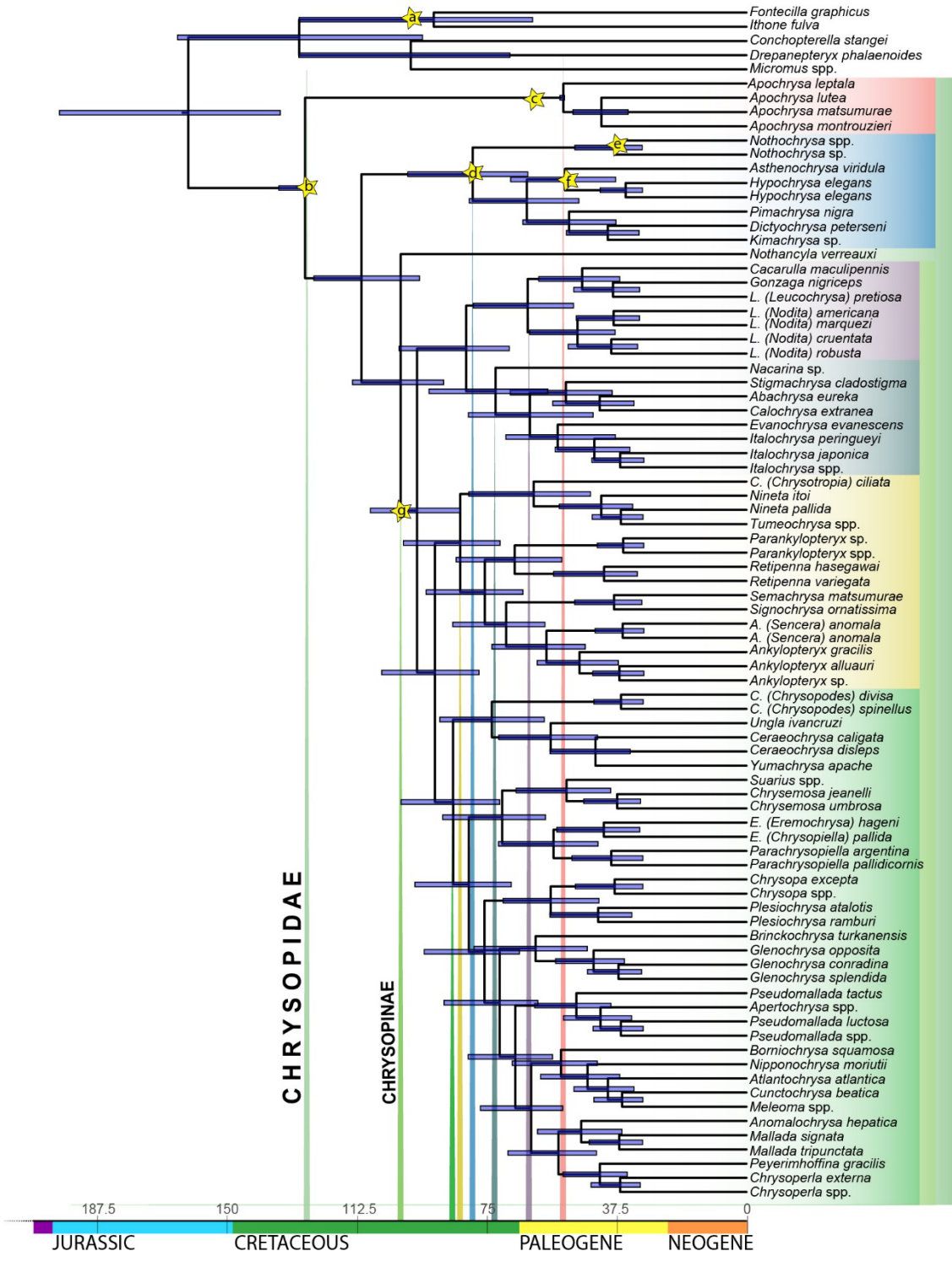
in a polytomy. In the analysis that included only species with molecular data present these nodes are resolved, although with partially low support. The *Chrysoperla*-group (PP= 1) includes the genera *Anomalochrysa*, *Mallada*, *Chrysoperla*, and *Peyerimhoffina*, where the former two are sister to the latter two. The *Meleoma*-group (PP= 0.91) is divided into two distinct clades, one including *Borniochrysa*, *Nipponochrysa*, *Atlantochrysa*, *Cunctochrysa*, and *Meleoma* and the other including *Brinckochrysa* and *Glenochrysa*. The last clade of Chrysopini is the *Chrysopa*-group (PP= 0.76), which is divided into a clade with *Apertochrysa* and *Pseudomallada* and another including *Ceratochrysa*, *Plesiochrysa*, *Furcochrysa*, and *Chrysopa*. Here, *Ceratochrysa* and *Plesiochrysa* are sister to *Furcochrysa* and *Chrysopa*.

Most genera that were of special interest to place in the tree of Chrysopidae are representatives of Chrysopini *s. st.*, but though studied could not be included in this analysis, due to the lack of molecular data. These are: *Rexa*, *Kostka*, *Austrochrysa*, *Chrysocerca*, *Chryptochrysa*, *Crassochochrysa*, *Titanochrysa*, and *Himalochrysa*. We attempted to place them with the morphological data only, but the inclusion of a single of these rogue taxa resulted in a significant drop of resolution, often placing them in a polytomy at the first node within Chrysopini. Further investigation of these genera is needed to place them correctly, including a more detailed study of their morphology and especially molecular data.

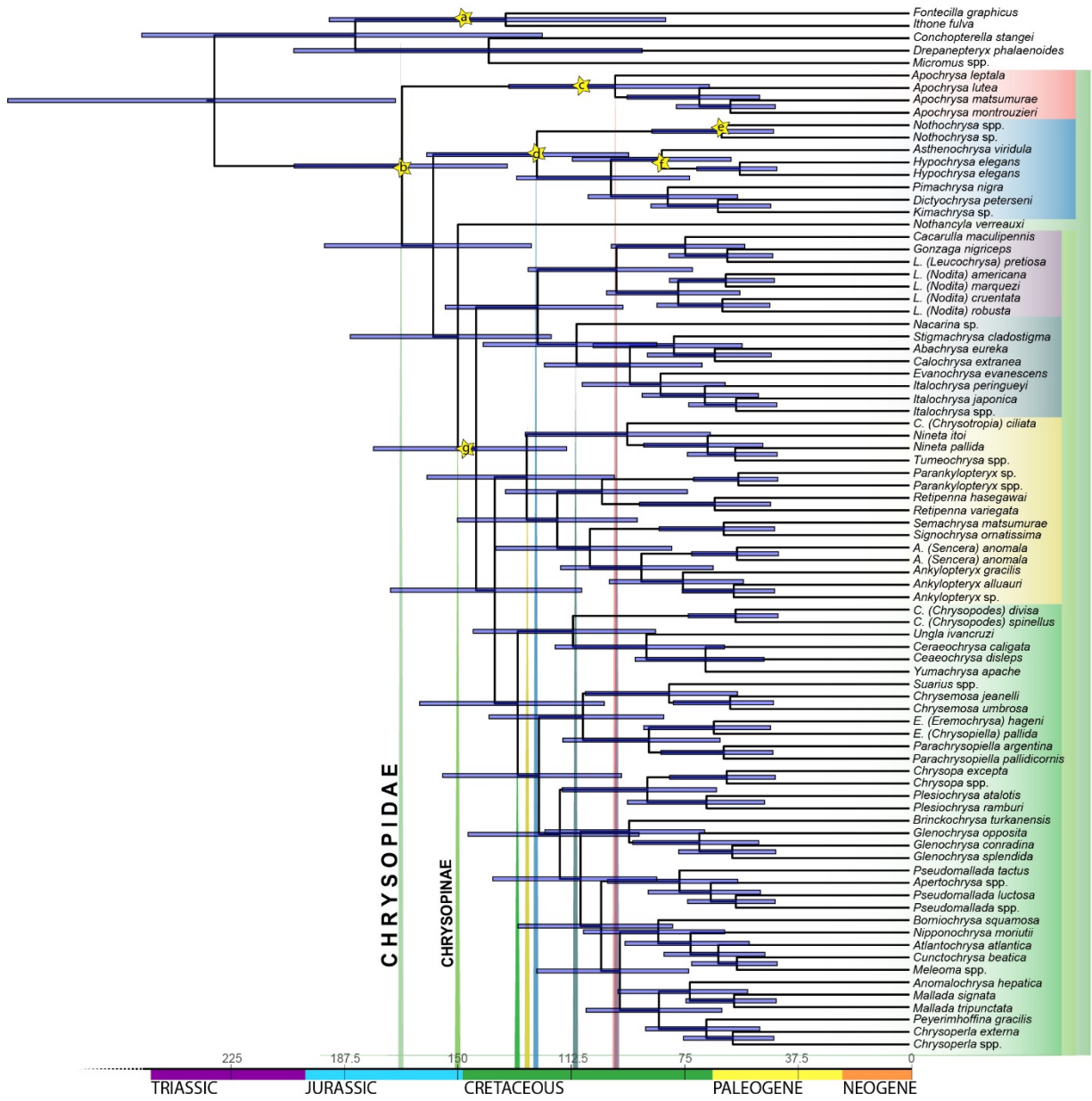
Analysis 10 and 11: combined data, Chrysopidae divergence times (fig. 11, 12)

Analysis 10 and 11 include multiple representatives of all subfamilies and tribes of Chrysopidae, and all terminal taxa for which molecular data was available – a total of 84 terminal taxa (79 ingroup). The two analyses with a strict (analysis 10) and relaxed (analysis 11) calibration point setting resulted in controversial divergence times, with all nodes being younger under the

strict settings. Analyses 10 reached an average SDSF of 0.01 after about 25 hours and ca. 15.5 million generations and was automatically terminated after reaching this given stop value. The ESS values were low, so the analysis cannot be considered as converged (LnL: 41, LnPr: 8, TH: 25, TL: 49), indicating that the posterior distribution of all parameters was not well sampled, but a longer run did not improve the ESS values significantly. Analyses 11 reached an average SDSF of 0.01 after about 35 hours and ca. 57 million generations and was automatically terminated after reaching this given stop value. The ESS values were low, so the analysis cannot be considered as converged (LnL: 3993, LnPr: 10, TH: 68, TL: 200), but a longer run did not improve the ESS values significantly. The ESS values were low in both analyses, but slightly higher in analysis 11. Because previous time tree analyses yielded differing results (e.g., paraphyletic Nothochrysinæ), we had to force the topology with the addition of constraints (Chrysopidae, Apochrysinæ, Chrysopinae + Nothochrysinæ, Nothochrysinæ, Chrysopinae, Belonopterygini + Leucochrysinini, Ankylopterygini, Chrysopini).



**Figure 12.** 50 % Majority rule consensus tree of the node-dated Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, with strict date settings; analysis 10. A. *Mesopolystoechus apicalis* Martynov 1937; b: *Mesypochrysa magna* Makarkin 1997; c: *Okanaganochrysa coltsunae* Makarkin and Archibald 2013; d: *Asiachrysa tadushiella* Makarkin 2014; e: *Nothochrysa praeclara* Stratz 1936; f: *Hypochrysa hercyniensis* Schlüter 1982; g: *Paleochrysa monteliensis* Séméria and Nel 1990.



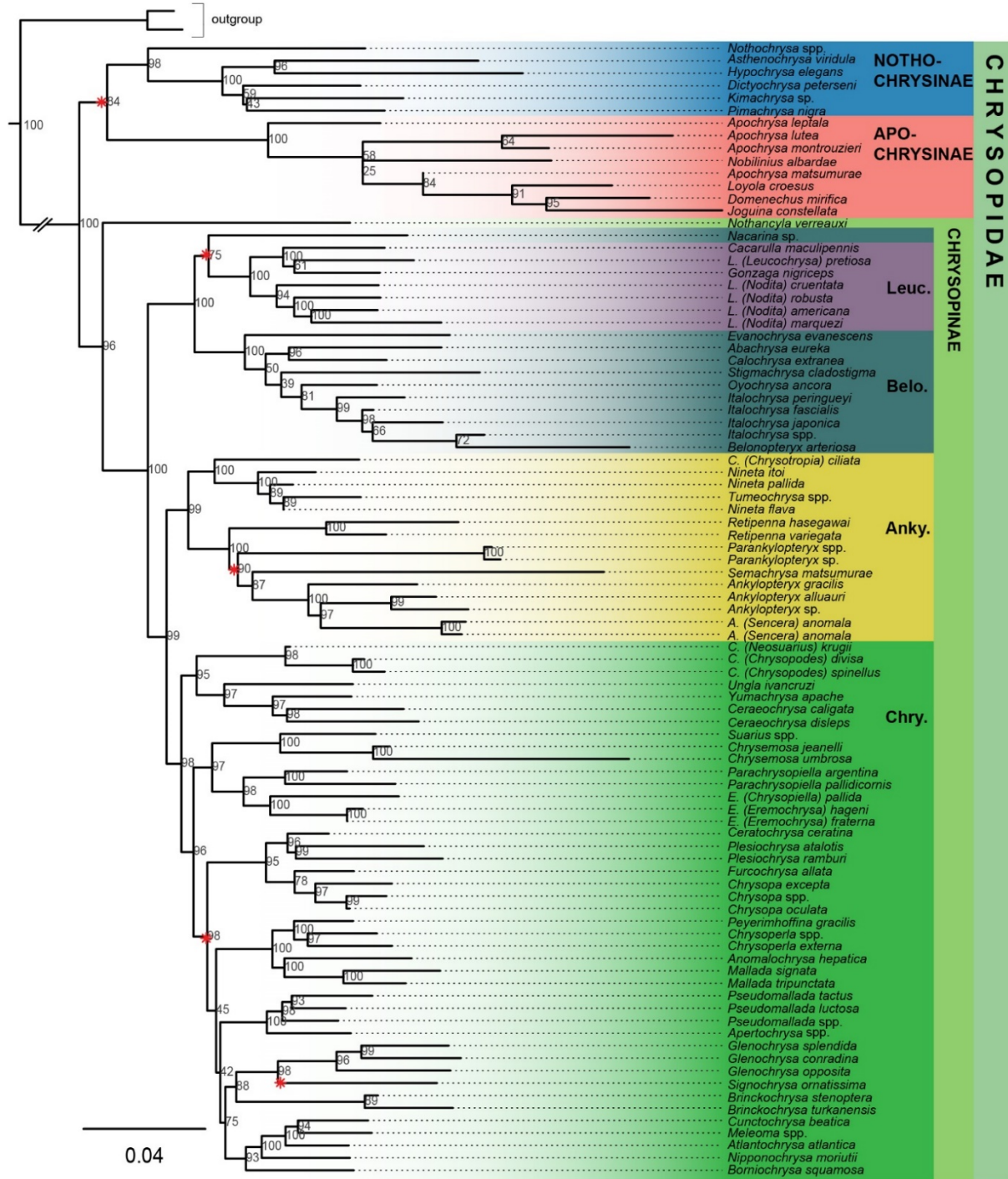
**Figure 13.** 50 % Majority rule consensus tree of the node-dated Bayesian inferred phylogenetic hypotheses from morphological and molecular data of Chrysopidae, with relaxed date settings; analysis 11. A. *Mesopolystoechus apicalis* Martynov 1937; b. *Mesypochrysa magna* Makarkin 1997; c. *Okanaganochrysa coltsunae* Makarkin and Archibald 2013; d. *Asiachrysa tadushiella* Makarkin 2014; e. *Nothochrysa praeclara* Stratz 1936; f. *Hypochrysa hercyniensis* Schlüter 1982; g. *Paleochrysopa monteliensis* Séméria and Nel 1990.



## Maximum Likelihood analysis

Analysis 12: combined data, Chrysopidae (fig. 13)

The maximum likelihood analysis recovered a phylogenetic hypothesis that is roughly similar to the results of the Bayesian analysis, with some important differences. ModelFinder in IQ-TREE found different best models for the 22 partitions than PartitionFinder, including TIM, TVM, TN, and K2 for most partitions and GTR for one. Ultra fast bootstrap (UFB) support values are fairly low for most higher nodes of Chrysopidae. The topology of the tree of analysis 12 is similar to those recovered in the Bayesian inference analyses with the same data set, with the following differences. Nothochrysinæ and Apochrysinæ form a monophyletic group (UFB= 84), and are sister to Chrysopinæ, which is monophyletic including *Nothancyla* (UFB= 96). The relationships of the tribes in Chrysopinæ are similar, in that Belonopterygini + Leucochrysinini (UFB= 100) are sister to Ankylopterygini (including *Nineta*-group) + Chrysopini (UFB= 99). *Nacarina* is not sister to all other Belonopterygini, but to Leucochrysinini, although with low support (UFB= 75), and the rest of the relationships in these two tribes are similar to that of the BI results. Ankylopterygini and the *Nineta*-group are sister taxa (UFB= 99), and the relationships within this clade are similar to that of the BI results, except for the position of *Parankylopteryx*, which is sister to *Semachrysa* + *Ankylopteryx* in this analysis. Additionally, *Signochrysa*, which is one of the ankylopterygine genera resulted within Chrysopini, which was never the case in any other analysis. The monophyly of Chrysopini is highly supported (UFB= 99) and the relationships are somewhat similar to those of the BI Analyses, with the *Chrysopodes*-group as sister to all other Chrysopini (UFB= 95), and the *Eremochrysa*-group sister to a clade of the *Chrysopa*-, *Chrysoperla*-, and *Meleoma*-group, but the relationships within this latter clade at the higher nodes are differently arranged, often with low support values. The nodes that differ in the resulting phylogenetic hypothesis of the ML analysis from the BI analyses are indicated by red asterisks in fig. 13.



**Figure 14.** Maximum likelihood inferred phylogenetic hypothesis from morphological and molecular data of Chrysopidae; analysis 12. Ultra fast bootstrap values indicated on nodes, red astrices indicate major differences to Bayesian inference analyses.

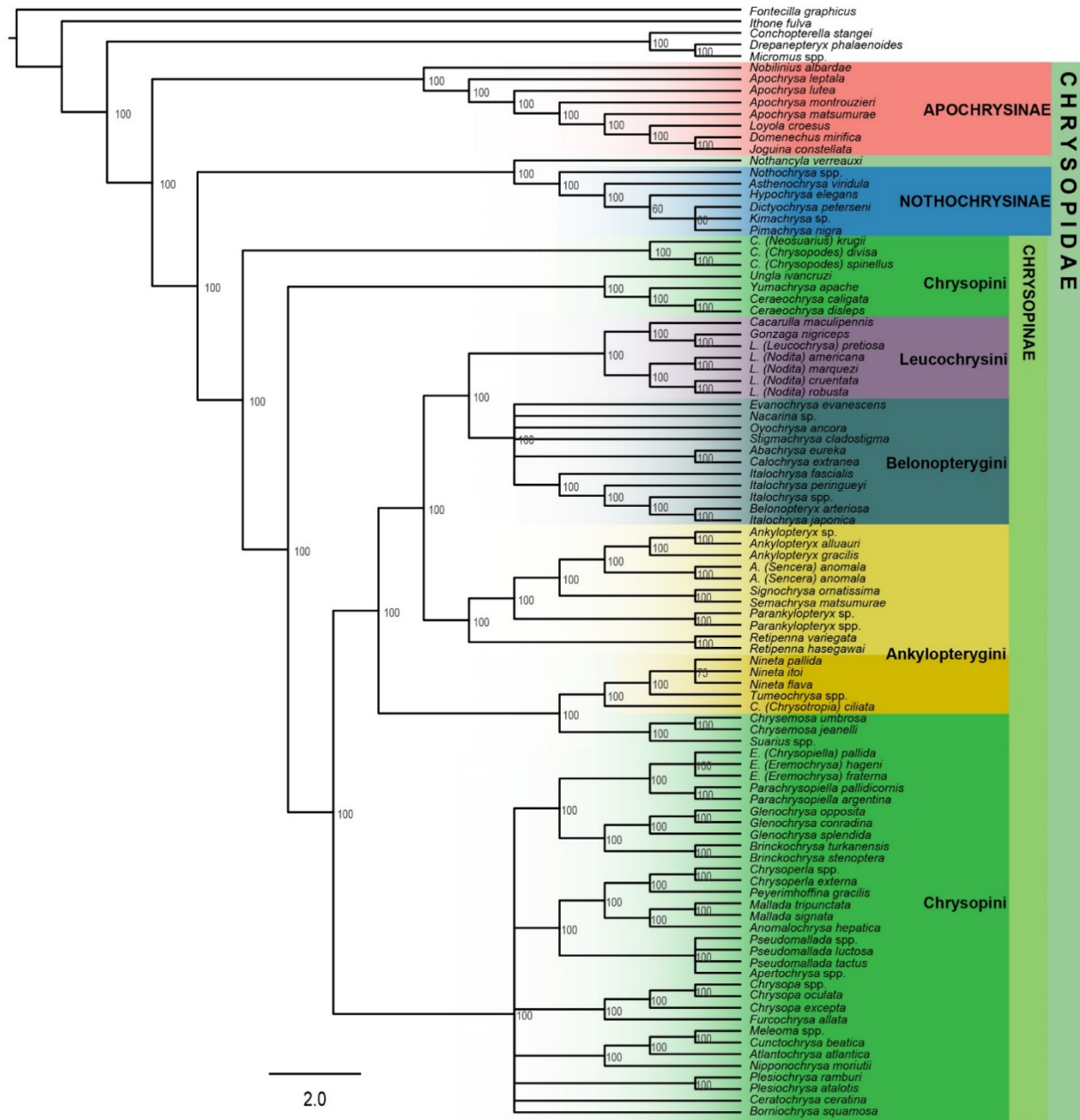
## Parsimony analyses

### Analysis 13: morphological data, Chrysopidae (fig. 14)

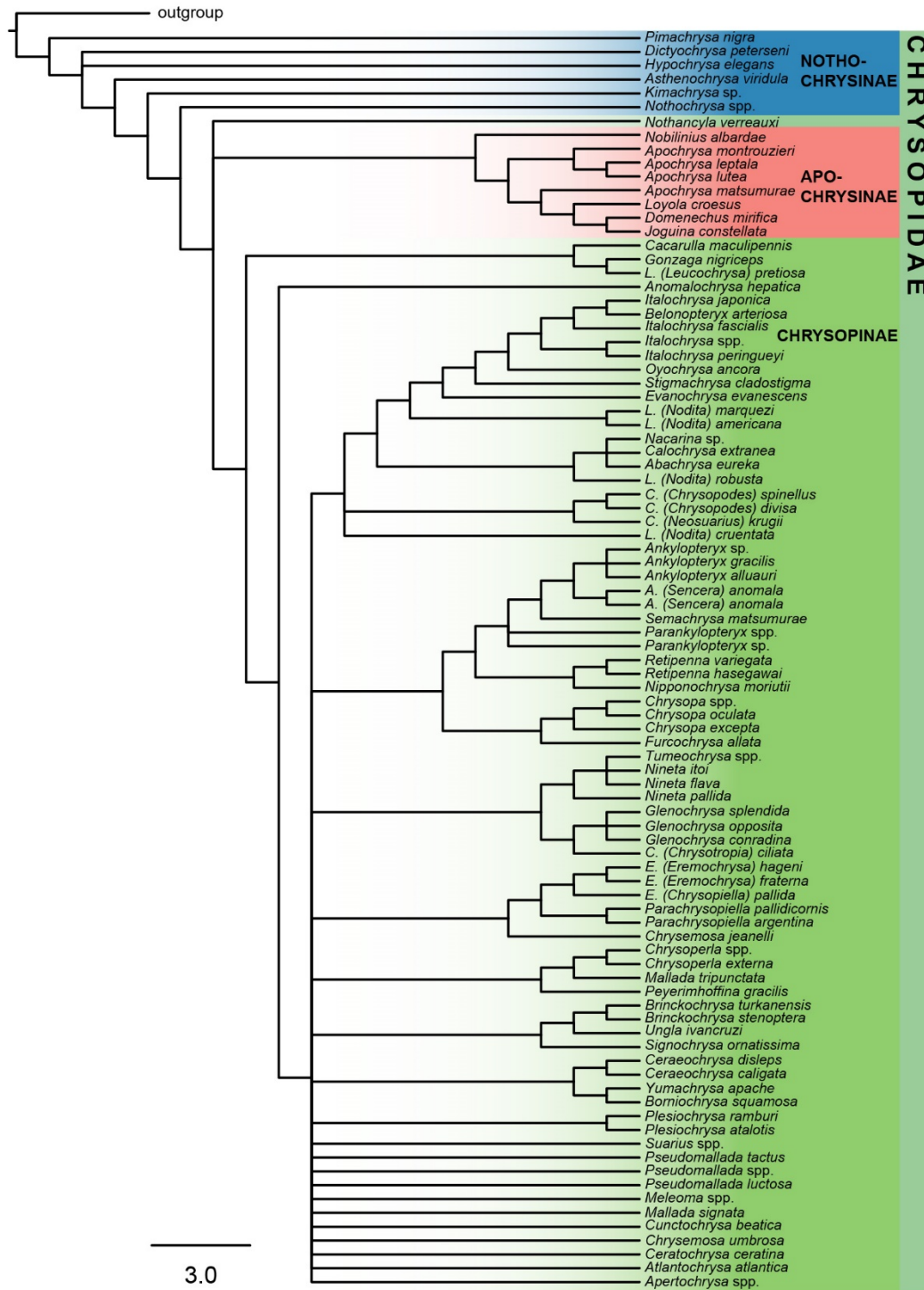
The parsimony tree inferred from the morphological data in TNT is slightly better resolved than the one from the Bayesian analysis. The 50% majority rule consensus tree was constructed from 633 equally parsimonious trees. Nothochrysinæ are paraphyletic and *Nothochrysa* is sister to a group of Apochrysinæ, Chrysopinæ, and *Nothancyla* forming a polytomy. Apochrysinæ is monophyletic and the relationships are similar to the combined data analyses. The position of *Nothancyla* as sister to all other Chrysopinæ is not supported well in the parsimony analysis. Chrysopinæ result in a large polytomy including most taxa. The resolution is low, but some monophyletic groups that were recovered in the other analyses are supported here as well, such as Belonopterygini + Leucochrysinini and several smaller clades within Chrysopini. Several genera were recovered in positions that are not plausible and are not recovered in any other analysis.

### Analysis 14: combined data, Chrysopidae (fig. 15)

The parsimony analysis of the combined data set in PAUP\* resulted in a fairly well resolved and supported 50% majority rule consensus tree, constructed from 640 equally parsimonious trees. As in the Bayesian analysis, Chrysopidae, the subfamilies and most tribes are monophyletic, but there are several strong differences to the results of the Bayesian analyses regarding the topology. *Nothancyla* is recovered as sister to Nothochrysinæ, Chrysopini are paraphyletic (split in four lineages) in regards to all other lineages of Chrysopinæ, Ankylopterygini are sister to Belonopterygini + Leucochrysinini, and not to the *Nineta*-group.



**Figure 15.** 50 % Majority rule consensus tree of the parsimony phylogenetic hypotheses from morphological data of Chrysopidae; analysis 13.



**Figure 16.** 50 % Majority rule consensus tree of the parsimony phylogenetic hypotheses from morphological and molecular data of Chrysopidae; analysis14. Support values indicated on nodes.

Table 3: Synapomorphies of the monophyletic groups, including support values and node age, combined from all analyses. Not all are unambiguous and can be reversed within the groups they define.

clade	pp (min-max)	apomorphies
Chrysopidae	1	Fusion of CuA and MP (39:1), leading to the formation of the pseudocubitus (PsC).
Apochrysinæ	1	4 or more veins fused in PsC (36:3); <i>im</i> cell absent (but also rarely absent in Chrysopinae) (34:3).
Chrysopinae + Nothochrysinæ	0.97-0.99	bsx present (except <i>Nothancyla</i> ) (13:1); <i>im</i> usually present (34:0,1,2,4).
Nothochrysinæ	1	PsM continuous with inner gradates (30:1); anal (44:1) and jugal lobe (45:1) present; small mediofrontal expansion of mesoscutum (7:1).
<i>Nothancyla</i> + Chrysopinae	1	Tympanal organ present (19:1), not reversed.
Chrysopinae	1	4 flagellar rings (2:1); 2 paired long setae between pretarsal claws (56:1) (but reversed few times, and present in few Apochrysinæ).
Belonopterygini + Leucochrysinini	1	* There are no unique synapomorphies for this clade, but in most members <i>microtholi</i> (61:1) and a <i>praegenitale</i> (62:1) are present, the lateral arms or the gonarcus are strongly expanded to an ear-like structure (74:2), and the entoprocessus is short or absent (77:0,1; 77:0). Mainly larval characters (see Tauber et al. 2014). Brooks and Barnard (1990) mention the form of the broad gonarcus and short, hooked mediuncus as apomorphies, but these can be found in other taxa.
Belonopterygini	0.81-0.95	<i>c2</i> shorter than <i>c1</i> (42:1); flagellomere wider than long (4:0); brown or yellow body color (1:1,2); basal most RP branch originating at <i>im</i> cell in hind wing (51:0).
Leucochrysinini	1	* There are no adult characters that could be identified as apomorphy for this clade in our analysis.
Chrysopini + Ankylopterygini	1	* There are no exceptional synapomorphies for this clade, but most members the flagellar setae are long (3:1), and there are numerous gonosetae present (86:2).
Ankylopterygini + <i>Nineta</i> -group	0.89-1	* There are no adult characters that could be identified as apomorphy for this clade in our analysis.
Ankylopterygini	1	Maxillar and labial palp apically thinly pointed; ra-rp present basal to the origin of the basal most RP branch in hind wing; tibial spurs absent (+Apo)
<i>Nineta</i> -group	1	* There are no unique synapomorphies for this clade, but most members have slightly elongate ectoprocts with a deep dorsal invagination and a varyingly strong apically expanded sternum VIII+IX.
Chrysopini	0.88-1	* There are no adult characters that could be identified as apomorphy for this clade in our analysis. The presence of a lighter colored dorsal median stripe on the entire body is present in most of the genera, but can be reversed, and it is present in some taxa outside of Chrysopini.
<i>Chrysopodes</i> -group	0.66-0.82	* There are no unique synapomorphies for this clade, but most members have short flagellar setae (3:0), and strongly expanded, ear-like lateral arms of the gonarcus (74:2) (both present in other clades).

<i>Eremochrysa</i> -group	0.88-1	More than 2 tibial spurs on meta and mesotibia (59:3; 60:3) (unique in Chrysopinae), yellow or brown body color (1:1,2) (unique in Chrysopini).
<i>Chrysoperla</i> -group	0.76-0.87	* There are no unique synapomorphies for this clade, but most members have a medially expanded median arch of the gonarcus (73:1), and usually apically expanded lateral arms (74:3). It is the only higher taxon in which all members have a tignum (71:1).
<i>Meleoma</i> -group	0.81-1	* There are no adult characters that could be identified as apomorphic for this clade in our analysis.
<i>Chrysopa</i> -group	0.76-0.96	* There are no exceptional synapomorphies for this clade, but most members have an elongate, thin and far removed mediuncus (80:0; 79:1) (except <i>Ankylopteryx</i> ).

\* These synapomorphies were determined with the “describtrees apolist=yes” command in PAUP\* (based on the results of analysis 3), and should be considered with caution, as the indicated clades lack unambiguous synapomorphies and existing character combinations are often reversed within, additionally these characters can also be found in other distantly related groups.

## Discussion

### Analyses

The majority of the analyses were well resolved and the relationships within Chrysopidae were recovered with good support on average. There were some minor to major discrepancies between the results of the different analyses. The parsimony analyses were generally less resolved, and the results of the Maximum Likelihood analyses had lower support values than the results of the Bayesian analyses and the topology was not as consistent with previous hypotheses. We therefore base this discussion on the Bayesian analyses and only point out some important differences from the ML analysis indicated as red arrows in fig. 14, where there are too many differences with the results of the parsimony analysis to indicate.

Morphological data alone was not able to resolve relationships among Chrysopidae, as can be seen in analyses 2 and 13, and Bayesian analyses based on molecular data only recovered a well-resolved tree, but not all taxa were included and not all nodes were well supported (fig. 2).



With the addition of morphological data to the molecular analysis we hoped to further support the relationships in analysis 1 and to widen our taxon sampling, with the inclusion of more species per genus and additional genera for which we did not have molecular data. The limited addition of morphological data had a positive effect on the convergence of the runs, the statistical support values of the analyses, and on the posterior probabilities of most relationships. With the inclusion of too many taxa without molecular data these positive effects disappeared, and in many cases the addition of a single terminal taxon with morphological data only resulted in the formation of polytomies. This is an indication that the phylogeny recovered with molecular data only is not as stable as we predicted, based on the support values of the results of analysis 1, most likely due to taxa for which we only have sequence data from one or two loci available (e.g., *Vieira*, *Kostka*). The inclusion of morphological data often obscured the placement of these taxa with little data, but was mostly beneficial, in addition to molecular data. The trees presented here are the results of the analyses with a compromise between maximal number of terminal taxa, high enough resolution of the tree and support values, as well as analyses that would converge. The more terminal taxa with exclusively morphological data we included, especially when the genus was not represented in the molecular data set, the lower the resolution was and the less likely that the runs would converge. The phylogenetic hypotheses discussed are the ones with the highest resolution and support values.

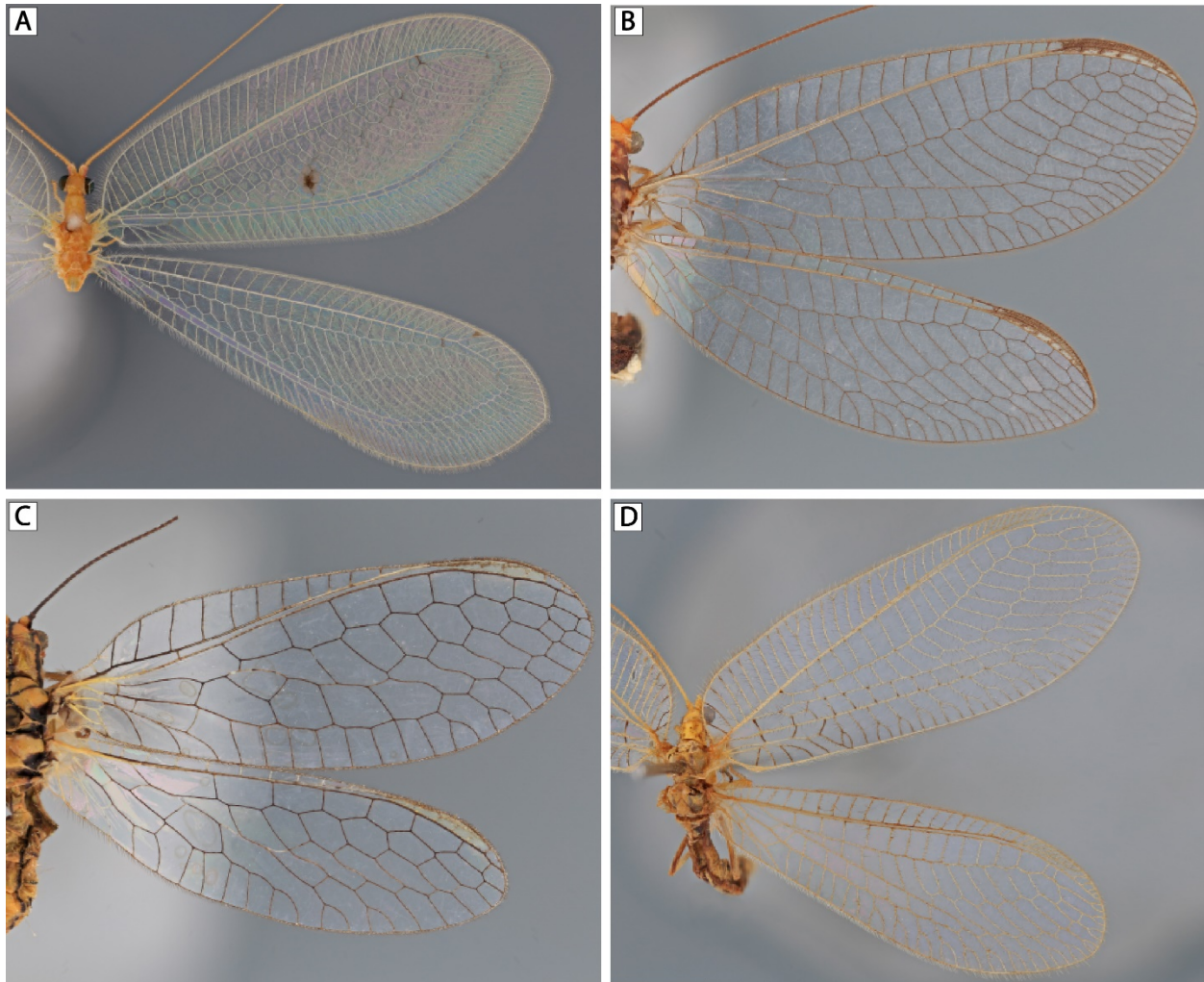
## Relationships of Chrysopidae and character evolution

### The family Chrysopidae

As in all previously conducted analyses, we recovered the family Chrysopidae as monophyletic (Brooks 1997, Winterton and Freitas 2006, Haruyama et al. 2008, Duelli et al. 2014,



Dai et al. 2017, Jiang et al. 2017, Garzón et al. in rev). Its representatives are grouped by the formation of the pseudocubitus (PsC) in the forewing due to the fusion of at least two longitudinal veins (see also chapter 4). In genera with an ill-defined PsC, such as some Nothochrysininae, there is still fusion on PsC between MP and CuA, and often also between MA and MP, as well as between MA and the first RP branch. In most higher Chrysopidae there is a much greater amount of fusion present, with usually three, but up to six veins. Another character supporting the monophyly of Chrysopidae is the path of CuA in the hind wing. All branches of CuA, but the regularly formed basalmost one diverge from PsC, leading to a *dcc*-cell (see chapter 4) which is completely bordered by CuA (figs. 16-18) – in contrast to the forewing of Chrysopidae and also the fore- and hind wing of other Neuroptera, where *dcc* is bordered by CuA, a crossvein, and CuP. These characteristics are not present in either of the hypothesized sister taxa Hemerobiidae or Myrmeleontoidea. The question of the most likely sister group of Chrysopidae is beyond the scope of this study and we direct the reader to recent studies using anchored phylogenomics (Winterton et al. 2017).



**Figure 17.** Photomicrographs of fore- and hind wing, in dorsal view. A: *Apochrysa matsumurae*; B: *Nothochrysa* sp.; C: *Hypochrysa elegans*; D: *Nothancylla verreauxi*.

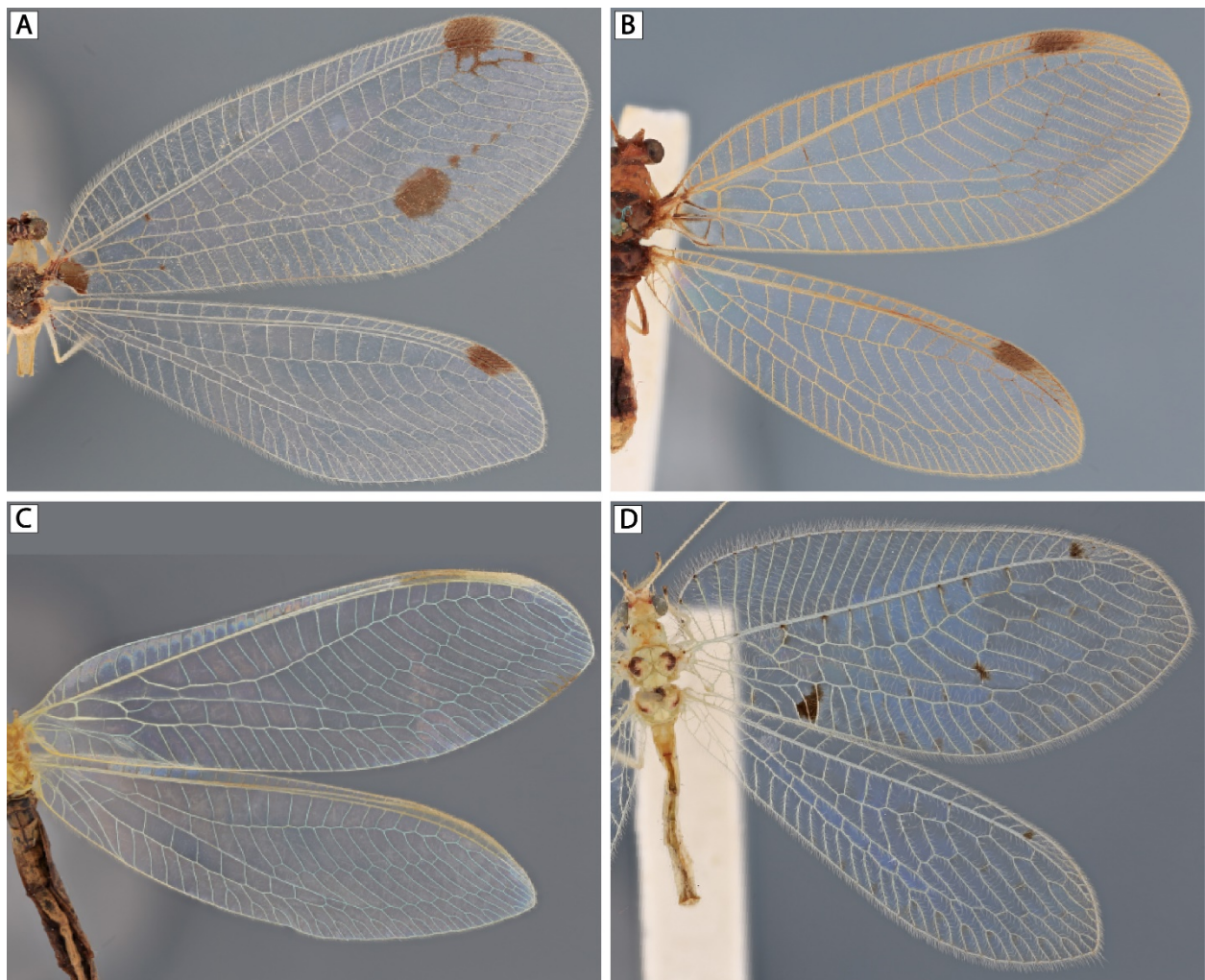
#### Relationships between subfamilies – Apochrysinæ, Nothochrysinæ, and Chrysopinæ

Although the three subfamilies Apochrysinæ, Nothochrysinæ, and Chrysopinæ have long been accepted to be monophyletic, the specific relationships between them have puzzled researchers for decades and are still not completely resolved. The position of Chrysopinæ as the youngest clade is widely accepted, and can be corroborated by a few autapomorphies and many plesiomorphic characters states shared by Apochrysinæ and Nothochrysinæ. The three main hypotheses regarding the relationships between the subfamilies are Nothochrysinæ +

(Apochrysinæ + Chrysopinæ), which is mostly outdated, but recovered in a recently published study on all Neuroptera (Winterton et al. 2017), (Nothochrysinæ + Apochrysinæ) + Chrysopinæ, as recovered in our ML analysis, or Apochrysinæ + (Nothochrysinæ + Chrysopinæ), as recovered in our BI analyses. The latter two have been common in analyses of the last several years (Nothochrysinæ + Apochrysinæ: Haruyama et al. 2008, Duelli et al. 2014, Jiang et al. 2017; Nothochrysinæ + Chrysopinæ: Winterton and Freitas 2006, Garzón et al. in rev; Apochrysinæ + Chrysopinæ: Dai et al. 2017,). It is curious that the relationship (Nothochrysinæ + Apochrysinæ) + Chrysopinæ often results from analyses under a ML framework and Apochrysinæ + (Nothochrysinæ + Chrysopinæ) from Bayesian inference.

Nothochrysinæ have long been perceived as the least derived and oldest of the three subfamilies, putatively as sister to Apochrysinæ + Chrysopinæ. This position was proposed because there is a comparatively large fossil record for Nothochrysinæ (or at least of fossil putatively assigned to Nothochrysinæ), including specimens from the Late Cretaceous that are currently recognized as nothochrysinæ, but none for Apochrysinæ and only a few, comparatively young exemplars of Chrysopinæ. Secondly, a basal position was assumed because the relatively simple wing venation of most nothochrysinæ genera reminds loosely of the non-fused venation of Hemerobiidae. It is now understood that Hemerobiidae are probably not sister to Chrysopidae and therefore not a reasonable point from which to extrapolate plesiomorphies for the MRCA (most recent common ancestor) of all Chrysopidae. Given that the “reduced” wings of nothochrysinæ cannot alone be a reason, particularly not *a priori*, for their placement as sister to all other Chrysopidae, concrete evidence for sorting subfamilial relationships remains to be established. Because of the old age of Chrysopidae but the comparatively young age of the subfamilies (resulting from putatively long ghost lineages leading from the origin to the crown-group of each

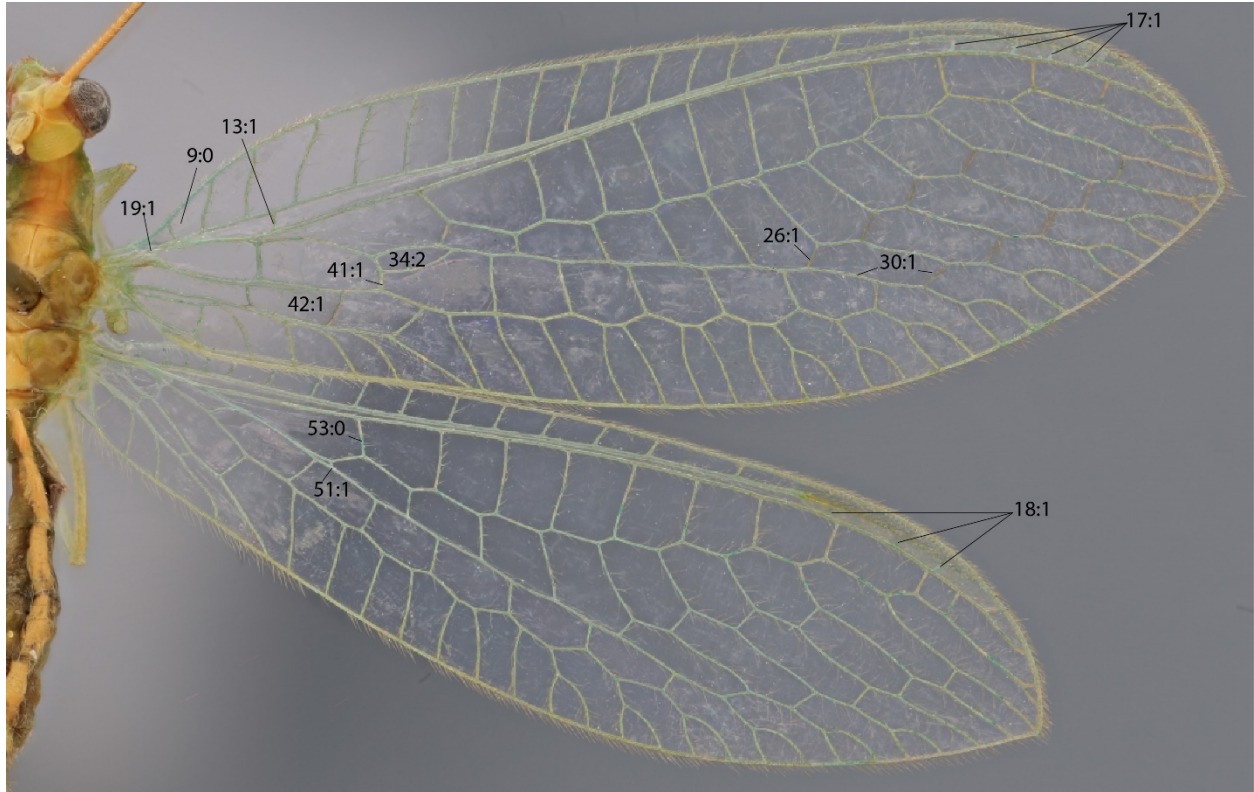
subfamily), we are most likely missing ample data for stem Apochrysinæ, stem Nothochrysinæ, and stem Chrysopinæ, leading to three highly derived groups with little in common (i.e., highly autapomorphic individual subfamilies achieving their crown-group features comparatively late in each lineage's evolution and extensive ghost records for their individual stem groups). The characters that are evidence for either grouping could just as well be retained plesiomorphies, in the light of the controversial hypotheses of relationship of most recent studies (Duelli et al. 2014, Dai et al. 2017, Jiang et al. 2014, Garzon et al. in rev).



**Figure 18.** Photomicrographs of fore- and hind wing, in dorsal view. A. *Gonzaga nigriceps*; B. *Stigmachrysa kervillei*; C. *Nineta flava*; D. *Parankylopteryx* sp.

In our analyses, Nothochrysininae form a monophyletic group with Chrysopinae and this clade is sister to Apochrysininae. This relationship between the three subfamilies is strongly supported, with posterior probabilities varying from 0.84 to 1.0 in the different nodes and analyses. The inclusion of fewer taxa resulted in a sister relationship between Apochrysininae and Nothochrysininae in our analyses, but the more terminal taxa we included the stronger was the support for Nothochrysininae + Chrysopinae. This relationship is supported by the presence of the basal subcostal crossvein (1sc-r = bsx) – a crossvein between Sc and R situated basally on the wing basad to the origin of RP (in Apochrysininae and *Nothancyla* 1sc-ra is located distally on the wing, below the pterostigma), although it can be found in other neuropteran lineages as well, such as Dilaridae, Sisyridae Coniopterygidae, or Osmylidae (see chapter 4, Breitkreuz et al. 2017). In the framework of the analyses presented here this character is apomorphic.





**Figure 19.** Photomicrograph of fore- and hind wing of *Borniochrysa squamosa*, in dorsal view, including character states (refer to list of characters).

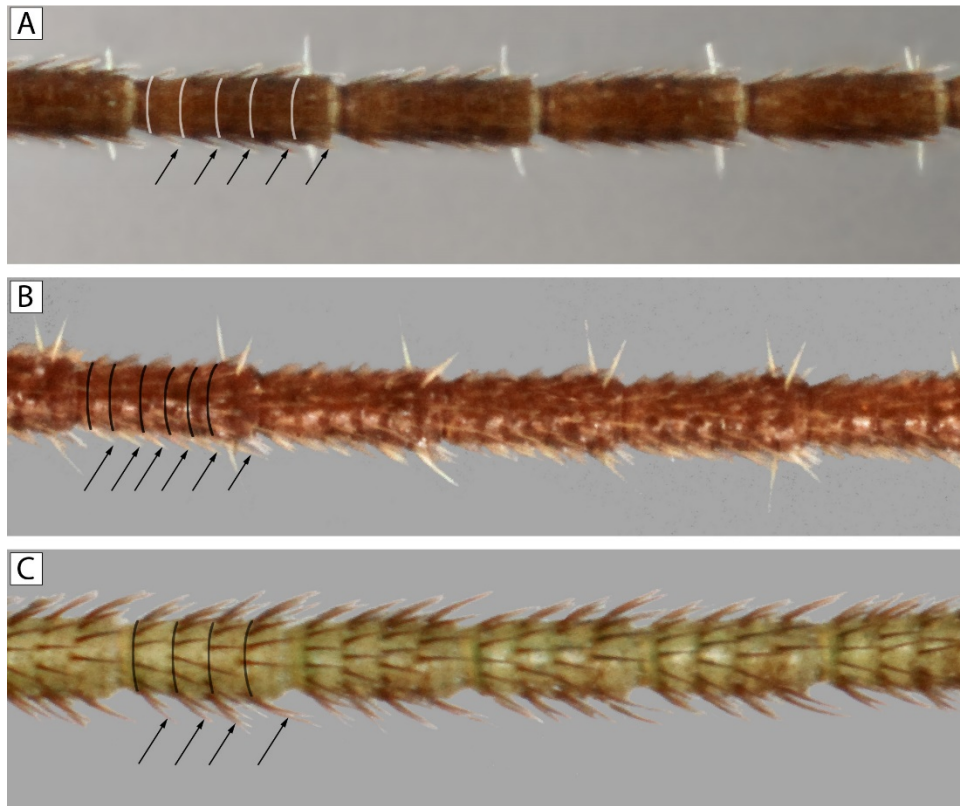
The **tympanal organ** at the wing base (swollen R) is reportedly present in Apochrysinæ and Chrysopinæ but not in Nothochrysinæ (Brooks and Barnard 1990). The absence of this character in Nothochrysinæ was traditionally one of the reasons for the sister-group relationship of this subfamily with all other Chrysopidae. For the newly recovered relationship of Apochrysinæ as sister to Nothochrysinæ + Chrysopinæ, this presence of a tympanal organ in Apochrysinæ would be potentially problematic. It would mean that the tympanal organ is either a plesiomorphic character for all Chrysopidae and subsequently lost in Nothochrysinæ, or independently gained in Apochrysinæ and Chrysopinæ. No other neuropteran lineages show a tympanal organ (New 1989) and its presence in fossils of stem-group Chrysopidae is unknown because the base of the wing is often not sufficiently preserved. This question leads to a more detailed re-examination of the

tympanal organ of Apochrysinæ and Chrysopinæ. The tympanal organ is an auditory structure situated subbasally on the forewing and which is mainly formed by the inflated radius, and the media fuses with the radius at that point (Miller 1984, Brooks and Barnard 1990). The inflated area includes multiple chordotonal organs, several sensilla, the tracheae, and a rippled tympanal membrane (Miller 1984). The structure of this membrane is visible in pinned specimens as a striated curved area within the basally inflated radius (R). Brooks and Barnard (1990) describe the apochrysinæ tympanal organ as an elongate and swollen R-vein close to the wing base. After thorough examination we conclude that it is highly doubtful that the structure in Apochrysinæ is a tympanal organ. Apart of the swollen character of R sub-basally in Apochrysinæ there is nothing that would characterize it as a tympanal organ, and there are other swollen vein areas in the wing base. The curved striated membrane, which is present in the tympanal organ of all Chrysopinæ, is lacking in Apochrysinæ and R and M are not fused, in that the tracheae follow a simple straight line within their respective veins (see chapter 4, Breitkreuz et al. 2017). The ability to detect high frequency bat calls with the tympanal organ has been tested for some genera of Chrysopidae but not for Apochrysinæ. Due to this lack of morphological as well as functional evidence, it is not parsimonious to assume that the swollen R in Apochrysinæ is a tympanal organ (Breitkreuz et al. 2017), particularly in the absence of a membrane in the vein or evidence for chordotonal organs for the detection of sound. This suggests that the tympanal organ evolved once in Chrysopidae, namely in the MRCA of Chrysopinæ, allowing for speculations about the role of this structure and associated behavior in the evolutionary radiation of this subfamily (Archibald et al. 2014). The presence of a fully developed tympanal organ also sheds light on the long uncertain placement of the monotypic genus *Nothancyla*. Traditionally, this curious species, which displays combined characteristics of all three subfamilies, was placed in Apochrysinæ, but is recovered as sister to

Chrysopinae in all current analyses (Dai et al. 2017, Jiang et al. 2017, Winterton et al. 2017, Garzón et al. in rev). This placement can easily be confirmed by the presence of a tympanal organ identical to that of all Chrysopinae. *Nothancyla* shares several characters with Apochrysinæ, such as five flagellar setal rings and the absence of a subbasal crossvein (bsx), but these characters are much less complex than a fully developed tympanal organ in the same position as in Chrysopinae.

Another character illuminating the relationships of Apochrysinæ + (Nothochrysinæ + Chrysopinae) is the **amount of fusion in the pseudoveins** of the fore- and hind wings, which is discussed in further detail in chapter 4 (Breitkreuz et al. 2017). Each subfamily has a certain set of fused veins. Apochrysinæ usually have no fusions in PsM or only two veins in the basal half of the wing but up to seven in PsC (although the pattern is subject to more plasticity than in the other subfamilies) leading to a highly derived venation pattern. Nothochrysinæ wings vary from no fusion in either pseudovein (*Dictyochrysa*) to two fused veins in PsM and three in PsC (*Nothochrysa*). The latter character state is the groundplan for Chrysopinae, which generally have a strict number of two fused veins in the PsM and three or rarely two in PsC. This set of characters suggests a closer relationship between Nothochrysinæ and Chrysopinae than to Apochrysinæ, and several analyses that we did not include here, due to low support values, showed Nothochrysinæ as paraphyletic in regard to Chrysopinae. The remarkable similarity in vein fusions between the genus *Nothochrysa* and many Chrysopinae, regarding the *im* cell (see below) and amount of fusion in the pseudoveins, could be evidence for a clade including both taxa, and should be investigated further, although it has not been recovered in any recent analysis.

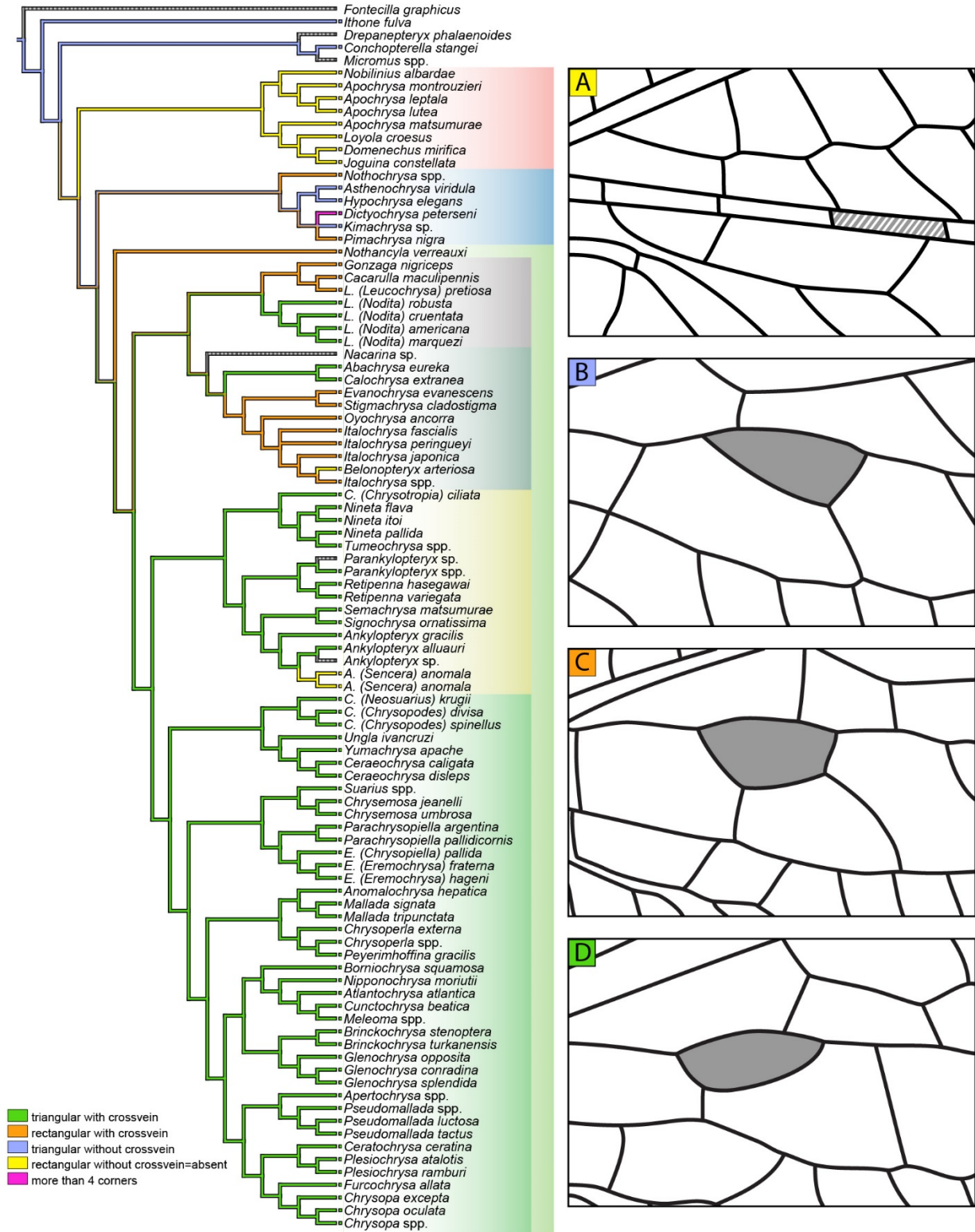




**Figure 20.** Photomicrographs of flagella, lateral view; curved lines indicate the base of the flagellar setae, and black arrows indicate the tip of the flagellar setae. A: *Hypochrysa elegans*, five setal rings; B: *Nothochrysa* sp., six setal rings; C: *Peyerimhoffina gracilis*, four setal rings.

Traditional characters to define the three subfamilies are: (1) the **continuation of PsM** with either the inner gradates (Nothochrysinæ) or the outer gradates (Chrysopinæ and Apochrysinæ). This character is less prominent in some Nothochrysinæ where the PsM is not fully developed. (2) The number of **setal rings on a flagellomere**, where Chrysopinæ always have four rings, except for the genus *Nothancyla* (five rings), Apochrysinæ have five rings, and Nothochrysinæ can have either five or six rings. This character is consistent between the subfamilies and Nothochrysinæ is the only one with variation, apart of *Nothancyla* in Chrysopidae. (3) The absence or presence of an **im cell** (= irregular *mamp1*), which is always absent in Apochrysinæ, present and normally triangular with a crossvein in Nothochrysinæ (except for the rectangular *im* cell in

*Nothochrysa*), and present (except *Ankylopteryx anomala* and *Belonopteryx arteriosa*) in Chrysopinae, with either a quadrangular or ovate shape (triangular without crossvein) (fig. 20). We here distinguish between the *im* cell and *mamp1*, in order to be able to define the states for the subfamilies. The *im* cell will be defined as an irregular *mamp1*: the first cell between MA and MP, and not occupying the entire space between PsM and PsC. Thus, Apochrysinæ have a *mamp1*, which is equal to the third cell between PsM and PsC, but no *im* cell.



**Figure 21.** *mamp1* character states traced on the BI tree inferred from combined data (analysis 4); *mamp1* shaded in grey. A: *Chrysopa perla* Linnaeus. B: *Hypochrysa elegans*. C: *Nacarina balboana* (Banks). D: *Apochrysa leptala* (Rambur).

The *im* cell is absent in Apochrysinæ, but the first cell between MA and MP (*mamp1*) is present by default. It is bordered by MA, a small crossvein between MA, and an RP branch in some taxa (visible only when observing the trachea), and MP as part of PsC. In Nothochrysinæ the *mamp1* can be regular, meaning that it is bordered only by a fairly straight MA, MP, and a crossvein between them, and that it occupies the full width between PsM and PsC, or it is irregular as in *Nothochrysa*, where *mamp1* occupies only half of the width between PsM and PsC. This is identical to many of the *mamp1* conditions in Chrysopinæ. This similarity means that *Nothochrysa* is either more related to Chrysopinæ than assumed, rendering Nothochrysinæ paraphyletic, or that the formation of *mamp1* in the form of a true *im* (occupying half of the width between PsM and PsC) is a convergence between *Nothochrysa* and Chrysopinæ, which is supported by the results of this analysis. In Chrysopinæ *mamp1* is always irregular, but can be present in different states. The least derived Chrysopinæ (Belochrysinini + Leucochrysinini) have a rectangular *im* cell with a crossvein plesiomorphically, which evolved into a triangular or ovate within the clade several times. The most common form of *mamp1* for all Chrysopinæ is the triangular or ovate *im*, which is due to the secondary fusion of MA and MP on PsM, posterior to *im*. In all other types MA and MP fuse (if at all) on PsC. The triangular or ovate *im* of most Chrysopidae is solely bordered by MA and MP and no crossveins are involved. The return to a quadrangular *im* cell has evolved independently in multiple lineages of Chrysopini (*Austrochrysa*, *Rexa*, *Kostka*, and rarely *Chrysopodes*), and is approximated at times in one or both wings, when the veins are somewhat deformed. The only documented cases of a *im* cell lacking in Chrysopinæ (apart of *Nothancyla*) are in the unrelated *Ankylopteryx* (*Sencera*) *anomala* and *Belonopteryx arteriosa*, where the two M branches split more apically.

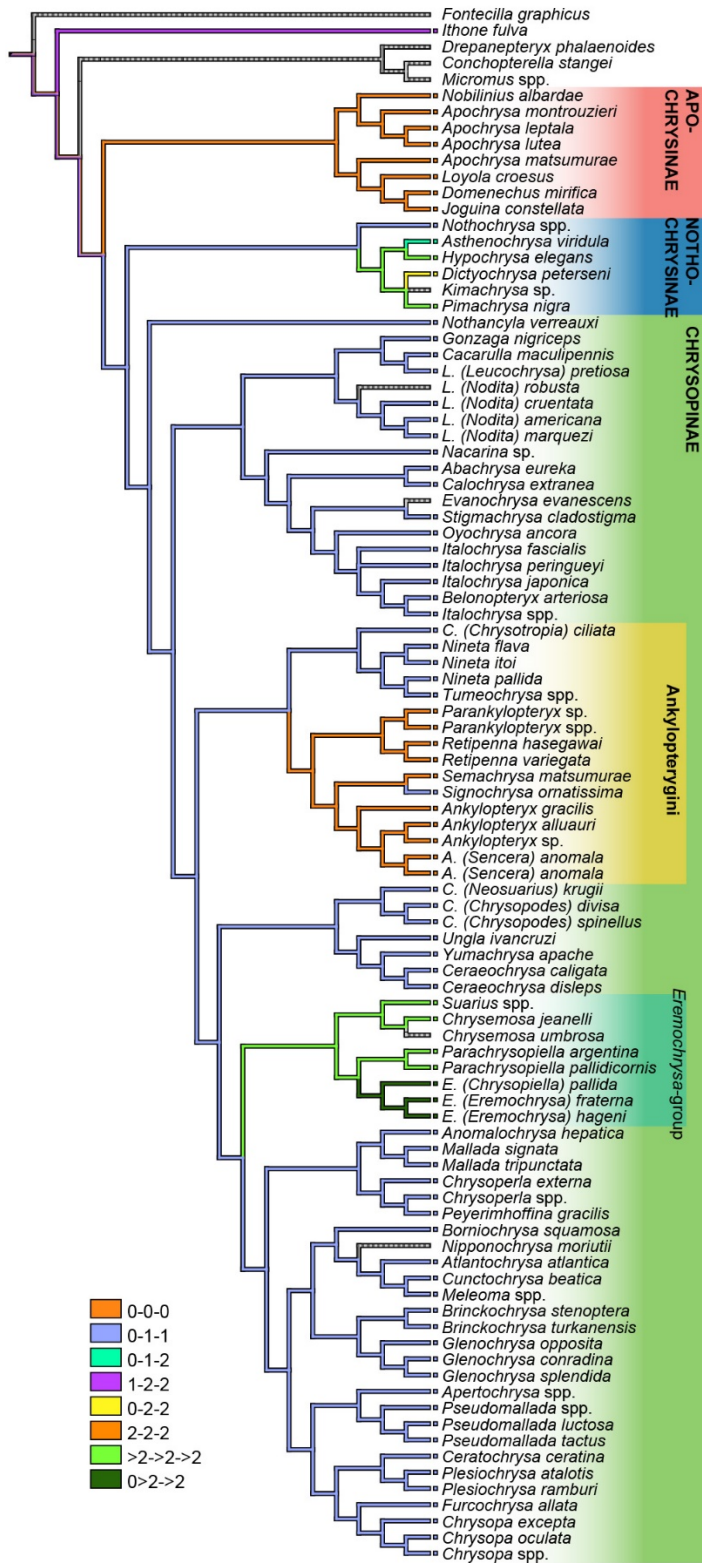
Two previously overlooked characters that are worth discussing when comparing the subfamilies are found on the **legs**. The tibia can have one or more apical spurs (fig. 21), and the presence and number of the spurs is specific to the subfamilies (fig. 22), with some exceptions. Apochrysinæ have no tibial spurs on any of their legs (0-0-0), a condition that can elsewhere only be found in Ankylopterygini (and possibly in the monotypic nothochrysin *Pamochrysa*). The genera of Nothochrysinæ are extremely variable regarding tibial spurs, with all states from absent spurs, over several states in-between (0-1-1, 0-1-2, 0-2-2), to multiple tibial spurs present on all legs. Chrysopinæ usually have no spur on the protibia, and one each on meso- and metatibia (0-1-1), except for the *Eremochrysa*-group, with multiple tibial spurs on each leg (0->2->2->2). The second noteworthy leg character is the number of long setae on the apical margin of tarsomere V. There are usually two long setae present in Apochrysinæ and Chrysopinæ, with few genera having four setae (including *Joguina*, *Domenechus*, *Nothancyla*, and few nested Chrysopini), and no prominently long setae present in Nothochrysinæ.



**Figure 22.** Photomicrographs of tarsi. A: *Hypochrysa elegans*, dorsal view, black arrows indicating four long setae; B: *Stigmachrysa kervillei*, dorsal view, black arrows indicating two long setae; C: *Parankylopteryx* sp. ventro-lateral view, arrow indicating the absence of a tibial spur on the metatibia; D: *Stigmachrysa kervillei*, ventro-lateral view, arrow indicating a tibial spur on the metatibia; E: *Suarius alisteri*, ventro-lateral view, arrows indicating multiple tibial spurs on the metatibia.

Most “characters” that were used to support a possible sister relationship between Nothochrysoinae and Apochrysoinae are plesiomorphic character states, that stand in contrast to the derived states in Chrysopinae, or are absence characters of chrysopine apomorphies, such as the presence of four setal rings (except for *Nothancyla*), or the tympanal organ.





**Figure 23.** Tibial spurs character states traced on the BI tree inferred from combined data (analysis 4), each formula summarizes number of tibial spurs on the pro-, meso-, and metathoracic leg.

## Relationships within Apochrysinæ

Apochrysinæ include representatives with the largest body sizes and wing spans among Chrysopidae, but only 26 species are currently recognized. The wings have ample fusion when compared to Chrysopinae, Nothochrysinæ, or fossils in the stem of Chrysopidae, and due to this strong disparity it is complicated to infer relationships to the other subfamilies. No apochrysinæ fossils are currently recognized, which is puzzling given their purportedly old age. We putatively associated the fossil *Okanaganochrysa coltsunae* with the stem of Apochrysinæ due to its large wings with strong reticulation and the absence of the basal subcostal crossvein (bsx), but this should be considered with caution due to the presence of an *im* cell in the fossil (which could be plesiomorphic at that relative level or convergent and autapomorphic to the fossil). Apochrysinæ are united by the missing bsx, which is only also absent in *Nothancyla*, the absence of the *im* cell (a condition also found in *Ankylopteryx* and *Belonopteryx*), and a combination of a PsM that is continuous with the outer gradates and the flagellar setae arrangement in five rings. In the phylogenetic analysis based on morphological data of Apochrysinæ conducted by Winterton and Brooks (2002), they synonymized several genera, especially under *Apochrysa*. Our analysis did not include all previously accepted genera, but confirmed many of the synonymizations. In the phylogeny of Winterton and Brooks, *Apochrysa* is sister to all other Apochrysinæ, a relationship that is supported by several apomorphies, such as the elongate PsC in *Nobilinius*, *Domenechus*, *Joguina*, and *Loyola*, and the long cell between RA and RP below the pterostigma as well as the presence of forked vein branches on the basal half of the posterior wing margin of *Apochrysa*. In our analyses we found that the addition or exclusion of a single character lead to changing topologies within the subfamily. In our analysis *Loyola*, *Joguina*, and *Domenechus* always group together, as do most species of *Apochrysa*, but the genus *Nobilinius* and the species *Apochrysa matsumurae* vary in their position between the different analyses. *Nobilinius* resulted as sister to



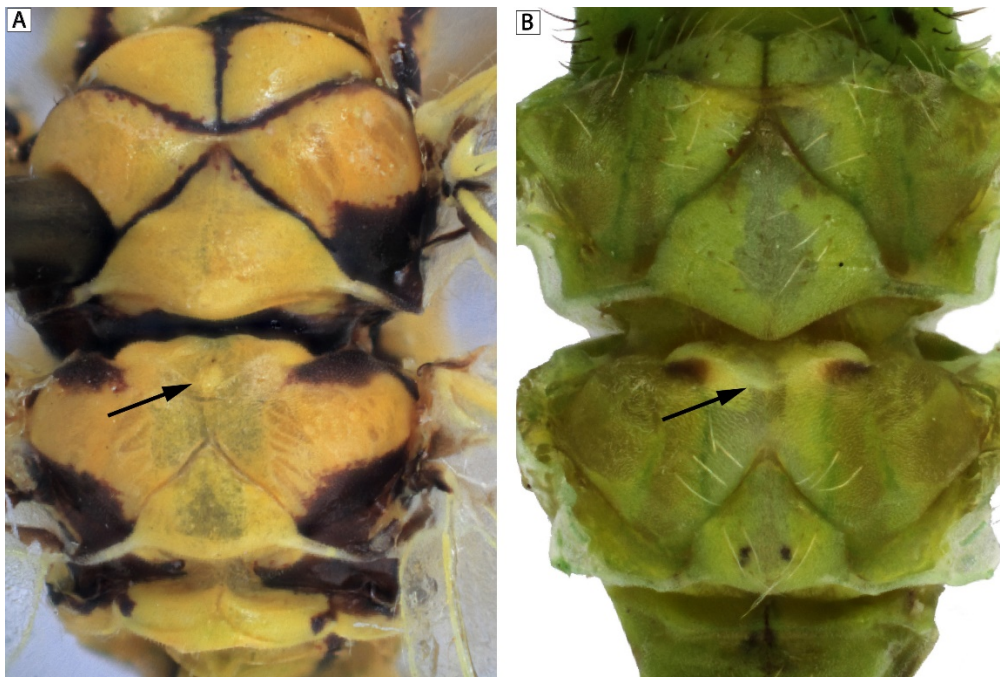
*Loyola*, *Joguina*, and *Domenechus* is an additional analysis with more apochrysine-significant characters, but *Apochrysa matsumurae* still does not group within *Apochrysa* and its generic attribution should be investigated further. Unfortunately, the apochrysine dataset is lacking many male characters with phylogenetic significance because we did not have males for all genera, as they are often unknown or only present as valuable types in collections, and therefore not available for dissection.

An expanded molecular data set with a more thorough taxon sampling could greatly help to resolve these issues, but most apochrysine genera are rare to find in the field. The main analysis was lacking the character of the elongate cell in RP below the pterostigma, and in a subsequent analysis we recovered a similar topology to that of Winterton and Brooks (2002). This shows that the inclusion of more internal characters and widely unknown larval characters could have a strong impact on the estimation of relationships for this subfamily.

#### Relationships within Nothochrysinæ

Nothochrysinæ display many primitive-looking representatives that have wing-venation characters often reminiscent of fossil Chrysopidae. Due to the presence of a sizeable fossil record among the subfamilies, it was long believed to be the oldest of Chrysopidae and therefore sister to Apochrysinæ and Chrysopinæ. Many genera are rare and most of them have unique morphologies, rendering the identification of relationships among all genera of Nothochrysinæ problematic. We were able to examine representatives of all genera but the monotypic *Leptochrysa*, only known from a single specimen, and *Triplochrysa*, a rare genus from Australia for which we added morphological character data from the literature. The inclusion of all genera resulted in *Nothochrysa* as sister to a large polytomy. Most nothochrysinæ have weakly developed

pseudoveins, often with no fusions on the scarcely straight PsM, and only two veins fused on the often short PsC. Nothochrysinæ are the only group of extant Chrysopidae in which the PsM is continuous with the inner gradates, but this character is common in most fossil taxa. All Nothochrysinæ have a small expansion on the anterior margin of the metascutum (fig. 23), which cannot be found in any other Chrysopidae. They have either five or six setal rings on each flagellomere. Most have five, like Apochrysinæ and *Nothancyla*, but a probably monophyletic group (PP=96) consisting of *Dictyochrysa*, *Kimochrysa*, and *Pimachrysa* has six rings. The genus *Nothochrysa* is the only one in which both six and five setal rings can be present. Therefore the six setal rings seem to be the apomorphic state, which likely had separate origins in Nothochrysinæ.



**Figure 24.** Photomicrographs of the meso- and metanotum, dorsal view. A: *Hypochrysa elegans*, black arrow indicates the presence of a small expansion on the anterior margin of the metascutum; B: *Chrysopa oculata*, black error indicates the simple metascutum, without medial expansion.

Contrary to previous concepts, *Nothochrysa* is not the most derived nothochrysine, but rather sister to all other taxa. Therefore, the supposedly “primitive” habitus of many nothochrysines (e.g., *Hypochrysa*, *Pimachrysa*), which was the reasoning for a sister-group relationship of Chrysopidae and Hemerobiidae, is more likely the expression of a derived and strongly reduced morphology, given our phylogenetic hypothesis. This raises concerns when comparing fossil taxa to extant Nothochrysinæ, in which the wing venation often is apparently similar, seemingly obviating the primary reason to assume this subfamily as the oldest of modern lineages of Chrysopidae.

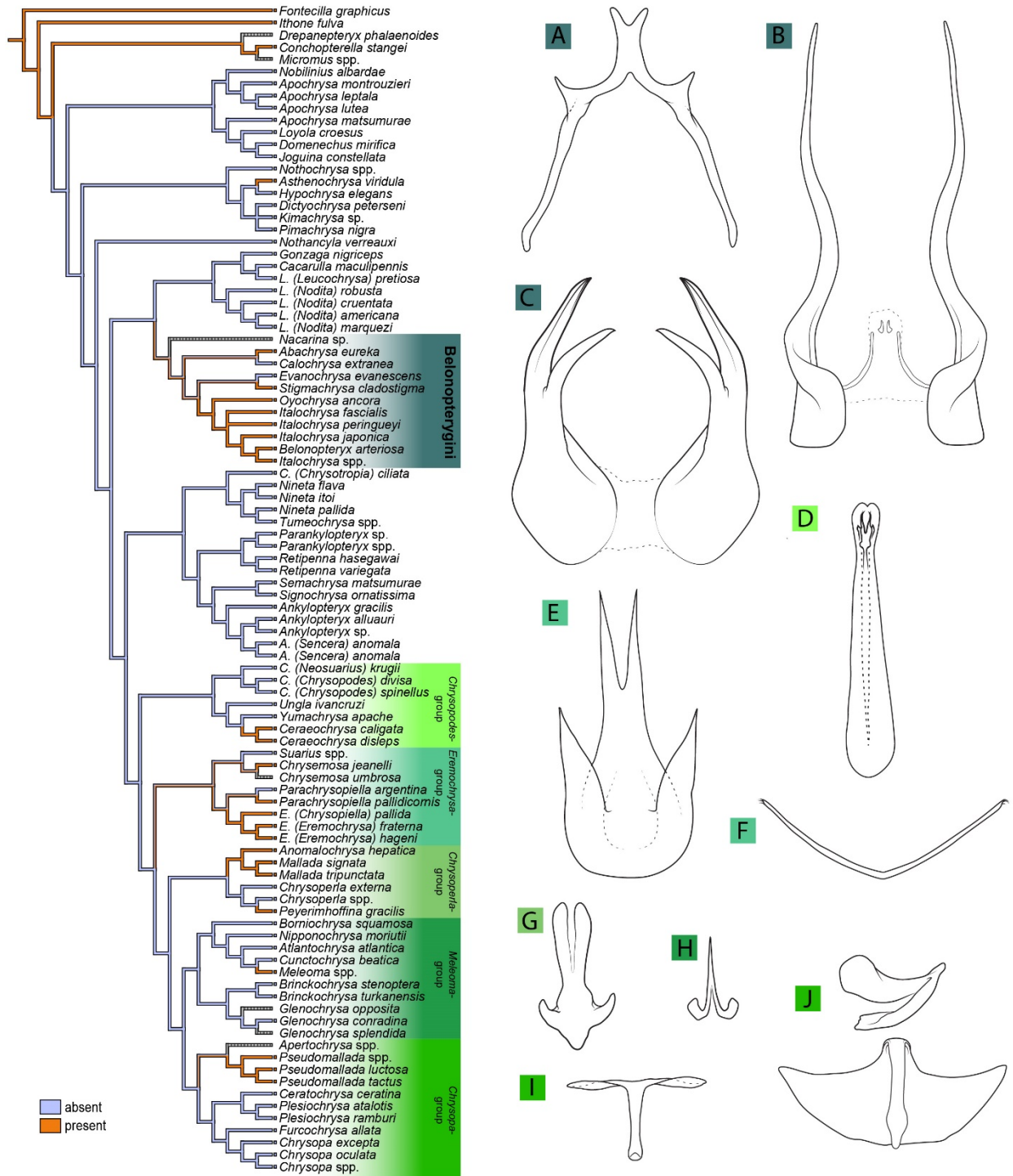
#### Relationships between the tribes of Chrysopinae

*Nothancyla* is strongly supported as sister to all other Chrysopinae (PP= 1) and not, as originally suggested, part of Apochrysinæ, which can be corroborated with several morphological characters. The most striking evidence is the presence of a tympanal organ in *Nothancyla* (as discussed above), as well as the combination of the presence of an *im* cell and the PsM being continuous with the outer gradates. The enigmatic genus has several characters usually occurring in Apochrysinæ or Nothochrysinæ, such as the flagellar setal arrangement in five rings, forked veinlets present in the costal field at the anterior wing margin, or the absence of the basal subcostal crossvein, which is otherwise limited to Apochrysinæ. Nonetheless, the sister relationship between *Nothancyla* and Chrysopinae is recovered in every recent analysis including the presented (Dai et al. 2017, Jiang et al. 2017, Winterton et al. 2017, Garzón in rev), and due to this relationship Garzón et al. (in rev) erected the tribe Nothancylini. We here refer to Chrysopinae including Nothancylini as Chrysopinae sensu lato, and without Nothancylini as Chrysopinae sensu strictu. The latter are mainly supported by the arrangement of the flagellar setae in four rows.

There are **five tribes** in Chrysopinae s. l.: Nothancylini, Belonopterygini, Leucochrysinini, Ankylopterygini, and Chrysopini, the latter one being the most species-rich. The monophyly of all five tribes in Chrysopidae, as currently accepted, could not be confirmed by our analysis. Belonopterygini, Leucochrysinini and Ankylopterygini are monophyletic, but Chrysopini, as is currently recognized, is rendered paraphyletic by the latter. Prominent morphological characters supporting these clades are rare and they are united by combinations of numerous characters (table 3), which can undergo reversals or transformations within the lineages. This morphological controversy is reflected in the phylogeny inferred from morphological data, where the tribes could not be recovered. Therefore the addition of molecular data is fundamental to the reconstruction of the relationships within Chrysopinae.

A character that has long been subject of discussion is the presence of **parameres** in Chrysopinae. We define parameres as a sternal sclerite in the male genitalia, ventral of the gonarcus complex, and situated apical to the hypandrium internum on the gonosaccus. All higher Chrysopinae clades, except for the sister taxa *Nineta*-group and Ankylopterygini, include representatives with parameres (see below) (fig. 24). They are present in most Belonopterygini, rarely in Leucochrysa, and in several Chrysopini genera. This character was termed “parameres” in Belonopterygini and many other Neuroptera (Brooks and Barnard 1990, Aspöck and Aspöck 2008), and “gonapsis” in Chrysopini, but Aspöck and Aspöck (2008) suggested that both structures originate from the ninth sternum. They are often differently shaped, but in the same position, and we therefore propose the synonymization of these terms. The nothochrysinine genus *Asthenochrysa* has a structure that is in the same position as the parameres and should be further investigated. Most Belonopterygini have paired parameres, with a thin membranous connection, that can appear as detached, except for *Nesochrysa*, which have a sclerotized medial area. The parameres (or

traditionally gonapsis) of Chrysopini are usually not paired, but a single structure which can vary greatly in shape (fig. 24, and see chapter 2). Some Chrysopini have parameres with a thin medial area and large lateral lobes, which renders the traditional distinction between paired parameres (especially with exceptions as in *Nesochrysa*) and unpaired gonapsis subjective. The presence of parameres and a gonapsis was thought to be apomorphic in Belonopterygini or Chrysopini respectively, but our analyses shows that it was most likely the plesiomorphic state for Chrysopidae, also given its presence in many other Neuroptera, and is still present in most clades, only completely lost in Ankylopterygini and Apochrysinæ. However, either scenario—plesiomorphic or convergence—seems similarly not parsimonious in Chrysopidae. The most plausible character evolution given our results is the plesiomorphic presence of paired parameres, as can be seen in Belonopterygini and possibly *Asthenochrysa*, which was reduced in several lineages, such as Apochrysinæ, most Leucochrysinini, Ankylopterygini, and some Chrysopini. The evolution of parameres within Chrysopini is even more puzzling, because they are not present in several clades, and have numerous different forms in others, due to which a reconstruction of the character transformation is complicated.



**Figure 25.** Parameres character states traced on the BI tree inferred from combined data (analysis 4). A. *Dysochrysa furcata*; B. *Italoichrysa* sp.; C. *Oyochrysa ancora*; D. *Ceraeochrysa cincta*; E. *Parachrysopiella talquensis*; F. *Chrysemosa* sp.; G. *Anomalochrysa hepatica*; H. *Meleoma schwarzi*; I. *Pseudomallada euryderus*; J. *Pseudomallada ventralis*.

The sister group relationship of **Belonopterygini and Leucochrysinini** is highly supported in every analysis (PP= 1), and can be grouped by few characters, such as the male genitalic characters: broad ear-like lateral arms of the gonarcus and the absence of entoprocessi, although these are not irreversible states. Unfortunately, we were not able to place many of the belonopterygine or leucochrysinine genera that were of most interest due to the lack of molecular data and their puzzling morphology. When included, the currently leucochrysinine genera *Nuvol*, *Berchmansus*, and *Santocellus*, usually resulted in different positions within Leucochrysinini, but with low support values. The rare species of *Belonopteryx* and *Turnerochrysa* resulted within the genus *Italochrysa* with low support values. *Vieira* resulted as sister to *Nacarina* in the phylogeny inferred from molecular data (PP=1), making it a belonopterygine, but the inclusion of morphological data did not support this relationship, while unable to place this genus. Tauber et al. (2007) officially transferred *Vieira* from Leucochrysinini to Belonopterygini, based on larval characters. The inclusion of *Vieira* in the combined data analysis lead to a polytomy between numerous Belonopterygini and Leucochrysinini taxa. The clade including Leucochrysinini and Belonopterygini is of strong need for a more detailed phylogenetic analysis with more molecular data and the inclusion of larval characters.

**Belonopterygini** are monophyletic in our analysis, but a more detailed analysis, including the rogue taxa currently placed in the tribe (*Belonopteryx*, *Chrysacanthia*, *Chrysaloisia*, *Nesochrysa*, and *Turnerochrysa*), is needed to confirm this. In every analyses including the monotypic genus *Belonopteryx* the species resolved within *Italochrysa*, but with low support. It is most likely that the inclusion of more species of the diverse genus *Italochrysa* would result in a paraphyly, in regard to many genera, such as *Evanochrysa*, *Oyochrysa* or *Stigmachrysa*, *Belonopteryx*, and *Triplochrysa*. The South American genus *Nacarina* is sister to *Vieira* in analysis

1, and either the monophyletic group of these, or, when *Vieira* was not included only *Nacarina* is sister to all other Belonopterygini. The monotypic *Abachrysa*, which is Nearctic, is sister to all included Old World belonopterygine genera (*Calochrysa*, *Stigmachrysa*, and *Italochrysa*). The parameres of Belonopterygini are usually paired, but they were reduced in several genera, such as *Calochrysa*, *Evanochrysa*, some *Nacarina*, one examined *Italochrysa* and *Belonopteryx*, and the parameres of *Nesochrysa* are medially fused with multiple long apical projections. Another character that loosely groups belonopterygine genera is the elongation of the first cubital cell, rendering it longer than the, often unusually short, second cubital cell (fig 17b), and most representatives have short flagellomeres with short setae. Additionally, contrary to most other Chrysopidae, the basal-most RP branch of the hind wing originates at the *mamp1* cell, and not distal to it. This feature is present in most belonopterygine genera, but not all, such as *Evanochrysa* or some *Italochrysa* species, nor in Leuchochrysinini. We have also found this character state in *Chrysotropia ciliata*, but not as pronounced and it seems to be an exception outside of Belonopterygini.

In **Leucochrysinini**, the subgenus *Nodita* is sister to a monophyletic group including *Leucochrysa* (*Leucochrysa*), *Gonzaga*, and *Cacarulla*, contrary to the current classification. Superficially, the subgenera *Leucochrysa* and *Nodita* can only be distinguished by the shape of the *im* cell, which is triangular in *Nodita* and quadrangular in *Leucochrysa*. The genitalia of the two subgenera are very similar, but Brooks and Barnard (1990) mentioned a small difference in the female subgenitale, where it has a small basally pointing extension in *Nodita*, but not in *Leucochrysa*. In the latter the subgenitale is expanded basally strongly in some species, forming a structure that can appear as a praegenitale, but which is connected to the subgenitale and not to



sternum VII. Brooks and Barnard (1990) suggested this structure in Leucochrysinini to be a predecessor of the praegenitale of Belonopterygini, but further study is needed to confirm this.

There were several genera that could not be placed here, but some characteristics, that are indicative for certain relationships can be found. *Nuvol* and *Santocellus* have a hind wing venation consistent with that of Leucochrysinini. *Vieira* has a hind wing venation close to that of Belonopterygini, supporting the sister-group relationship of this genus with the rest of the belonopterygine tribe. This relationship was proposed before, on the basis of larval characters (Tauber 2007), but unfortunately we were not able to place the genus in our analyses, where the small amount of molecular data, combined with the unusual morphology resulted in an uncertain placement in a polytomy including numerous belonopterygine and leucochrysinine taxa. *Berchmansus cincticeps* (Banks) has a hindwing venation that is otherwise only found in Ankylopterygini s. str., with the basal most RP branch originating from RP distad to 1ra-rp, but the male and female genitalia are consistent with Leucochrysinini. The tribe is in need of a more detailed phylogenetic reconstruction, including molecular data for the rogue taxa of our analyses and with a higher taxon sampling of the diverse genera *Leucochrysa* and *Nodita*.

**Ankylopterygini** are monophyletic, but not as previously thought a sister clade to all Chrysopinae. A monophyletic group including the chrysopine genera *Nineta*, *Chrysopidia* (*Chrysopidia*), *Chrysopidia* (*Chrysotropia*), and *Tumeochrysa* (= *Nineta*-group), is most closely related to the tribe Ankylopterygini. This relationship has been recovered in all recent phylogenetic studies inferred from molecular data (Duelli et al. 2014 in part, Garzón et al. in rev). Within the *Nineta*-group, *Chrysopidia* is sister to *Nineta*, which is rendered paraphyletic by *Tumeochrysa*. The latter two share numerous morphological characters, such as the elongation of the male sternum VIII+IX or the scape in various degrees. Given our results, *Tumeochrysa* is a species of

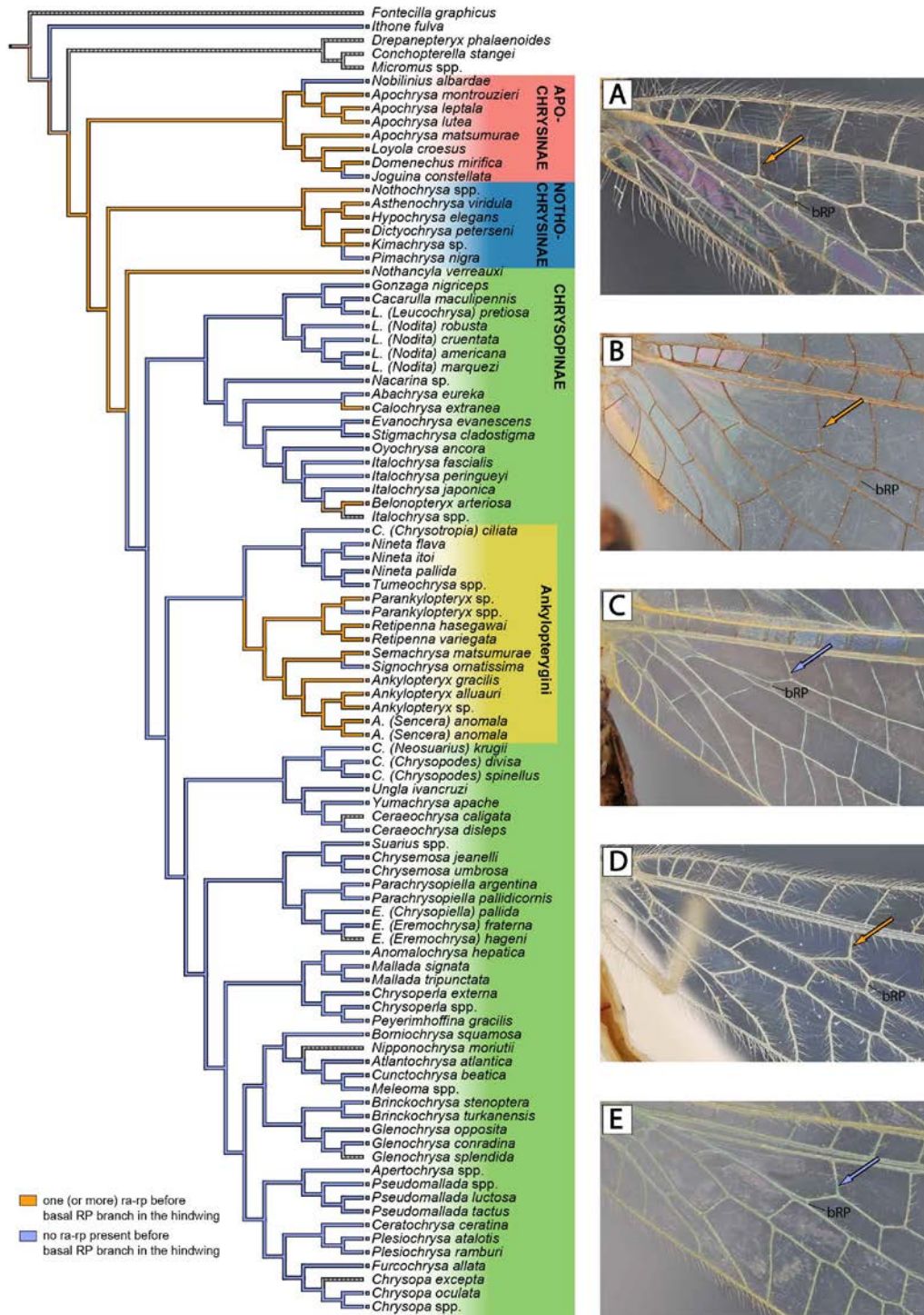
*Nineta* in which the male sternum VIII+IX and the scape are strongly elongate, but with more than two gradate series present in *Nineta*. *Chrysopidia* is traditionally defined by their elongate scape and sternum VII+IX in the male, but these characters are also present to a different extent in most *Nineta* and all *Tumeochrysa*. The thin and elongate sternum VII+IX in the male can be found in some Ankylopterygini s. str., such as *Signochrysa* and *Retipenna*, but also in unrelated Chrysopini, such as some species of *Mallada* or *Meleoma*. The genus *Chrysopidia* is divided into three subgenera: *Anachrysa*, *Chrysopidia*, and *Chrysotropia*. The latter two group together in our analyses, but *Anachrysa* consistently placed within Chrysopini sensu lato. The genitalia of *Anachrysa* are very similar to those of *Mallada*, with a tignum and parameres present, which is never the case in Ankylopterygini sensu lato. Apart of the elongate scape and sternum VIII+IX, which is also present in *Mallada* in a less expressed form, there are no distinctive characters to support a placement in the *Nineta*-group. In the constrained analysis (tree 9, see box in figure) we forced *Anachrysa* in Chrysopini and it resulted as part of the *Chrysoperla*-group with high support (see also below, *Chrysoperla*-group paragraph). The male genitalia of all Ankylopterygini s. l. are comparatively simple, with no parameres, or tignum and an often long and narrow mediuncus. Most Ankylopterygini s. str. have a basally expanded costal area, that is similar to that of Apochrysinæ, and developed strongest in *Ankylopteryx* and *Parankylopteryx*. These two genera, plus *Sencera*, are currently recognized as subgenera of *Ankylopteryx*, but we could not confirm such a relationship. As suggested before (Breitkreuz et al. 2015), *Sencera* is simply a morphologically derived species of *Ankylopteryx*, as it resulted within the genus in every analysis. It has a fully reduced *im* cell, but all other morphological characters are consistent with *Ankylopteryx*, and there are several species of the latter genus, which have a small, and almost reduced *im* cell (Brooks 1983, Brooks and Barnard 1990, Tsukaguchi 1995). *Parankylopteryx* and

*Ankylopteryx* are not recovered as sister genera, which is surprising given their similar morphology. The most significant difference between the genera is the far detached mediuncus in *Ankylopteryx*, whereas it is close to the medial arch of the gonarcus in *Parankylopteryx*. Other characters, such as the dark coloration of the costa basally, or the dark tarsus in *Parankylopteryx*, can be used as a guideline but there are *Ankylopteryx* species with markings in these areas. *Parankylopteryx* is sister to *Retipenna*, and *Ankylopteryx* is sister to *Semachrysa* + *Signochrysa*, but we could not find apomorphies for either group. All genera of Ankylopterygini s. str. but *Parankylopteryx* and *Ankylopteryx* do not have the typical broadened basal costal area, but many have narrow and pointed terminal palpi. The tibial spurs are absent in Ankylopterygini s. str., as in Apochrysinæ, but present in the *Nineta*-group. Ankylopterygini s.str have a unique state of the basal most hind wing RP branch (fig. 25). In the majority of examined species this RP branch originates from RP distal to the first crossvein between RA and RP (1ra-rp). This is contrary to the majority of Chrysopidae, in which the basal most RP branch originates from RP, where MA meets RP or only slightly distad. Therefore, the first apparent crossvein between RP and PsM is the basal most RP branch in Ankylopterygini s. str., and not the second most basal RP branch, as in other Chrysopinae, where the basal most one is not apparent as a crossvein, but immediately fused with PsM after its origin from RP.

As suggested before, we here formally include the genera *Nineta*, *Tumeochrysa*, and *Chrysopidia* in the tribe Ankylopterygini. We also suggest the exclusion of *Anachrysa* from the genus *Chrysopidia* and instead a closer relationship with *Mallada*, but await further phylogenetic and detailed morphological studies for the formal placement.

It is curious that Ankylopterygini s. str. and Apochrysinæ share several characters, given that the two taxa are not closely related. Both have a broad basal costal area and no tibial spurs

present, additionally *Ankylopteryx anomala* is, with *Belonopteryx arteriosa*, the only known species of Chrysopinae without an *im* cell. These convergences open up room for speculations on the factors favoring such a habitus, which should be further investigated.



**Figure 26.** ra-rp crossveins presence or absence basal to basal most RP branch traced on the BI tree inferred from combined data (analysis 4), including Photomicrographs of the respective character states; bRP (basal most RP branch). A. *Apochrysa matsumurae*, orange arrow indicating 1ra-rp basal to bRP; B: *Nothochrysa* sp., orange arrow indicating 1ra-rp basal to bRP; C: *Nineta flava*, blue arrow indicating 1ra-rp distal to bRP; D: *Parankylopteryx* sp., orange arrow indicating 1ra-rp basal to bRP; E: *Borniochrysa squamosa*, blue arrow indicating 1ra-rp distal to bRP.

**Chrysopini** (not including the *Nineta*-group) are well supported, but no true synapomorphies could be identified, and all the included clades result in a large polytomy in the phylogeny based on morphological data. There is a high amount of homoplasy in Chrysopini, due to retained plesiomorphies amongst apomorphies of genera, as well as many convergences between unrelated genera, especially in coloration. It is difficult to place taxa without molecular data in the morphologically very similar Chrysopini. Most Chrysopini are small and green, with a similar wing venation, including a usually ovate *im* cell, but can vary greatly in the male genitalia. A character that is only present in the male genitalia of Chrysopini (and only in the more derived lineages) is the tignum. This thin, arched structure can only be found in some members of the *Chrysoperla*-, *Meleoma*-, and *Chrysopa*-group. These three groups form a monophyletic group, but the genera with a tignum are not all closely related, although the form of it is conserved throughout the groups. Given our results it is most likely that it was gained once in the lineage of the clade including the three groups, and then lost in multiple occasions (fig. 26). The tignum is present in all representatives of the *Chrysoperla*-group, which is sister to the *Meleoma*-group + *Chrysopa*-group according to the larger scale combined data analyses (analyses 1, 3, and 4), but this relationship is not well supported, and the conclusion should be taken with caution.

We here divide the tribe Chrysopini into five monophyletic groups, in order to discuss generic relationships: the *Chrysopodes*-group, the *Eremochrysa*-group, the *Chrysoperla*-group, the *Meleoma*-group, and the *Chrysopa*-group.



**Figure 27.** Tignum absence and presencetraced on the BI tree inferred from combined data (analysis 4), including schematic drawing of male terminalia, tignum orange. Dashed line in *Nothancyla* indicates the uncertainty of the presence of a tignum in this species; additional orange square in *Plesiochrysa* indicates that a tignum is present in few (not included) species of the genus.

The ***Chrysopodes*-group** consists of *Chrysopodes*, *Neosuarius*, *Ungla*, *Yumachrysa*, and *Ceraeochrysa*, and is sister to all other Chrysopini. The phylogenetic hypotheses differ between the analyses based solely on molecular data and those including morphological data. *Chrysopodes* is sister to a clade including *Ungla*, *Yumachrysa*, and *Ceraeochrysa* in all analyses. The placement of *Neosuarius* as a subgenus of *Chrysopodes* could be confirmed by including a species based on morphological data. The males of both subgenera have a ventral expansion of the dorsal apodeme, which is forming a ventral tip of the ectoproct, and the female spermatheca is unusually elongate for a chrysopine genus. In the molecular analysis, *Yumachrysa* and *Chrysopodes* are sister genera and in the combined analysis *Ungla* is sister to *Yumachrysa* + *Ceraeochrysa*, but either phylogenetic hypothesis is not highly supported, therefore the inclusion of additional taxa would be beneficial to identify relationships within this group. *Ceraeochrysa* is the only genus within this clade that has parameres. The structure is a medially fused elongate rod, which is significantly longer than the gonarcus complex. In the molecular analysis we included the enigmatic and monotypic genus *Kostka*, which resulted within the *Chrysopodes*-group. Unfortunately the inclusion of morphological data did could not support this relationship, probably also influenced by the low amount of molecular data present for the genus (1 gene= CO1), due to which the previously recovered relationship was not stable in the light of additional data. We therefore recommend further testing with additional molecular data before suggesting a phylogenetic placement of *Kostka*.

The ***Eremochrysa*-group** includes the genera *Suarius*, *Chrysemosa*, *Parachrysopiella*, *Chrysopiella*, and *Eremochrysa*, and is sister to the clade including the *Chrysoperla*-, *Meleoma*-, and *Chrysopa*-groups. *Suarius* + *Chrysemosa* are sister to the remaining three genera and all monophylies are strongly supported in this group. All representatives of the group have multiple



tibial spurs on all legs (although in *Eremochrysa* and *Chrysopiella* there are none on the protibia), which is unique among Chrysopinae, and can otherwise only be found in some nothochrysines. The living specimens of the *Eremochrysa*-group are mostly light brown, and easily distinguished from the otherwise green Chrysopini, also by their often reduced wing venation with only one or even absent gradate rows in fore- or hind wings. The two clades in the *Eremochrysa*-group represent two geographic ranges, where *Suarius* and *Chrysemosa* occur in the Palearctic and Afrotropics, and *Parachrysopiella*, *Chrysopiella*, and *Eremochrysa* occur in the Nearctic and Neotropics. *Parachrysopiella* is sister to the subgenera of *Eremochrysa* (*Eremochrysa* and *Chrysopiella*). Most members of the *Eremochrysa*-group have parameres (medially fused single structure) except for a few species of *Parachrysopiella* and *Suarius*. The shape of the parameres (fig. 24) varies from a thin elongate arch in *Chrysemosa*, to a long and prominent medial rod in *Eremochrysa* or a large structure with four apical pointing elongate teeth in *Parachrysopiella*. The males of both *Eremochrysa* and *Chrysopiella* have a small additional external sclerite laterally, ventral of tergum IX + ectoproct, which is not present in any other Chrysopidae.

The relationship between the *Chrysoperla*-, *Meleoma*-, and *Chrysopa*-groups is not well resolved and the genera result in a polytomy in most analyses. In some analyses (3 and 4) the *Chrysoperla*-group is sister to *Meleoma*-group + *Chrysopa*-group, but the support values are usually low (pp<65).

The ***Chrysoperla*-group** is a clade including the genera *Anomalochrysa*, *Mallada*, *Peyerimhoffina*, and *Chrysoperla*, where the former two are sister to the latter two. All genera have a tignum in the male genitalia (with few exceptions in some *Mallada* and *Anomalochrysa* species), and all but *Chrysoperla* also have parameres. The combination of both tignum and parameres present is elsewhere only found in the not closely related *Meleoma* and *Pseudomallada*. The

parameres of the *Chrysoperla*-group are usually smaller than the gonarcus complex, a medially fused, singular structure and often have two apical lobes, but they can vary greatly even within genera (see chapter 2). The Hawaiian genus *Anomalochrysa* is sister to *Mallada*, confirming their close relationship, which Brooks and Barnard (1990) suggested based on their morphological similarities, especially of the genitalia. Most species of *Anomalochrysa*, and few species of *Mallada*, have more than two gradate series in fore and hindwing. In an additional analysis that included *Chrysopidia* (*Anachrysa*), and in which we included the genus in the constrained Chrysopini, it resulted as sister to *Anomalochrysa* with fairly high support (PP= 88), and high support when just considering its placement in close relationship to *Anomalochrysa* and *Mallada* (PP= 96). *Anachrysa* is currently recognized as a subfamily of *Chrysopidia*, which resulted within Ankylopterygini in our analysis. The inclusion of *Anachrysa* in the main analysis led to a polytomy between the tribes of Chrysopinae and the genus. Due to the presence of a tignum and parameres we are confident to exclude the genus from Ankylopterygini, as these features are never found in that tribe. Adding a constraint to include *Anachrysa* in Chrysopini resulted in a confident placement of the genus as part of the *Chrysoperla*-group. We therefore suggest the elevation of *Anachrysa* to genus level (see chapter 2). Brooks and Barnard (1990) also suggested a close relationship between *Peyerimhoffina* and *Chrysoperla* and, based on our results, it is likely that the monotypic *Peyerimhoffina* renders the diverse *Chrysoperla* paraphyletic, suggesting a synonymization of the small genus. Further phylogenetic analyses, based on molecular data, including many of the cryptic species of *Chrysoperla*, are needed to solve this question.

The ***Meleoma*-group** is a large clade that includes two monophyla – one with *Borniochrysa*, *Nipponochrysa*, *Atlantochrysa*, *Cunctochrysa*, and *Meleoma*, and the other with *Brinckochrysa* and *Glenochrysa*. Parameres are absent in all members but *Meleoma*, where they

have a thin v-shape, and reportedly one *Cunctochrysa* species (Tsukaguchi 1995), and a tignum is only present in *Meleoma* and monotypic genus *Atlantochrysa*. *Meleoma* is a distinct genus, with several characters that are subject to sexual dimorphism (see chapter 2), and which cannot be found in any other Chrysopidae, such as the strong ornamentation of the supraantennal frons, and the curved and elongate basal antenna. These characters do not occur in the closely related *Cunctochrysa* or *Atlantochrysa*, but the three genera share a hammerhead or beak-like mediuncus with a thick basal part. *Borniochrysa* and *Nipponochrysa* do not share distinctive characters with *Atlantochrysa*, *Cunctochrysa* or *Meleoma*, but possess several autapomorphies respectively (see chapter 2). As such, *Borniochrysa* is the only representative of the *Meleoma*-group with more than two gradate series in fore or hind wing, and the monotypic genus *Nipponochrysa* has an elaborate entoprocessus in the male genitalia. The second clade in the *Meleoma*-group consists of the sister genera *Brinckochrysa* and *Glenochrysa*. The latter has been shown to have eversible glandular sacks on the dorsal pronotum in the males, which has not been found in *Brinckochrysa* and we were not able to identify these structures, although they can be difficult to detect in dried specimens.

The fifth clade in Chrysopini is the ***Chrysopa*-group**, which includes *Pseudomallada* (this genus name is no longer valid, for nomenclatural changes see chapter 2) as sister to a clade of *Ceratochrysa*, *Plesiochrysa*, *Furcochrysa*, and *Chrysopa*. *Apertochrysa* is a highly diverse genus, and has recently been subject to a detailed phylogenetic analysis (Mochizuki 2017). It was shown that the genus, as it is currently recognized, is paraphyletic and emerges in four different lineages of Chrysopini. The species examined by us (*A. edwardsi* + *euryderus*, and *A. crassinervis*) are closest to *Pseudomallada* and have been officially included in the genus by Mochizuku (2017), which we can confirm with the results of the study presented here (although the wrong name was

given priority, see chapter 2 for discussion and nomenclatural change). The group of *Apertochrysa* species examined here is distinct from *Pseudomallada* in the absence of a tignum, which is well developed in the latter. The type species of *Apertochrysa* (*A. umbrosa*) could not be included here, but was recovered within *Pseudomallada* in Mochizuki (2017). In the second monophylum of the *Chrysopa*-group, *Ceratochrysa*, and *Plesiochrysa* form a clade that is sister to *Furcochrysa* and *Chrysopa*. All representatives of this clade have a long and thin mediuncus which is clearly detached from the median arch of the gonarcus. This character can also be found in few other Chrysopinae, such as *Ankylopteryx*, but not in the closely related genera. *Ceratochrysa* is a distinct genus, with a reduced number of inner gradates and long, thin entoprocessi as well as a large gonocornua. It is recovered as sister to *Plesiochrysa*, which was suggested due to the wing venation and elongate prothorax by Brooks and Barnard (1990), but with a fairly low support (PP=73). *Plesiochrysa* also have more outer than inner gradates, but the male genitalia differ in the size of the entoprocessus, a tignum is present in few species, and some have an additional sclerotized structure below the mediuncus, which are not parameres, but rather attached to the apex of the mediuncus and therefore classified as a pseudopenis, a rare character in Chrysopidae. The monotypic genus *Furcochrysa* is sister to *Chrysopa*, and we suggest a synonymization (see chapter 2), due to the lack of characters that would support the genus status of *Furcochrysa*. The genitalia of both genera are identical and the wing venation characters that were the base for the erection of the genus *Furcochrysa* are merely forked vein terminals (Freitas and Penny 2000).

There were several rogue taxa that we examined, but could not include in analyses because the inclusion of any single one of them resulted in the formation of polytomies between the five major clades of Chrysopini. These are: *Austrochrysa*, *Chrysocerca*, *Chryptochrysa*, *Himalochrysa*, *Kostka* (which was placed close to *Ceraeochrysa* in the molecular-only analysis but could not be

placed in the phylogeny inferred from combined data), *Kymachrysa* (which constantly resulted in a polytomy with several Leucochrycini), *Rexa* (one of the few Chrysopini with a quadrangular *im* cell), and *Titanochrysa*. The inclusion of molecular data for these taxa would be imperative to recover them in the correct position in the tree of Chrysopidae, but many are rare to find in the field.

### Age of Chrysopidae

The results of our divergence-time analyses differ with the currently accepted view on the age of Chrysopidae and their subfamilies. We used a different set of fossils to date the nodes, due to the lack of the deterministic characteristic of the respective groups in the fossils currently treated as the oldest Chrysopidae. The synapomorphy of all Chrysopidae is the fusion of veins to form the PsC, which is not present in *Mesypochrysa minuta*, widely used as the oldest chrysopid fossil in previous analyses (Wang et al. 2017, Garzón et al. in rev). Based on our divergence-time analysis, Chrysopidae are around 130 million years old. This age for the family is situated between previous suggestions such as ca. 100 million (Wang et al. 2017), ca. 180 million (Garzón et al. in rev), or 200 million years old (Jiang et al. 2017). Our results set the origin of crown Chrysopidae in the Early Cretaceous, around the Barremian age.

There are about 90 fossils that are placed in Chrysopidae and their stem, including the extinct Limaiinae, or the extinct sister family Mesochrysopidae (some authors recognize it as a basal subfamily of Chrysopidae s. l.) (Adams 1967, Martins-Neto and Vulcano 1988, Nel et al. 2005, Jepsen et al. 2012, Makarkin et al. 2012, Makarkin and Archibald 2013, Archibald and Makarkin 2015). The oldest known fossil that can confidently be placed in Chrysopidae, due to the presence of a fused PsC is *Mesypochrysa magna* Makarkin, from Baissa, Russia (early

Barremian, 131–126 MA). There are other fossils from that age, or slightly older, without a fused PsC, but in which the wing venation is similar to *M. magna* in other regards. The majority of chrysopid fossils are attributed to Mesochrysopidae, Limmatae, or less frequently Nothochrysininae, and therefore most have been considered as stem-chrysopids, whereas crown-group fossils are much rarer (Nel et al. 2005). Many fossils that were described as Nothochrysininae, are generally similar to modern members of this subfamily, but because they are only preserved as wing compression fossils we cannot confidently place them in the subfamily. In previous analyses Nothochrysininae was calibrated with the fossil *Adamsochrysa aspera* Makarkin and Archibald, but this species does not have a single bsx in the forewing, which is present in all members of the subfamily, and is in general too different from actual nothochrysinine wings. Instead we selected *Asiachrysa tadushiella* as the oldest member of crown Nothochrysininae due to the presence of a bsx, an *im* cell, and a PsC continuous with the outer gradates. We putatively included *Okanaganochrysa coltsunae* as the oldest stem apochrysinine, due to the large and strongly reticulate wing, but this placement should be considered with caution due to the presence of an *im* cell in the fossil. The inclusion of this calibration point did not have a large impact on the divergence times in our analysis. Most crown-group chrysopid fossils are nothochrysinines (*Archaeochrysa*, *Nothochrysa*, *Hypochrysa*), there are none known for Apochrysininae (with the sole possible exception of the aforementioned *O. coltsunae*), and only a few chrysopines (e.g., *Chrysopa glaesaria*, *C. martinovae*, *C. vetula*, *Leucochrysa prisca*). *Paleochrysopa monteliensis* is the oldest chrysopid fossil with a PsM continuous with the outer gradates and the presence of an *im* cell, and can therefore be attributed to Chrysopinae. Apart from this Priabonian representative, those fossils in Chrysopinae were described in either *Chrysopa* or *Leucochrysa*, but due to the absence of genital characters these placements should be considered with caution. A study of chrysopid fossils,

including a phylogeny proposed for the stem groups based on wing-venation characters, can be found in Nel et al. (2005), although some of the fossils reported therein are likely not chrysopids.

According to our analysis, Chrysopidae originated in the Early Cretaceous (Barremian), modern Apochrysinæ in the Eocene (Ypresian), Nothochrysinæ + Chrysopinæ shared their MRCA in the Early Cretaceous (Albian), modern Nothochrysinæ originated in the Late Cretaceous (Campanian), Chrysopinæ between the Early and Late Cretaceous (Albian–Cenomanian). None of the modern genera are younger than 35 million years, which is a surprising result, and in other time trees (relative time), that were not calibrated (not included here), some taxa seemed to diverged more recently.

These results are greatly dependent on the fossils chosen as calibration points and vary widely when less strict time intervals are employed (see analysis 12). Therefore, we suggest further analyses, after a thorough study of the fossil Chrysopidae and their relatives.

## Conclusion

We present the results of multiple phylogenetic analyses of Chrysopidae inferred from combined molecular and morphological data. The recovered relationships generally confirm most recent studies of the family (Duelli et al. 2014, Dai et al. 2017, Jiang et al. 2017, Garzón et al. in rev). Apochrysinæ are sister to a clade including Nothochrysinæ and Chrysopinæ. The enigmatic genus *Nothancylla* is sister to Chrysopinæ and was included in the subfamily based on the presence of a tympanal organ. The four tribes (excluding the monotypic Nothancylini) are grouped in two monophyla: Belonopterygini + Leucochrysinini and Ankylopterygini + Chrysopini. The *Nineta*-group, whose members were formerly classified in Chrysopini, are now included in the tribe

Ankylopterygini. Within the diverse tribe Chrysopini we recognized five distinct clades: *Chrysopodes*-, *Eremochrysa*-, *Chrysoperla*-, *Meleoma*-, and *Chrysopa*-groups. Additionally, we find Chrysopidae to be younger than previously suggested, based on a divergence-time analysis calibrated with fossils that can reliably be placed in the respective taxa. According to this analysis modern Chrysopidae originated in the Late Cretaceous. We identified several characters that allow the diagnosis of higher taxa, but there are few synapomorphies consistent within the clades. The mapping of characters such as the parameres, the tignum, the *im* cell, or the tibial spurs illuminate the evolution of those traits in Chrysopidae. Based on the examination of the parameres and gonapsis, and their presence throughout the tree, we suggest that these structures are homologous.

The different types of analyses (BI, ML, and parsimony) yielded varying phylogenetic hypotheses and Bayesian inference performed best regarding support values and resolved topology. Further analyses with a larger taxon sampling in the molecular matrix would be beneficial for the placement of many genera we had to exclude due to the lack of data. Detailed morphological analyses of specific taxa could help to resolve questions about missing apomorphies. A principle component analysis (PCA) could shed light on the morphological data set, where many of the gathered character data could not be included in the final analysis. Measuring which characters have a higher influence on the phylogenetic hypothesis would be a convenient first step for future analyses.

## References

- Adams, P. A. 1967. A review of the Mesochrysinæ and Nothochrysinæ (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology* 135(4): 215–238.



- Archibald, S. B., and V. N. Makarkin. 2015. A new species of *Archaeochrysa* Adams (Neuroptera: Chrysopidae) from the early Eocene of Driftwood Canyon, British Columbia, Canada. *The Canadian Entomologist* 147(4): 359–369.
- Archibald, S. B., Makarkin, V. N., Greenwood, D.R., and G.F. Gunnell. 2014. The red queen and court jester in green lacewing evolution: bat predation and global climate change. *Palaios* 29(5): 185–191.
- Aspöck, U., and H. Aspöck. 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology* 33(1): 97–127.
- Beutel, R. G., Friedrich, F., and U. Aspöck. 2010a. The larval head of Nevrorthidae and the phylogeny of Neuroptera (Insecta). *Zoological Journal of the Linnean Society*. 158: 533–562.
- Briggs, D. E., and R. A. Fortey. 2005. Wonderful strife: systematics, stem groups, and the phylogenetic signal of the Cambrian radiation. *Paleobiology* 31(5): 94–112.
- Brooks, S. J., 1983. A new genus of oriental lacewings (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History, Entomology* 47: 1–26.
- Brooks, S. J. 1997. An overview of the current status of Chrysopidae (Neuroptera) systematics. *Deutsche Entomologische Zeitschrift*, 44(2): 267–275.
- Brooks, S. J. and P. C. Barnard. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History, Entomology* 59(2): 117–286.

- Chernomor, O., von Haeseler, A., and B. Q. Minh. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–1008. <https://doi.org/10.1093/sysbio/syw037>.
- Dai, Y., Winterton, S. L., Garzón-Orduña, I. J., Liang, F., and X. Liu. 2017. Mitochondrial phylogenomic analysis resolves the subfamily placement of enigmatic green lacewing genus *Nothancyla* (Neuroptera: Chrysopidae). *Austral Entomology* 56(3): 322–331.
- Duelli, P., Henry, C. S., and A. Mochizuki. 2014. The endemic *Atlantochrysa atlantica* (McLachlan) (Neuroptera: Chrysopidae) on Atlantic Islands: African or American origin? *Journal of Natural History* 48(41–42): 2595–2608.
- Engel, M. S., Winterton, S., and L. Breitkreuz. 2018. Phylogeny and Evolution of Neuropterida: Where Have Wings of Lace Taken Us? *Annual Review of Entomology* 63(1).
- De Freitas, S., Penny, N. D. and P. A. Adams. 2009. A revision of the New World genus *Ceraeochrysa* (Neuroptera: Chrysopidae). Revisión del género *Ceraeochrysa* (Neuroptera: Chrysopidae) del Nuevo Mundo. *Proceedings of the California Academy of Sciences* 60(15/20): 503–610.
- Garzón-Orduña, I., Winterton, S., Jiang, Y., Breitkreuz, L., Duelli, P., Engel, M.S., Penny, N., Tauber, C., Mochizuki, A., and X. Liu. A molecular supermatrix approach to green lacewing phylogeny reveals higher-level relationships and a single origin of larval camouflaging behavior (Neuroptera: Chrysopidae). (in review, *Molecular Phylogenetics and Evolution*).
- Goloboff, P. A., Farris, J. S., and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24(5): 774–786.

- Haring, E., and U. Aspöck. 2004. Phylogeny of the Neuropterida: a first molecular approach. *Systematic Entomology* 29(3): 415–430.
- Haruyama, N., Mochizuki, A., Duelli, P., Naka, H., and M. Nomura. 2008. Green lacewing phylogeny, based on three nuclear genes (Chrysopidae, Neuroptera). *Systematic Entomology* 33(2): 275–288.
- Haruyama, N., Mochizuki, A., Sato, Y., Naka, H., and M. Nomura. 2011. Complete mitochondrial genomes of two green lacewings, *Chrysoperla nipponensis* (Okamoto, 1914) and *Apochrysa matsumurae* Okamoto, 1912 (Neuroptera: Chrysopidae). *Molecular Biology Reports* 38: 3367–3373.
- Heath, T. A., Huelsenbeck, J. P., and T. Stadler. 2014. The fossilized birth–death process for coherent calibration of divergence–time estimates. *Proceedings of the National Academy of Sciences* 111(29): E2957–E2966.
- Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M.M., and A. Mochizuki. 2012. Parallel evolution in courtship songs of North American and European green lacewings (Neuroptera: Chrysopidae). *Biological Journal of the Linnean Society* 105(4): 776–796.
- Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., and A. Mochizuki. 2013. Obligatory duetting behaviour in the *Chrysoperla carnea*-group of cryptic species (Neuroptera: Chrysopidae): its role in shaping evolutionary history. *Biological Reviews* 88(4): 787–808.
- Henry, C. S., and M. L. M. Wells. 2004. Adaptation or random change? The evolutionary response of songs to substrate properties in lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Animal Behaviour* 68(4): 879–895.

- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B. Q., and L.S. Vinh. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 2: 518–522.
- Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- Jepson, J. E., Makarkin, V. N., and R. A. Coram. 2012. Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group of southern England. *Cretaceous Research* 34: 31–47.
- Jiang, Y., Garzón-Orduña, I. J., Winterton, S. L., Yang, F., and X. Liu. 2017. Phylogenetic relationships among tribes of the green lacewing subfamily Chrysopinae recovered based on mitochondrial phylogenomics. *Scientific Reports* 7(1): 7218. <https://doi.org/10.1038/s41598-017-07431-1>.
- Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., and L. S. Jermin. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>.
- Lanfear, R., Calcott, B., Ho, S. Y. W., and S. Guindon. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29(6): 1695–1701.
- Lee, M. S., and A. Palci. 2015. Morphological phylogenetics in the genomic age. *Current Biology* 25(19): R922–R929.
- Lepage, T., Bryant, D., Philippe, H., and N. Lartillot. 2007. A general comparison of relaxed molecular clock models. *Molecular Biology and Evolution* 24(12): 2669–2680.

- Maddison, W. P. and D. R. Maddison. 2018. Mesquite: a modular system for evolutionary analysis. Version 3.40. <http://mesquiteproject.org>.
- Makarkin, V. N., and S. B. Archibald. 2013. A Diverse New Assemblage of Green Lacewings (Insecta, Neuroptera, Chrysopidae) from the Early Eocene Okanagan Highlands, Western North America. *Journal of Paleontology* 87(1): 123–146.
- Makarkin, V. N., Yang, Q., Peng, Y., and D. Ren. 2012. A comparative overview of the neuropteran assemblage of the Lower Cretaceous Yixian Formation (China), with description of a new genus of Psychopsidae (Insecta: Neuroptera). *Cretaceous Research* 35: 57–68.
- Martins-Neto, R. G., and M. A. Vulcano. 1988. Neurópteros (Insecta: Planipennia) da Formação Santana (Cretáceo inferior), Bacia do Araripe, Nordeste do Brasil. I: Família Chrysopidae. *Anais da Academia Brasileira de Ciências* 60(2): 189–201.
- McEwen, P. K., New, T. R., and A. E. Whittington, eds. 2007. Lacewings in the crop environment. Cambridge University Press pp. 547.
- Miller, L. A. 1984. Hearing in Green Lacewings and their Responses to the Cries of Bats, in Canard, M., Séméria, Y., & New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Miller, M. A., Pfeiffer, W., and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA pp. 1–8.
- Minh, B. Q., Nguyen, M. A. T., and A. von Haeseler. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30: 1188–1195.

- Mochizuki, A., Henry, C. S., and P. Duelli. 2017. *Apertochrysa* (Neuroptera: Chrysopidae): A heterogeneric phantom? *Zootaxa* 4238(1): 58–72.
- Nel, A., Delclos, X., and A. Hutin. 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société Entomologique de France* 41(1): 29–69.
- New, T. R. 1989. *Handbuch der Zoologie, Band/Volume IV Arthropoda: Insecta, Planipennia: lacewings*. Walter de Gruyter, Berlin, New York.
- Nguyen, L. T., Schmidt, H. A., von Haeseler, A., and B. Q. Minh. 2014. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274.
- Oswald, J. D. 2018. *Neuropterida Species of the World. Version 5.0*. <http://lacewing.tamu.edu/SpeciesCatalog/Main>. Last accessed on March 05 2018.
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and M. A. Suchard. 2018. Tracer v1.7. Available from <http://tree.bio.ed.ac.uk/software/tracer/>.
- Ridgway, R. L., and W. L. Murphy. 1984. Biological control in the field. pp. 220–228. in Canard, M., Séméria, Y., & New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.
- Ronquist, F. and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Swofford, D. L. 2003. PAUP\*. *Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

- Tauber, C. A. 2007. Review of *Berchmansus* and *Vieira* and description of two new species of *Leucochrysa* (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America* 100(2): 10–138.
- Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2014. Debris-carrying in larval Chrysopidae: unraveling its evolutionary history. *Annals of the Entomological Society of America* 107(2): 295–314.
- Tsukaguchi, S. 1995. *Chrysopidae of Japan: (insecta, Neuroptera)*. Yutaka Insatsu, Osaka, Japan.
- Wang, Y., Liu, X., Garzón-Orduña, I. J., Winterton, S. L., Yan, Y., Aspöck, U., Aspöck, H., and D. Yang. 2017. Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. *Cladistics* 33(6): 617–636. DOI: 10.1111/cla.12186.
- Winterton, S. L., and S. J. Brooks. 2002. Phylogeny of the apochrysine green lacewings (Neuroptera: Chrysopidae: Apochrysinae). *Annals of the Entomological Society of America* 95(1): 16–28.
- Winterton, S., and S. De Freitas. 2006. Molecular phylogeny of the green lacewings (Neuroptera: Chrysopidae). *Australian Journal of Entomology* 45(3): 235–243.
- Winterton, S. L., Hardy, N. B., and B. M. Wiegmann. 2010. On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Systematic Entomology* 35(3): 349–378.
- Winterton, S. L., Lemmon, A. R., Gillung, J. P., Garzon, I. J., Badano, D., Bakkes, D. K., Breitkreuz, L., Engel, M. S., Lemmon, E. M., Liu, X., and R. J. Machado. 2017. Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology*. DOI: 10.1111/syen.12278.

Zhang, C. 2017. Molecular clock dating using MrBayes. arXiv preprint arXiv:1603.05707.



## Supplementary Material

S1\_Table 1: summary of molecular data present, and its source.

VOUCHER	MITOGENOME	16S	COI	CAD	WG	PepCK	ATPase	18S
<i>Abachrysa eureka</i>	(X. Liu)	DQ399263	ABA x	ABA x	–	–	–	ABA x
<i>Ankylopteryx gracilis</i>	–	ANTHA (sp.) x	–	ANTHA (sp.) x	<i>gracilis</i> AB2879 16	<i>gracilis</i> AB287915	<i>gracilis</i> AB2879 17	ANTHA (sp.) x
<i>Ankylopteryx (Sencera) exquisita</i>	–	x	x	x	–	–	–	x
<i>Ankylopteryx (Sencera) exquisita</i>	–	x	x	–	–	–	–	x
<i>Ankylopteryx alluaudi</i>	–	DQ399264	x	x	–	–	–	x
<i>Ankylopteryx</i> sp.	–	x	–	x	–	–	–	x
<i>Anomalochrysa hepatica</i>	–	x	x	x	–	–	–	x
<i>Apertochrysa (=Pseudomallada)</i> CHIMERA	–	APED ( <i>edwardsi</i> ) DQ399265	APED ( <i>edwardsi</i> ) DQ414484	APED ( <i>edwardsi</i> ) x	<i>eurydera</i> AB2942 29	<i>eurydera</i> AB294228	<i>eurydera</i> AB2942 30	APE D ( <i>edwardsi</i> ) x
<i>Apochrysa leptalea</i>	–	AY620155	x	–	–	–	–	x
<i>Apochrysa lutea</i>	–	DQ399285	–	EU860139	–	–	–	EU815269
<i>Apochrysa matsumurae</i>	AP011624 (Haruyama et al. 2011)	Included in mitogenome	Included in mitogenome	–	AB287533	AB287532	AB287534	–
<i>Apochrysa montrouzieri</i>	–	x	–	–	–	–	–	x
<i>Asthenochrysa viridula</i>	–	x	–	–	–	–	–	–
<i>Atlantochrysa atlantica</i>	–	ATLAT x	ATLAT x	–	AB820322	AB820321	AB820323	–

<i>Borniochrysa squamosa</i>	–	x	x	x	AB287886	AB287885	AB287887	x
<i>Brinckochrysa turkanensis</i>	–	x	x	x	AB287581	AB287580	AB287582	x
<i>Cacarulla maculipennis</i>	–	x	x	x	–	–	–	x
<i>Calochrysa extranea</i>	–	DQ399266	DQ414485	x	–	–	–	x
<i>Ceraeochrysa cecla</i>	–	–	x	x	–	–	–	x
<i>Ceraeochrysa displepis</i>	–	–	x	x	–	–	–	x
<i>Chrysemosa jeanneli</i>	–	x	x	x	AB287584	AB287583	AB287585	x
<i>Chrysemosa umbratilis</i>	–	x	–	x	–	–	–	x
<i>Chrysopa</i> CHIMERA	<i>C. pallens</i> NC_019618 (Henry et al. 2012)	CPERLA ( <i>perla</i> ) AY620151	CPERLA ( <i>perla</i> ) KJ592454	CPERLA ( <i>perla</i> ) KC213148	–	–	–	CPERLA ( <i>perla</i> ) x
<i>Chrysopa excepta</i>	–	x	DQ414489	DQ414471				x
<i>Chrysoperla</i> CHIMERA	<i>nippone nsis</i> AP011623 (Haruyama et al. 2011)	Included in mitogenome	Included in mitogenome	CFUR x	<i>furcifera</i> AB287653	<i>furcifera</i> AB287652	<i>furcifera</i> AB287654	CFUR x
<i>Chrysoperla externa</i>	–	AY743738	AY743807	x	AB287650	AB287649	AB287651	x
<i>Chrysopidia</i> ( <i>Chrysotropia</i> ) <i>ciliata</i>	–	x	AB354066	x	AB287686	AB287685	AB287687	KC413703
<i>Chrysopodes divisa</i>	–	–	DQ414491	DQ414472	–	–	–	x
<i>Chrysopodes spinella</i>	–	DQ399274	DQ414493	DQ414473	–	–	–	x
<i>Conchopterella stangei</i>		EU734855	DQ414494	DQ414474	–	–	–	EU815236
<i>Cunctochrysa baetica</i>	–	x	–	x	AB820325	AB820324	AB820326	x

<i>Dictyochrysa peterseni</i>	–	DQ399275	DQ414495	–	–	–	–	x
<i>Drepanopteryx phalaenoides</i>	<i>phalaenoides</i> KT425075 (Wang et al. 2017)	Included in mitogenome	Included in mitogenome	HEME	–	–	–	–
<i>Eremochrysa hageni</i>	–	x	x	x	–	–	–	x
<i>Eremochrysa pallida</i>	–	x	x	x	–	–	–	x
<i>Evanochrysa evanescens</i>	–	x	x	–	–	–	–	–
<i>Fontecilla graphicus</i>	KT425072 (Wang et al. 2017)	EU734863	DQ414496	EU860115	–	–	–	EU815244
<i>Glenochrysa conradina</i>	–	x	x	x	–	–	–	x
<i>Glenochrysa opposita</i>	–	DQ399276	DQ414497	x	–	–	–	x
<i>Glenochrysa splendida</i>	–	x	x	x	–	–	–	–
<i>Gonzaga nigriceps</i>	–	x	x	x	–	–	–	x
<i>Hypochrysa elegans</i>	–	x	KJ592497	–	–	–	–	–
<i>Italochrysa</i> CHIMERA	<i>insignis</i> (X. Liu)	Included in mitogenome	Included in mitogenome	<i>insignis</i> ITAL EU860117	<i>italica</i> AB287554	<i>italica</i> AB287553	<i>italica</i> AB287555	<i>insignis</i> ITAL EU815246
<i>Italochrysa japonica</i>	–	x	x	x	–	–	–	x
<i>Italochrysa peringueyi</i>	–	x	x	x	–	–	–	x
<i>Ithone fulva</i>		EU734865	–	EU860118	–	–	–	EU815247
<i>Kimochrysa africana</i>	–	x	x	x	AB287889	AB287888	AB287890	x
<i>Kosta nacaratus</i>	–	–	x	–	–	–	–	–

<i>Leucochrysa (Nodita) marquezii</i>	–	DQ39 9280	DQ414498	DQ414476	–	–	–	x
<i>Leucochrysa (Nodita) cruentata</i>	–	x	x	x	–	–	–	–
<i>Leucochrysa (Nodita) robusta</i>	–	DQ39 9281	DQ414499	DQ414477	–	–	–	x
<i>Leucochrysa (Nodita) texana</i>	–	DQ39 9279	DQ414502	DQ414478	–	–	–	x
<i>Leucochrysa pretiosa</i>	(X. Liu)	Included in mitogenome	Included in mitogenome	–	–	–	–	–
<i>Mallada signatus</i>	–	x	AB354081	x	AB2878 30	AB287829	AB2878 31	x
<i>Mallada tripunctatus</i>	–	x	x	x	–	–	–	x
<i>Meleoma</i> CHIMERA	–	MEL E (emuncta)	MELE (emuncta) KM535160	MELE (emuncta)	arizonensis AB2942 31	arizonensis AB287832	arizonensis AB2878 33	MEL E (emuncta)
<i>Micromus</i> CHIMERA	sp. KT4250 87 (Wang et 2017)	Included in mitogenome	Included in mitogenome	–	linearis AB2875 27	linearis AB287526	linearis AB2875 28	sp. AF42 3789
<i>Nacarina</i> sp.	–	x	x	x	–	–	–	x
<i>Nineta itoi</i>	–	x	AB354083	x	AB2878 47	AB287846	AB2878 48	x
<i>Nineta pallida</i>	–	x	KJ592563	x	AB2878 53	AB287852	AB2878 54	x
<i>Nipponochrysa moriutii</i>	–	–	AB354086	NIPPON x	AB2878 65	AB287864	AB2878 66	NIPPON x
<i>Nothancyla verreauxi</i>	KP2646 29 (Dai et al. 2017)	Included in mitogenome	Included in mitogenome	DQ414481	–	–	–	x
<i>Nothochrysa</i> CHIMERA	californica KP2646 30	Included in mitogenome	Included in mitogenome	NOTH (californica) DQ414480	fulviceps AB2875 30	fulviceps AB287529	fulviceps AB2875 31	NOTH (californica)

	(Dai et al. 2017)	genome						a) EU815265
<i>Parachrysoptera argentiniae</i>	–	x	x	x	–	–	–	x
<i>Parachrysoptera pallidicornis</i>	–	x	x	x	–	–	–	x
<i>Parankylopteryx multipunctata</i>	(sp.) (X. Liu)	Included in mitogenome	Included in mitogenome	PANK (sp.) x	–	–	–	PANK (sp.) x
<i>Parankylopteryx</i> sp.	–	x	x	–	–	–	–	x
<i>Peyerimhoffina gracilis</i>	–	x	KJ592481	x	AB287868	AB287867	AB287869	x
<i>Pimachrysa nigra</i>	–	EU734889	EU839756	EU860142	–	–	–	EU815273
<i>Plesiochrysa atalotis</i>	–	DQ399287	DQ414508	x	–	–	–	x
<i>Plesiochrysa ramburi</i>	–	x	x	x	AB294226	AB294225	AB294227	x
<i>Pseudomallaeluctuosus</i>	–	DQ399288	DQ414509	DQ414483	AB287752	AB287751	AB287753	x
<i>Pseudomallada</i> CHIMERA	–	PSEMA (marianus) x	PSEMA (marianus) x	–	<i>prasinus</i> AB287779	<i>prasinus</i> AB287778	<i>prasinus</i> AB287780	–
<i>Pseudomallada tactus</i>	–	AY620154	x	x	AB287791	AB287790	AB287792	x
<i>Retipenna hasegawai</i>	–	x	x	–	–	–	–	–
<i>Retipenna variegata</i>	–	x	x	–	–	–	–	–
<i>Semachrysa matsumurae</i>	–	SEMA A x	–	SEMA x	AB287548	AB287547	AB287549	SEMA A x
<i>Signochrysa ornatissima</i>	–	x	x	–	–	–	–	–
<i>Stigmachrysa cladostigma</i>	–	–	x	–	–	–	–	–

<i>Suarius walsinghmi</i>	–	SUAR (sp.) x	SUAR (sp.) x	SUAR (sp.) x	<i>walsingh ami</i> AB2878 74	<i>walsingha mi</i> AB287873	<i>walsingh ami</i> AB2878 75	SUAR (sp.) x
<i>Tumeochrysa</i> sp.	–	x	–	x	–	–	–	x
<i>Ungla ivancruzi</i>	–	x	x	x	–	–	–	x
<i>Vieira leschenaulti</i>	–	x	x	–	–	–	–	x
<i>Yumachrysa apache</i>	–	x	–	–	AB2878 77	AB287876	AB2878 78	x



## Chapter 2

### Generic Revision of Chrysopidae (Neuroptera)



## Introduction

The widely distributed family Chrysopidae is one of the largest in Neuroptera, although small, in terms of species richness, when compared to other insect orders. There are presently recognized three subfamilies, five tribes, 80 genera, and 1,399 species (Oswald 2018). The adults of most Chrysopidae are delicate green insects, with an intricate wing venation pattern, giving the group the common name “green lacewings”. In comparison to the mostly nectar- and pollen-feeding adults, the larvae are predacious, feeding on several kinds of small soft-bodied insects. Due to this trait, lacewings are widely used in biological pest control programs in sustainable agriculture. Chrysopidae are intensely studied, especially in regards to their behavior, but also the underlying alpha taxonomy to understand local diversity in agricultural ecosystems worldwide.

Although thoroughly studied, a comprehensive generic revision of the family has been lacking. Chrysopidae were described by Schneider in 1851, with *Chrysopa* Leach as the type genus, for the green members of Hemerobiidae exhibiting a distinctive wing venation. In the 20<sup>th</sup> century, numerous genera were added to Chrysopidae, either by splitting *Chrysopa* or by the new discovery of distinct lacewings. Many of these were established by the most prolific authors in chrysopid research, such as Esben-Petersen, Banks, or especially Navás, who authored about 35% of the currently recognized genera. Over the course of the last century, several of the genera described by early authors were synonymized (e.g., Tjeder 1966, New 1980, Brooks and Barnard 1990). With their groundbreaking work on chrysopid systematics, Brooks and Barnard (1990) provided a foundation for numerous projects on chrysopid genera. The tremendous work of Brooks and Barnard forms the basis of this study, and many previous contributions on chrysopid diversity during the last 30 years. Their monograph summarized a century of publications on Chrysopidae, and thus created an astonishing resource, including descriptions of all genera, illustrations, a key,

and a checklist. Due to the many nomenclatural changes since this revision, a revised classification of Chrysopidae is needed, and one that is in accordance with our modern understanding of phylogenetic relationships within the family.

Three subfamilies are currently recognized: Apochrysinæ, Nothochrysinæ, and Chrysopinæ, of which the latter holds the vast majority of the family's diversity.

Apochrysinæ are large lacewings that are distinctive in the size of their wings with numerous posterior radial (RP) branches. Their pseudocubitus (PsC) is usually formed by the fusion of multiple longitudinal veins (up to 6), and PsC and the pseudomedia (PsM) are close together along at least two thirds of the wing. The basal subcostal crossvein is absent, meaning, that the first crossvein between the subcosta (Sc) and the radius (R) (1sc-r) is positioned apically on the wing, at the pterostigma. Outside of Apochrysinæ, this condition is only found in the peculiar genus *Nothancyla* Navás. The subfamily was long thought to be sister to Chrysopinæ, or possibly to Nothochrysinæ, but recent phylogenetic analyses have revealed that they are probably sister to all other Chrysopidae (see chapter 1). Apochrysinæ were established in 1908 by Handlirsch, on the basis of the genus *Apochrysa* Schneider, and reviewed by Winterton and Brooks (2002), who synonymized numerous genera. Apochrysinæ currently include 24 species in five genera (Oswald 2018), and are distributed in the tropics.

Nothochrysinæ are sturdy lacewings, often small and most genera have a seemingly reduced wing venation. The subfamily is mainly defined by the continuation of PsM with the inner gradates (although variably distinguished), and several absence characters. The genera of Nothochrysinæ are variable in their morphology, such as the form of *mamp1* or the number of flagellar setal rings, and especially *Nothochrysa* McLachlan shows considerable variation in character states that are similar to some members of Chrysopinæ rather than other nothochrysinæ.

The subfamily was erected by Navás in 1910 on the basis of the genus *Nothochrysa*, and is in desperate need of a detailed revision, including the various fossil taxa attributed to it. Nothochrysoidea include 27 species in nine genera (Oswald 2018), and are distributed worldwide except for South America.

Chrysopinae are a diverse subfamily, accounting for more than 95% of all species in the family. All members of Chrysopinae have a tympanal organ at the base of the forewing, and all but *Nothancyla* have the flagellar setae arranged in four rings. Chrysopinae vary greatly in their general appearance, wing venation, and especially genitalia. Thus, not all higher taxa within the subfamily are supported by well-defined synapomorphies. Currently, five tribes are recognized in Chrysopinae: Ankylopterygini, Belonopterygini, Chrysopini, Leucochrysinini, and Nothancylini. Belonopterygini and Leucochrysinini form a monophyletic group (see chapter 1) and are sister to Ankylopterygini and Chrysopini. These clades lack unambiguous synapomorphies in the adults, but Belonopterygini and Leucochrysinini share larval characters (Tauber 2007). The larvae of Chrysopini and Ankylopterygini are in need of comparison (see chapter 1 for further discussion of shared characters).

The tribe Ankylopterygini were established by Navás in 1910 for the genus *Ankylopteryx* and its relatives. Previous to the present work, this tribe included all genera with finely pointed palpi (*Ankylopteryx* Brauer, *Parankylopteryx* Tjeder, *Retipenna* Brooks, *Semachrysa* Brooks, and *Signochrysa* Brooks and Barnard), but on the basis of phylogenetic analyses (see chapter 1) the genera of the *Nineta*-group are now included within the tribe. This leads to the distinction of Ankylopterygini sensu lato, with all genera included and Ankylopterygini sensu strictu, which excludes the genera of the *Nineta*-group. Synapomorphies for Ankylopterygini s. str. are numerous, such as the pointed palpi, reduced tibial spurs in most taxa, and an often enlarged costal

area at the wing base. Ankylopterygini s. l., in contrast, have no unifying unambiguous synapomorphies, but all generally lack parameres and a tignum. A transition of character states can be observed between the *Nineta*-group and the lesser-derived Ankylopterygini s. str., such as the elongate sternum VIII+IX and scape in most *Nineta*-group species, as well as in *Signochrysa* and *Retipenna*. The tribe currently includes 150 species in seven genera (Oswald 2018), and is distributed in the Old World, with two exceptions of species of *Nineta* in the Nearctic.

The tribe Belonopterygini was established in 1913 by Navás on the basis of the genus *Belonopteryx* Gerstaecker. It now includes the former tribe Italochrysinini and therefore some of the most common large chrysopids of the Old World. The members of Belonopterygini are often stout looking, usually have a short *c*2 cell, short flagellomeres and flagellar setae, lack entoprocessi, and have broad lateral arms to the gonarcus. Paired parameres are present in most genera and the females of many have a praegenitale. The subfamily currently includes 159 species in 14 genera (Oswald 2018), and is distributed worldwide.

Chrysopini are the most species rich tribe in Chrysopinae. There are no unambiguous synapomorphies defining this tribe, and members are variable, but they normally have a triangular *im* cell, are green (except for the *Eremochrysa*-group), and entoprocessi are present in most. Chrysopini are the only tribe in which a tignum is present. Parameres can be absent or present, and are medially fused, forming a single structure in the vast majority of species. Currently 843 species in 32 genera are recognized (Oswald 2018), and they occur throughout the world.

The tribe Leucochrysinini is solely present in the New World and was established by Adams in 1978 based on the genus *Leucochrysa* McLachlan. The tribe is morphologically diverse, including small species to some of the largest of Chrysopidae, approximating Apochrysininae in wingspan and reticulation of the veins. Adult synapomorphies for the tribe are lacking, but most

members have no parameres, no entoprocessi, broad lateral arms to the gonarcus, relatively long flagellomeres, and are often marked on the thorax and the wings. Currently 192 species in eight genera are recognized (Oswald 2018), and these are distributed across the New World.

The tribe Nothancylini was only recently erected (Garzón et al. in rev.), to accommodate the enigmatic and monotypic genus *Nothancylla*. Phylogenetic analyses recovered the genus as sister to Chrysopinae (see chapter 1), and it has a unique combination of characters occurring in all three subfamilies.

Although there have been great efforts to revise the diversity of Chrysopidae (such as recent generic revisions: *Ceraeochrysa* (see De Freitas and Penny 2009), *Leucochrysa* (see Tauber 2004), or *Ungla* (see Tauber et al. 2017)), many genera are in need of a detailed study, and we suspect that some will subsequently be split or require synonymization. Unfortunately, our sampling of species individual in genera was not large enough to go beyond suggesting areas in need of further investigation.

This chapter provides an overview of the currently recognized taxa in Chrysopidae. A dichotomous key is given to identify all chrysopids to the generic level. This key reflects the morphological homoplasy in the taxa of Chrysopidae, with tribes and genera broken up in several areas of the key. Detailed descriptions of all genera are provided, including diagnoses, remarks, and illustrations. Several changes in the systematics of Chrysopidae since the last revision of the family (Brooks and Barnard 1990) are discussed. The classification proposed in this chapter is based on the generic relationships recovered in the most recent phylogenetic analyses (chapter 1). Although most genera are included and described in detail, there are a few genera for which material was not accessible and the original descriptions lacked sufficient detail to make meaningful comparisons or evaluations of their identity, even lacking enough information to place

them in a higher taxon. These taxa are listed and briefly discussed at the end of the chapter.

## Material and Methods

Representatives of all currently recognized genera were examined, except for the following: *Berchmansus* Navás, *Himalochrysa* Hölzel, *Kymachrysa* Tauber and Garland, *Leptochrysa* Adams and Penny, *Neula* Navás, *Nipponochrysa* Tsukaguchi, *Nuvol* Navás, *Santocellus* Tauber et al., *Triplochrysa* Kimmins, *Sinochrysa* Yang, *Tibetochrysa* Yang et al., and *Yunchrysopa* Yang and Wang. Most of these genera could be added on the basis of the primary literature. Examined material was gathered from the following institutions: The Natural History Museum, London, United Kingdom (BMNH); California Academy of Sciences, San Francisco, CA, USA (CAS); California Department of Food and Agriculture, Sacramento, CA, USA (CDFA); Museum für Naturkunde Berlin, Germany (ZMNB); Muséum National d'Histoire Naturelle, Paris, France (MHNM); Naturhistorisches Museum Wien, Austria (NHMW); and Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, KS, USA (SEMC). Additionally, photographs of specimens from the BMNH (taken by L.B.), as well as provided by C. Martens from the University of São Paulo and Lukas Kirschey from the ZMNB were used to determine character states for select taxa. For species for which material was unavailable, we relied on the original and subsequential literature relating to particular genera.

The generic descriptions were generated with the matrix key development program Lucid. The characters and character states were entered in a natural language format and the states of all morphological characters were subsequently scored manually for each genus. Finally, the descriptions were exported in html-format, and edited in a text editor program. The diagnoses

focus on externally visible characters and male genitalic traits, where possible. As such, some genera might have distinctive mandibles (noted in remarks), but that character is rarely visible in non-dissected heads (cleared and stained dissections of the head are usually not present in collections).

Line drawings were produced in Adobe Illustrator CC 2017. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and then arranged in Adobe Photoshop and Illustrator CC 2017.

## Key of to the genera of Chrysopidae

(*Sinochrysa*, *Tibetochrysa*, and *Yunchrysope* not included, see generic descriptions)

For a detailed definition of the morphological characters mentioned in this key, including a glossary of all common characters in Chrysopidae, see chapter 3.

- |    |   |                          |
|----|---|--------------------------|
| 1. | bsx absent (1c-sc apically on wing) .....           | 2                        |
| —. | bsx present (1c-sc basally on wing) (fig. 1D) ..... | 7                        |
| 2. | <i>im</i> cell present (as in fig. 1G) .....        | <i>Nothancyla</i> p. 477 |
| —. | <i>im</i> cell absent (as in fig. E) .....          | 3                        |
| 3. | gradates in costal area .....                       | <i>Joguina</i> p. 162    |
| —. | gradates absent in costal area .....                | 4                        |

4. ra-rp crossveins absent below pterostigma, leading to the presence of a long cell (fig. 2A)  
..... *Apochrysa* p. 153
- . ra-rp crossveins present below pterostigma, leading to multiple short cells ..... 5
5. gradates absent between RA and RP ..... *Nobilinius* p. 169
- . gradates present between RA and RP ..... 6
6. crossveins present between vein endings in posterior marginal area; forewing veins 1A and  
2A forked; spermatheca with lateral striations ..... *Domenechus* p. 158
- . Cells in posterior marginal area simple; forewing vein 1A sometimes forked, 2A simple;  
spermatheca without lateral striations ..... *Loyola* p. 165
7. flagellar setae arranged in five or six rings (figs. 1I, J) ..... 8
- . flagellar setae arranged in four rings (fig. 1K) ..... 16
8. more than two gradate series in forewing (e.g., fig. 5A) ..... 9
- . two gradate series in forewing (e.g., fig. 7A) ..... 10
9. three gradate series in forewing, parallel; mamp1 cell regular, occupying entire space



	between PsC and PsM .....	<i>Triplochrysa</i> p. 202
—.	more than three gradate series in forewing, irregularly arranged; mamp1 cell irregular, not occupying entire space between ill-defined PsC and PsM, but instead three cells present (fig. 5) .....	<i>Dictyochrysa</i> p. 176
10.	2m-cua originating from MP .....	11
—.	2m-cua originating from M .....	13
11.	wing narrow and elongate (more than 4 times longer than wide), microsetae on entire wing .....	<i>Leptochrysa</i> p. 187
—.	wing not narrow and elongate (less than 4 times longer than wide), microsetae only present on wing base and between 3A and posterior wing margin .....	12
12.	more than 10 RP branches, tergum IX + ectoproct fused, lateral gonapophyses simple, without spoon-like setae (fig. 7) .....	<i>Nothochrysa</i> p. 190
—.	less than 10 RP branches, tergum IX + ectoproct separated, lateral gonapophyses simple, with spoon-like setae, pointing ventral .....	<i>Pimachrysa</i> p. 198
13.	flagellar setae arranged in six rings (fig 1J) .....	<i>Kimochrysa</i> p. 184
—.	flagellar setae arranged in five rings (fig. 1I).....	14

14. dorsal apodeme of male with long ventral process ..... *Hypochrysa* p. 180
- dorsal apodeme of male regular, without long ventral process ..... 15
15. *im* cell triangular with crossvein (fig. 1F), with no strong angle in MA .....  
..... *Asthenochrysa* p. 173
- *im* cell short and quadrangular, with an almost right angle in MA (fig. 8) .....  
..... *Pamochrysa* p. 194
16. gradates absent or only one gradate series present in forewing ..... 17
- two or more gradates in the forewing ..... 19
17. gradates usually absent (or 1 crossvein present in outer gradates); *c1* longer than *c2* .....  
..... *Turnerochrysa* p. 298
- outer gradates present (more than 1 crossvein); *c1* as long as or longer than *c2* ..... 18
18. parameres with four tips; tergum IX simple, without small separate lateral sclerotized area  
(fig. 50) ..... *Parachrysopiella* p. 414
- parameres shaped as a single rod; tergum IX with small separate lateral sclerotized area .....  
..... *Eremochrysa (Chrysopiella)* p. 379

19. one gradate series in hind wing ..... *Eremochrysa (Eremochrysa)* (in part) p. 382
- more than one gradate series in hind wing ..... 20
20. palpi finely pointed (fig. 1A); tibial spur usually absent on all legs (fig, 1L) ..... 21
- palpi tapered or rounded, but not finely pointed (fig. 1B); at least one tibial spur present on meso- and metatibiae (fig, 1L) ..... 24
21. microtholi present; costa narrow basally; sternum VIII+IX elongate, with long setae apically; parallel gradates; mediuncus trifurcate (fig. 16) ..... *Signochrysa* p. 240
- microtholi absent; costa usually broad basally (not all genera); sternum VIII+IX not very strongly elongate, without long setae apically; gradates not parallel ..... 22
22. costa narrow basally; ventral apodeme with dorsal process; wings unmarked (fig. 14) .....  
..... *Retipenna* p. 231
- costa broad basally; ventral apodeme without dorsal process; wings usually marked ..... 23
23. mediuncus closely attached to the gonarcus; costa marked at base (fig. 13) .....  
..... *Parankylopteryx* p. 228
- mediuncus clearly detached from gonarcus; costa unmarked at base (fig. 10) .....

.....	<i>Ankylopteryx</i> p. 207
24. cell <i>c1</i> longer than <i>c2</i> (e.g., fig. 24A) .....	25
— cell <i>c1</i> as long as or shorter than <i>c2</i> (e.g., fig. 1D) .....	44
25. sternum VIII+IX strongly elongate, occurring in Hawaii (fig. 31) .....	
.....	<i>Anomalochrysa</i> (in part, rare) p. 309
— sternum rounded or slightly elongate, not in Hawaii .....	26
26. <i>im</i> cell absent (fig. 1E) .....	27
— <i>im</i> cell present (fig. 1G, H) .....	28
27. wings narrow, with two elongate markings .....	<i>Belonopteryx</i> p. 249
— wings regular, rounded, without markings except for pterostigma (fig. 26A) .....	
.....	<i>Nesochrysa</i> p. 282
28. <i>im</i> cell quadrangular (fig. 1G) .....	29
— <i>im</i> cell triangular (fig. 1H) .....	35
29. present in the New World .....	<i>Nacarina</i> (in part) p. 277

—.	present in the Old World .....	30
30.	praegenitale absent .....	31
—.	praegenitale present .....	32
31.	pterostigma unmarked or weakly marked; parameres shaped as paired rods, with one tip (fig. 24) .....	<i>Italochrysa</i> p. 272
—.	pterostigma marked; parameres paired with forked tips (fig. 28) .....	<i>Oyochrysa</i> p. 290
32.	parameres absent (fig. 23) .....	<i>Evanochrysa</i> p. 268
—.	parameres present (e.g., 26C, 29B) .....	33
33.	praegenitale on apex of sternum VII; parameres with three pointed processes on each side (6 medially connected rods total) (fig. 26) .....	<i>Nesochrysa</i> (in part) p. 282
—.	praegenitale within sternum VII; parameres not with three tips .....	34
34.	<i>im</i> cell short (equal sided quadrangular); gradates diverging; parameres short and close to mediuncus (fig. 29) .....	<i>Stigmachrysa</i> p. 294
—.	<i>im</i> cell elongate, almost triangular (crossvein short); gradates parallel; parameres positioned ventrally (fig. 27) .....	<i>Nodochrysa</i> (in part) p. 286

35.	present in the New World .....	36
—.	present in the Old World .....	39
36.	body light yellow with black spots throughout thorax and abdomen .....	<i>Abachrysa</i> p. 245
—.	body dark yellow, green, or brown, unmarked or with markings, but not with round spots .....	37
37.	flagellomeres shorter than long, flagellar setae shorter than flagellomere width; pterostigma unmarked or weakly marked; parameres often present; body usually unmarked .....	<i>Nacarina</i> (in part) p. 277
—.	flagellomeres as long as or longer than wide, flagellar setae as long or longer than flagellomere width; pterostigma usually marked; parameres absent; body usually marked .....	38
38.	wings strongly marked; RP sinuous .....	<i>Vieira</i> (in part) p. 301
—.	wings unmarked or with scarce markings; RP straight .....	<i>Nodita</i> (in part) p. 466
39.	CuP forked at <i>dcc</i> ; parameres absent (figs. 19, 21) .....	40
—.	CuP forked at <i>c2</i> ; parameres present .....	41

40.	thick spines on apex of sternum VIII+IX; Africa .....	<i>Chrysaloisia</i> p. 261
—.	thick spines absent on sternum VIII+IX; Australia .....	<i>Calochrysa</i> p. 253
41.	parameres with three pointed processes on each side (6 medially connected rods total) (fig. 26) .....	<i>Nesochrysa</i> (in part) p. 282
—.	parameres not with three tips .....	42
42.	parameres not paired, medially fused (fig. 22B) .....	<i>Dysochrysa</i> p. 264
—.	parameres paired, not fused medially .....	43
43.	parameres paired simple rods; wings strongly marked (fig 20) .....	<i>Chrysacanthia</i> p. 261
—.	parameres shaped as two ‘U’-shaped sclerites; wings not strongly marked (fig. 27) .....	..... <i>Nodochrysa</i> (in part) p. 286
44.	three or more gradate series in forewing (e.g., fig. 32A) .....	45
—.	two gradate series in forewing (e.g., fig. 1D) .....	55
45.	parameres present .....	46
—.	parameres absent .....	50

46.	tignum present; mediuncus elongate and thin, without lateral processes .....	47
—.	tignum absent; mediuncus laterally expanded, apically forked .....	49
47.	present in Hawaii .....	<i>Anomalochrysa</i> (in part) p. 309
—.	not in Hawaii .....	48
48.	parameres arranged as thin, elongate structure with a basal fork and an apical fork with recurved tips .....	<i>Anachrysa</i> p. 306
—.	parameres shaped as a broad ‘X’ with two basal and two apical lobes .....	..... <i>Mallada</i> (in part) p. 402
49.	<i>im</i> cell triangular; parameres with round apices .....	<i>Himalochrysa</i> (in part) p. 391
—.	<i>im</i> cell triangular or quadrangular; parameres with four sharply pointed teeth .....	..... <i>Rexa</i> (in part) p. 462
50.	gradates present between RA and RP .....	<i>Cacarulla</i> p. 452
—.	gradates absent between RA and RP .....	51
51.	tignum present .....	<i>Austrochrysa</i> p. 324



—.	tignum absent .....	52
52.	wing markings present; entoprocessus absent (fig. 30) .....	<i>Vieira</i> (in part) p. 301
—.	wing markings absent except for pterostigma; entoprocessus present and long .....	53
53.	hind wing with more than two gradate series; CuA endings forked; more than 15 RP branches .....	<i>Nineta (Tumeochrysa)</i> p. 224
—.	hind wing with two gradate series; CuA endings simple, not forked; less than 15 RP branches .....	54
54.	gonarcus medially separated (as in fig. 11B); scape elongate (more than 1.5x as long as wide) .....	<i>Chrysopidia (Chrysopidia)</i> p. 212
—.	gonarcus medially fused; scape not strongly elongate (less than 1.5x as long as wide) (fig. 35) .....	<i>Borniochrysa</i> p. 328
55.	parameres present .....	56
—.	parameres absent .....	72
56.	tignum present .....	57
—.	tignum absent .....	60

57.	tergum IX + ectoproct tapering apicodorsally; 1r-m meeting PsM distal to <i>im</i> (fig. 52)....	
	.....	<i>Peyrimhoffina</i> p. 418
—.	tergum IX + ectoproct rounded, not tapering apicodorsally; 1r-m meeting PsM at <i>im</i> ...	58
58.	sternum VIII+IX rounded; parameres shaped as ‘T’, or with a ventral broad and flat flange and a dorsal medial thin rod (fig. 32B) .....	<i>Apertochrysa</i> (in part) p. 314
—.	sternum VIII+IX usually elongate; parameres not shaped as ‘T’, or with a ventral broad and flat wing and a dorsal medial thin rod, but broadly ‘X’, or roughly ‘W’ shaped .....	59
59.	vertex of male without ornamentation; parameres broadly ‘X’ shaped; entoprocessi usually absent (fig. 49) .....	<i>Mallada</i> (in part) p. 402
—.	vertex of male usually with ornamentation; parameres roughly ‘W’ shaped; entoprocessi usually present .....	<i>Meleoma</i> (in part) p. 406
60.	<i>im</i> cell quadrangular (fig. 1G) .....	61
—.	<i>im</i> cell triangular (fig. 1H) .....	63
61.	New World .....	<i>Leucochrysa</i> (in part, rare) p. 460
—.	Old World .....	62

62. parameres with broadly 'X' shaped (fig. 49) ..... *Mallada* (in part, rare) p. 402
- parameres with four sharp teeth ..... *Rexa* (in part) p. 426
63. parameres longer than gonarcus ..... 64
- parameres shorter than gonarcus ..... 68
64. parameres shaped as a single rod ..... 65
- parameres not shaped as a single rod, with at least two lobes or rods ..... 67
65. Old World ..... *Crassochrysa* (in part) p. 371
- New World ..... 66
66. ventral apodeme basally extended; RP branches curved between gradates .....  
..... *Kymachrysa* p. 398
- ventral apodeme simple, basally not extended; RP branches fairly straight between gradates  
(fig. 37) ..... *Ceraeochrysa* p. 336
67. tergum IX + ectoproct greatly elongate (fig. 38) ..... *Chrysocerca* p. 349
- tergum IX + ectoproct rounded, not elongate ..... *Himalochrysa* (in part) p. 391

68.	parameres shaped as a single rod; palpomeres usually dark (fig. 56) ....	<i>Titanochrysa</i> p. 435
—.	parameres not shaped as single rod, but with more than one tip or broadly expanded; palpomeres mostly unmarked or slightly marked .....	69
69.	parameres shaped roughly as broad ‘W’, with a medial and and two lateral lobes (fig. 49); frons of male usually with ornamentation .....	<i>Meleoma</i> (in part) p. 406
—.	parameres shaped differently (‘X’, with four sharp teeth, or thin arch); frons without ornamentation .....	70
70.	parameres ‘X’ shaped .....	<i>Mallada</i> (in part) p. 402
—.	parameres shaped differently (with four sharp teeth, or thin arch) .....	71
71.	parameres with four sharp teeth .....	<i>Rexa</i> (in part, rare) p. 426
—.	parameres shaped as a thin arch (fig. 39) .....	<i>Chrysemosa</i> p. 345
72.	tignum present .....	73
—.	tignum absent .....	75

73.	1rp-ma joining PsM distal to <i>im</i> , or on apex of <i>im</i> .....	<i>Chrysoperla</i> p. 358
—.	1rp-ma joining PsM at <i>im</i> .....	74
74.	number of crossveins higher in outer gradates than inner gradates (more than 2) .....	..... <i>Plesiochrysa</i> (in part) p. 422
—.	number of crossveins about the same in outer and inner gradates (+/- 1) .....	..... <i>Atlantochrysa</i> p. 320
75.	1r-m originating basal to RP .....	<i>Berchmansus</i> p. 449
—.	1r-m originating from RP .....	76
76.	<i>im</i> cell quadrangular (fig. 1G) .....	77
—.	<i>im</i> cell triangular (fig. 1H) .....	80
77.	crossveins present between few ra-rp crossveins (fig. 48) .....	<i>Kostka</i> p. 395
—.	crossveins absent between ra-rp crossveins .....	78
78.	wing markings absent, except for pterostigma .....	<i>Leucochrysa</i> (in part) p. 460
—.	wing markings present .....	79

79.	tergum IX + ectoproct with ventral lobes (fig. 60) .....	<i>Gonzaga</i> p. 456
—.	tergum IX + ectoproct simple, without ventral lobes .....	<i>Santocellus</i> p. 473
80.	2 or more tibial spurs on all legs (fig. 1N) .....	<i>Suarius</i> (in part) p. 403
—.	tibial spur absent on prothoracic leg, one present on meso- and metathoracic legs (fig. 1M) .....	81
81.	dorsal apodeme with a ventral process .....	82
—.	dorsal apodeme simple, without ventral process .....	83
82.	tergum IX + ectoproct basally simple, not narrowly expanded (fig. 42) .....	..... <i>Chrysopodes (Chrysopodes)</i> (in part) p. 363
—.	tergum IX + ectoproct basally narrowly expanded .....	<i>Chrysopodes (Neosuarius)</i> p. 367
83.	tergum IX + ectoproct apically elongate or with ventral lobes, not simple and rounded ..	84
—.	tergum IX + ectoproct simple and rounded, without lobes or elongation .....	90
84.	tergum IX + ectoproct apically with ventral lobes .....	85
—.	tergum IX + ectoproct apically elongate .....	87

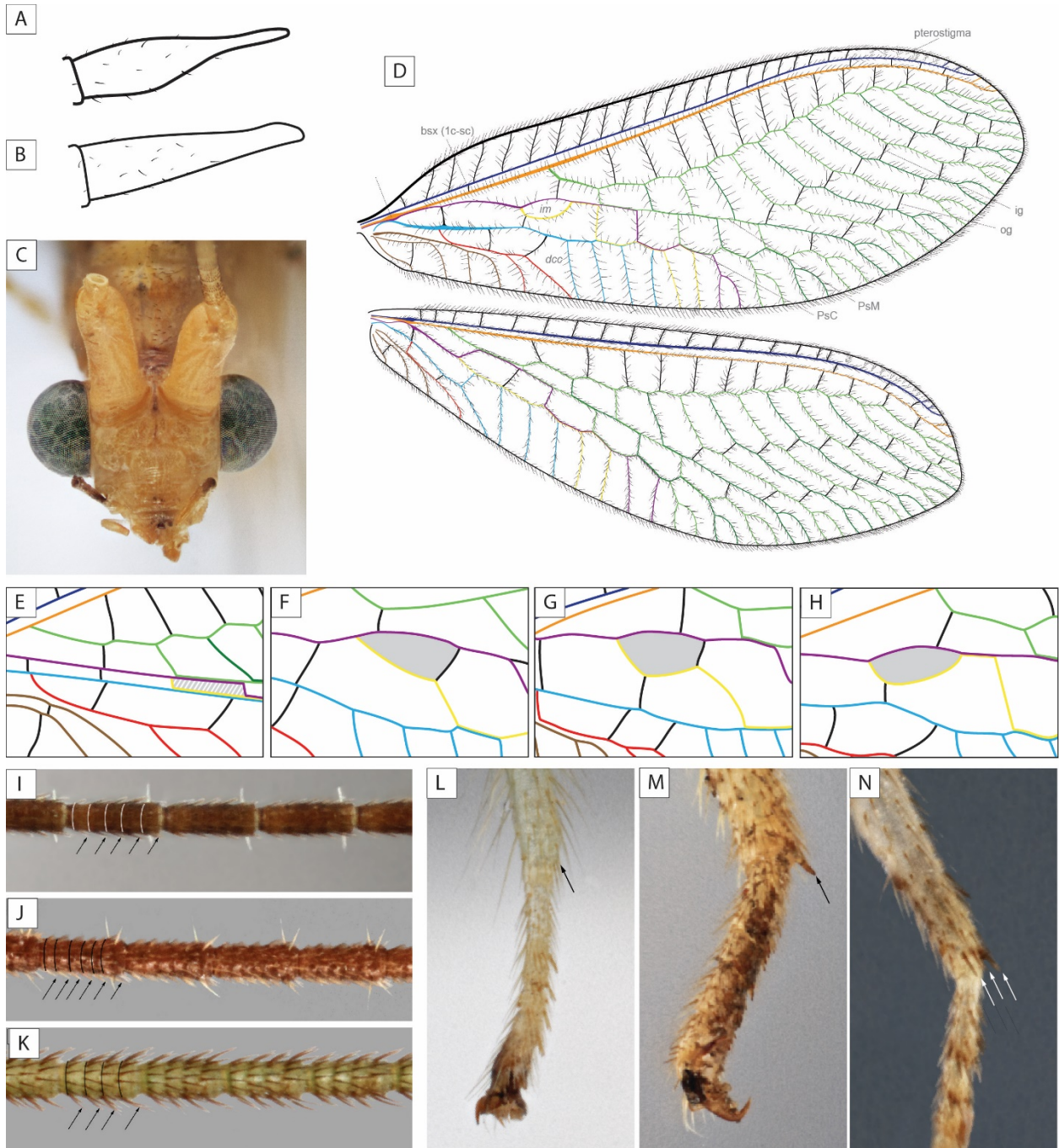
85. sternum VIII+IX strongly tapered and curved towards dorsal (fig. 36) .....  
..... *Brinckochrysa* p. 332
- . sternum VIII+IX slightly elongate but not strongly tapered .....86
86. number of crossveins higher in outer gradates than inner gradates (more than 2) (fig. 58)  
..... *Yumachrysa* p. 444
- . number of crossveins about the same in outer and inner gradates (+/- 1) .....  
..... *Ungla* (in part) p. 439
87. wings usually strongly marked, often thick setae present on pronotum and basal posterior  
wing margin; glenofinger present; three lobes with patches of gonocristae present apically  
on sternum VIII+IX (fig. 47) ..... *Glenochrysa* (in part) p. 386
- . wings usually unmarked (except for pterostigma), thick setae absent; glenofinger absent;  
sternum VIII+IX without lobes and gonocristae apically ..... 88
88. patch of long setae present apically on tergum IX + ectoproct (fig. 35) .....  
..... *Borniochrysa* p. 328
- . setae on tergum IX + ectoproct uniformly distributed, patch of long setae apically absent ..  
..... 89
89. sternum VIII+IX elongate and curved towards dorsal, with thick patch of setae apically ....

.....	<i>Nineta (Nineta)</i> p. 219
—.	sternum VIII+IX elongate, fairly straight, without thick patch of setae apically (fig. 11) ...
.....	<i>Chrysopidia (Chrysotropia)</i> (in part) p. 215
90.	wing markings present ..... 91
—.	wing markings absent ..... 92
91.	often thick setae present on pronotum and basal posterior wing margin; glenofinger present; three lobes with patches of gonocristae present apically on sternum VIII+IX (fig. 47) ..... <i>Glenochrysa</i> (in part) p. 386
—.	thick setae absent; glenofinger absent; sternum VIII+IX without lobes and gonocristae apically ..... <i>Vieira</i> (in part) p. 301
92.	2 or more tibial spurs on all legs (fig. 1N) ..... <i>Suarius</i> (in part) p. 430
—.	tibial spur absent on prothoracic leg, one present on meso- and metathoracic legs (fig. 1M) ..... 93
93.	number of crossveins higher in outer gradates than inner gradates (more than 2) ..... 94
—.	number of crossveins about same in outer and inner gradates (+/- 1) ..... 96



94. entoprocessi thin and longer than lateral arm of gonarcus, and projecting towards apex of abdomen, not arching (fig. 38) ..... *Ceratochrysa* p. 341
- . entoprocessi, short, long or arching, but not longer than lateral arm of gonarcus, and projecting towards apex of abdomen ..... 95
95. mediuncus elongate and thin, pseudopenis present (fig. 53) .....  
..... *Plesiochrysa* (in part) p. 422
- . mediuncus broad in lateral view, triangular in dorsal view, shaped like an axe head .....  
..... *Cunctochrysa* (in part) p. 374
96. often thick setae present on pronotum and basal posterior wing margin; glenofinger present; three lobes with patches of gonocristae present apically on sternum VIII+IX (fig. 47) ..... *Glenochrysa* (in part) p. 386
- . thick setae absent; glenofinger absent; sternum VIII+IX without lobes and gonocristae apically ..... 97
97. gonocornua strongly elongate, often pointing beyond apex of abdomen, about as long as or slightly longer than lateral arm of gonarcus ..... *Nipponochrysa* p. 411
- . gonocornua absent or less than half length of lateral arm of gonarcus ..... 98
98. mediuncus clearly detached from gonarcus ..... *Chrysopa* p. 353

—.	mediuncus closely connected with gonarcus, with membranous connection .....	99
99.	mediuncus broad in lateral view, triangular in dorsal view, shaped like an axe head .....	
	..... <i>Cunctochrysa</i> (in part) p. 374	
—.	mediuncus shaped differently .....	100
100.	Old World .....	101
—.	New World .....	102
101.	sternum VIII+IX elongate, longer than tergum XI + ectoproct (fig. 11) .....	
	..... <i>Chrysopidia</i> ( <i>Chrysotropia</i> ) (in part) p. 215	
—.	sternum VIII+IX simple, not longer than tergum XI + ectoproct .....	
	..... <i>Crassochochrysa</i> (in part) p. 371	
102.	entoprocessi present .....	<i>Ungla</i> (in part) p. 439
—.	entoprocessi absent .....	103
103.	meso- and metanotum often marked; mediuncus sclerotized .....	<i>Nodita</i> (in part) p. 466
—.	meso- and metanotum usually unmarked; mediuncus weakly sclerotized, with sclerotized apical hook (fig. 42) .....	<i>Chrysopodes</i> ( <i>Chrysopodes</i> ) (in part) p. 362



**Figure 28.** Illustrations relevant to the key to genera. A. Schematic line drawing of finely pointed apical palpomere (Ankylopterygini). B. Schematic line drawing of tapered, but not finely pointed apical palpomere (most non-Ankylopterygini). C. *Nineta (Tumeochrysa)* sp., strongly elongate scape. D. *Chrysopa oculata*, fore- and hind wing, schematic line drawing, venation based on

tracheation pattern; dark blue: Sc (subcosta); orange: RA (radius anterior); green: RP (radius posterior); purple: MA (media anterior), yellow: MP (media posterior); light blue: CuA (cubitus anterior); red: CuP (cubitus posterior); brown: A (anal); bsx: basal costal crossvein (1c-sc positioned basally); *dcc*: distal cubital cell; *ig*: inner gradates; *im*: intermediate cell; *og*: outer gradates; PsC: pseudocubitus; PsM: pseudomedia; dark blue: subcosta (Sc); orange: radius anterior (RA); green: radius posterior (RP); violet: media anterior (MA); yellow: media posterior (MP); light blue: cubitus anterior (CuA); red: cubitus posterior (CuP); brown: anal veins. E-H. Line drawings of the variation of *mamp1*, *mamp1* shaded in grey, refer to figure 1D for color legend. E. *im* cell absent, *mamp1* quadrangular without crossvein, *Apochrysa leptala* (Rambur). F. *im* cell triangular with crossvein, *Hypochrysa elegans* (Burmeister). G. *im* cell quadrangular, with crossvein, *Nacarina balboana* (Banks). H. *im* cell triangular without crossvein, *Chrysopa perla* Linnaeus. I-K. Photomicrographs of flagella, lateral view, curved lines indicate the base of the flagellar setae, and black arrows indicate the tip of the flagellar setae. I. *Hypochrysa elegans* (Burmeister), five setal rings; J. *Nothochrysa* sp., six setal rings; K. *Peyerimhoffina gracilis* (Schneider), four setal rings. L-N. Photomicrographs of apical metatibia and tarsi, ventro-lateral view. L. *Parankylopteryx* sp., arrow indicating the absence of a tibial spur on the metatibia. M. *Stigmachrysa kervillei* Navás, arrow indicating a tibial spur on the metatibia. N. *Suarius alisteri* (Navás), ventro-lateral view, arrows indicating multiple tibial spurs on the metatibia.

## Classification of Chrysopidae

### Family Chrysopidae Scheider 1851

(1396 species, 80 genera)

Diagnosis: Chrysopidae can be distinguished from other Neuroptera by the presence of fused veins in at least the pseudocubital (PsC), but often also in the pseudomedia (PsM), as well as the unique path of the anterior cubitus (CuA) in the hind wing, which joins PsC posterior to its first vein ending, forming a ‘*dcc*’ that is completely bordered by CuA.

Description of the general chrysopid (also see chapter 3 for detailed description and illustration of morphological characteristics of the common chrysopid *Chrysopa oculata* Say):

Most Chrysopidae light green, with some yellow or brown taxa; head marked or unmarked; three labial and five maxillary palpomeres present; labium usually medially indented; pronotum

varying in dimensions but commonly slightly longer than wide, and unmarked or strongly marked with red or brown; meso- and metanotum marked or unmarked, with a yellow longitudinal median stripe often present; meso- and metapleuron usually unmarked (marked red or brown in a few genera); legs usually unmarked (marked red or brown in a few genera); tibial spurs present, varying in number from absent on all legs to numerous spurs present on all legs (most common formula 0-1-1); tarsae usually unmarked and tarsomere V bearing two long apical setae in most genera (no or numerous long setae in some genera); wings with fusion between longitudinal veins R, M, and Cu and thus pseudoveins present (amount of fusion in veins varies across family); fusion always present in PsC (with usually 3 veins fused, but 2 veins or up to 6 in some genera), and usually present in PsM (with usually 2 veins fused, but no fusion or 3 veins in some genera); *mamp1* usually irregular (*im* present) and triangular without a crossvein in most genera (or regular to irregular and quadrangular with a crossvein); wing veins and integument vary from unmarked to strongly marked brown, and pterostigma can be unmarked, weakly defined, or strongly marked; absomen usually unmarked (but red or brown markings sometimes present); males and females with nine visible terga (+ectoproct, usually fused with tergum IX), and nine sterna in male (sternum VIII+IX usually fused), and seven sterna in female; terminalia of both sexes greatly variable with differences in external sclerites (such as elongate ectoprocts, or presence of lobes), as well as internal genitalia; female genitalia consisting of subgenitale, spermatheca, spermathecal duct, and vela; praegenitale in some genera (usually Belonopterygini); male genitalia always consisting of gonarcus, mediuncus, and hypandrium internum, additionally entoprocessi, parameres, tignum, gonosetae, and/or gonocristae sometimes present.

### Subfamily **Apochrysinæ** Handlirsch 1908

(24 species, 5 genera)

Apochrysidae Handlirsch 1908: 1251. Type genus: *Apochrysa* Schneider 1851. Tillyard 1926: 318 [subfamily level, Apochrysinæ], Adams 1978a: 221 [tribe level, Apochrysinini].

DIAGNOSIS: Apochrysinæ are the only chrysopids with no basal subcostal crossvein (1sc-r apically on wing), except for *Nothancyla*, and the only subfamily in which the *im* cell is entirely absent (*mamp1* regular, occupying the entire space between PsM and PsC). They have large wings with numerous RP branches, including the only representatives with gradates in the costal area, the PsM is continuous with the outer gradates, and the distance between PsM and PsC is shorter than in most other chrysopids. The flagellar setae are arranged in five rings. No tibial spurs are present, and many species have multiple setae apically on fifth tarsomere. The genitalia are simple, with only a thin gonarcus and triangular mediuncus present.

REMARKS: Apochrysinæ include the largest green lacewings, and are easily recognizable by their wings. Winterton and Brooks (2002) provided a comprehensive review of the subfamily, including a phylogeny inferred from morphological data. As a result of their analysis, they synonymized several apochrysinine genera. Previous authors have stated that a tympanal organ is present, but strongly elongate in Apochrysinæ. After thorough examination we propose that this structure is absent in all Apochrysinæ and therefore a character unique to Chrysopinae including *Nothancyla*.

Genus *Apochrysa* Schneider 1851

(10 species) figures 1E, 2.

*Apochrysa* Schneider 1851: 157. Type species: *Hemerobius leptaleus* Rambur 1842.

*Synthochrysa* Needham 1909: 202. Type species: *Hemerobius stigma* Girard 1862. Winterton and Brooks 2002: 22 [synonymy under *Apochrysa*].

*Nacaura* Navás 1913c: 280. Type species: *Apochrysa matsumurae* Okamoto 1912. Winterton and Brooks 2002: 22 [synonymy under *Apochrysa*].

*Oligochrysa* Esben-Petersen 1914: 639. Type species: *Oligochrysa gracilis* Esben-Petersen 1914. Winterton and Brooks 2002: 22 [synonymy under *Apochrysa*].

*Anapochrysa* Kimmins 1952b: 932. Type species: *Anapochrysa africana* Kimmins 1952. Winterton and Brooks 2002: 22 [synonymy under *Apochrysa*].

*Lauraya* Winterton 1995: 139. Type species: *Lauraya retivenosa* Winterton 1995. Winterton and Brooks 2002: 22 [synonymy under *Apochrysa*].

DIAGNOSIS: *Apochrysa* is the only chrysopid genus with a combination of the flagellar setae arranged in five rings, PsM continuous with the outer gradates, *mamp1* regular (*im* absent), no *ra-rp* crossveins below pterostigma, and PsC not extending beyond two thirds of the forewing.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, Oriental.

DESCRIPTION: Large lacewing (ca. 2.5 cm), body green in living individual.

Head: colored same as body; genal marking absent, or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape marked laterally, equal to, or greater than 2x width, rarely less than 1.5x as long as wide; pedicel marked laterally, or entirely pale; flagellar setal arrangement in

five rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark laterally, or uniformly pale; antenna longer than forewing length, rarely shorter than, or equal to forewing length; carina on dorsal torulus margin present, pilosity short, surface smooth and matte, or unevenly textured.

Thorax: prothorax markings absent, continuous, in lateral longitudinal stripe, or in spots, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long, rarely predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; gradates in costal field absent; forked costal crossveins absent, rarely present; apical costal area broad; pterostigma absent, diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc crassate basally; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; ra-rp crossveins below pterostigma absent; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent, rarely present; number of gradate series: 2, 3, or rarely 4 or more; number of gradate crossveins more in inner series than outer series; gradate series diverging; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP, joining M basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 15 or more; PsC not present up to more



than 2/3 of wing; *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 4 or more; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup, meets CuA basal to 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked, or simple; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale, or longitudinal veins pale, crossveins dark; wing markings on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: 2 or 3; number of crossveins between PsM and PsC: 15 or more; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 4; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; legs unmarked.

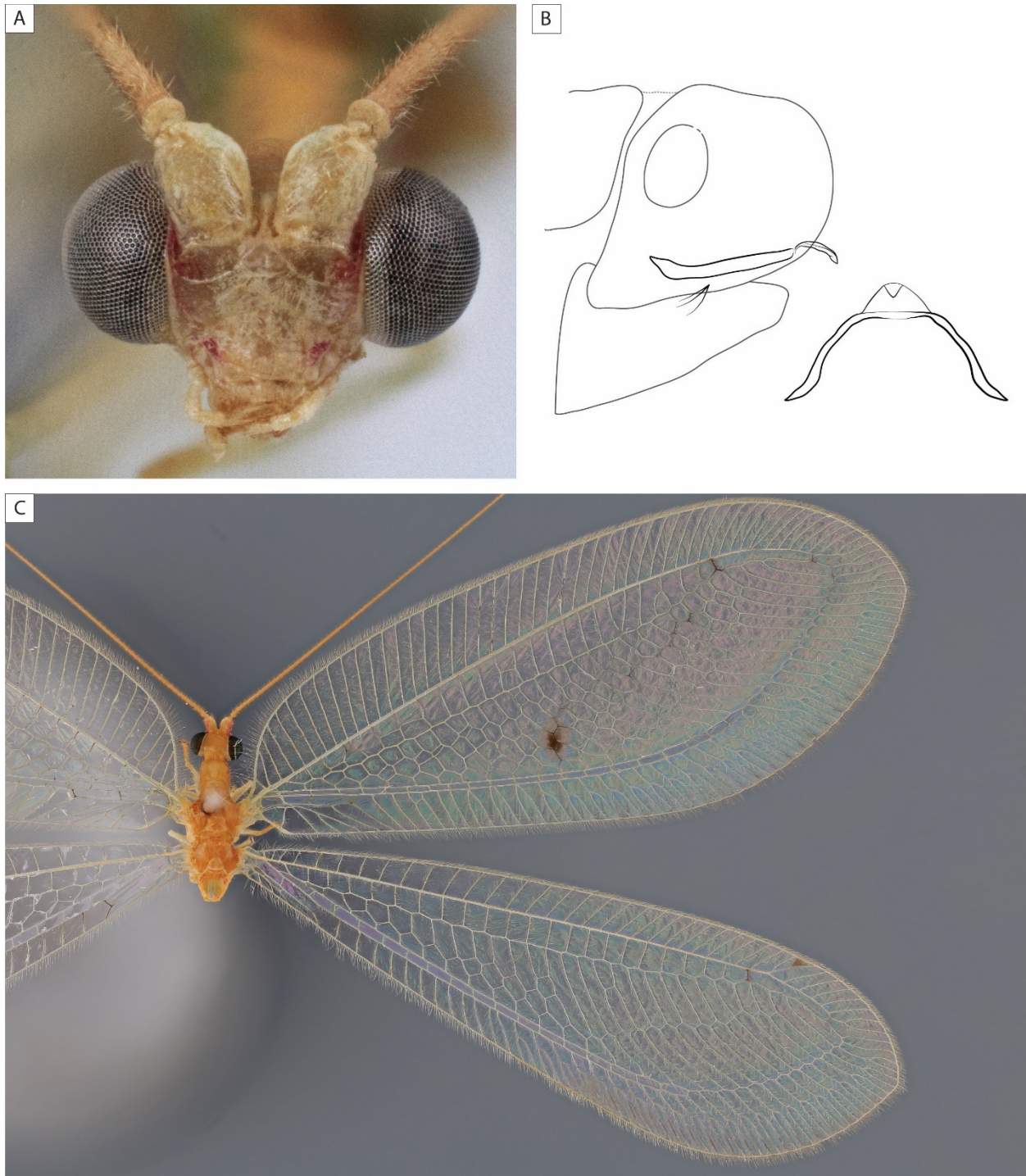
Abdomen: markings sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded, or with small subapical cone ventrally; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca large, or thick, surface with transverse ridges or smooth; vela smaller than spermatheca; spermathecal duct long and strongly coiled, or long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not

fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially not fused, membraneously separated, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: Winterton and Brooks (2002) synonymized several apochryine genera with *Apochrysa* on the basis of the PsC not extended beyond the basal two thirds of the forewing. The wing venation of the genus is comparatively variable (especially the number of gradate series), and it was this variation upon which the various genera not synonymized were originally established. The species *A. matsumurae* (formerly *Nacaura*) fell outside of the genus in all phylogenetic hypotheses inferred from combined data (see chapter 1), and its generic status should be further examined. Winterton (2006) noted a specimen of *Apochrysa* with extremely altered wing venation in which a strongly reticulate irregular venation was present. Larvae are only known from *A. matsumurae* and were reported to be debris-carrying (Tsukaguchi 1995), and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 29.** *Apochrysa*. A. *Apochrysa lutea* (Walker), head, frontal view, photomicrograph. B. *Apochrysa lutea* (Walker), male genitalia, lateral and detailed dorsal view, schematic line drawing. C. *Apochrysa matsumurae* (Okamoto), fore- and hind wing, dorsal view, microphotograph.

Genus *Domenechus* Navás 1913

(2 species) figure 3.

*Domenechus* Navás 1913b: 298. Type species: *Domenechus sigillatus* Navás 1913, by monotypy.

DIAGNOSIS: *Domenechus* is the only chrysopid genus with the combination of the flagellar setae arranged in five rings, PsM continuous with the outer gradates, *mamp1* regular (*im* absent), ra-rp crossveins present below pterostigma, PsC extending beyond 2/3s of the forewing, vein 2A forked, typically no forked costal crossveins (or very few), a gradate series between RA and AP, and 2, round, elevated markings on the forewing and one large ill-defined marking posterior to PsC.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape marked dorsally, equal to, or greater than 2x width; pedicel marked apically; flagellar setal arrangement in five rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons with unbroken band; carina on dorsal torulus margin absent; vertex flat in profile, markings absent, ornamentation absent, pilosity elongate, surface smooth and matte.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae dark, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity dense, setae pale, predominantly long;

metathorax unmarked, pilosity dense, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; gradates in costal field absent; forked costal crossveins absent; apical costal area broad; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc crassate basally; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma:  $>7$ ; tympanal organ absent; RP strongly curved; ra-rp crossveins below pterostigma present; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP present; number of gradate series:  $>4$ ; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP, joining M basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 15 or more; PsC present up to more than  $2/3$  of wing; *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: up to 7; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup; 2m-cua originated from M; cubital cell number: more than three; cell *c1* as long, or shorter than *c2*; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings on *dcc*, on spots in RP sector, and on posterior margin medially.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 4 or more; number of crossveins between PsM and PsC: 15 or more; maximum number of fused veins on

PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae four in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca thick, surface smooth; vela about same size as spermatheca; spermathecal duct long and strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX separate, regular, without strong apical spines or dense setae; sternum VIII with small process along posteromedial margin; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; mediuncus attached to gonarcus, without membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: Members of *Domenechus* have similar wing markings to some *Joguina* species, but do not have gradates between the costal crossveins, or posterior to PsC. They can be differentiated from *Loyola* by the large ill-defined marking posterior to PsC, and the striated

surface of the spermatheca, both of which are absent in the latter. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 30.** *Domenechus mirifica* (Gerstaecker), head, frontal view, photomicrograph.

Genus *Joguina* Navás 1912

(5 species)

*Joguina* Navás 1912: 98. Type species: *Apochrysa nicobarica* Brauer 1864, by original destination.

*Lainius* Navás 1913b: 300. Type species: *Lainius constellatus* Navás 1913. Winterton and Brooks 2002: 24 [synonymy under *Joguina*].

DIAGNOSIS: *Joguina* is the only chrysopid genus with gradates present between costal crossveins and between the twigs of the longitudinal veins posterior to PsC.

DISTRIBUTION: Neotropical, Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape marked completely, or laterally, less than 1.5x as long as wide; pedicel marked completely, or laterally; flagellar setal arrangement in five rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons with unbroken band; carina on dorsal torulus margin present; vertex flat in profile, markings absent or present, ornamentation absent, pilosity elongate, surface smooth and matte.

Thorax: prothorax markings absent, or continuous, red, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly red, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; gradates in costal field present; forked costal crossveins present; apical costal area broad; pterostigma absent; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc crassate basally; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: >7; tympanal organ absent; RP almost straight; ra-rp crossveins below pterostigma absent or present; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP present; number of gradate series: >4; gradate series



irregularly arranged; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP, joining M basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 15 or more; PsC present up to more than 2/3 of wing; *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 4 or more; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua originated from M; cubital cell number: more than three; crossvein 2cua-cup meeting basal *dcc* vein; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings on spots in RP sector.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: >4; number of crossveins between PsM and PsC: 15 or more; maximum number of fused veins on PsM: 3; maximum number of fused veins on PsC: 4; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae four in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca large, surface with transverse ridges; vela smaller than spermatheca; spermathecal duct long and strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sternum VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus attached to gonarcus, without membranous connection, flattened, or short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent, or numerous short setae on apex present; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: Winterton and Brooks (2002) synonymized the neotropical genus *Lainius* with the oriental *Joguina* on the basis of their phylogenetic analysis and the similarity in wing venation characters (e.g., gradates present between costal crossveins and the twigs of the longitudinal veins posterior to PsC). There are more gradate series present on the entire wing in the two Neotropical species than in the three Oriental species. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Loyola* Navás 1913

(3 species)

*Loyola* Navás, 1913a: 297. Type species: *Apochrysa croesus* Gerstaecker 1893, by original designation.

*Claverina* Navás, 1913b: 164. Type species: *Apochrysa beata* Walker 1858, by monotypy.

Winterton and Brooks 2002: 25 [synonymy under *Loyola*].

DIAGNOSIS: *Loyola* is the only chrysopid genus with the combination of the flagellar setae arranged in five rings, PsM continuous with the outer gradates, *mamp1* regular (*im* absent), ra-rp crossveins present below pterostigma, PsC extending beyond 2/3s of the forewing, typically no forked costal crossveins (or very few), a gradate series between RA and AP, and 2, round, elevated markings on the forewing, and no markings posterior to PsC.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape unmarked, or ventrally, equal to, or greater than 2x width; pedicel marked laterally, or entirely pale; flagellar setal arrangement in five rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex flat in profile, markings absent or present, ornamentation absent, pilosity elongate, surface smooth and matte.

Thorax: prothorax markings in lateral longitudinal stripe, red, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly red, pilosity sparse, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin

absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; gradates in costal field absent; forked costal crossveins absent; apical costal area broad; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc crassate basally; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: >7; tympanal organ absent; RP strongly curved; ra-rp crossveins below pterostigma present; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP present; number of gradate series: >4; number of gradate crossveins approximately same number in each series; gradate series irregularly arranged; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on R, or originating on RP, joining M basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 15 or more; PsC present up to more than 2/3 of wing; *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 4 or more; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings on inner gradates, and on spots in RP sector.

Hind wing: sc-r crossveins below pterostigma: >7; number of gradate series: >4; number of crossveins between PsM and PsC: 15 or more; maximum number of fused veins on PsM: 2;

maximum number of fused veins on PsC: 4; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca thick, surface with transverse ridges; vela about same size as spermatheca; spermathecal duct long and strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: Winterton and Brooks (2002) synonymized *Claverina* with *Loyola* on the basis of their similar wing venation. Both genera have elevated and somewhat sclerotized, marked spots between RP and PsM in the forewing, although less pronounced in *Claverina*. Members of *Loyola*

are the largest green lacewings, with a wingspan of about 10cm. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Nobilinus* Navás 1913

(4 species) figure 4.

*Nobilinus* Navás 1913a: 25. Type species: *Nobilinus insignitus* Navás 1913.

DIAGNOSIS: *Nobilinus* is the only chrysopid genus with a combination of the flagellar setae arranged in five rings, PsM continuous with the outer gradates, *mamp1* regular (*im* absent), ra-rp crossveins present below pterostigma, and PsC extending beyond 2/3s of the forewing, and no gradates present between RA and RP.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in five rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons with unbroken band; carina on dorsal torulus margin present; vertex flat in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and matte.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae pale,

predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; gradates in costal field absent; forked costal crossveins absent; apical costal area broad; pterostigma absent; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc crassate basally; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: >7; tympanal organ absent; RP almost straight; ra-rp crossveins below pterostigma present; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 3; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP, joining M basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 15 or more; PsC present up to more than 2/3 of wing; *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 4 or more; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins entirely pale; wing markings on inner gradates.

Hind wing: sc-r crossveins below pterostigma: >7; number of gradate series: 3; number of

crossveins between PsM and PsC: 15 or more; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; spermatheca thick, surface with transverse ridges; vela smaller than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Nobilinius* is similar to *Apochrysa* in its general wing venation pattern, but the RP branches are more numerous present and there are ra-rp crossveins present below the



pterostigma in the former. The genus resulted as sister to *Apochrysa* in some of the analyses presented in chapter 1, and further investigation into the status of it is suggested. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 31.** *Nobilenius albardae* (McLachlan), head, frontal view, photomicrograph.

### Subfamily **Nothochrysinæ** Navás 1910

(27 species, 9 genera)

Nothochrysinos (nomen incorrectum, nec. Nothochrysinæ) Navás 1910a: 59. Type genus:

*Nothochrysa* McLachlan 1868. Navás 1913b: 303 [tribe level, Nothochrysinini].

Dictyochrysinæ Esben-Petersen 1918: 26. Type genus: *Dictyochrysa* Esben-Petersen 1917.

Adams 1967: 219 [synonymy under Nothochrysinæ].

DIAGNOSIS: Nothochrysinæ are the only chrysopids in which the PsM is continuous with the inner gradates (this character can be less prominent in genera, where the PsM is not strongly pronounced, such as *Hypochrysa* or *Dictyochrysa*). The flagellar setae are arranged in five or six rings. The basal subcostal crossvein is present, and the *mamp1* is various (regular, but triangular, triangular with a crossvein present, or quadrangular with a crossvein present). The genitalia are simple, with the gonarcus as a thin arch and a triangular gonarcus, but some species have additional structures, which could be parameres.

REMARKS: Nothochrysinæ are stout, often primitive looking lacewings, usually small (with a few large species in *Nothochrysa*). The subfamily is in great need of a comprehensive revision, possibly including the fossil taxa assigned to Nothochrysinæ as well, because relationships within the subfamily are still unclear (see chapter 1), and many of the genera include a single derived species.

Genus *Asthenochrysa* Adams and Penny 1992

(1 species)

*Asthenochrysa* Adams and Penny 1992: 217. Type species: *Hypochrysa viridula* Adams 1978.

DIAGNOSIS: *Asthenochrysa* is the only chrysopid genus with the flagellar setae arranged in five rings, and a sclerotized plate present ventral of gonarcus complex with thick, short spines in the male genitalia.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented, unknown; frons in profile raised laterally, markings absent; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in five rings; flagellar setae shorter than flagellomere width; flagellum uniformly dark; antenna shorter than, or equal to forewing length; vertex raised in profile, markings absent, ornamentation absent, pilosity short, surface smooth and glossy.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin present.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C fused proximal to pterostigma; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 0-3; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; pseudoveins absent; *mamp1* irregular (*im* cell present), triangular, with crossvein;

maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *dcc*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: 2; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae absent; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale large, consisting of 2 parts, on broad sclerotized structure; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused,

median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or tapering medioapically, mediuncus process absent; sclerotized plate ventral of gonarcus complex with thick, short spines present; parameres absent; gonosetae sparsely present (<10); gonocristae present apically on ectoproct; microtholi absent.

REMARKS: *Asthenochrysa* is externally similar to *Hypochrysa*, especially in the wing venation, but can be distinguished through the male genitalia. The monotypic genus is the only nothochry sine known from South America. Larvae and feeding habits of the adults are unknown.

Genus *Dictyochrysa* Esben-Petersen 1917

(3 species) figure 5.

*Dictyochrysa* Esben-Petersen 1917: 214. Type species: *Dictyochrysa fulva* Esben-Petersen 1917, by original designation and monotypy.

DIAGNOSIS: *Dictyochrysa* is the only chrysopid genus with the flagellar setae arranged in six rings, and more than two gradate series (arranged irregularly).

DISTRIBUTION: Australasian, Oceanian.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus marked on apical 2

palpomeres; maxillary palpus marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked medially, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in six rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface smooth and matte.

Thorax: prothorax markings in spots, or in bands, brown to black, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly short; metathorax marked, pilosity sparse, setae dark, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin present.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 5, or six; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C fused proximal to pterostigma; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: >4; number of gradate crossveins approximately same number in each series; gradate series irregularly arranged; 1r-m originating on RP; 1rp-ma joining M at

*mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe recurved, angular; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: >4; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae absent; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 2; number of metatibial spurs: 2; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

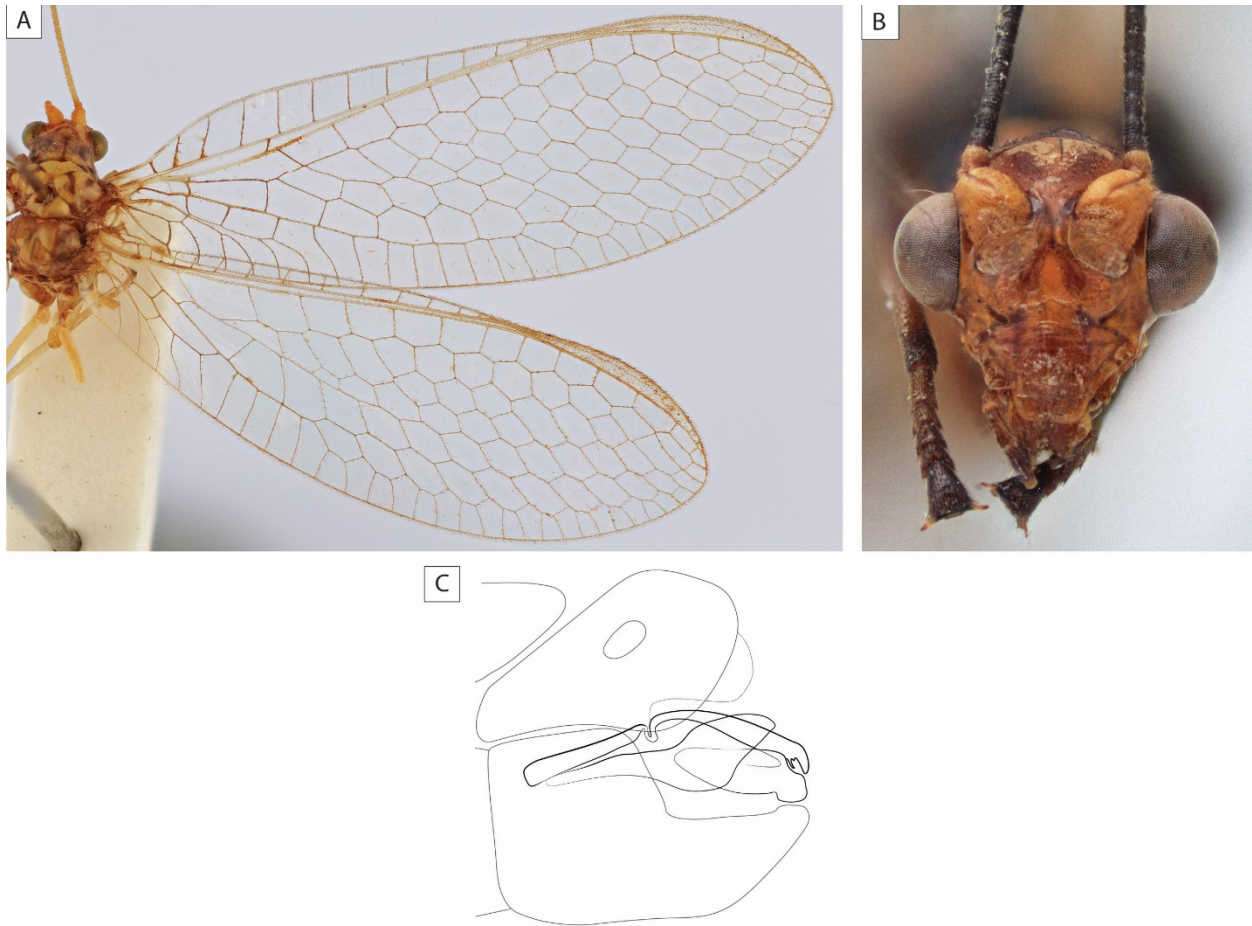
Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca thick; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines

on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned distally on lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, larger than lateral arms of gonarcus, mediuncus process present as ventral hook; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *Dictyochrysa* is easily recognizable amongst Nothochrysinæ by its strongly reticulate wing venation. The larvae of *Dictyochrysa fulva* are not debris-carrying (New 1981a), and the eggs are stalked and laid singly (Brooks and Barnard 1990). No insect remains were found in the guts of adults (Brooks and Barnard 1990).





**Figure 32.** *Dictyochrysa peterseni* Kimmins. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral view, schematic line drawing.

Genus *Hypochrysa* Hagen 1866

(1 species) figures 1F, I, 6.

*Hypochrysa* Hagen 1866: 377. Type species: *Chrysopa nobilis* Schneider 1851, by monotypy.

Leraut 1980: 243 [replacement name for *Hypochrysa*: *Hypochrysodes*], Oswald 1987

[*Hypochrysopodes* is unnecessary replacement name for *Hypochrysa*].

DIAGNOSIS: *Hypochrysa* is the only chrysopid genus with the flagellar setae arranged in six rings, and a long ventral, pointed extension of the dorsal apodeme in the male. They are also recognizable by their distinct markings on head and pronotum.

DISTRIBUTION: Nearctic.

DESCRIPTION: body colored pale green, or yellow.

Head: colored same as body; genal marking brown; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus finely pointed; labrum straight; frons in profile flat; scape marked laterally, or medially, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in five rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark; antenna shorter than, or equal to forewing length; frons with medial longitudinal stripe; carina on dorsal torulus margin present; vertex raised in profile, markings present (medial longitudinal stripe and small lateral markings), ornamentation absent, pilosity short, surface smooth and matte.

Thorax: prothorax markings in three longitudinal stripes, brown to black, pilosity uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin present.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in

costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C fused proximal to pterostigma; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins mostly dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae absent; tarsi entirely dark or entirely pale (unmarked); number of protibial spurs: more than two; number of mesotibial spurs: more than two;

number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae short; leg extensively marked.

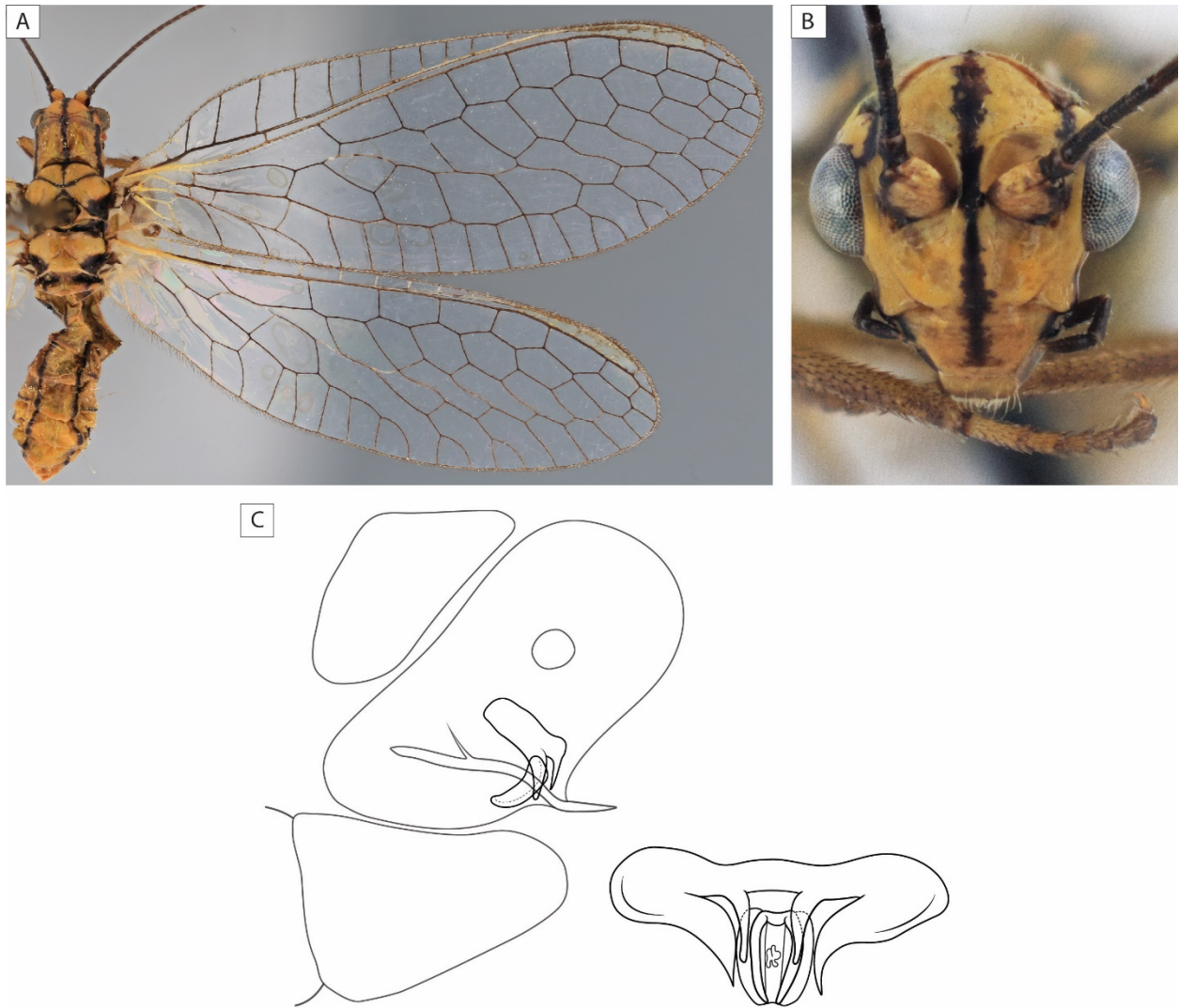
Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or elongate basally; spermatheca elongate, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme with ventral process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, rounded and bilobed, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: The single species of *Hypochrysa* is easily recognized among nothochrysinines by its distinct coloration. The pronotum is marked with three thin, longitudinal black bands that are continued on markings on the vertex, gena, and frons. As in all nothochrysinines except for *Dictyochrysa* and *Nothochrysa*, vein 1A is not forked in the forewing. The larvae are elongate, light green and not debris carrying (Brauer 1867, Principi 1956, Gepp 1983, Tauber et al. 2014). No insect remains were found in the guts of the adults; instead, they contained pollen grains

(Brooks and Barnard 1990).



**Figure 33.** *Hypochrysa elegans* (Burmeister). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and caudal view, schematic line drawing.

Genus *Kimochrysa* Tjeder 1966

(3 species)

*Kimochrysa* Tjeder 1966: 254. Type species: *Kimochrysa impar* Tjeder 1966, by original

designation.

DIAGNOSIS: *Kimochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in six rings, a triangular mamp1 including a crossvein, and tergum IX and ectoproct not fused (numerous sc-r crossveins are present in most but not all specimens basal to the pterostigma, which is not present in any other Chrysopidae).

DISTRIBUTION: Afrotropical.

DESCRIPTION:

Head: colored same as body; genal marking absent, or brown; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape marked dorsally, laterally, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in six rings; flagellomeres as wide as long, or shorter; flagellum uniformly dark or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; vertex raised in profile, markings absent or present, ornamentation absent, pilosity short, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings continuous, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; number of maximal

c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, and additional crossveins between Sc ad R present basal to pterostigma; veins Sc and C fused proximal to pterostigma; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; additional sc-r crossveins present basal to pterostigma in some species; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), triangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins scarcely dark; wing markings absent.

Hind wing: number of gradate series: 2; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); femoral setae short; leg extensively marked.

Abdomen: markings abundant; setae short, dark; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, or extended ventrally backwards, on narrow elongate membranous structure; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct long and strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, flattened, or short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Kimochrysa* and *Hypochrysa* are quite similar in their wing venation, the only difference being the numerous sc-r crossveins present basal to the pterostigma. However, this character seems to be variable, as we have seen specimens of *K. africana* (Kimmins) that lack these crossveins. The larvae are not debris carrying, slender and green (Tauber et al. 2014). No insect remains were found in the guts of the adults; instead, they contained pollen grains (Brooks and Barnard 1990).

Genus *Leptochrysa* Adams and Penny 1992



(1 species)

*Leptochrysa* Adams and Penny 1992: 219. Type species: *Leptochrysa prisca* Adams and Penny 1992, by original designation and monotypy.

DIAGNOSIS: *Leptochrysa* is the only chrysopid genus with microsetation on the entire wing integument.

DISTRIBUTION: Neotropical.

DESCRIPTION: general body colored brown.

Head: colored same as body, or marked brown entirely; genal marking absent; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; scape marked completely, equal to, or greater than 2x width; pedicel marked completely; flagellar setal arrangement in five rings; flagellomeres at least 1.5x as long as wide; flagellum dark basally; frons uniformly brown; vertex raised in profile, markings absent, ornamentation absent.

Thorax: prothorax markings in lateral longitudinal stripe, or in spots, brown to black, setae dark, predominantly short, thick long setae patches on pronotum absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent.

Forewing: microtrichia present on entire wing; costal area narrow basally; costal crossveins (c-sc) simple, straight; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present; veins Sc and C fused proximal to pterostigma;

number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins mostly dark; wing markings between PsM and PsC, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsi entirely dark; femoral setae short; leg extensively marked.

Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; subgenitale longer than broad, close to sternum.

REMARKS: We were not able to examine a specimen of *Leptochrysa*, and based the

description on Adams and Penny (1992). The species is a primitive looking chrysopid, regarding the wing venation and especially the microsetation on the integument, which is not present in any other living chrysopid species. The venation resembles fossil chrysopid species more so than other extant species. The biology of *Leptochrysa* is unknown, and only a single specimen is known from Peru.

Genus *Nothochrysa* McLachlan 1868

(10 species) figures 1J, 7.

*Nothochrysa* McLachlan 1868: 195. Type species: *Chrysopa fulviceps* Stephens 1836, by subsequent designation by Banks 1903.

*Nothanica* Navás 1913c: 180. Type species: *Hemerobius capitatus* Fabricius 1793, by original designation. Tjeder 1941: 30 [synonymy under *Nothochrysa*].

DIAGNOSIS: *Nothochrysa* is the only chrysopid genus with an irregular *mamp1*, forming a quadrangular, elongate *im* cell and the PsM continuous with the inner gradates, and more than 10 RP branches.

DISTRIBUTION: Nearctic, or Palaearctic.

DESCRIPTION: general body colored brown or yellow.

Head: orange; genal marking absent; labial palpus marked on apical 3 palpomeres, or uniformly marked; maxillary palpus marked on apical 2 palpomeres, or uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical,

broad, regular shaped, with basal tooth on one side; frons in profile flat; scape marked dorsally, laterally, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in five rings, or six rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, or uniformly dark; antenna shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex flat in profile, markings absent or present, ornamentation absent, pilosity absent, or short, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings large and discontinuous, brown to black, pilosity uniformly distributed, setae dark or pale and dark admixed, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked, predominantly brown to black, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; metathorax marked, pilosity dense, or sparse, setae dark or pale, predominantly long, or predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin present.

Forewing: tegula marked or unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: >7; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) sinuous, or straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same

number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 2, or 3; MA and MP rejoining on PsC; MA and CuA fused, or not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins mostly dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: >7; number of gradate series: 2; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

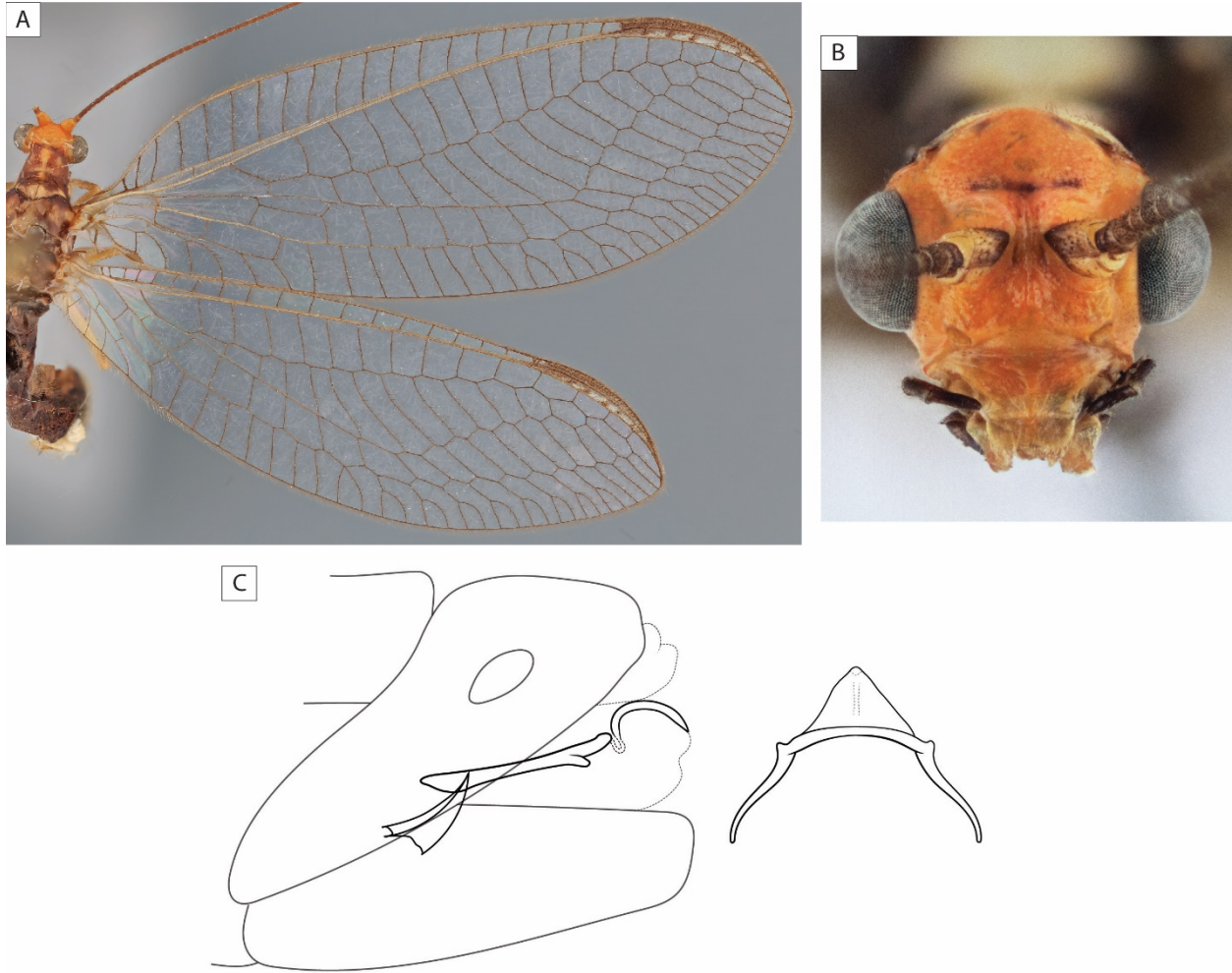
Legs: pretarsal claw dilated, or simple; tarsal setae absent; tarsi entirely dark or entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings abundant; setae short, dark or pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not completely fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Nothochrysa* is seemingly the nothochryesine with the closest wing venation to Chrysopinae and forms a distinct clade, sister to all other genera of Nothochrysoidea (see chapter 1). In some specimens PsM does not seem completely continuous with the inner gradates, but there is instead a slight extension of PsM beyond the basal most inner gradate. In both *Dictyochrysa* and *Nothochrysa* vein 1A is not forked, but they can be easily distinguished by the different wing venation pattern. Larvae of three species of the genus have been described, and are all debris carrying (Killington 1937, Kimmins 1939, Toschi 1965, Gepp 1983, Tauber et al. 2014), which are the only known debris-carriers in Nothochrysoidea. No insect remains were found in the guts of the adults (Brooks and Barnard 1990).



**Figure 34.** *Nothochrysa*. A. *Nothochrysa fulviceps* (Stephens) A. Fore- and hind wing, dorsal view, photomicrograph. B. *Nothochrysa fulviceps*, head, frontal view, photomicrograph. C. *Nothochrysa* sp., male genitalia, lateral view, schematic line drawing.

Genus *Pamochrysa* Tjeder 1966

(1 species) figure 8.

*Pamochrysa* Tjeder 1966: 248. Type species: *Pamochrysa stellata* Tjeder 1966, by monotypy.

DIAGNOSIS: *Pamochrysa* is the only chrysopid genus with the flagellar setae arranged in five rings, the ill-defined PsM continuous with the inner gradates, separated tergum XI and

ectoproct in the male and female, and an irregular *mamp1* (forming a quadrangular *im* cell).

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked laterally, medially, or ventrally, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in five rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark distally; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface smooth and glossy.

Thorax: prothorax markings large and discontinuous, brown to black, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae dark, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin present.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 6; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly



defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), quadrangular and short, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins mostly dark; wing markings absent, or scarsly at some vein joints.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae absent; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae short; leg extensively marked.

Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.

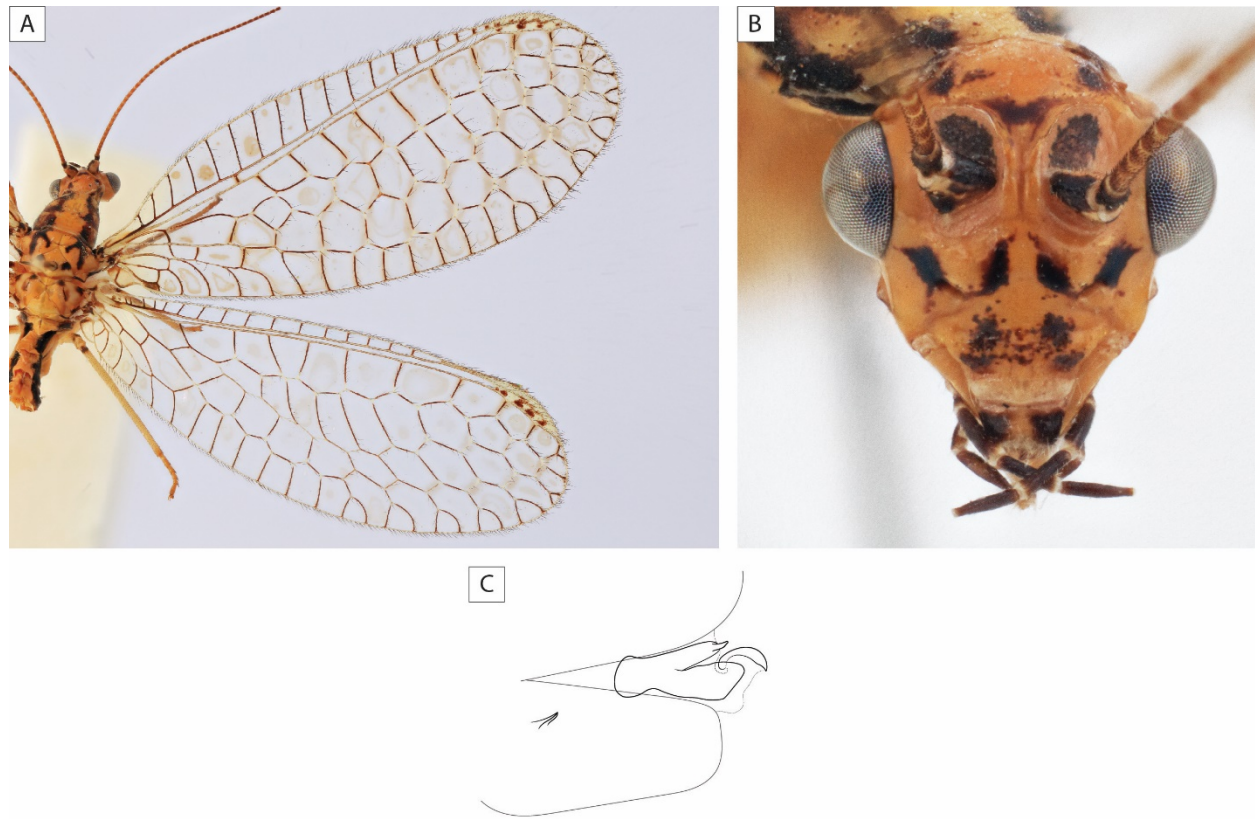
Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded;

praegenitale absent; subgenitale as long as broad; spermatheca average, surface smooth; vela smaller than spermatheca; spermathecal duct very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: *Pamochrysa* is similar to *Pimachrysa*, but they can be differentiated by the number of flagellar setal rings (five in *Pamochrysa*, six in *Pimachrysa*). The quadrangular *im* cell of *Pamochrysa* is much shorter than in any other chrysopid species with a quadrangular *im* cell, and in comparison to others, MA forms two of abscissae of *im*, due to a strongly curved MA towards RP. The three genera *Kimochrysa*, *Pamochrysa*, and *Pimachrysa* have a separated tegum IX and ectoproct, which is comparatively rare in Chrysopidae. It is likely that *Pamochrysa* and *Pimachrysa* are closely related, due to their many similarities in wing venation and genitalia. They are the only chrysopids, in which the spiracle of the eighth tergum of the females is positioned on the sclerotized tergum and not in the membranous area between terga and sterna. Additionally *Pamochrysa* does not have the very distinct spoon shaped setae on the lateral gonapophyses, which are present in *Pimachrysa*. Larvae of the genus are unknown, and no insect remains were found in

the guts of the adults; instead, they contained pollen grains (Tjeder 1966, Brooks and Barnard 1990).



**Figure 35.** *Pamochrysa stellata* Tjeder. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral view, schematic line drawing.

Genus *Pimachrysa* Adams 1956

(5 species) figure 9

*Pimachrysa* Adams 1956: 67. Type species: *Pimachrysa grata* Adams 1956, by original designation.

DIAGNOSIS: *Pimochrysa* is the only chrysopid genus with the flagellar setae arranged in six

rings, the ill-defined PsM continuous with the inner gradates, separated tergum XI and ectoproct in the male and female, and an irregular *mamp1* (forming a quadrangular *im* cell). Females are easily recognizable by the thick ventrally pointing spoon-shaped setae on the lateral gonapophyses.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape marked dorsally, laterally, or medially, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in six rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark; antenna shorter than, or equal to forewing length; frons with unbroken band, or with medial longitudinal stripe; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface unevenly textured.

Thorax: prothorax markings continuous, brown to black, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity sparse, setae dark, predominantly short; metathorax marked, pilosity sparse, setae dark, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin present.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined

marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ absent; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA basal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A simple, unforked; anal lobe recurved, angular; wing veins mostly dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae absent; tarsi entirely dark; number of protibial spurs: more than two; number of mesotibial spurs: more than two; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae short; leg extensively marked.

Abdomen: markings sparse; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; gonapophysis enlarged bearing thick

spoon-shaped setae; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale consisting of 2 parts, apparently detached; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX separate, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or strongly curved towards base, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi present.

REMARKS: *Pimachrysa* has a similar wing venation to *Pamochrysa* but can be distinguished by the flagellar setal rows and terminalia. Larvae of the genus are unknown, and no insect remains were found in the guts of the adults; instead, they contained pollen grains (Brooks and Barnard 1990).



**Figure 36.** *Pimachrysa nigra* Adams, head, frontal view, photomicrograph.

Genus *Triplochrysa* Kimmins 1952

(2 species)

*Triplochrysa* Kimmins 1952a: 69. Type species: *Triplochrysa pallida* Kimmins 1952, by monotypy and original designation.

DIAGNOSIS: *Triplochrysa* is the only chrysopid genus with the flagellar setae arranged in five rings, and three gradate series.

DISTRIBUTION: Australasian, Oceanian.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus truncated apically; labrum indented; mandibles asymmetrical,

broad, regular shaped, with basal tooth on one side; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in five rings; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with medial longitudinal stripe; vertex flat in profile, markings absent, ornamentation absent.

Thorax: prothorax markings absent, fronterolaterally, small spot, or diffuse and sparse, brown to black, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black; small expansion on frontal metascutum margin present.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal crossveins (c-sc) simple, straight; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 3; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on R; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM terminating between inner and outer gradates; PsM and PsC relatively wide apart; *mamp1* regular, with more than 4 corners (*im* cell absent), or irregular (*im* cell present), triangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets



CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A simple, unforked; vein 2A forked; anal lobe recurved, angular; wing veins scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2 or 3; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 2; jugal lobe expanded; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); femoral setae short; leg unmarked.

Abdomen: markings absent; setae short; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or extended ventrally backwards, on narrow elongate membranous structure; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent;

mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: Both species of *Triplochrysa* have three gradate series and a generally similar venation pattern, but differ in the form of *mamp1*. The wing venation of *Triplochrysa* is unique among living Chrysopidae, with a regular *mamp1*, which is usually found in Apochrysininae, but their wing venation pattern is extremely different from that of *Triplochrysa*. Apart of the third gradate series, *Triplochrysa* is similar to *Hypochrysa* but can additionally be distinguished by the absence of an elongate process of the forsal apodeme in the former. *Dictyochrysa* is the only other nothochrysinine with more than two gradate series, but has an otherwise very different wing venation pattern than *Triplochrysa*. Larvae of the genus are unknown, and no insect remains were found in the guts of the adults (Brooks and Barnard 1990).

## Subfamily **Chrysopinae** Schneider 1815

(1345 species, 62 genera)

Chrysopina Schneider 1851: 35. Type genus: *Chrysopa* Leach 1815. Esben-Petersen 1918: 27  
[raised to subfamily: Chrysopinae].

DIAGNOSIS: Chrysopinae are the only chrysopids in which the flagellar setae are arranged in four rings (with the exception of *Nothancyla*: five rings), and the only with a tympanal organ present. PsM is continuous with the outer gradates, and an im cell is usually present (with the exception of few species, such as *Ankylopteryx anomala*, *Nesochrysa* rarely, or *Belonopteryx*

*arteriosa*), and either quadrangular with a crossvein or triangular without a crossvein.

REMARKS: Chrysopinae is by far the largest of the three subfamilies, holding the greatest extant diversity, and thus morphologically extremely variable. It is distributed world wide, with only Leucochrysinini restricted to the New World. *Nothancyla* was recently included in Chrysopinae on the basis of a phylogenetic analysis (Garzón et al. in rev.). Chrysopinae including Nothancylini share a single unambiguous synapomorphy: a tympanal organ on the wing base, formed mainly by the radius (although the media is included).

Tribe **Ankylopterygini** Navás 1910

(150 species, 7 genera)

Ancilopteryginos Navás 1910a: 59, nomen incorrectum [recte Ankylopterygini Hölzel 1970: 51]

Type genus: *Ankylopteryx* Brauer 1864.

DIAGNOSIS: Ankylopterygini including the *Nineta*-group has no unambiguous synapomorphies. All members of the tribe have a triangular im cell, no parameres, or tignum, and no praegenitale. The *Nineta*-group and some Ankylopterygini s. str. have an elongate sternum VIII+IX in the male, and a variously pronounced elongation of the scape. Ankylopterygini s. str. can be diagnosed by the finely pointed apical palpi, and there are usually no tibial spurs present (except in *Signochrysa*).

REMARKS: Based on the recent phylogenetic hypotheses (Garzón et al. in prep, chapter 1), we here include the genus *Nineta*, and the subgenera *Chrysopidia* and *Chrysotropia* in the tribe Ankylopterygini). The three included taxa form a monophylum (*Nineta*-group) which is sister to

all genera originally placed in Ankylopterygini (*Ankylopteryx*, *Parankylopteryx*, *Retipenna*, *Semachrysa*, and *Signochrysa* = Ankylopterygini sensu stricto) (see chapter 1). Most members of the *Nineta*-group have an elongate sternum VII+IX in the male and often an elongate scape. As in all Ankylopterygini, the tignum and parameres are absent.

Genus *Ankylopteryx* Brauer 1864

(45 species) figure 10.

*Ankylopteryx* Brauer 1864: 899. Type species: *Chrysopa venusta* Hagen 1853, by subsequent designation by Tjeder 1966: 493.

*Ethiochrysa* Fraser 1952: 57. Type species: *Ethiochrysa polychlora* Fraser 1952, by monotypy. Brooks and Barnard 1990: 155 [synonymy under *Ankylopteryx*].

*Sencera* Navás 1925a: 26. Type species: *Sencera scioneura* Navás 1924, by original designation and monotypy. Brooks and Barnard 1990: 157 [as subgenus of *Ankylopteryx*]. **Syn. nov.**

DIAGNOSIS: *Ankylopteryx* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, a strongly broadened basal costal area, which is usually unmarked at the wing base, and an elongate mediuncus, which is clearly detached from the medial arch of the gonarcus.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, or Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on

apical 3 palpomeres, or uniformly pale; maxillary palpus marked on apical palpomere, or uniformly pale; apical palpus finely pointed; labrum indented, narrow, without basal tooth; frons in profile flat; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and matte.

Thorax: prothorax markings fronterolaterally, small spot, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 0-3; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series

diverging, or parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate), rarely regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM, rarely PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP, rarely M; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC, rarely meeting basal *dcc* vein; distal cubital cell (*dcc*) open, rarely closed; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins marked weakly in irregular pattern; wing markings between PsM and PsC, on *dcc*, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi with tarsomere 5 dark; number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; leg unmarked, or with band on tibia.

Abdomen: markings absent, or sparse; setae long, pale; sternum II without stridulatory organ.

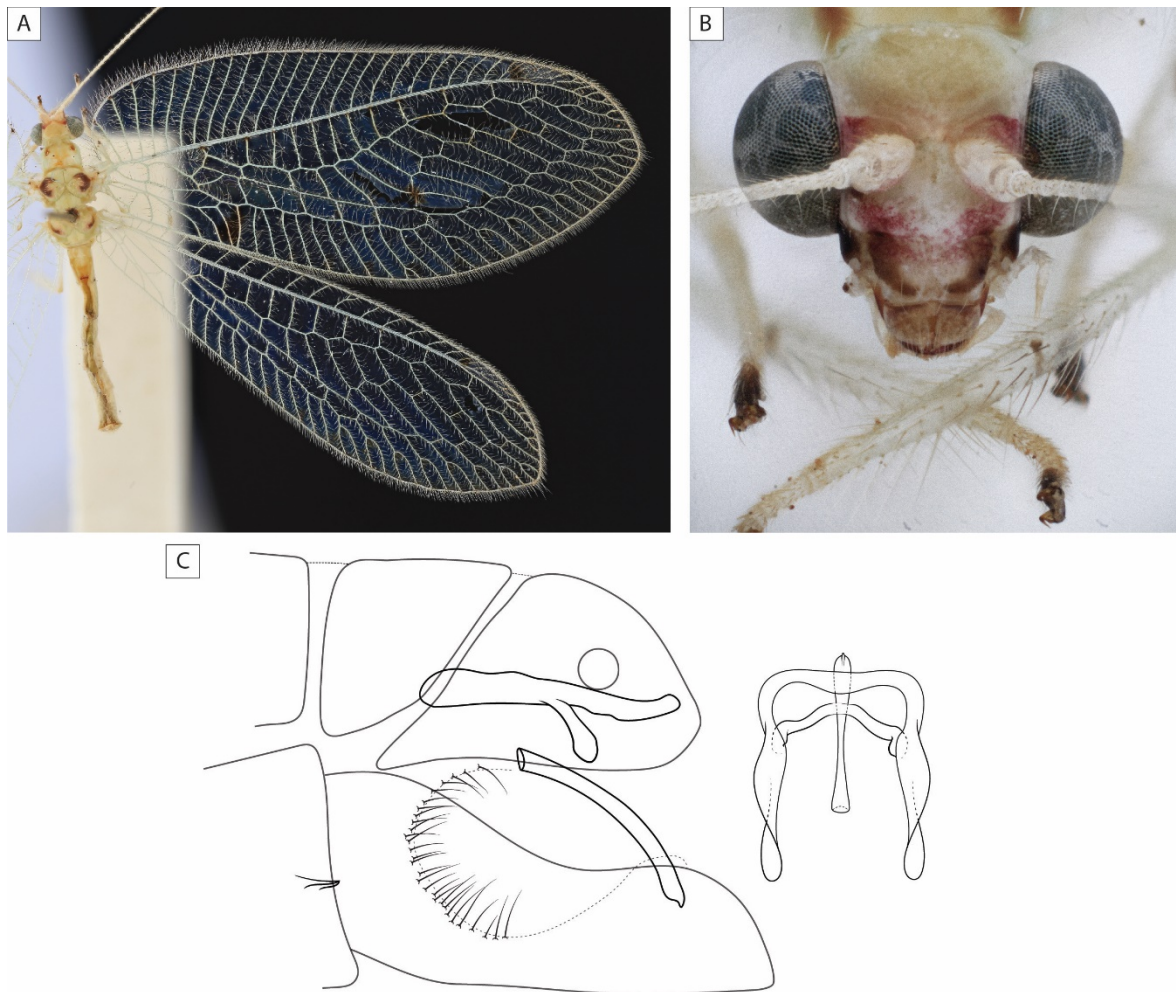
Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale

as long as broad, close to sternum; spermatheca thick; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, or long and arching around mediuncus, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, larger than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent, rarely numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: The four species of the former subgenus *Sencera* have recently been synonymized (Breitkreuz et al. 2015), and the phylogenetic analyses (see chapter 1) have confirmed that this species is well nested within *Ankylopteryx*. We therefore include *Sencera anomala* in *Ankylopteryx*. It is nearly a derived form of the genus, with a missing *im* cell, which is approximated in several other *Ankylopteryx* species, where the *im* cell is somewhat smaller and reduced. *Ankylopteryx* and *Parankylopteryx* are remarkable similar externally, and can only be distinguished by the unmarked tarsi and the small dark marking on the basis of the costa in *Parankylopteryx*, which we have found to be varying within the genus, and sometimes approximated in *Ankylopteryx*. The main difference between the two genera is the detached mediuncus of *Ankylopteryx*, whereas it is closely associated with the median arch of the gonarcus in *Parankylopteryx*. Due to this similarity, it was long suspected that these two genera are closely

related. In recent phylogenetic hypotheses (see chapter 1, and Garzón et al. *in rev*) this could not be confirmed. Larvae of two species are described (*A. collarti* and *A. octopunctata*) and both are debris-carriers (Brooks and Barnard 1990, Hölzel et al. 1990, Tsukaguchi 1995, and Tauber et al. 2014). No insect remains were found in the guts of the adults (Brooks and Barnard 1990).



**Figure 37.** *Ankylopteryx* sp.. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysopidia* Navás 1910

(20 species, 2 subgenera)



REMARKS: We excluded the former subgenus *Anachrysa* from *Chrysopidia*, due to the presence of parameres and a tignum, which is never present in Ankylopterygini. The wing venation, elongate scape, and elongate sternum VIII+ IX, which were the base for its former placement in *Chrysopidia*, can also be found in taxa of Chrysopini, to which its genitalia are more similar (see below, and chapter 1).

Subgenus *Chrysopidia* Navás 1910

(17 species)

*Chrysopidia* Navás 1910a: 54. Type species: *Chrysopidia nigrata* Navás 1910, by monotypy.

DIAGNOSIS: *Chrysopidia* is the only chrysopid subgenus with the combination of the flagellar setae arranged in four rings, three gradate series in the forewing, no integumental markings on the wings, the absence of parameres and tignum, and an elongate sternum VIII+IX in the male, and a medially separated gonarcus.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or rarely red; apical palpus slightly tapered apically, not finely pointed; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; scape marked laterally, or entirely pale, equal to, or greater than 2x width; pedicel marked laterally; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark laterally, or uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length;

frons unmarked, or with small red lateral marking, or with small spot medially on supra-, or intra-antennal frons; vertex raised in profile, markings absent, ornamentation absent.

Thorax: prothorax markings absent, or diffuse and sparse, brown to black, or red, setae pale, predominantly short, thick long setae patches on pronotum absent; mesothorax marked or unmarked, predominantly red; metathorax marked or unmarked; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 3; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal

cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2 or 3; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca thin, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate, with dense setal patch apically; tignum absent; gonarcus medially not fused, membraneously separated, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus or longer, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent.

REMARKS: *Chrysopidia* (*Chrysopidia*) is similar to *Tumeochrysa* and *Nineta*, but can be distinguished from *Nineta* by the presence of three gradate series and from *Tumeochrysa* by the medially separated median arch of the gonarcus in *Chrysopidia*, and the basally extended inner gradates, parallel to PsM in *Tumeochrysa*. The subgenus is one of the few chrysopids with the combination of three gradate series and no parameres or tignum. Besides *Tumeochrysa*, this combination is also present in *Vieira* and *Cacarulla*, which can easily be distinguished from *Chrysopidia* by their general wing venation and markings. Larvae of the subgenus are unknown, and no insect remains were found in the guts of the adults (Brooks and Barnard 1990).

Subgenus *Chrysotropia* Navás 1911

(3 species) figure 11.

*Chrysotropia* Navás 1911: 12. Type species: *Chrysotropia lacroixi* Navás 1911 (= *C. ciliata* Wesmael 1841), by monotypy. Hölzel 1967: 36 [subgenus of *Chrysopa* Leach], Hölzel 1973b: 354 [raised to genus], Brooks and Barnard 1990: 209 [subgenus of *Chrysopidia* Navás].

DIAGNOSIS: *Chrysotropia* is the only chrysopid subgenus with the combination of the flagellar setae arranged in four rings, two gradate series in the forewing, a strongly elongate sternum VIII+IX in the male, the absence of parameres and tignum, an elongate and thin mediuncus, and symmetrical mandibles with a tooth on each side.

DISTRIBUTION: Oriental, or Palaearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, or asymmetrical, with basal tooth, with basal tooth on one side; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex flat in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae dark, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent or present.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches curved between inner and outer gradates; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally

extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, or longitudinal veins pale, crossveins dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*, or apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

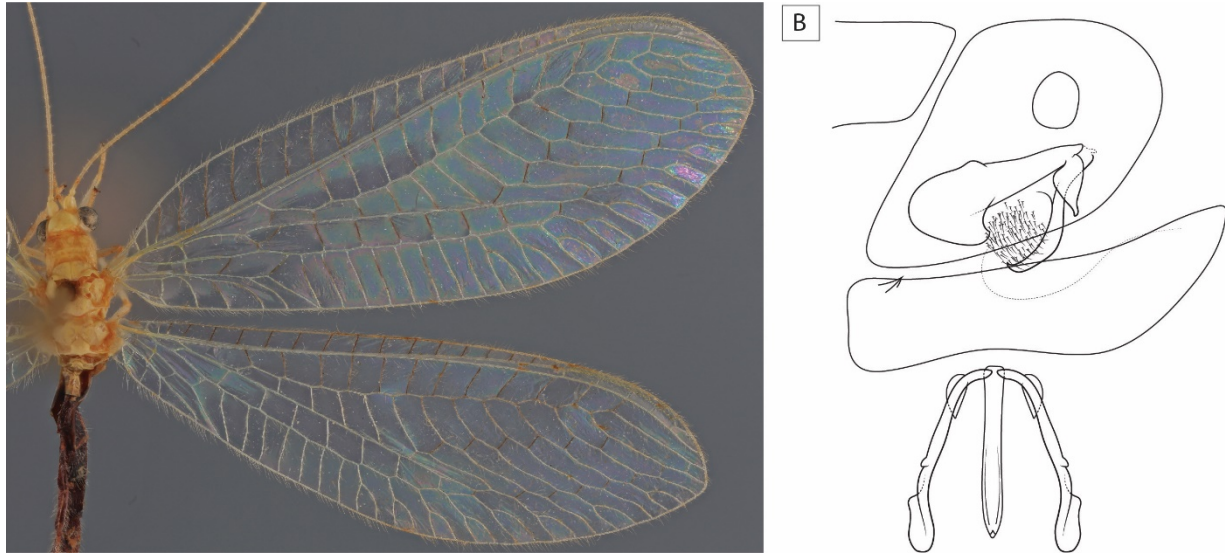
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca average; vela larger than spermatheca, or smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct apically elongate, or normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, with dense setal patch apically; tignum absent; gonarcus medially not fused, membraneously separated, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: The two subgenera *Chrysopidia* and *Chrysotropia* result as sister genera in the latest phylogenetic hypothesis (see chapter 1), but only one species of *Chrysopidia* was included. The largest difference between the two taxa is the presence of an additional gradate series in *Chrysopidia*, but a variation in the number of gradate series within a genus is present in other chrysopid genera. Given the main diagnostic characters above, *Chrysotropia* would key out with *Ungla* and *Borniochrysa*. *Ungla* has a neotropical distribution and it can be distinguished from *Chrysotropia* by its asymmetrical mandibles; additionally, the sternum VII+IX is usually much more elongate in *Chrysotropia*. *Borniochrysa* has a cone like expansion of the male tergum IX + ectoproct, which is absent in *Chrysotropia*, and the mandibles of the former are asymmetrical. Larvae of one species are described (*C. cilliata*) as debris-carrying (Killington 1937, Gepp 1983, Brooks and Barnard 1990, and Tauber et al. 2014). No insect remains were found in the guts of the adults (Brooks and Barnard 1990).



**Figure 38.** *Chrysopidia (Chrysotropia)*. A. *Chrysopidia (Chrysotropia) ciliata* (Wesmael), fore- and hind wing, dorsal view, photomicrograph. B. *Chrysopidia (Chrysotropia) obliquita* (Banks), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Nineta* Navás 1912

(32 species, 2 subgenera)

REMARKS: We here instate *Tumeochrysa* as a subgenus of *Nineta*, based on the results of the recent phylogenetic analysis (see chapter 1). The two subgenera are similar in their elongate sternum VII+IX in the male and the often elongate scape. The members of both subgenera are often large with narrow wings and numerous RP branches.

Subgenus *Nineta* Navás 1912

(18 species) figure 12.

*Nineta* Navás 1912: 98. Type species: *Hemerobius flavus* Scopoli 1763, by original designation.

Banks 1940: 187 [subgenus of *Chrysopa* Leach], Tjeder 1966: 345 [reinstated as genus].



*Parachrysa* Nakahara 1915: 121. Type species: *Nothochrysa olivacea* Gerstaecker 1894, by original designation and monotypy. Kuwayama 1962 [synonymy under *Nineta*].

DIAGNOSIS: *Nineta* is the only chrysopid subgenus with the combination of the flagellar setae arranged in four rings, two gradate series in the forewing, and the absence of parameres and tignum, and especially a strongly elongate and sternum VIII+IX in the male, which is apically curved towards dorsal, bearing a patch of long setae.

DISTRIBUTION: Nearctic oriental, or Palaearctic.

DESCRIPTION: body colored pale green. large

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, broad, regular shaped, with basal tooth; frons in profile flat, or raised laterally; scape unmarked, equal to, or greater than 2x width, or less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or uniformly brown; carina on dorsal torulus margin absent or present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity denser laterally, setae dark or pale, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale,

predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6, or >7; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6, or >7; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9, or 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

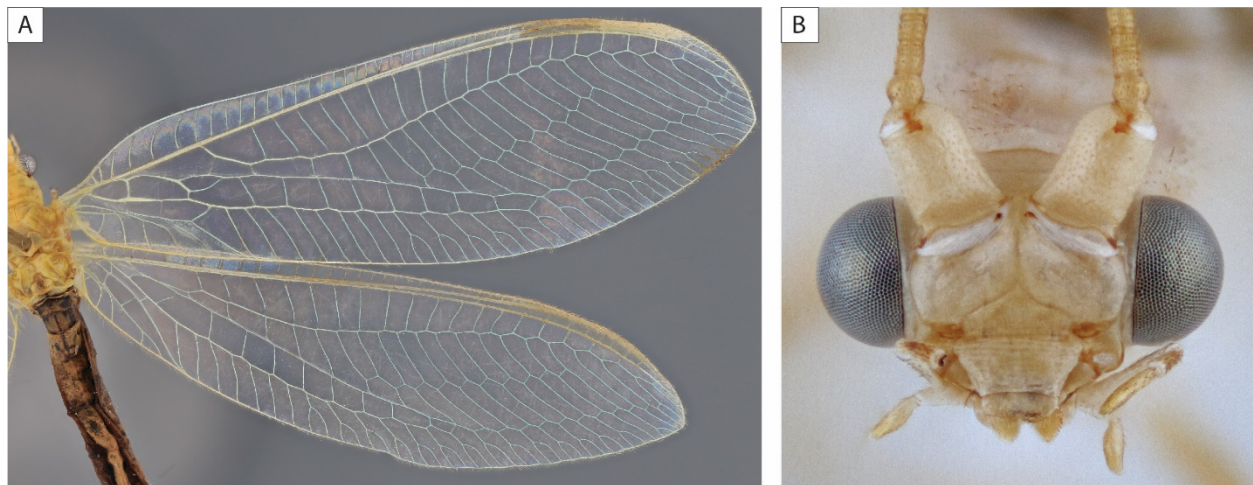
Abdomen: markings absent, or sparse; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, close to sternum; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct apically elongate; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent or present apically; ventral apodeme regular; sterna VIII and IX fused, elongate and curved towards dorsal apically, or with single apical expansion, with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with broad medial projection, or with 2 forward projecting horns medially, lateral arms apically flat expanded, or strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus attached to gonarcus, without membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process

absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent or present.

REMARKS: Within its distribution *Nineta* is often quite easily recognizable by its general habitus, being a comparatively large lacewing, with numerous RP branches and unmarked wings, but pinpointing concrete diagnostic characters for all species, which do not occur in this combination in other genera is more complicated. The vast majority of species has a strongly upwards curved sternum VIII+IX in the male. It is also present in *Tumeochrysa* and *Anomalochrysa*, but these genera have more than two gradate series in the forewing, as well as approximated in *Chrysopidia* and *Mallada*, where the curvature is not as expressed. It can also be distinguished from *Anomalochrysa* and *Mallada* by the presence of parameres in these genera. The larvae of several species have been described, and are all naked and not debris-carrying (Brooks and Barnard 1990, and Tauber et al. 2014, and cited literature within both). No insect remains were found in the guts of the adults (Brooks and Barnard 1990).



**Figure 39.** *Nineta*. A. *Nineta flava* (Scopoli) fore- and hind wing, dorsal view, photomicrograph. B. *Nineta vittata* (Wesmael), head, frontal view, photomicrograph

Subgenus *Tumeochrysa* Needham 1909 **stat. nov.**

(14 species) figure 1C.

*Tumeochrysa* Needham 1909: 204. Type species: *Tumeochrysa indica* Needham 1909, by original designation and monotypy.

*Chrysoplecta* Navás 1910a: 55. Type species: *Chrysoplecta immaculata* Navás 1910, by monotypy. Banks 1940: 187 [synonymy under *Tumeochrysa*].

DIAGNOSIS: *Tumeochrysa* is the only chrysopid subgenus with the combination of the flagellar setae arranged in four rings, three or more gradate series in the forewing, where the inner gradates are usually extended basally parallel to PsM, no integumental markings on the wings, and the absence of parameres and tignum, and a medially fused and sclerotized gonarcus.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus marked on apical 3 palpomeres, or uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, broad, regular shaped, without basal tooth; frons in profile flat; scape unmarked, equal to, or greater than 2x width, or less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity

uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity dense, setae dark, predominantly short; metathorax marked or unmarked, pilosity sparse, setae dark, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: >7; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 3 or 4; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC close; number of crossveins between PsM and PsC: 10-14, or 15 or more; *mamp1* irregular (*im* cell present), triangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuA forked present; CuP forked at *c2*; vein

1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale, or dark on gradates; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: >7; number of gradate series: 3 or 4; number of crossveins between PsM and PsC: 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long or short, dark or pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded, or with long and narrow apical projection; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate and curved towards dorsal apically, without strong apical spines or dense setae, or with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, or with 2 forward projecting lobes medially, lateral arms apically flat expanded; entoprocessus long, positioned at

the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, or closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, larger than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: We here included *Tumeochrysa* as a subgenus of *Nineta* due to the similarity of the terminalia, genitalia and elongation of the scape. Both are also fairly large lacewing, with numerous RP branches in the forewing, but *Tumeochrysa* has more gradate series than *Nineta*. Brooks and Barnard (1990) pointed out the similarities between the two genera and suggested a close relationship. This was confirmed in our phylogenetic analysis, including multiple species of both genera (see chapter 1). In the different analyses *Tumeochrysa* resulted either as sister or more often within *Nineta*, so that we are confident to place it as a subgenus, but suggest further investigation in these two genera to assess whether *Tumeochrysa* is a valid genus. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Parankylopteryx* Tjeder 1966

(8 species) figure 1L, 13.

*Parankylopteryx* Tjeder 1966: 508 [as subgenus of *Ankylopteryx* Brauer]. Type species:

*Ankylopteryx neavei* Navás 1913, by original designation and monotypy. Brooks and Barnard 1990: 157 [raised to genus level].



DIAGNOSIS: *Parankylopteryx* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, a strongly broadened basal costal area, which is usually marked at the wing base, and an elongate mediuncus, which is closely associated with the medial arch of the gonarcus, by a visible membrane.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus finely pointed; labrum indented; mandibles symmetrical, narrow, without basal tooth; frons in profile flat; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin absent; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and matte.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal

field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 0-3; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked weakly in irregular pattern, or dark along integumental marking pattern; wing markings between PsM and PsC, on *dcc*, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent or present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0;

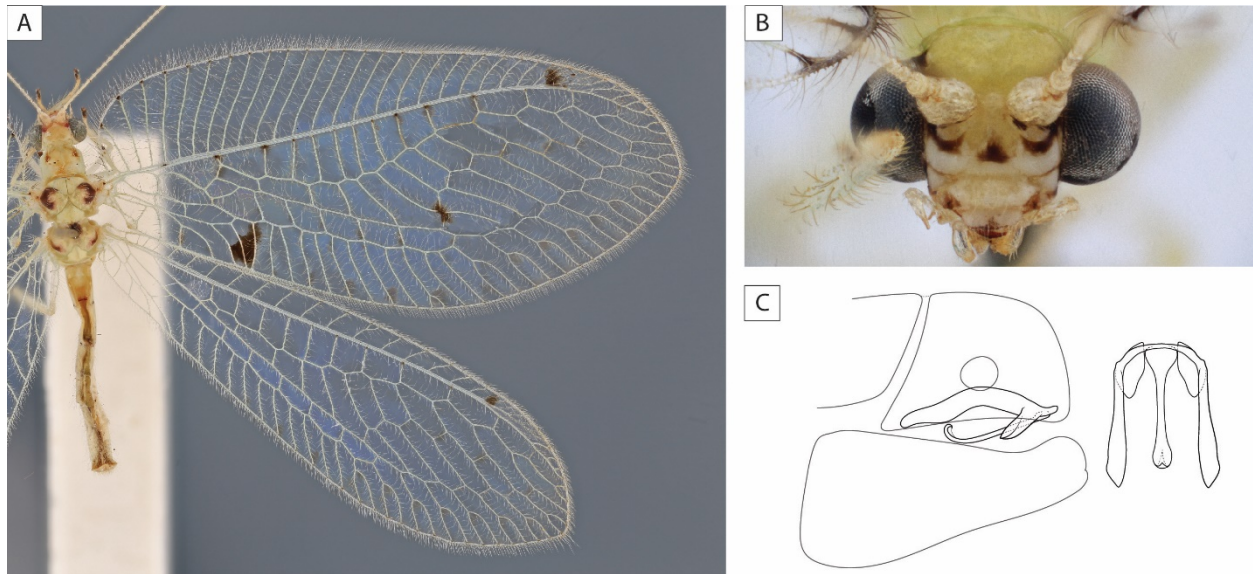
metatibia on inner surface smooth; femoral setae long.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average, surface smooth; vela smaller than spermatheca; spermathecal duct very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: As discussed above (see *Ankylopteryx* remarks) *Parankylopteryx* and *Ankylopteryx* are externally very similar but can be distinguished by their genitalia, and most often by their coloration of the costa at the wing base and the tarsi. In the recent phylogenetic hypotheses *Parankylopteryx* results as sister genus to *Retipenna*, but we were not able to find characters to support this relationship. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 40.** *Parankylopteryx*. A. *Parankylopteryx polystictia* Navás, fore- and hind wing, dorsal view, photomicrograph. B. *Parankylopteryx polystictia*, head, frontal view, photomicrograph. C. *Parankylopteryx* sp., male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Retipenna* Brooks 1986

(16 species) figure 14.

*Retipenna* Brooks 1986: 36. Type species: *Chrysopa notata* Navás 1910, by original designation.

DIAGNOSIS: *Retipenna* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, two gradate series in the forewing, finely pointed palpaе, a dorsally projecting ventral apodeme in the male terminalia, a mediuncus, that is clearly detached from the gonarcus, and a medially separated gonarcus.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or brown; labial palpus marked on

apical palpomere, or uniformly pale; maxillary palpus uniformly pale; apical palpus finely pointed; labrum indented; mandibles symmetrical, narrow, without basal tooth; frons in profile flat, rarely raised laterally; scape marked dorsally, or entirely pale, less than 1.5x as long as wide; pedicel marked basally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, rarely present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or fronterolaterally, small spot, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved, rarely almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series

diverging; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, but in some specimens almost open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, longitudinal veins pale, crossveins dark or veins dark basally, pale distally; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked), or with tarsomere 5 dark; number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

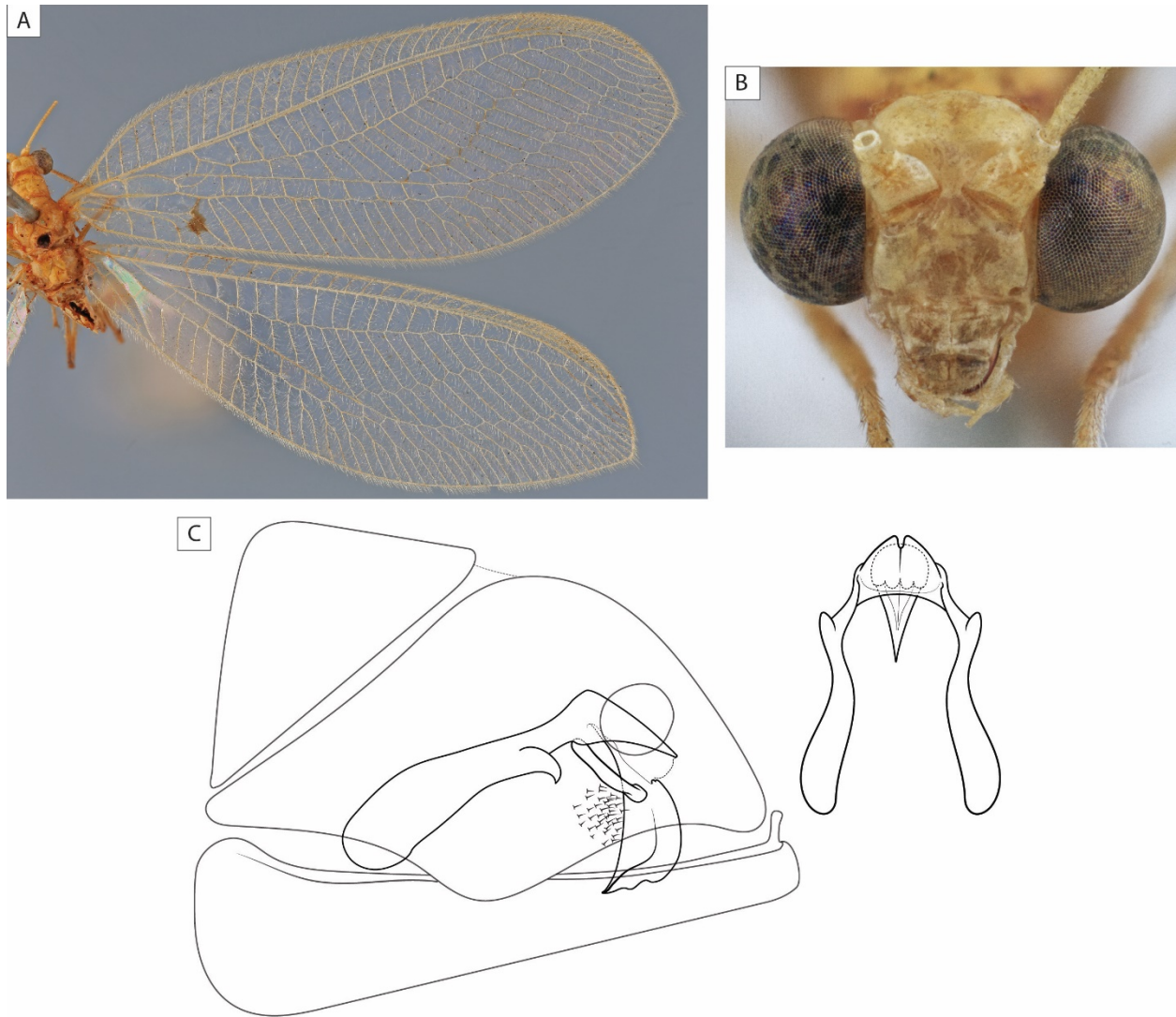
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or extended ventrally backwards, close to sternum; spermatheca average, surface

smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled, or very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme with dorsal process; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially not fused, membraneously separated, median arch with 2 forward projecting lobes medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms present; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: Although *Retipenna* is a member of Ankylopterygini, most characters of the genus are very similar to *Chrysopa*. It can be distinguished from this genus, by several characters, such as the finely pointed palpi, the medially separated gonarcus, and the diverging (and not parallel) gradate series in the forewing. *Retipenna* has broader hind wings than the other Ankylopterygini, in which it is usually thinner than in other Chrysopidae. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 41.** *Retipenna*. A. *Retipenna grahami* (Banks), fore- and hind wing, dorsal view, photomicrograph. B. *Retipenna grahami* (Banks), head, frontal view, photomicrograph. C. *Retipenna variegata* Brooks, male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Semachrysa* Brooks 1938

(20 species) figure 15.

*Indochrysa* Banks 1938a: 225. [Unavailable name: no type species designated.]

*Semachrysa* Brooks 1983: 6. Type species: *Semachrysa minuta* Brooks 1983, by original designation.



DIAGNOSIS: *Semachrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, finely pointed apical palpaе, three dark spots on the frons, a strongly broadened basal costal area, few gonosetae present, and the base of the mediuncus associated with the apex of the entoprocessi.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3 palpomeres, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, or uniformly marked; apical palpus finely pointed; labrum straight; mandibles symmetrical, narrow, without basal tooth; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, or short, surface smooth and matte, or unevenly textured.

Thorax: prothorax markings absent, or fronterolaterally, small spot, brown to black, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series diverging; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale, marked weakly in irregular pattern, or dark along integumental marking pattern; wing markings absent, on *dcc*, on inner gradates, along RS, or on basal third of wing.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2;

maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

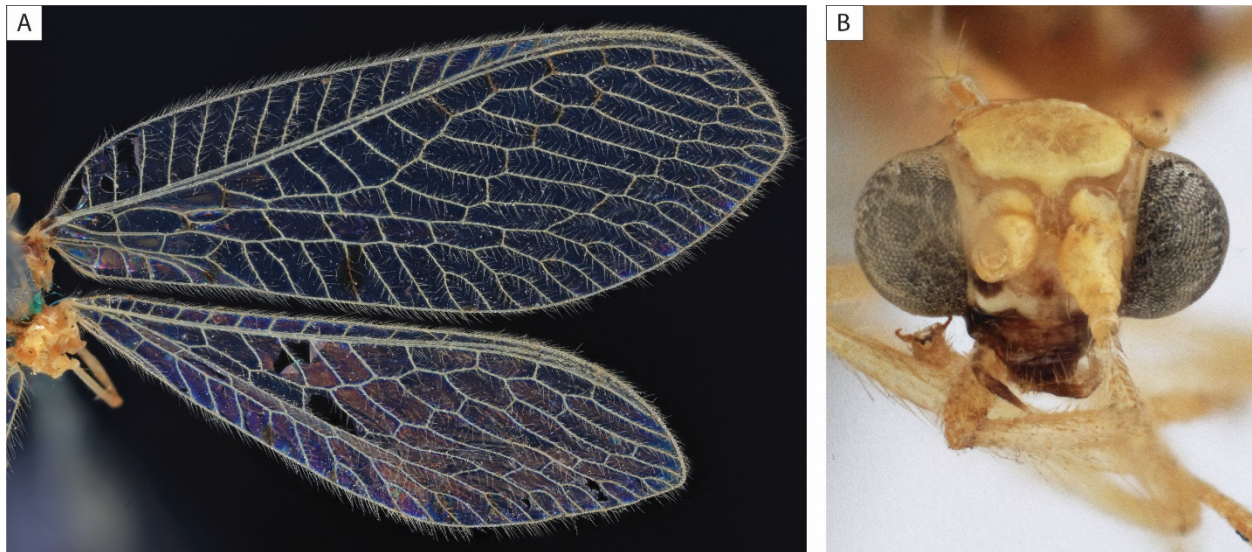
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent, or sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII apically exerted, pointy, or simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca small, surface smooth; vela about same size as spermatheca, or smaller than spermatheca; spermathecal duct very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular, or with dorsal process; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long and arching around mediuncus, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, base at apex of entoprocessi, elongate and laterally expanded, shorter or about as long as lateral arms of gonarcus, mediuncus process present as apical fork in horizontal plane; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi absent

REMARKS: The wings of *Semachrysa* are similar to those of *Ankylopteryx* and *Parankylopteryx*, due to their broad costal area at the wing base, but they are usually not marked as in the other two genera. The costal areal is not as broad as in *Ankylopteryx* and *Parankylopteryx*. It can be distinguished from the two genera by the male genitalia, where the mediuncus is membraneously associated with the gonarcus, but somewhat removed, and seemingly articulating with the apices of the entoprocessi. Additionally, there are less gonosetae present in *Semachrysa*, with usually two on each side of the mediuncus. The larvae are debris-carriers (Tauber et al. 2014), and no insect remains were found in the guts of the adults (Brooks and Barnard 1990).



**Figure 42.** *Semachrysa matsumurae* (Okomoto). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Signochrysa* Brooks and Barnard 1990

(9 species) figure 16.

*Signochrysa* Brooks and Barnard 1990: 162. Type species: *Leucochrysa mira* Navás 1913.

DIAGNOSIS: *Signochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, finely pointed apical palpa, a narrow basal costal area, a strongly elongate sternum VIII+IX in the male, which is apically curved towards dorsal, and a patch of long setae pointing apically on the apex of the ectoproct. It is also the only ankylopterygine with *microtholi* present.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3 palpomeres, or uniformly marked; maxillary palpus marked on apical 2 palpomeres, or uniformly pale; apical palpus finely pointed; labrum indented; mandibles symmetrical, narrow, without basal tooth; frons in profile raised laterally; scape marked dorsally, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked, or with small spot medially on supra-, or intra-antennal frons; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings in lateral longitudinal stripe, or fronterolaterally, small spot, brown to black, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or barely open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, scarcely dark or dark along integumental marking pattern; wing markings between PsM and PsC, on *dcc*, on inner gradates, along RS, and along apical margin.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp

crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

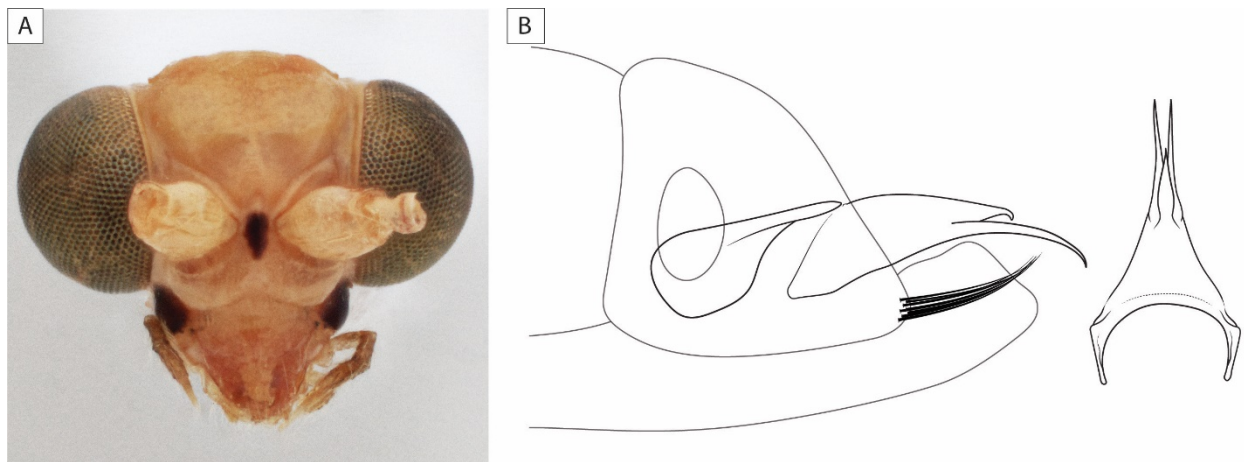
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca thin, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct tapering towards apicoventrally; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent, patch of long setae present apicoventrally; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, larger than lateral arms of gonarcus, mediuncus process present as apical forks in horizontal plane and vertical plane; parameres absent; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi present.

REMARKS: *Signochrysa* is a genus with very distinctive male terminalia and genitalia. Its elongate sternum VIII+IX reminds of the terminalia of the *Nineta*-group, but *Signochrysa* has the

typically pointed palps of *Ankylopterygini sensu stricto*. The genus has a unique mediuncus form, with a broadened base, and the apex forked in a horizontal and vertical plane, leading to a trifurcate apex, in which the dorsal, unpaired process is shorter than the paired, ventrally positioned and elongate processes. Additionally, it can be distinguished from all other *Ankylopterygini* by the presence of microtholi in the male. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 43.** *Signochrysa* sp. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Tribe **Belonopterygini** Navás 1913

(159 species, 14 genera)

Belonopterygini Navás 1913a: 163. Type genus: *Belonopteryx* Gerstaecker 1863.

Nadivini Banks 1943: 100. Type genus: *Nadiva* Navás 1919. Brooks and Barnard 1990: 163  
[synonymy under Belonopterygini].

Italochrysinini Hölzel 1970: 51. Type genus: *Italochrysa* Principi 1946. Adams and Penny 1986:  
120 [synonymy under Belonopterygini].



DIAGNOSIS: In most Belonopterygini the first cubital cell (*c1*) is longer than the second (*c2*), which is not the case in other Chrysopidae. Few Belonopterygini have a somewhat shorter *c1*, but can be recognized by the additional characters shared in the tribe: short flagellomeres, short flagellar setae, usually no entoprocessi present, a praegenitale is present in most, and parameres are present in most genera, often large and paired. These character states can be reversed throughout the lineages of Belonopterygini.

REMARKS: Belonopterygini are in need of a detailed revision, based on a phylogenetic analysis including molecular data for all genera, and numerous species of *Italochrysa*, which is likely to be paraphyletic in regard to many other belonopterygines (see chapter 1). The presence and state of the praegenitale should be further examined, as there seem to be several intermediate states in Belonopterygini, as well as in Leucochrysinini and possibly Chrysopini (e.g., *Kymachrysa*, or *Chrysopa*).

Genus *Abachrysa* Banks 1938

(1 species) figure 17.

*Abachrysa* Banks 1938b: 75. Type species: *Chrysopa eureka* Banks 1931, by original designation and monotypy.

DIAGNOSIS: *Abachrysa* is the only chrysopid genus with a whitish yellow body color, marked with distinct black spots throughout the body. Apart from its unique coloration it can be recognized by the combination of short flagellomeres (less than 1.5x as long as wide), paired and

amedially separated, rod-shaped parameres, and a triangular im cell, without a crossvein.

DISTRIBUTION: Nearctic.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical 2 palpomeres; apical palpus slightly tapered apically, not finely pointed; labrum indented, unknown; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum dark basally; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in spots, brown to black, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP

almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins marked strongly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely dark; number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg extensively marked.

Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.

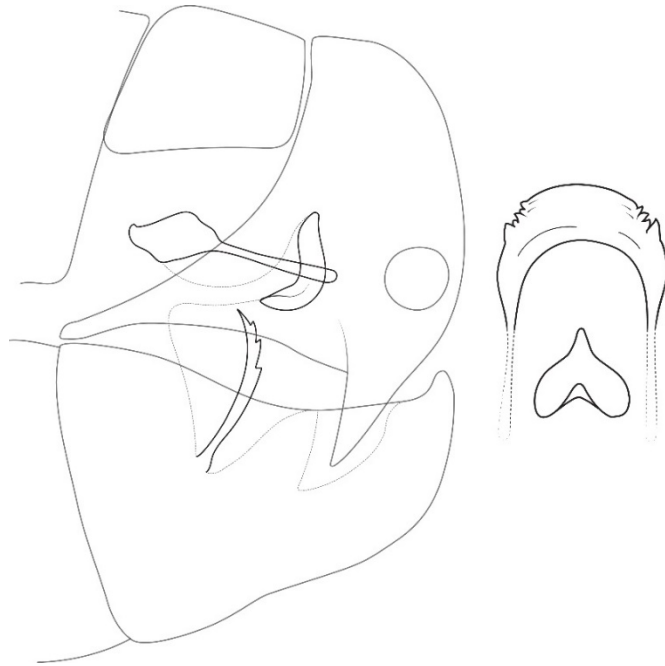
Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present within sternum; small sclerotized plate between subgenitale and sternum

absent; subgenitale broader than long, on narrow elongate membranous structure; spermatheca thick; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX separate, with con-like invagination for dorsal structure, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus clearly separate from gonarcus, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as two sclerites medially connected membraneously, shaped as paired simple rods, pointing towards apex, about as long as gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Abachrysa* is one of the most recognizable chrysopids, with its unique markings, and is the only belonopterygine present in the Nearctic (i.e., Southeastern USA). According to our phylogenetic analyses, (see chapter 1) it is sister to the Australian *Calochrysa*, which have similarly shaped parameres, and a triangular *im* cell, but the coloration of these two is very different. As Brooks and Barnard (1990) pointed out, the apical most flagellar ring on each flagellomere is often less pronounced in *Abachrysa*, *Belonopteryx*, and *Nacarina*, bearing fewer setae and suggested a close relationship between these genera. We can confirm the reduced setae in the apical ring of these genera, and we were able to find this condition in other Belonopterygini, such as *Calochrysa*, *Dysochrysa*, and possibly *Vieira*. The larvae of *Abachrysa* are unknown, and

no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 44.** *Abachrysa eureka* (Banks), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Belonopteryx* Gerstaecker 1863

(1 species) figure 18.

*Belonopteryx* Gerstaecker 1863: 169. Type species: *Belonopteryx arteriosa* Gerstaecker 1863, by monotypy.

DIAGNOSIS: *Belonopteryx* is the only chrysopid genus with the combination of narrow, elongate, and apically pointed wings, with the *mamp1* cell regular (*im* absent), and markings along the outer gradates as well as along RP.

DISTRIBUTION: Neotropical.

#### DESCRIPTION:

Head: orange; genal marking brown; labial palpus marked on apical 2 palpomeres; maxillary palpus uniformly marked; apical palpus truncated apically; labrum indented, broad, regular shaped, with basal tooth; frons in profile raised laterally; scape marked dorsally, less than 1.5x as long as wide; pedicel marked apically; flagellar setal arrangement in 2-3 rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum uniformly dark; frons unmarked; carina on dorsal torulus margin present, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in lateral longitudinal stripe, brown to black, pilosity uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity dense, setae pale, predominantly long; metathorax marked, pilosity dense, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent, or rarely present, between few grossveins; number of gradate series: 2; number of gradate crossveins approximately same number in each

series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; *mamp1* regular (*im cell* absent); 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked strongly in irregular pattern; wing markings on inner gradates, and along RS.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 10-14; maximum number of fused veins on PsM: 2; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg with spots on femora.

Abdomen: markings abundant, or dorsal and lateral longitudinal stripe; setae short, pale; sternum II without stridulatory organ.

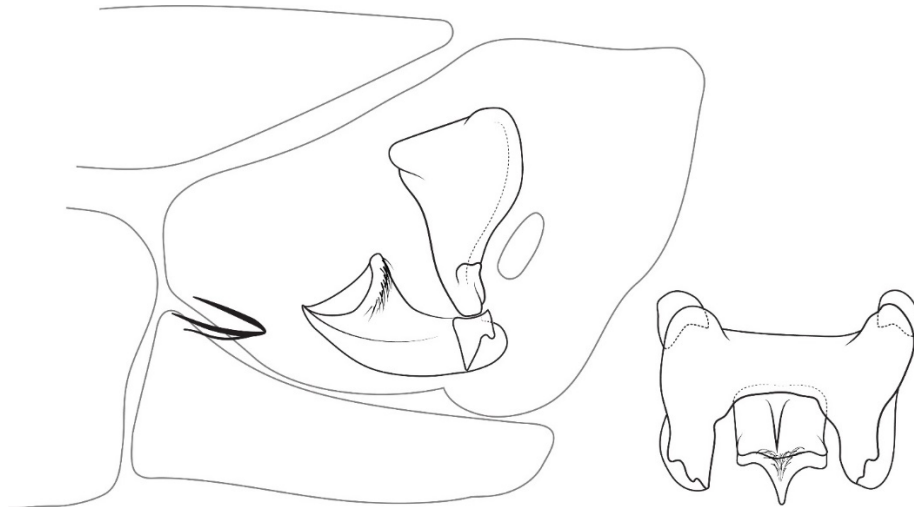
Female genitalia: praegenitale absent; small sclerotized plate between subgenitale and sternum absent; spermatheca large, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused;

ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or tapering medioapically, about as long as lateral arms of gonarcus, mediuncus process present as ventral extension with setae; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi present.

REMARKS: *Belonopteryx* is a very rare and monotypic genus, with only three known specimens present in collections. It is easily recognizable by its – for chrysopids – unusually elongate wings marked with two longitudinal bands. In our phylogenetic analysis (see chapter 1) the genus results within *Italochrysa*, when included. The relationships within Belonopterygini are often poorly supported and the lack of molecular data for *Belonopteryx* leads to an unstable placement of this genus. Brooks and Barnard (1990) suggested a close relationship to *Abachrysa* and *Nacarina* due to the reduced number of setae in the apical flagellar ring or each flagellomere in these genera. This relationship is possible, also due to the absence of parameres in both, *Belonopteryx* and *Nacarina*, but needs detailed investigation, because we found the reduced number of flagellar setae in further belonopterygine genera. The larvae of *Belonopteryx* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).





**Figure 45.** *Belonopteryx arteriosa* Gerstaecker, male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Calochrysa* Banks 1943

(1 species) figure 19.

*Calochrysa* Banks 1943: 100. Type species: *Chryopa extranea* Esben-Petersen 1917, by original designation and monotypy.

DIAGNOSIS: *Calochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, *c1* longer than *c2*, and CuP forked at *dcc* (not at *c2*, as in most Chrysopidae), and no thick spines at the apex of sternum VIII+IX in the male.

DISTRIBUTION: Australasian, Oceanian.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented;

mandibles symmetrical, with basal tooth on each side; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum dark distally; antenna shorter than, or equal to forewing length; frons with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in lateral longitudinal stripe, brown to black, pilosity denser laterally, setae dark, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly short; metathorax marked, pilosity sparse, setae dark, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal

to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *dcc*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked strongly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

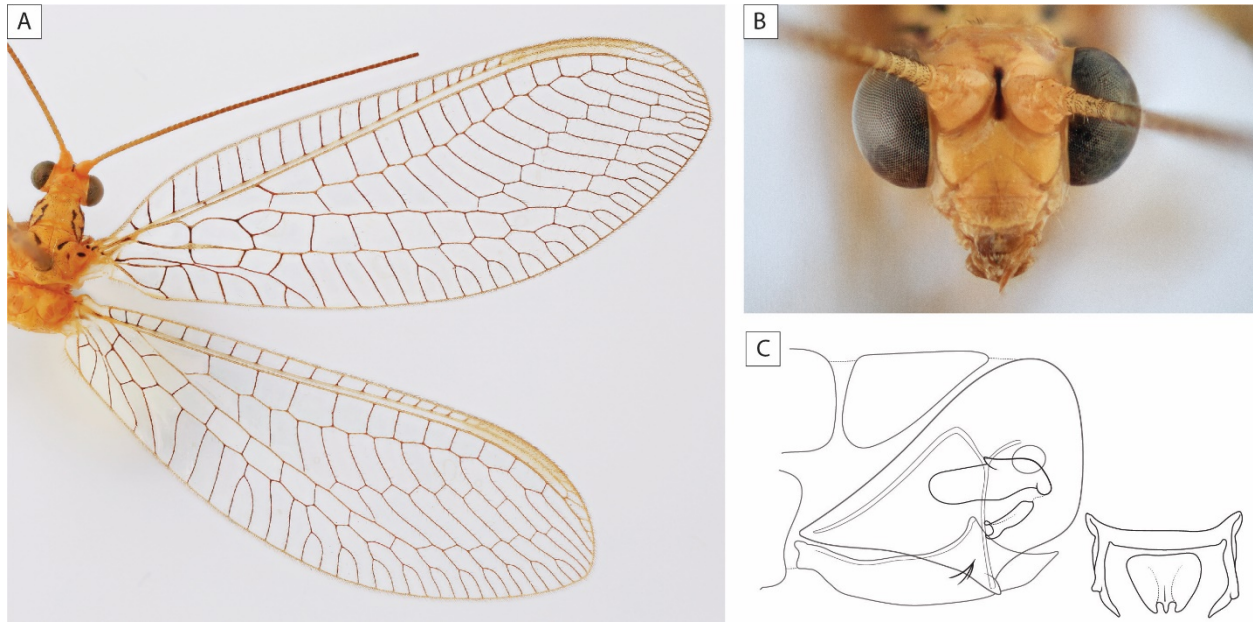
Abdomen: markings sparse; setae short, dark; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present within sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, on broad membranous structure; spermatheca average; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme with ventral process; tergum IX and ectoproct fused; ectoproct with ventral lobes; dorsal invagination between ectoprocts shallow; thick spines on

ectoproct absent, patch of long setae absent; ventral apodeme with dorsal process; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent (or present, arranged as two sclerites medially connected membraneously, shaped as paired, simple rods, basally expanded, opened towards apex, longer than gonarcus, positioned ventrally, in sternum 9; see remarks); gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: Brooks and Barnard (1990) described the parameres as present and shaped as long paired rods in *Calochrysa*. We were not able to find parameres in the material present, and New (1980) did not mention a ventral structure. It is possible that the specimens described by Brooks and Barnard (1990), New and in this study are not from the same species, but all are otherwise identical. Although not mentioning parameres, New (1980) stated that the tignum is present in this genus, which neither Brooks and Barnard (1990), nor this study could confirm. The sex of the type is not stated in the original description, but if it is a male, the genitalia should be examined to assess the presence of parameres. *Calochrysa* and *Chrysaloyisia* are the only belonopterygines in which CuP is forked at *dcc*, which could suggest a close relationship. The parameres are absent in both genera, and the gonarcus is similar, but *Calochrysa* is significantly smaller than *Chrysaloyisia*, and the latter is distributed in the afrotropics. The larvae are debris-carrying (New 1986, Tauber et al. 2014), and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 46.** *Calochrysa extranea* (Esben-Petersen). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysacanthia* Lacroix 1923

(4 species) figure 20.

*Chrysacanthia* Lacroix 1923: 120. Type species: *Chrysacanthia esbeniana* Lacroix 1923, by monotypy.

*Nesochrysa* Fraser 1951: 29, nomen praeoccupatum (nec *Nesochrysa* Navás 1910). Type species: *Nesochrysa varicella* Fraser 1951, by monotypy. Fraser 1955: 134 [synonymy under *Glenochrysa* Esben-Petersen, and homonym of *Nesochrysa* Navás 1910], Brooks and Barnard 1990: 168 [synonymy under *Chrysacanthia*].

DIAGNOSIS: *Chrysacanthia* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, *c1* longer than *c2*, and a small conical process medially at

the posterior margin of sternum VII in the male and medially in the female, bearing an additional apical pointing expansion.

DISTRIBUTION: Afrotropical, or Oriental.

DESCRIPTION: general body colored brown.

Head: colored same as body; genal marking brown; labial palpus marked on apical 2 palpomeres; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked completely, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna longer than forewing length; frons uniformly brown; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface unevenly textured.

Thorax: prothorax markings continuous, brown to black, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6;

tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA basal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked weakly in irregular pattern; wing markings between PsM and PsC, on *dcc*, on inner gradates, and along RS.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg with band on tibia.

Abdomen: markings white in basal half, dark brown in apical half; setae short; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII with small subapical cone ventrally; praegenitale present within sternum; subgenitale broader than long; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; sternum VIII with small process along posteromedial margin; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute, secondary process on lateral arms absent; mediuncus closely associated with gonarcus, with membranous connection, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as two sclerites medially connected membraneously, shaped as paired simple rods, often expanded at base, opened towards apex, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae present apically on ectoproct; microtholi absent.

REMARKS: *Chrysacanthia* has distinctively marked wings (spotted), which is common in Leucochrysini, but all other characters are in accordance with Belonopterygini (such as the presence of the large parameres, *c1* longer than *c2*, or short flagellomeres and flagellar setae). Apart of *Vieira*, it is the only belonopterygine, with strongly marked wings. *Oyochrysa* is similar to *Chrysacanthia*, but the wing markings are not as extensive as in *Chrysacanthia* and *Vieira*, and it can be distinguished from *Chrysacanthia* by the different genitalia (especially the shape of the parameres). Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).





**Figure 47.** *Chrysacanthia hainana* (Yang and Yang) A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Chrysaloyisia* Navás 1928

(1 species) figure 21.

*Chrysaloyisia* Navás 1928: 87. Type species: *Chrysaloyisia somalica* Navás 1928, by original designation and monotypy.

DIAGNOSIS: *Chrysaloyisia* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, short flagellomeres and flagellar setae, *c1* longer than *c2*, CuP forked at *dcc*, and thick spines at the apex of sternum VIII+IX in the male.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked;

flagellar setal arrangement in four rings; flagellomeres as wide as long or shorter; flagellar setae shorter than flagellomere width; flagellum uniformly pale; antenna longer than forewing length; frons with unbroken band; carina on dorsal torulus margin absent; vertex flat in profile, markings present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, pilosity denser laterally, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity dense, setae dark, predominantly short; metathorax unmarked, pilosity sparse, setae dark, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins

on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *dcc*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins longitudinal veins pale, crossveins dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: unknown.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, apically with three lobes bearing thick spines; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus

process absent; gonosaccus membrane thickened ventrally of gonarcus; parameres absent; gonosetae sparsely present (<10); gonocristae present apically on sternum IX; microtholi absent.

REMARKS: *Chrysaloysia* and *Calochrysa* are the only belonopterygine genera in which CuP is forked at *dcc*. The two genera can be distinguished by the presence of the prominent thick spines, positioned on three small lobes on the apex of sternum VIII+IX in the male. Brooks and Barnard (1990) described the parameres as absent, but suggested that they were probably destroyed and not conserved in the dissection. The male specimens examined here did not have parameres. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 48.** *Chrysaloysia somalica* Navás. A. Fore- and hind wing, dorsal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Dysochrysa* Tjeder 1966

(2 species) figure 22.

*Dysochrysa* Tjeder 1966: 335. Type species: *Dysochrysa furcata* Tjeder 1966, by original designation.

DIAGNOSIS: *Dysochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, *c1* longer than *c2*, usually a triangular *im* cell, and parameres, that are fused medioapically (towards the apex of the abdomen) and opened towards the base.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape unmarked; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres as wide as long, or shorter; flagellum uniformly pale; antenna longer than forewing length; frons with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field

absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2 or with an additional medial, irregularly arranged series; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate) (rarely quadrangular, with crossvein); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1;

metatibia on inner surface smooth; femoral setae short; leg unmarked.

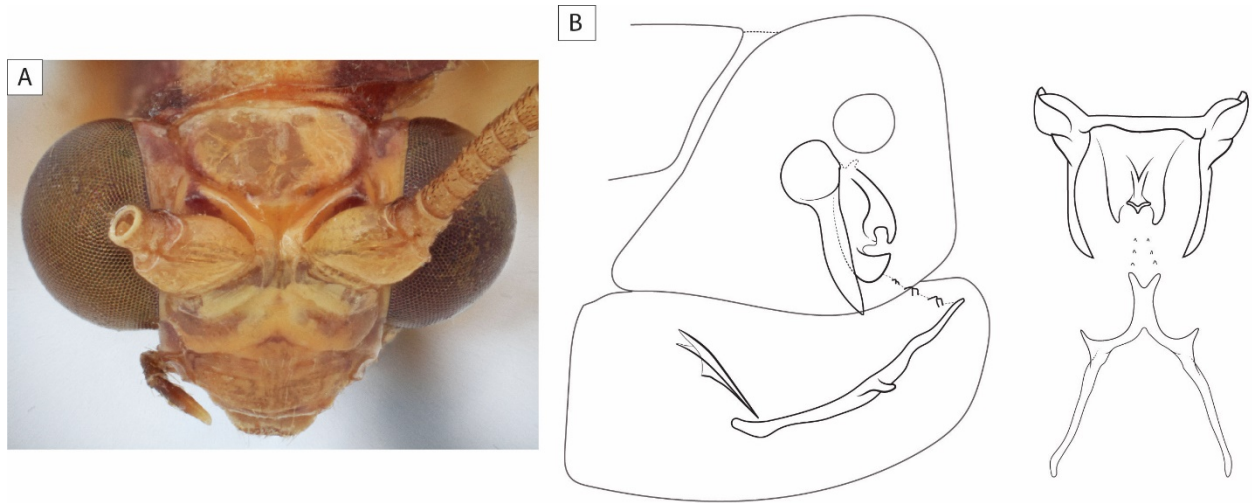
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present within sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca elongate, surface smooth; vela larger than spermatheca; spermathecal duct long and strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as lateral sclerotized lobes; parameres present, arranged as single sclerite, shaped as thin arch, with a forked process medio-apically and small expansions apico-laterally, opened towards base, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi present.

REMARKS: *Dychochrysa* can externally be mistaken as an *Italochrysa*, but is distinguishable by the male genitalia. Brooka and Barnard (1990) mention the high possibility that the two species of the genus are conspecific. *Dysochrysa* is described to have a triangular, but we have collected specimens with a quadrangular on one or both wings in South Africa, so this character seems to be somewhat variable in the genus. Their larvae are unknown, and no insect

remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 49.** *Dysochrysa furcata* Tjeder. A. Fore- and hind wing, dorsal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Evanochrysa* Brooks and Barnard 1990

(3 species) figure 23.

*Evanochrysa* Brooks and Barnard 1990: 172. Type species: *Italochrysa evanescens* McLachlan 1869.

DIAGNOSIS: *Evanochrysa* is the only chrysopid species with the combination of the flagellar setae arranged in four rings, and shorter than the flagellomere width, *c1* longer than *c2*, wing markings absent, parameres absent, and the praegenitale present in the female.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary



palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark distally, or uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, continuous, or in lateral longitudinal stripe, brown to black, or red, pilosity denser laterally, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate

series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9, or 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

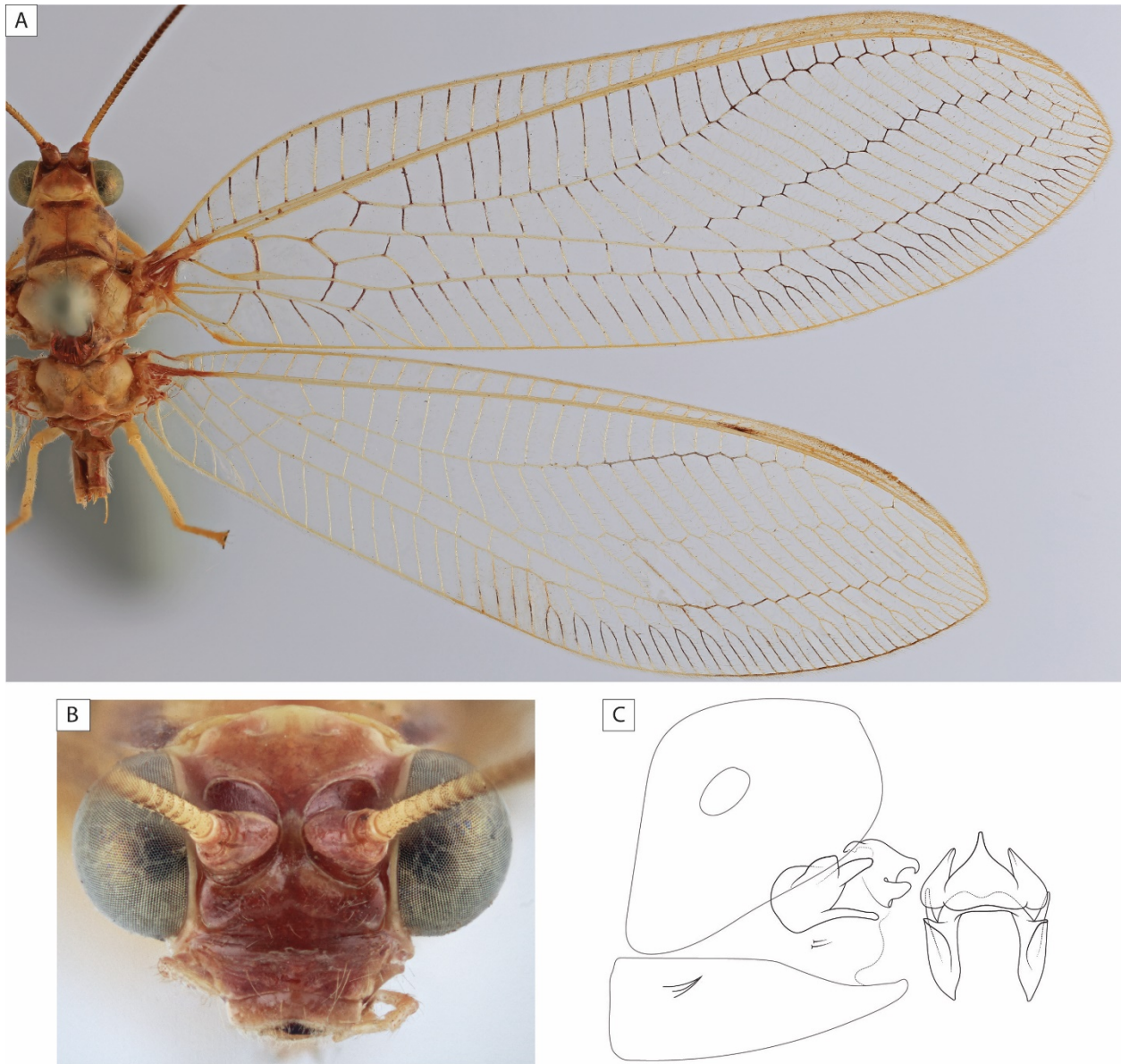
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent, or sparse; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present on apex of sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca average, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as lateral sclerotized lobes; parameres absent; gonosetae sparsely present (<10); gonocristae present apically on sternum IX; microtholi present.

REMARKS: *Evanochrysa* is a large and robust lacewing, which is externally similar to *Italochrysa*, but does not have parameres. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990). The three species can be distinguished by their pronotal and antenna markings (*E. infecta* is entirely yellow, including yellow antennae, *E. evanescens* has lateral red-brown stripes and pale antennae, and *E. levasseuri* has dark spots and dark antennae). Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 50.** *Evanochrysa infecta* (Newman). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Italochrysa* Principi 1946

(104 species) figure 24.

*Italochrysa* Principi 1946: 86. Type species: *Hemerobius italica* Rossi 1790, by monotypy.

DIAGNOSIS: *Italochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, short flagellomeres and flagellar setae, *c1* longer than *c2*, wing markings absent, a quadrangular im cell, with a crossvein, a weakly defined, and not strongly marked pterostigma, and parameres present (shaped as paired rods), and occurring in the Old World.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, Oriental, or Palearctic.

DESCRIPTION: body colored pale green, or yellow.

Head: orange, or same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked apically, basally, completely, dorsally, laterally, medially, entirely pale, or ventrally, less than 1.5x as long as wide; pedicel marked apically, basally, completely, dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum dark basally, dark distally, uniformly dark or uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length; frons with broken band, spots, or with unbroken band; carina on dorsal torulus margin present; vertex flat in profile, or raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, continuous, large and discontinuous, or fronterolaterally, small spot, brown to black, or red, pilosity denser laterally, or uniformly

distributed, setae dark or pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked or unmarked, predominantly brown to black, or predominantly red, pilosity dense, setae dark or pale, predominantly short; metathorax marked or unmarked, pilosity dense, or sparse, setae pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula marked or unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA basal to origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets

CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting basal *dcc* vein, or meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or scarcely dark; wing markings absent, between PsM and PsC, or on *dcc*.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*, or apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg extensively marked or unmarked.

Abdomen: markings abundant, or dorsal and lateral longitudinal stripe; setae short, pale; sternum II without stridulatory organ.

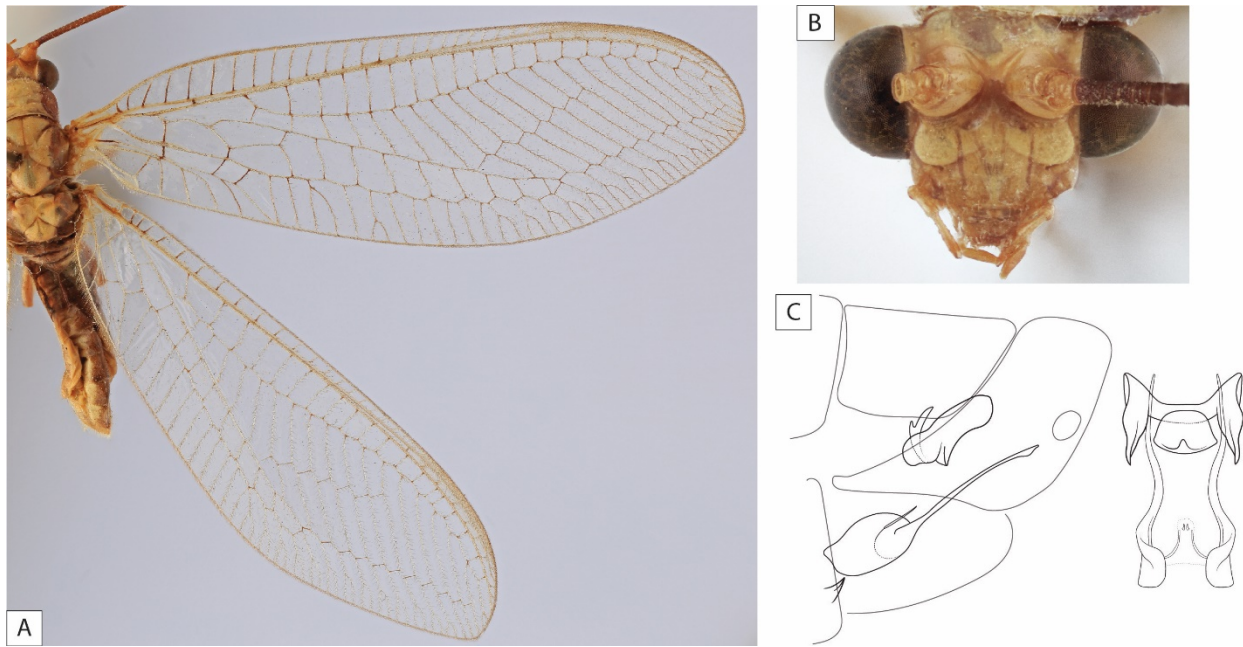
Female genitalia: tergum IX and ectoproct fused; sternum VII apically medially inserted, v-shaped, or simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, on narrow elongate membranous structure; spermatheca average, surface smooth; vela larger than spermatheca; spermathecal duct long and strongly coiled, or neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, or with three lobes bearing thick spines, without strong apical spines or dense setae, or with strong apical spines;

tignum absent; gonarcus medially fused, median arch with broad medial projection, or without expansion medially, lateral arms apically flat expanded, or strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, shaped as a 'v', or as paired simple rods, often expanded at base, opened towards apex, large, extending externally beyond abdomen apex, longer than gonarcus, or shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent, present apically on sternum IX, or present in 2 patches; microtholi absent or present.

REMARKS: *Italochrysa* is by far the largest group of Belonopterygini, with more than 80% of species. It is likely that the genus is rendered paraphyletic by several smaller genera, such as *Evanochrysa*, *Oyochrysa*, *Nesochrysa*, and others. Due to this it is difficult to pinpoint characters to unambiguously define the genus. The old world genus shares many characters with the neotropical *Nacarina*, in which parameres can be absent, but the two genera are otherwise lacking unambiguous characters in regard to each other. We have examined few unidentified oriental *Italochrysa* specimens in which the parameres are strongly reduced to small lobes. The *im* cell is quadrangular with a crossvein in most specimens, but can rarely be triangular, without a crossvein, in one or both forewings. The larvae of two species have been described and are debris carrying and usually associated with ants (Principi 1946, New 1983, Brooks and Barnard 1990, Tauber et al. 2014). No insect remains were found in the guts of adults (Brooks and Barnard 1990).





**Figure 51.** *Italochnrysa*. A. *Italochnrysa italica* (Rossi), fore- and hind wing, dorsal view, photomicrograph. B. *Italochnrysa italic*, head, frontal view, photomicrograph. C. *Italochnrysa* sp., male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Nacarina* Navás 1915

(20 species) figure 1G, 25.

*Nacarina* Navás 1915:133. Type species: *Nacarina furcata* Navás 1915, by original designation and monotypy.

*Nadiva* Navás 1919:303. Type species: *Goliva pletorica* Navás 1919, by original designation and monotypy. Stange 1967: 303 [synonymy under *Nacarina*].

*Goliva* Navá, 1920a:49. Type species: *Goliva deletangi* Navás 1920, by original designation and monotypy. Banks 1924: 49 [synonymy under *Nadiva*].

*Rameta* Navás 1920b:60. Type species: *Rameta sanguinea* Navás 1920, by original designation and monotypy. Banks 1924: 60 [synonymy under *Navida*].

*Mesochrysa* Navás 1927b:55. Type species: *Mesochrysa megaptera* Navás 1927, by original designation and monotypy. Brooks and Barnard 1990: 175 [synonymy under *Nacarina*].

DIAGNOSIS: *Nacarina* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, short flagellomeres and flagellar setae, *c1* longer than *c2*, wing markings absent, a weakly defined, and not strongly marked pterostigma, usually parameres absent, or present (shaped as paired rods), and occurring in the Neotropics.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent, brown or red; labial palpus uniformly pale, rarely marked on apical 3 palpomeres, or marked on apical palpomere; maxillary palpus uniformly pale, rarely marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked dorsally, laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum dark laterally, uniformly dark or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, large and discontinuous, in lateral longitudinal stripe, or in spots, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly

short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, or predominantly red, pilosity dense, setae dark or pale, predominantly short; metathorax marked or unmarked, pilosity dense, or sparse, setae dark or pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2, rarely three; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM, rarely basally extending parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein, rarely, triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC, rarely PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-

cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, entirely pale, longitudinal veins pale, crossveins dark or dark on gradates; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9, or 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple, rarely dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII apically medially inserted, v-shaped, or simple, apically rounded; small sclerotized plate between subgenitale and sternum absent or present; subgenitale as long as broad, or broader than long, apparently detached, or on broad membranous structure; spermatheca elongate, surface smooth; vela about same size as spermatheca, or larger than spermatheca; spermathecal duct long and strongly coiled, neither very long nor short, somewhat coiled, or very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded, or with ventral lobes; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sternum VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent;

gonarcus medially fused, median arch with 2 forward projecting horns medially, with narrow projection medially, or without expansion medially, lateral arms apically flat expanded, or strongly expanded to ear-like structure; entoprocessus absent, or minute, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent or present as ventral hook; parameres present, arranged as two sclerites medially connected membraneously, shaped as paired simple rods, often expanded at base, or as long and curved paired rods, opened towards apex, about as long or longer than gonarcus, positioned ventrally, in sternum IX, rarely absent; gonosetae numerously present (>10), or sparsely present (<10); gonocristae absent; microtholi absent or present.

REMARKS: Brooks and Barnard (1990) stated that the parameres are absent in *Nacarina*, but they are present in many species. There are several new species that are currently being described (Penny et al. in prep). *Nacarina* is similar to *Italochrysa* but the distributions of the two genera do not overlap (*Nacarina*: Neotropical, *Italochrysa*: entire old world). The larvae of *N. valica* were described by Weber (1942) and are associated with ant nests and not debris carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 52.** *Nacarina megaptera* (Navás), head, frontal view, photomicrograph.

Genus *Nesochrysa* Navás 1910

(9 species) figure 26.

*Nesochrysa* Navás 1910a: 53. Type species: *Nesochrysa grandieri* Navás 1910, by original designation and monotypy.

*Oviedus* Navás 1913b: 326. Type species: *Oviedus auricollis* Navás 1913, by monotypy. Brooks and Barnard 1990: 177 [synonymy under *Nesochrysa*].

*Madachrysa* Navás 1934: 62. Type species: *Madachrysa seyrigi* Navás 1934, by original designation and monotypy. Brooks and Barnard 1990: 177 [synonymy under *Nesochrysa*].

DIAGNOSIS: *Nesochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in for rings, short flagellomeres and flagellar setae, and parameres that are not medially separated, with three long rods on each side, and larger than the gonarcus, extending

beyond the apex of the abdomen.

DISTRIBUTION: Afrotropical.

DESCRIPTION: general body colored brown.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum uniformly pale; antenna longer than forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, or red, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified;

R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; irregular (*im* cell present), quadrangular, with crossvein, or triangular, without crossvein (ovate), or *mamp1* regular (*im* cell absent); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC, or PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark or veins dark basally, pale distally; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

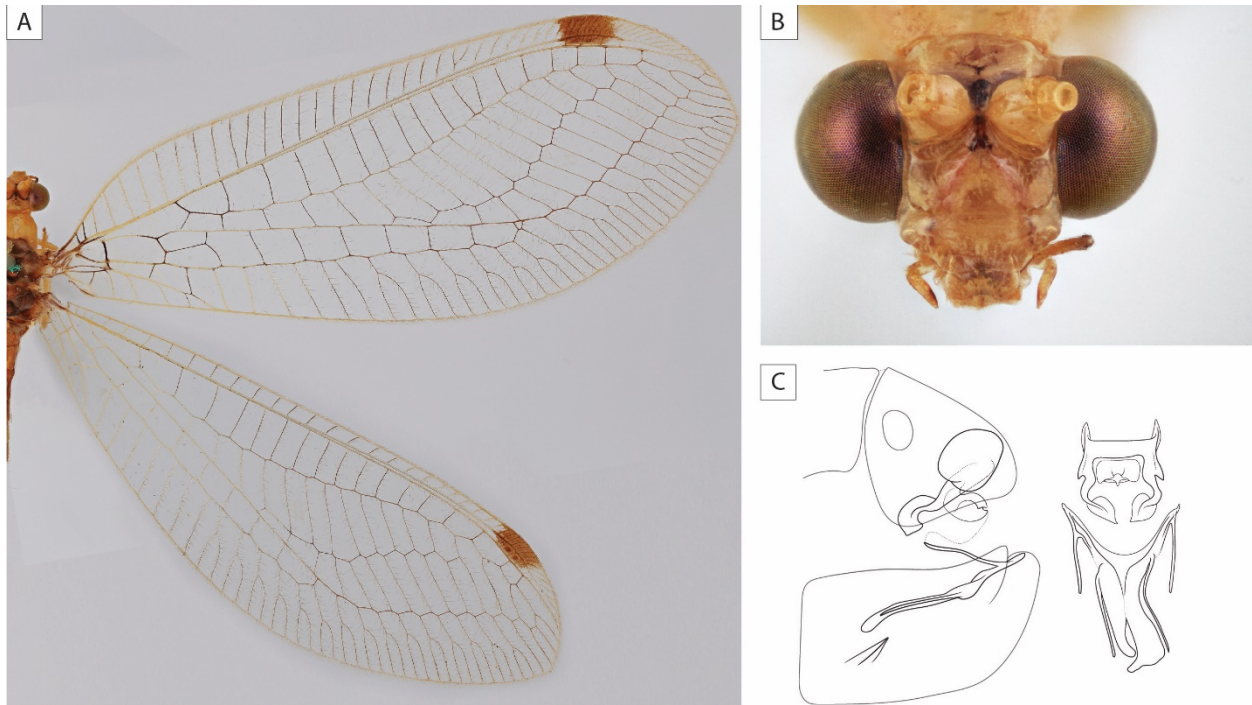
Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.



Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present on apex of sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca average, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with dorsal projecting horn, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus; parameres present, arranged as single sclerite, shaped as three long and pointed rods on each side, medially connected, opened towards apex, large, extending externally beyond abdomen apex, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: The parameres of *Nesochrysa* are unique among Chrysopidae, regarding their three long rods that are medially connected. Externally the genus is similar to *Stigmachrysa*, especially in regard of the well-marked pterostigma, but can be easily be distinguished by the male genitalia. Brooks and Barnard (1990) describe the *im* cell as quadrangular or absent, but we were not able to find specimens in which the *im* cell is absent, so this condition seems to be rare. Their larvae are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 53.** *Nesochrysa macrostigma* (Gerstaecker). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Nodochrysa* Banks 1938

(1 species) figure 27.

*Nodochrysa* Banks 1938a: 226 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa necrota* Banks 1920, by monotypy. Brooks 1984: 80 [raised to genus level].

**DIAGNOSIS:** *Nodochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, short flagellomeres and flagellar setae, and two small, pointed subapical cones on the female sternum VII.

**DISTRIBUTION:** Oriental.

DESCRIPTION: general body colored brown or yellow.

Head: colored same as body; genal marking absent; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked; carina on dorsal torulus margin present; vertex flat in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in three longitudinal stripes, brown to black, pilosity uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of

gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein, rarely triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC, or PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark; wing markings scarcely at base.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg extensively marked.

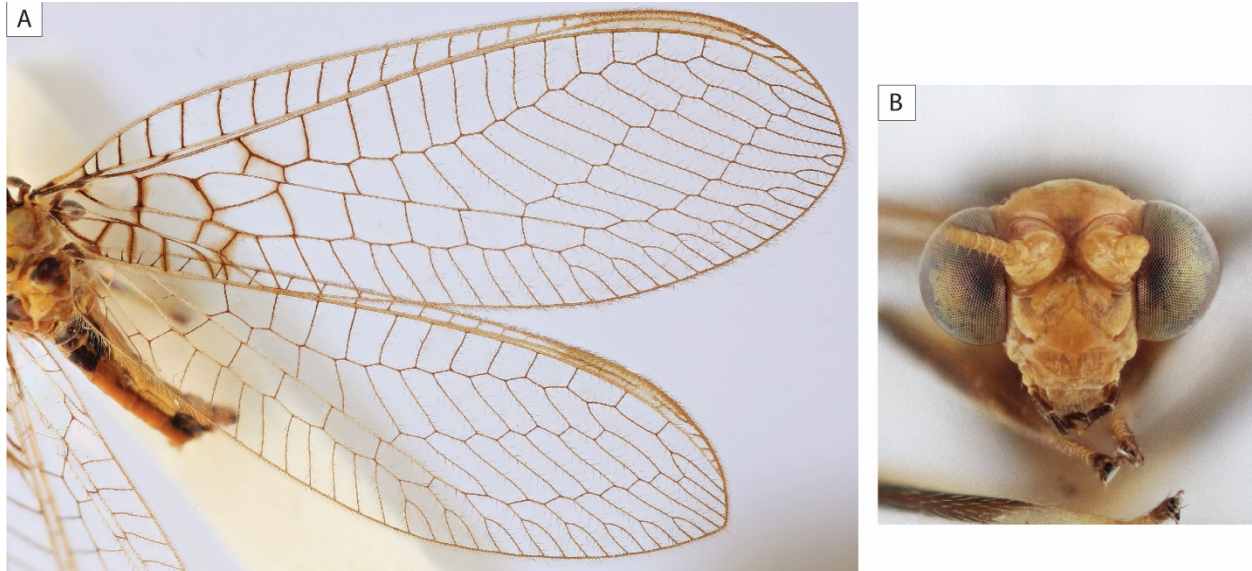
Abdomen: markings abundant; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded, or with two small subapical spines; praegenitale present within sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, close to sternum;

spermatheca elongate, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct with ventral lobes; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with three lobes bearing thick spines, with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with lateral, pointed gonocornua, lateral arms simple, not expanded; entoprocessus short, positioned medially on lateral arms, secondary process on lateral arms absent; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process present as lateral sclerotized lobes, or present as ventral hook; parameres present, arranged as two sclerites medially connected membraneously, shaped as a 'U' on each side, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi present.

REMARKS: Brooks and Barnard (1990) described the *im* cell as broadly triangular, but it is most often quadrangular, although with a short crossvein. They suggested a relationship with *Nesochrysa* due to the long antennae, the lobed apices of sternum VIII+IX and the sternum IX + ectoproct. The genus was not placed in our phylogenetic analysis (see chapter 1), due to the absence of molecular data. The larvae of *Nesochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 54.** *Nodochrysa necrota* (Banks). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Oyochrysa* Brooks 1985

(3 species) figure 28.

*Oyochrysa* Brooks 1985: 80. Type species: *Oyochrysa ancora* Brooks 1985, by original designation.

DIAGNOSIS: *Oyochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in rings, short flagellomeres and flagellar setae, and long parameres shaped as paired, and basally membraneously connected, rods that are slightly curved and strongly forked, with one tip longer than the other.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking brown; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel marked dorsally, or entirely pale; flagellar setal arrangement in four rings; flagellomeres as wide as long, or shorter, or at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings large and discontinuous, or in three longitudinal stripes, brown to black, or red, pilosity denser laterally, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, or predominantly red, pilosity sparse, setae pale, predominantly short; metathorax marked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; number of maximal c-sc crossveins basal to 1sc-r: 5; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate

series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 2, or 3; MA and MP rejoining on PsC; MA and CuA fused, or not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA basal to origin of CuP; 2m-cua meets CuA at 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark; wing markings between PsM and PsC, on *dcc*, and along RS.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings predominant; setae short, pale; sternum II without stridulatory organ.

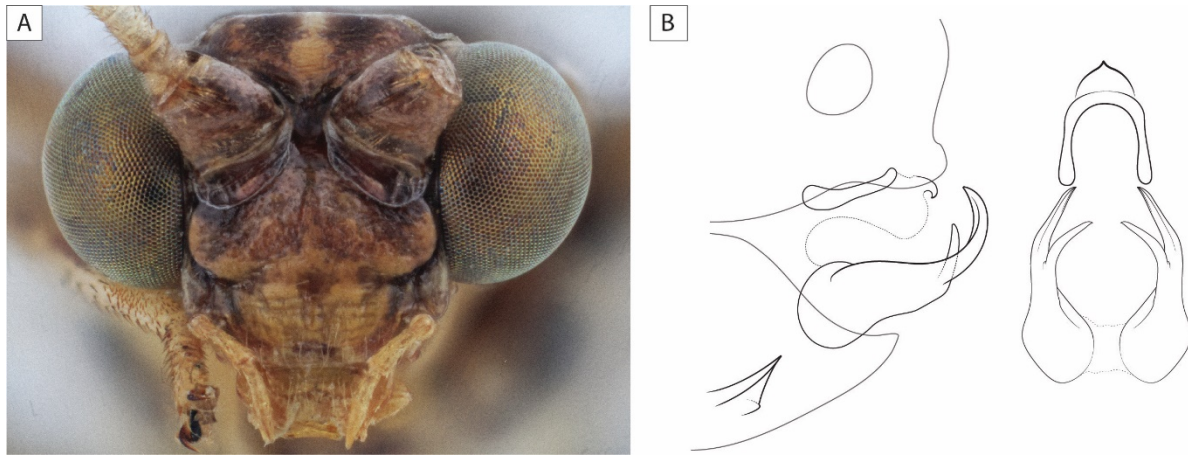
Female genitalia: tergum IX and ectoproct fused; sternum VII apically medially inserted, v-shaped; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, on narrow sclerotized structure, bearing setae; spermatheca elongate, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short,



somewhat coiled.

Male genitalia: dorsal apodeme with ventral process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sternum VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as two sclerites medially connected membraneously, shaped as paired, slightly curved and strongly forked rods, with pointed apices, one apex longer than other, opened towards apex, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent or present.

REMARKS: *Oyochrysa* is closely related to *Italochrysa*, due to the many external similarities (Brooks and Barnard 1990), and the two genera were recovered as sister in our phylogenetic analysis (see chapter 1), but an analysis including further *Italochrysa* species is needed. The parameres are large in both genera, but simple rods in *Italochrysa* and forked in *Oyochrysa*. The sclerotized structure apical to sternum VII in the female is characterized as a praegenitale, which is absent in *Italochrysa*. It is possible that the elongate membranous process in *Italochrysa* is a homologous structure to the praegenitale in *Oyochrysa*. The larvae of *Oyochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 55.** *Oyoichrysa ancora* Brooks. A. Head, frontal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Stigmachrysa* Navás 1925

(3 species) figure 1M, 29.

*Stigmachrysa* Navás 1925b: 570. Type species: *Stigmachrysa kervillei* Navás 1925, by original designation and monotypy.

**DIAGNOSIS:** *Stigmachrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, short flagellomeres and flagellar setae, *c1* longer than *c2*, a quadrangular im cell with a crossvein, and a prominently marked pterostigma, and short parameres that are positioned close to the mediuncus.

**DISTRIBUTION:** Oriental.

**DESCRIPTION:** body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented;

frons in profile raised laterally; scape marked dorsally, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter, or at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with small spot medially on supra-, or intra-antennal frons; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity dense, setae pale, predominantly short; metathorax unmarked, pilosity dense, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series diverging; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart;

number of crossveins between PsM and PsC: 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins dark on gradates; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

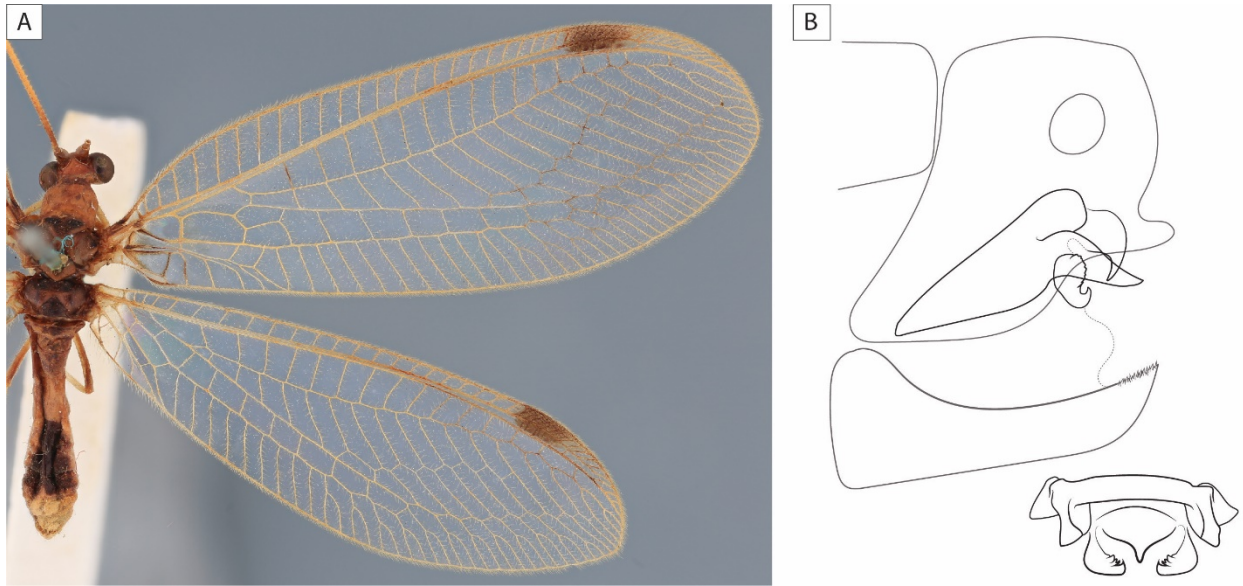
Abdomen: markings abundant, or sparse; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present within sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca elongate, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused;

ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or tapering medioapically, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as two sclerites medially connected membraneously, shaped as paired small spoon-like structures with apical teeth, opened towards apex, shorter than gonarcus, positioned proximal to mediuncus; gonosetae absent; gonocristae present apically on sternum IX; microtholi present.

Remarks: Both *Nesochrysa* and *Stigmachrysa* have a strongly marked pterostigma, as do few *Italochrysa* species, but *Stigmachrysa* can be distinguished by the comparatively small parameres, that are close to the mediuncus, whereas they are large and ventrally positioned in the other two genera. Additionally, *Stigmachrysa* has a praegenitale in the female sternum VII that is positioned within the sclerotized integument (as in *Abachrysa*, *Calochrysa*, *Dysochrysa*, and *Nodochrysa*), whereas it is absent in *Italochrysa* (as in *Belonopteryx*, *Vieira*, and *Oyochrysa*) or apically present in *Nesochrysa* (as in *Evanochrysa*). The larvae of *Stigmachrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 56.** *Stigmachrysa*. A. *Stigmachrysa kervillei* Navás, fore- and hind wing, dorsal view, photomicrograph. B. *Stigmachrysa cladostigma* (Navás), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Turnerochrysa* Kimmins 1935

(1 species)

*Turnerochrysa* Kimmins 1935: 576. Type species: *Turnerochrysa mirifica* Kimmins 1935, by monotypy.

DIAGNOSIS: *Turnerochrysa* is the only chrysopid genus with no gradate series (or a single crossveins in the inner gradates).

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented;

scape unmarked, less than 1.5x as long as wide; pedicel marked apically; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark; antenna shorter than, or equal to forewing length; frons unmarked, markings present, ornamentation absent, surface smooth and glossy.

Thorax: prothorax markings in spots, brown to black, pilosity denser laterally, setae pale and dark admixed, predominantly short, thick long setae patches on pronotum absent; mesothorax marked, predominantly brown to black; metathorax marked; pale medial stripe present; small expansion on frontal metascutum margin present.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 6; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 0-3; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 0 (or 1, due to the presence of a single crossvein in the inner gradates of one wing); number of gradate crossveins more in inner series than outer series; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with inner gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at

origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*, or at *dcc*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark; wing markings sparsely at some vein joints.

Hind wing: sc-r crossveins below pterostigma: 0-3; number of gradate series: 1, or zero; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; leg with markings on femora, tibiae, and tarsi.

Abdomen: markings sparse; setae short.

Female genitalia: unknown.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sternum VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus absent, or minute; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, about as long as lateral arms of gonarcus; parameres present, arranged as single sclerite, shaped as a broad 'U' with small expansion medially (inner margin forming 'W'), with small teeth on lateral apices (or possibly paired rods, see remarks), opened towards apex, about as long as gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi present.



REMARKS: *Turnerochrysa* is easily identified by the absence of gradate series, but the type specimen in the BMNH has a single crossvein present in the inner gradates of the right forewing. Only one specimen of this genus is known. Although the wing venation of *Turnerochrysa* is very different to *Italochrysa*, it seems to be closely related (see chapter 1). Brooks and Barnard described the parameres as small paired rods, but they are clearly connected in the original description. Unfortunately, we were not able to study the genitalia, and the type specimen should be reexamined to address this issue. The larvae of *Turnerochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Vieira* Navás 1913

(5 species) figure 30.

*Vieira* Navás 1913a: 152. Type species: *Leucochrysa leschenaulti* Navás 1911, by original designation and monotypy.

DIAGNOSIS: *Vieira* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, strongly marked wings (especially a large marking around the origin of RP, which is rare), two gradate series, that are divergent to each other in most species, and sinuate costal crossveins, at the level of the origin of RP, and antennae about as long as the forewing or shorter.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly marked; maxillary palpus marked on apical palpomere, or uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, or asymmetrical, with basal

tooth, with basal tooth on one side; frons in profile flat, or raised laterally; scape marked completely, or entirely pale, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally; antenna shorter than, or equal to forewing length; frons uniformly brown, with broken band, spots, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, or short, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly long; metathorax marked, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked or unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally, rarely broad basally; costal setae relatively long, or relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent, rarely present; apical costal area narrow, rarely broad; pterostigma diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous, or

straight; gradates in area between RA and RP absent; number of gradate series: 2, rarely three; number of gradate crossveins approximately same number in each series or more in inner series than outer series; gradate series diverging, or parallel; inner gradate series rarely not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on R, or, RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA at 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*, or longer than *c2*; crossvein 2cua-cup meeting basal *dcc* vein, or meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or dark along integumental marking pattern; wing markings between PsM and PsC, on inner gradates, on spots in RP sector, on basal third of wing, along apical margin, and in costal area on basal half of wing.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long or short; leg unmarked.

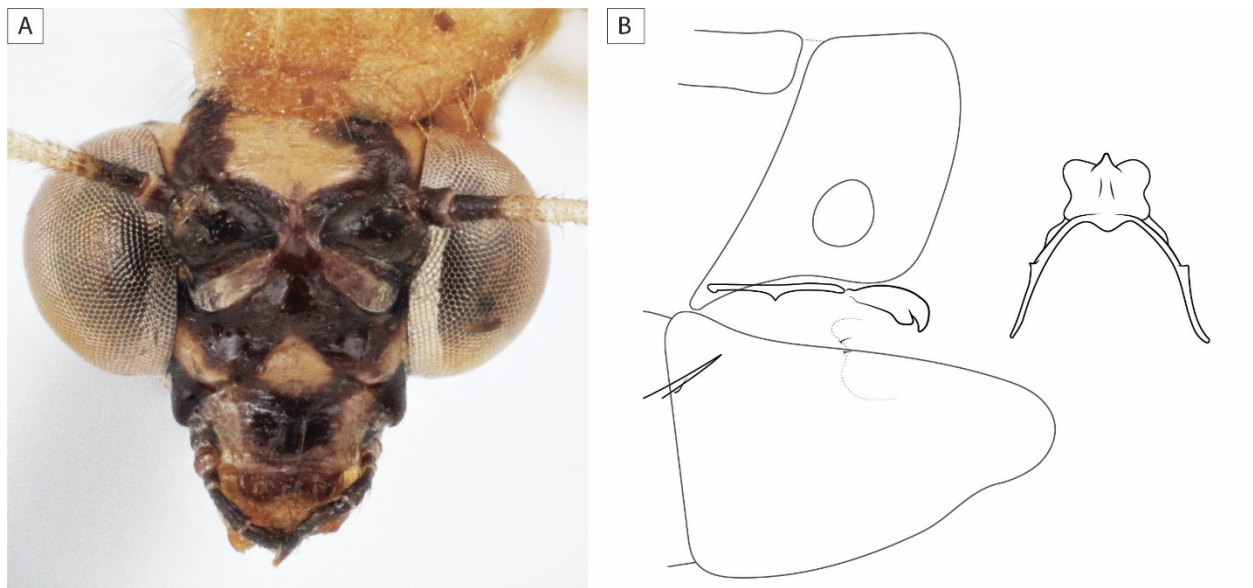
Abdomen: markings abundant; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; gonapophysis rarely enlarged bearing thick spoon-shaped setae; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, close to sternum, or on broad membranous structure; spermatheca thick, thin, or average, surface smooth; vela about same size as spermatheca, or larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, or with lateral, pointed gonocornua, lateral arms apically flat expanded, or simple, not expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or tapering medioapically, with single gonoseta on each side, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae sparsely present (<10); gonocristae absent; microtholi present.

REMARKS: *Vieira* was originally placed in Leucochrysinini, but transferred to Belonopterygini by Tauber (2007), on the basis of larval characters, and this placement was confirmed in our phylogenetic analysis, (see chapter 1). Tauber also transferred *Vieira brooksi* and *V. elegans* from *Berchmansus*. As in *Berchmansus*, 1r-m originates from R and not RP in some species of *Vieira*. These species can be distinguished from *Berchmansus* by the very long antennae

of the latter, and the wings are generally marked stronger in *Vieira*. Tauber (2006) described the male genitalia of *V. elegans* and stated that the parameres are present and very elongate and coiled, but this character was not mentioned in the subsequent literature (e.g., Tauber et al. 2007, Sosa and Tauber 2017). We were not able to identify a ventral sclerite in dissection of our specimen of *V. elegans*. Larvae of *V. elegans* were described by Tauber et al. (2006) and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 57.** *Vieira elegans* (Guerin). A. Head, frontal view, photomicrograph. b. Male genitalia, lateral and dorsal view, schematic line drawing.

#### Tribe **Chrysopini** Schneider 1851

(843 species, 32 genera)

Chrysopina Schneider 1851: 35. Type genus: *Chrysopa* Leach 1815. Navás 1914a: 76 [as tribe, Chrysopini].

Chrysopiscini Navás 1910a: 59. Type genus: *Chrysopisca* McLachlan 1875 [synonymy under Chrysopini].

Suarini Navás 1914a: 73. Type genus: *Suarinus* Navás 1914 [synonymy under Chrysopini].

DIAGNOSIS: Chrysopini usually have the flagellar setae arranged in four ring, the *im* cell most often triangular without a crossvein, *c1* as long as or shorter than *c2*, the basal RP branch is positioned apical to *mamp1*, and there is no ra-rp crossvein basal to the origin of the basal most RP branch absent, and sterna VIII and IX usually fused in the male.

REMARKS: The tignum is a character unique to Chrysopini, but is not present in all genera. If present, the parameres are usually a single structure, and not medially separated (as in many Belonopterygini).

Genus *Anachrysa* Hölzel 1973 **stat. nov.**

(2 species)

*Anachrysa* Hölzel 1973b: 356 [as subgenus of *Chrysopidia* Navás]. Type species: *Chrysopidia* (*Anachrysa*) *elegans* Hölzel 1973, by original designation.

DIAGNOSIS: *Anachrysa* is the only chrysopid genus with the combination of three gradate series, a tignum, and parameres arranged single sclerite, shaped as a thin and straight rod, which is broadened at base, and bifurcate apically.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3

palpomeres, or marked on apical palpomere; maxillary palpus marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellum dark distally; antenna shorter than, or equal to forewing length; frons unmarked, ornamentation absent, surface smooth and glossy.

Thorax: prothorax markings in spots, red; mesothorax unmarked; metathorax unmarked; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 3; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital

cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins entirely pale, or veins dark basally, pale distally; wing markings on *dcc*.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 3; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 4; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); metatibia on inner surface smooth; leg unmarked.

Abdomen: markings absent.

Female genitalia: tergum IX and ectoproct fused; sternum VII apically exerted, pointy; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca thin, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate, with dense setal patch apically; tignum present; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; mediuncus clearly separate from gonarcus, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as a thin and



straight rod, broad at base, and bifurcate apically in some, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent.

REMARKS: We excluded the former subgenus *Anachrysa* from *Chrysopidia*, and reinstate the genus status, due to its extremely different genitalia. It has parameres and a tignum, which is never present in *Chrysopidia*, nor in any Ankylopterygini. It was originally placed in the genus, due to the three gradate series, the elongate scape and the elongate sternum VIII+IX in the male, but these are all characters that can be found in different combinations in *Anomalochrysa* and *Mallada*. In our phylogenetic analysis (see chapter 1), *Anachrysa* results within a monophylum with these two genera. We therefore also place the genus *Anachrysa* in Chrysopini, and not as *Chrysopidia* in Ankylopterygini. *Anachrysa*, *Mallada*, and *Anomalochrysa* are the only genera in Chrysopidae with the combination of three gradate series (not present in all species of *Mallada* and *Anomalochrysa*), parameres, and a tignum. Many of the species in *Anomalochrysa* and *Mallada* also have an elongate sternum VIII+IX in the male, as does *Anachrysa*. It is likely that the two species of *Anachrysa* can be synonymized with *Mallada*, but a more detailed phylogenetic study is needed to assess this relationship. The larvae of *Anachrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Anomalochrysa* McLachlan 1883

(19 species) figure 31.

*Anomalochrysa* McLachlan 1883: 298. Type species: *Anomalochrysa hepatica* McLachlan 1883, by subsequent designation by Zimmerman 1957: 95.

DIAGNOSIS: *Anomalochrysa* is the only chrysopid genus with the combination of 3 or more gradate series, tignum and parameres present, and a broad sclerotized external structure ventrally of ectoproct apex, bearing setae.

DISTRIBUTION: Hawaii.

DESCRIPTION: general body colored brown or green.

Head: colored same as body; genal marking absent, brown or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, with broken band, spots, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, in lateral longitudinal stripe, or in medial longitudinal stripe, red, pilosity denser laterally, or uniformly distributed, setae pale, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, setae dark or pale, predominantly short, setae dark or pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally, or narrow basally and apically, but broadened on basal half; costal setae

relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent, rarely present; apical costal area narrow; pterostigma absent, diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 3, 4, or more; number of gradate crossveins more in inner series than outer series; gradate series irregularly arranged, or parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*, rarely longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 3, 4, or more; number of crossveins between PsM and PsC: 0-9, or 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to

*mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae four in number, or two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent, or sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum, rarely on small sclerotized structure with setae; spermatheca thin, or average, surface smooth; vela about same size as spermatheca, or larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct apically elongate, or normally shaped, rounded; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent, patch of long setae absent; sclerotized external structure present ventrally of ectoproct apex, bearing setae; ventral apodeme regular; sternum VIII and IX fused, elongate, or elongate and curved towards dorsal apically, with dense setal patch apically; tignum present; gonarcus medially fused, median arch with narrow projection medially, or without expansion medially, lateral arms apically flat expanded; entoprocessus absent, or minute, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as a structure with two elongate medial lobes, partially

fringed apically, and a smaller, thin lobe on each side, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *Anomalochrysa* is endemic to Hawaii, but quite similar to *Mallada*. Brooks and Barnard (1990) noted the similarity between the two genera, and especially with a group around *M. basalis*. Indeed, the genitalia of the two genera are extremely similar, and can only be distinguished by the presence of an additional sclerotized external plate ventral to the apex of the ectoproct in *Anomalochrysa*. The parameres are similarly shaped in *Mallada* and *Anomalochrysa*. The two genera and *Anachrysa* are the only genera in which three or more gradates are present in combination with a tignum and parameres. Our phylogenetic analysis confirms a close relationship of these three genera (see chapter 1). The larvae of *Anomalochrysa* have been described and are not debris carrying (Terry 1905, Perkins 1913, New 1986b, and Tauber et al. 2014) and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

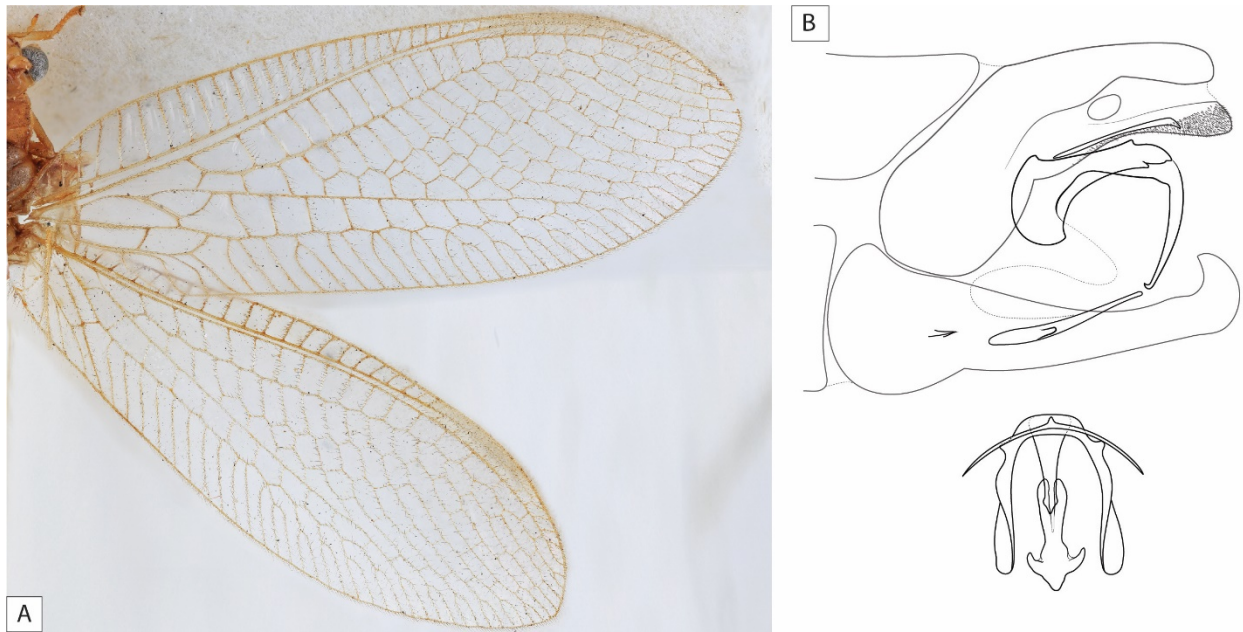


Figure 58. *Anomalochrysa hepatica* McLachlan. A. Fore- and hind wing, dorsal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing

Genus *Apertochrysa* Tjeder 1966

(182 species) figure 32.

*Apertochrysa* Tjeder 1966: 480 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa umbrosa* Navás, 1914, by original designation. Hölzel 1973: 341 [as subgenus of *Anisochrysa* Nakahara], Tsukaguchi 1985: 505 [reinstated as genus].

*Triadochrysa* Adams 1978: 294 [as subgenus of *Mallada*]. Type species: *Mallada (Triadochrysa) triangularis* Adams, 1978, by original designation and monotypy. Brooks and Barnard 1990: 223 [synonymy under *Mallada*], Tsukaguchi 1995: 67 [synonymy under *Pseudomallada*].

*Navasius* Yang and Yang 1990: 327 [homonym of *Navasius* Esben-Petersen, 1936]. Type species: *Navasius eumorphus* Yang and Yang, nomen nudum [= *Dichochrysa eumorphus* Yang and Yang 1999]. Unavailable name as not based upon an available species-group name at time

of original description.

*Dichochrysa* Yang 1991: 150 [unavailable name as type species is autobasic with *Navasius* Yang and Yang, an unavailable genus-group name]. [nom. nov. for *Navasius* Yang and Yang 1990 (homonym of *Navasius* Esben-Petersen 1936, Mrymeleontidae)]. Aspöck et al. 2001:93 [synonymy *Pseudomallada* under *Dichochrysa*], ICZN 2010 [synonymy under *Pseudomallada*, due to originally unavailable type species].

*Pseudomallada* Tsukaguchi 1995: 67. Type species: *Chrysopa cognatella* Okamoto 1914, by original designation. **Syn. nov.**

DIAGNOSIS: *Apertochrysa* is the only chrysopid genus with the combination of a simple, rounded sternum VIII+IX in the male, a tignum, and parameres shaped as a flattened structure with a laterally broadly extended dorsal part, and ventrally with a thin rod medially projecting backwards, V-shaped in lateral view.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, Nearctic, Oriental, or Palearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, or uniformly marked; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, or uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat, or raised laterally; scape marked dorsally, laterally, or entirely pale, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than

flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with small spot medially on supra-, or intra-antennal frons; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, or short, surface smooth and glossy, or smooth and matte.

Thorax: prothorax markings absent, in lateral longitudinal stripe, fronterolaterally, small spot, or in spots, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, or predominantly red, pilosity sparse, setae dark or pale, predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series, rarely more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM,



rarely meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, scarcely dark, entirely pale, or veins dark basally, pale distally; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth or with row of small tubercles; femoral setae long or short; leg unmarked.

Abdomen: markings absent, abundant, or sparse; setae long or short, dark or pale; sternum II with stridulatory organ, or without stridulatory organ.

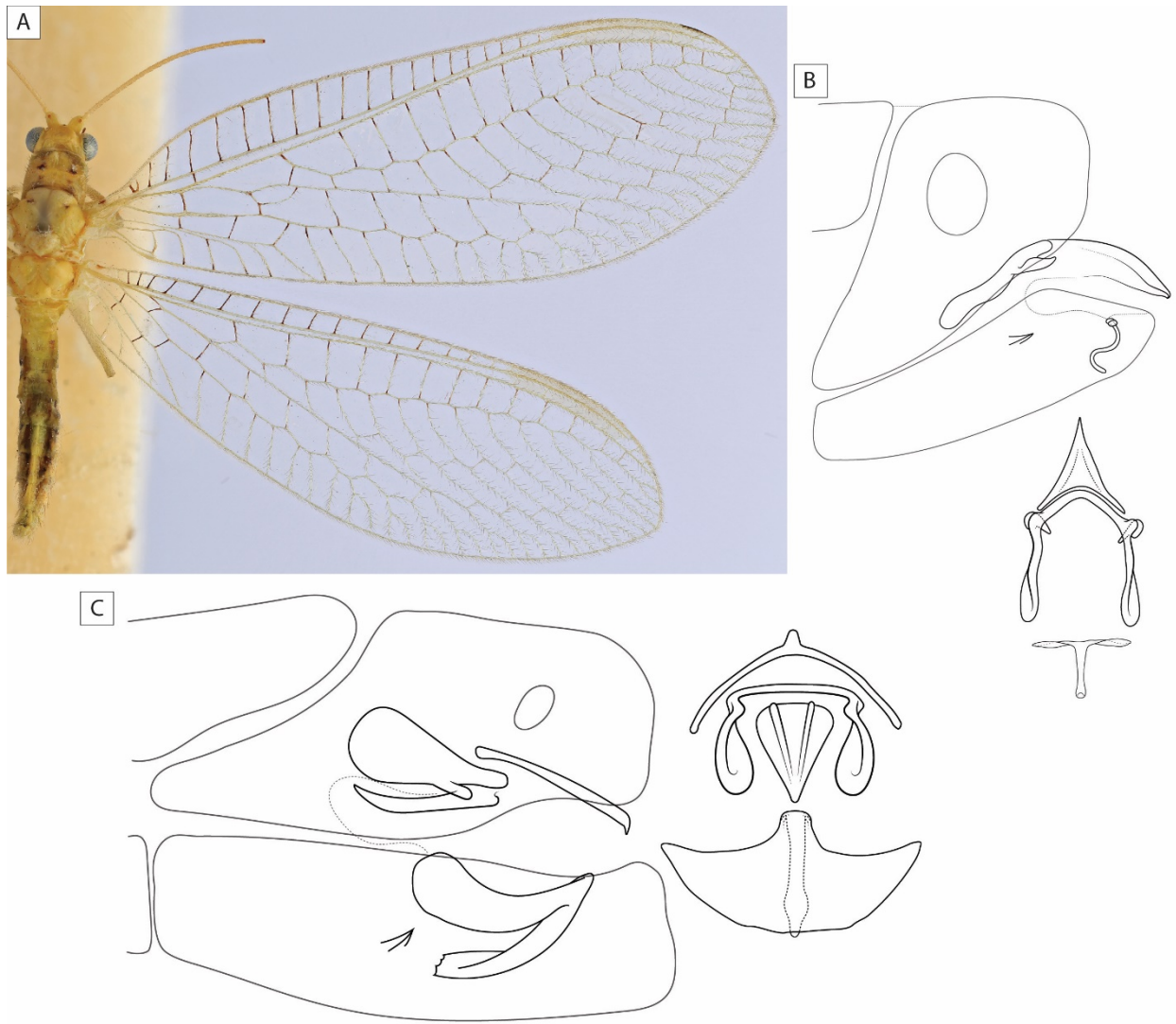
Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale

as long as broad, close to sternum; spermatheca thin, or average, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum present, rarely absent; gonarcus medially fused, or not fused, membraneously separated, median arch without expansion medially, lateral arms apically flat expanded, or simple, not expanded; entoprocessus long, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or shaped like axe head, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as a flattened structure with a laterally broadly extended dorsal part, and ventrally with a thin rod medially projecting backwards, V-shaped in lateral view, opened towards base, about as long as gonarcus, or shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: The hitherto established name for most species in this genus was *Pseudomallada*, but we here synonymize *Pseudomallada* with *Apertochrysa*, on the basis of Mochizuki et al. (2017). The type species was nested within the genus in the phylogenetic analysis including numerous species of *Pseudomallada* and *Apertochrysa* (Mochizuki et al. 2017), but does not have a tignum. There are several species of *Apertochrysa* that did not fall within *Pseudomallada* and many were not included in the phylogenetic analysis, so while we synonymize

*Apertochrysa* on the basis of the type species, the placement of other putative taxa included in the genus need evaluation. The name of *Pseudomallada* has been source of confusion over the last 20 years, with both *Dichochrysa* and *Pseudomallada* used in current literature. *Pseudomallada* was established by Tsukaguchi in 1995, based on the type species *P. cognatella* Okamoto 1914, and *Dichochrysa* was established in 1991 by Yang, but was a replacement name for an unavailable generic name (see taxonomic summary, above) and therefore it too is unavailable. Aspöck (2001) synonymized *Pseudomallada* with *Dichochrysa*, unaware that the latter was unavailable. In 2010 the ICZN ruled in a case submitted by Oswald (conservation of *Dichochrysa*), and confirmed *Pseudomallada* as the correct generic name when these two names are considered synonymous (Oswald 2008, ICZN 2010). However, owing to the results of the phylogenetic analysis of Mochizuki et al. (2017) both names are now synonyms of *Apertochrysa*, which was established well before *Dichochrysa* or *Pseudomallada*. Given the precedence, *Triadochrysa* would have been the correct name for this genus before the synonymy under *Apertochrysa*. There are a total of 17 species in the original *Apertochrysa* of which not all fell within the *Pseudomallada*-group (Mochizuki et al. 2017). The type species (*A. umbrosa*) as well as *A. eurydera*, and *A. edwardsi* were shown to be in the *Pseudomallada*-group, but *A. kichijoi* fell in the *Eremochrysa*-group, and *A. albolineatoides* in the *Chrysopa*-group (Mochizuki et al. 2017). The remaining 12 species need to be reexamined in order to securely place them in a genus. The larvae of *Apertochrysa* have been described (e.g. Smith 1926b, Killington 1937, Tjeder 1966, Gepp 1983, New 1984, Tsukaguchi 1995, Monserrat and Díaz-Aranda 2012, Tauber et al. 2014, Tauber and Tauber 2015) and are debris-carrying. The adults of *A. edwardsi* have been reported to be predacious (New 1981, Brooks and Barnard 1990).



**Figure 59.** *Apertochrysa*. A. *Apertochrysa crassinervis* (Esben-Petersen), fore- and hind wing, dorsal view, photomicrograph. B. *Apertochrysa crassinervis* (Esben-Petersen), male genitalia, lateral and dorsal view, schematic line drawing. C. *Apertochrysa ventralis* (Curtis), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Atlantochrysa* Hölzel 1970

(1 species) figure 33.

*Atlantochrysa* Hölzel 1970: 48 [as subgenus of *Anisochrysa* Nakahara]. Type species: *Chrysopa atlantica* McLachlan 1882, by original designation. Aspöck et al. 1980: 379 [raised to

genus].

DIAGNOSIS: *Atlantochrysa* is the only chrysopid genus with the combination of a triangular *im* cell without a crossvein, 1rp-ma joining M at the *im* cell, a tignum, a mediuncus that is shorter than the lateral arms of the gonarcus, no parameres, and numerous gonosetae present.

DISTRIBUTION: Atlantic Islands.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin absent; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface unevenly textured.

Thorax: prothorax markings large and discontinuous, brown to black, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly short; metathorax marked, pilosity dense, setae dark, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked);

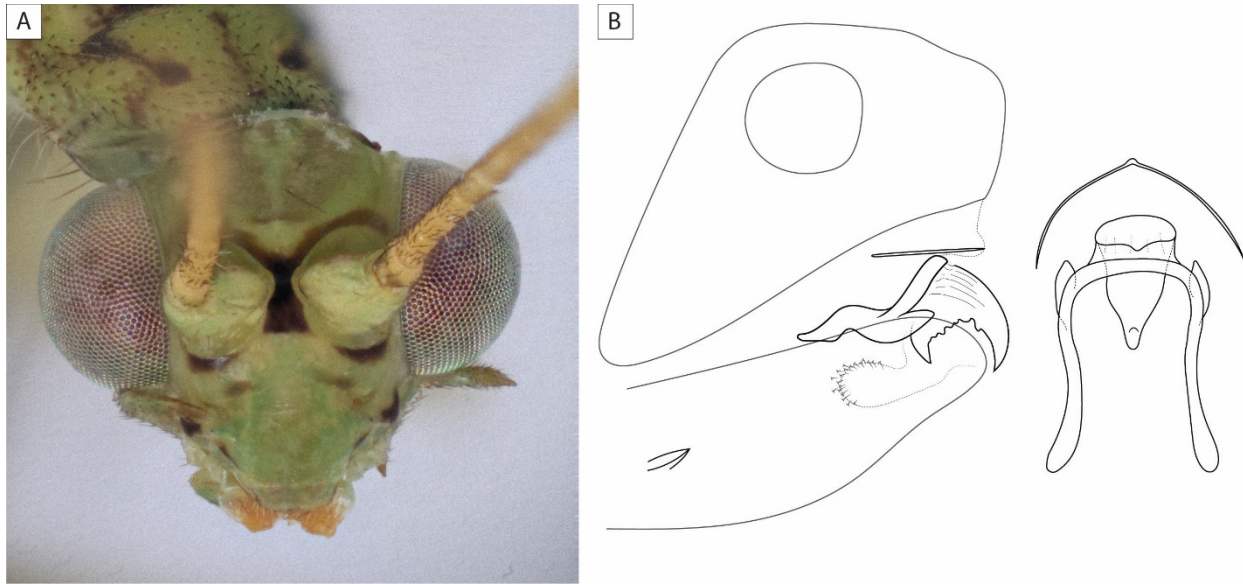
number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings sparse; setae long, dark or pale; sternum II without stridulatory organ.

Female genitalia: sternum VII simple, apically rounded; praegenitale absent; subgenitale as long as broad; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum present; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as ventral hook; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: Brooks and Barnard (1990) describe small parameres in *Atlantochrysa*, but, as in the original description, we were not able to find parameres in our dissections of male specimens. *Atlantochrysa* is one of the few genera that has a tignum and no parameres (as does *Austrochrysa*, *Chrysoperla*, *Plesiochrysa*, and possibly *Nothancyla*). The larvae of *A. atlantica* have been described and are debris-carrying (Monserrat 1977, Tauber et al. 2014) and the guts of adults contained insect remains (Brooks and Barnard 1990).



**Figure 60.** *Atlantochrysa atlantica* (McLachlan). A. Head, frontal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Austrochrysa* Esben-Petersen 1928

(6 species) figure 34.

*Austrochrysa* Esben-Petersen 1928: 98. Type species: *Austrochrysa samoana* Esben-Petersen 1928, by original designation.

*Scoliochrysa* Navás 1929: 365. Type species: *Scoliochrysa loriana* Navás 1929, by original designation and monotypy. Banks 1937: 149 [synonymy under *Chrysopa* Leach], Brooks and Barnard 1990: 190 [synonymy under *Austrochrysa*].

DIAGNOSIS: *Austrochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, a quadrangular im cell with a crossvein, a tignum, and no parameres.

DISTRIBUTION: Australasian, Oceanian.



DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in one posterolateral spot, brown to black, pilosity denser laterally, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 2 or 3; number of gradate crossveins more in outer series than inner series; gradate series diverging, or parallel; basal

crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins longitudinal veins pale, crossveins dark; wing markings between PsM and PsC, or on *dcc*.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2 or 3; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

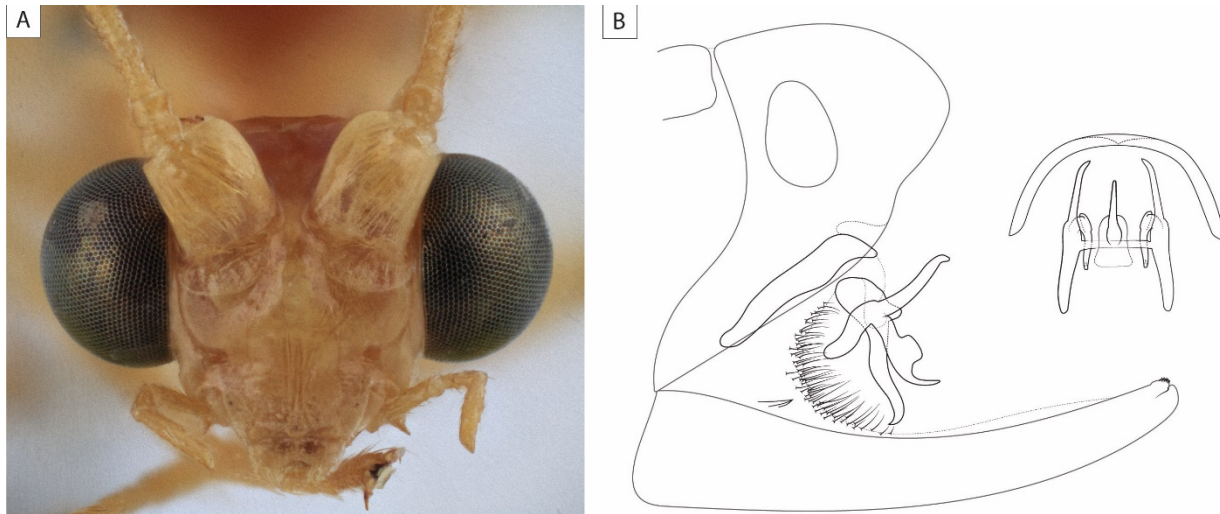
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: sternum VII simple, apically rounded; praegenitale absent; subgenitale longer than broad; spermatheca average, surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled; tergum IX and ectoproct fused.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused;

ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate, with strong apical spines; tignum present; gonarcus medially not fused, membraneously separated, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, shorter than lateral arms of gonarcus; parameres absent; gonosetae numerously present (>10); gonocristae absent; microtholi absent.

REMARKS: Brooks and Barnard (1990) stated that the tignum was absent in *Austrochrysa*, but after a reexamination of the male genitalia we concluded, that one of the arches in the complex genitalia is the tignum. *Austrochrysa* is one of few genera in which a tignum is present and the parameres are absent (as *Atlantochrysa*, *Chrysoperla*, *Plesiochrysa*, and possibly *Nothancyla*). The larvae of *Austrochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 61.** *Austrochrysa abnormis* (Albarda). A. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Borniochrysa* Brooks and Barnard 1990

(5 species) figure 35.

*Bornia* Navás 1928: 123 [homonym of *Bornia* Philippi 1836: 13]. Type species: *Bornia winkleri* Navás 1928, by original designation and monotypy. Banks 1931: 381 [synonymy under *Chrysopa* Leach], Kuwayama 1962: 372 [synonymy under *Anomalochrysa* McLachlan].

*Borniochrysa* Brooks and Barnard 1990: 192, nom. nov. for *Bornia* Navás 1928. Type species: *Bornia winkleri* Navás 1928, autobasic with *Bornia* Navas 1928.

**DIAGNOSIS:** *Borniochrysa* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, a triangular im cell, without a crossvein, apically elongate ectoprocts in the male, with very thick setae apically, and no tignum or parameres.

**DISTRIBUTION:** Afrotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking red; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth; frons in profile raised laterally; scape marked laterally, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity dense, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in outer series than inner series; gradate series parallel; inner gradate series

not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

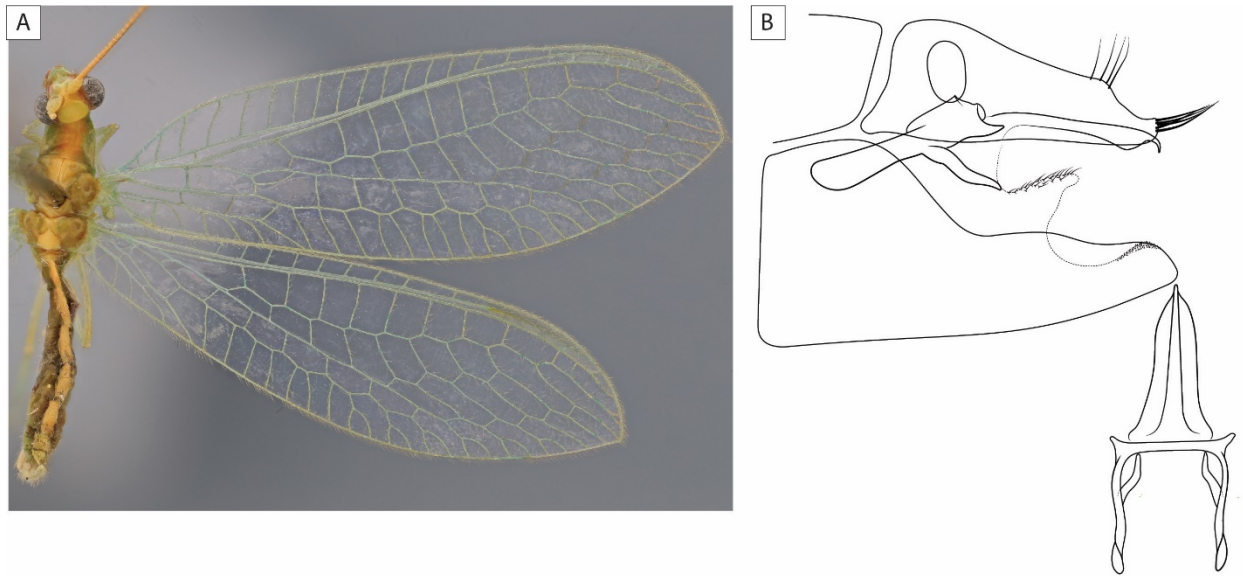
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct apically elongate; dorsal invagination between ectoprocts deep; thick setae on ectoproct present apically, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms simple, not expanded; entoprocessus long, positioned medially on lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, elongate, thin, flattened, or tapering medioapically, larger than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae present apically on sternum IX; microtholi absent or present.

REMARKS: Even though there are two or three gradate series in the forewing of *Borniochrysa*, there are only two gradate series in the hind wing of all species, which is in contrast to all other chrysopines with three gradate series in the forewing (except for some *Chrysopodes* species). The larvae of *Borniochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 62.** *Borniochrysa squamosa* (Tjeder). A. Fore- and hind wing, dorsal view, photomicrograph. B. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Brinckochrysa* Tjeder 1966

(23 species) figure 36.

*Neda* Navás 1933: 106. [homonym of *Neda* Muslant 1850: 274]. Type species: *Neda decaryella*

Navás 1933, by original designation. Brooks and Barnard 1990: 193 [synonymy under *Brinckochrysa*].

*Brinckochrysa* Tjeder 1966: 360 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa peri*

Tjeder 1966, by original designation. Hölzel 1970: 51 [raised to genus].

DIAGNOSIS: *Brinckochrysa* is the only chrysopid genus with a prominent stridulatory structure on sternum II in the male. Besides that structure it is unique in the combination of a triangular im cell without a crossvein, ventral lobes in the ectoprocts in the male, a strongly tapered sternum VIII+IX in the male, where the sternum is apically reduced to a small area surrounding



the apex of the ventral apodeme, which is curved towards dorsal, long entoprocessi, and no parameres.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, red, pilosity uniformly distributed, setae dark, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly red, pilosity dense, setae pale, predominantly long; metathorax marked or unmarked, pilosity dense, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field

absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series, or more in outer than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1;

metatibia on inner surface with row of thickened setae; leg unmarked.

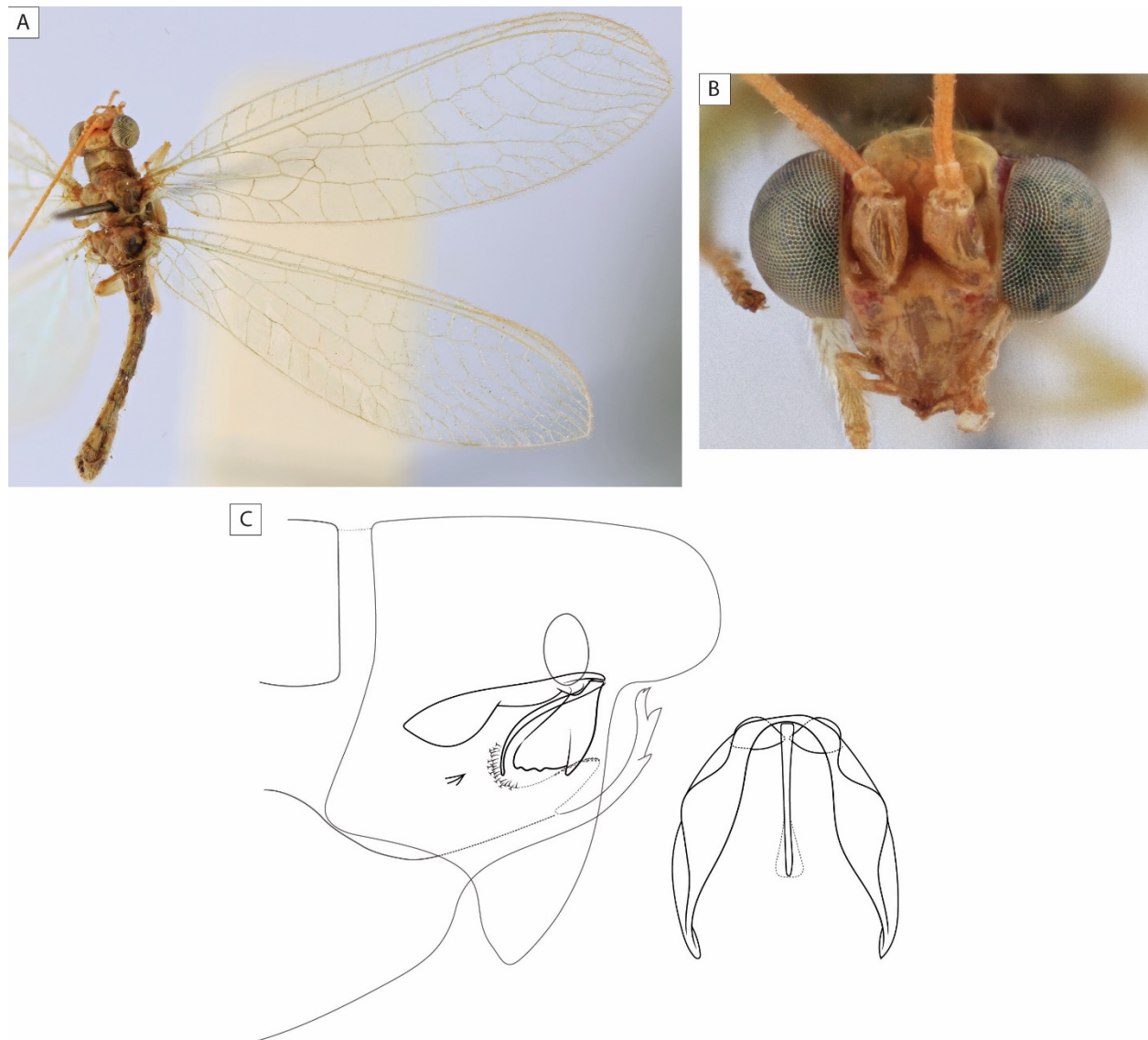
Abdomen: markings absent; setae long, pale; sternum II with stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average; vela smaller than spermatheca.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct with ventral lobes; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme with dorsal process; sterna VIII and IX fused, strongly tapered (to only apodeme) and upward turned, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae present apically on sternum IX; microtholi absent.

REMARKS: *Brinckochrysa* is the only chrysopid in which a prominent stridulatory structure is present. This structure is manifested in a combination of a serrated area on sternum II and a row of thick spines, that can be rounded or pointed, on the metatibia. These structures can be found in a less prominent pronunciation in few *Apertochrysa* species (e.g., *A. ventralis*), some *Meleoma* and one species of *Chrysocerca*. *Brinckochrysa* and *Apertochrysa* are probably not closely related (see chapter 1), but the genus is in the same genus group as *Meloma*. The larvae of several species have been described and are not debris-carrying (Adams 1959, Tsukaguchi 1979, Brooks and

Barnard 1990, Tauber et al. 2014). The feeding habits of the adult are unknown.



**Figure 63.** *Brinckochrysa*. A. *Brinckochrysa stenoptera* (Navás), fore- and hind wing, dorsal view, photomicrograph. B. *Brinckochrysa* sp., head, frontal view, photomicrograph. C. *Brinckochrysa* sp., male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Ceraeochrysa* Adams 1982

(61 species) figure 37.

*Ceraeochrysa* Adams 1982b: 70. Type species: *Chrysopa cincta* Schneider 1851, by original

designation.

DIAGNOSIS: *Ceraeochrysa* is the only chrysopid genus with the combination of the basal crossvein of the inner gradates meeting PsM, parameres present as a single sclerite, shaped as a long, single rod, and gonocristae present apically on sternum VIII+IX.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape marked completely, dorsally, or laterally, less than 1.5x as long as wide; pedicel marked completely, dorsally, or laterally; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna longer than forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, rarely present, ornamentation absent, pilosity absent, surface smooth and glossy, rarely unevenly textured.

Thorax: prothorax markings in lateral longitudinal stripe, red, rarely brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin

absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in outer series than inner series, rarely approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, marked strongly in irregular pattern, or dark on gradates; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum

number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long or short; leg unmarked.

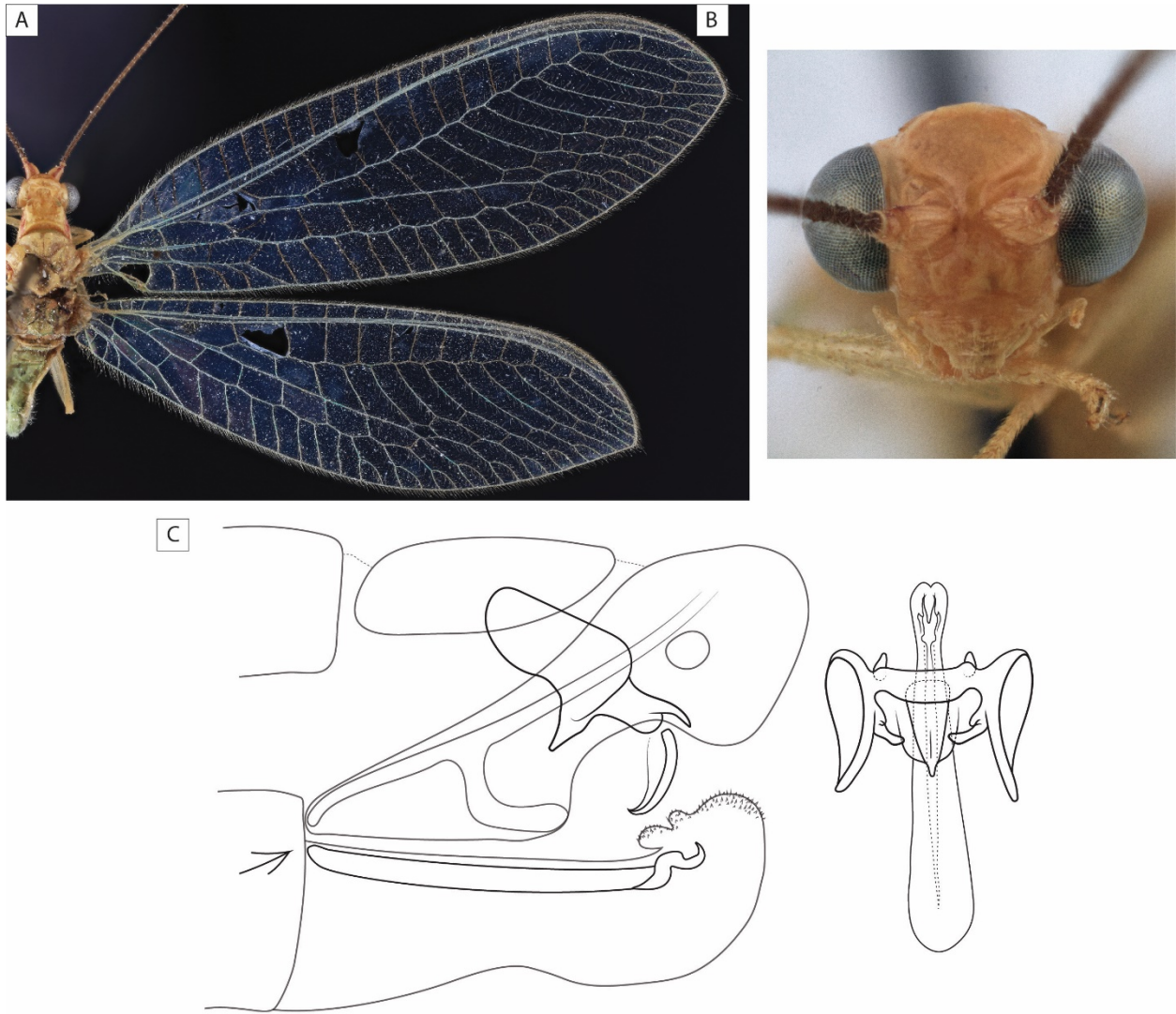
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, close to sternum; spermatheca elongate, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process, rarely with ventral process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sternum VIII and IX fused, regular, or with two pointed lobes bearing thick setae, with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent or present as lateral sclerotized lobes; parameres present, arranged as single sclerite, shaped as single rod, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent, or numerous present (>10); gonocristae present apically on sternum IX; microtholi absent.

REMARKS: *Ceraeochrysa* is a fairly large genus and it is not easily identified by its external characters, but only few genera have parameres shaped as a single elongate rod (especially in the neotropics). A relationship with *Leucochrysa* has been proposed (Adams 1982), but Brooks and Barnard suggested that the genus is rather part of Chrysopini. According to our phylogenetic analysis, *Ceraeochrysa* is closely related to *Ungla* and *Yumachrysa*. The larvae of several species were described (e.g., Smith 1926, 1932, Muma 1957, Tauber et al. 2000, Tauber and De Leon 2001, Tauber et al. 2014) and they are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).





**Figure 64.** *Ceraeochrysa cincta* (Schneider). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Ceratochrysa* Tjeder 1966

(3 species) figure 38.

*Musola* Navás 1929: 367. [homonym of *Musola* Roewer 1927: 398 (Arachnida)]. Type species:

*Musola impar* Navás 1929, by original designation and monotypy.

*Ceratochrysa* Tjeder 1966: 352 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa*

*ceratina* Navás 1910, by original designation. Barnard and Brooks 1984: 36 [raised to genus].

DIAGNOSIS: *Ceratochrysa* is the only chrysopid genus with strongly elongate entoprocessi, that usually pointing beyond the apex of the abdomen. The genus also has more crossveins in the outer gradates than the inner gradates, sterna VIII and IX separate, and sternum IX elongate.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus laterally compressed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally; antenna longer than forewing length; frons unmarked, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, red, pilosity denser laterally, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked);

number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

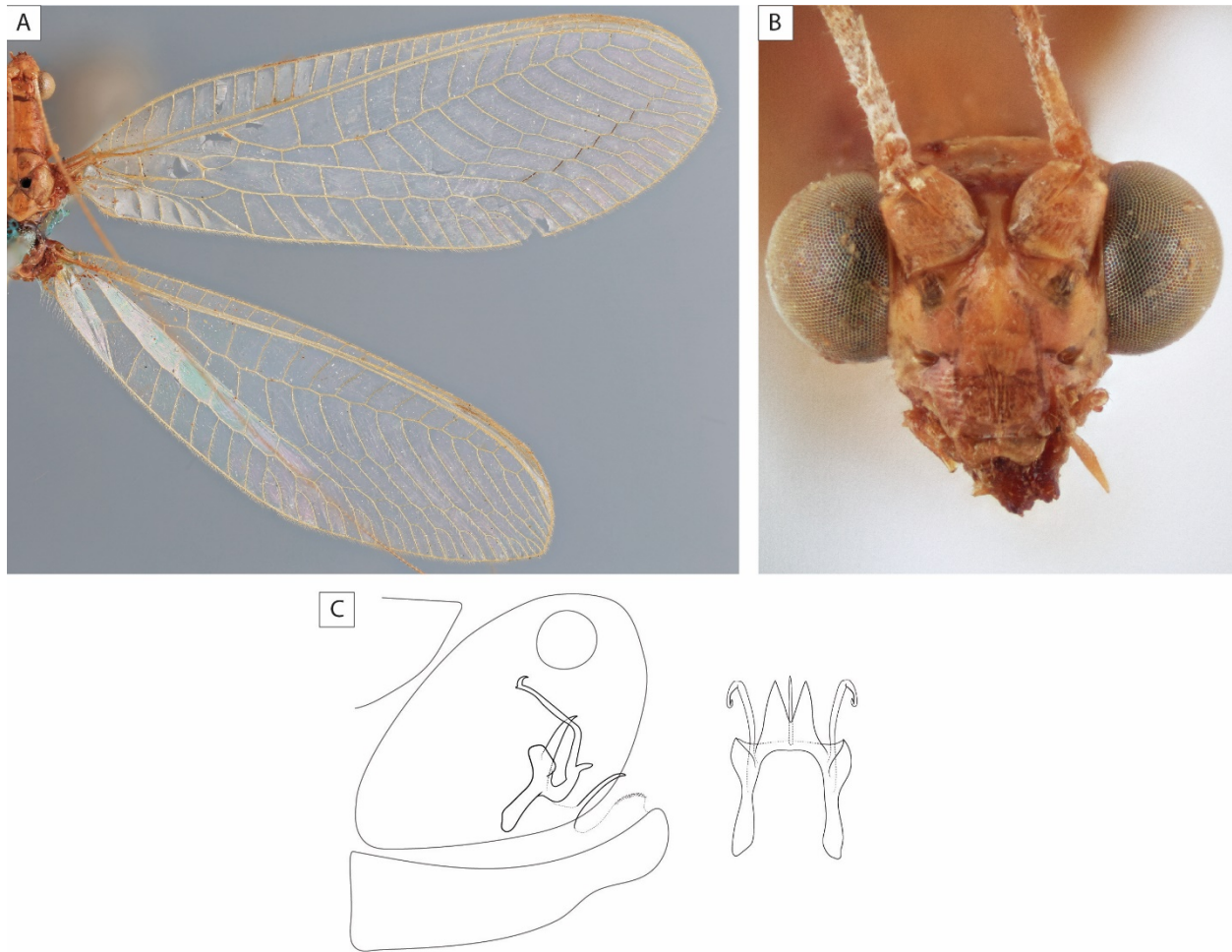
Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, on small sclerotized structure with setae; spermatheca average; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX separate, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms simple, not expanded; entoprocessus long and arching around mediuncus, as well as often pointing beyond the apex of the abdomen, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms present; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae present apically on sternum IX; microtholi absent.

REMARKS: The combination of the few inner gradate crossveins and the strongly elongate entoprocessi are unique in *Ceratochrysa*. The genus was recovered as sister to *Plesiochrysa* in our phylogenetic analysis (see chapter 1). Most *Plesiochrysa* species also have fewer crossveins in the inner gradates, and no parameres or tignum present, and fairly elaborate entoprocessi. The larvae of *C. antica* have been described (Barnard and Brooks 1984) and they are debris-carrying. The gut

content of the adults is unknown.



**Figure 65.** *Ceratochrysa ceratina* (Navás). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysemosa* Brooks & Barnard, 1990

(11 species) figure 39.

*Mesochrysa* Navás 1936a: 169 [homonym of *Mesochrysa* Navás 1927]. Type species: *Mesochrysa stigmata* Navás 1936, by original designation and monotypy.

*Chrysemosa* Brooks and Barnard, 1990: 198, nom. nov. pro *Mesochrysa* Navás 1927. Type

species: *Mesochrysa stigmata* Navás 1936, by autotypy.

DIAGNOSIS: *Chrysemosa* is the only chrysopid genus with the combination of two gradate series, a triangular *im* cell, without a crossvein, no tignum and parameres present as a thin arch.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent, brown or red; labial palpus uniformly marked, or uniformly pale; maxillary palpus uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked basally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; frons with broken band, spots, or with unbroken band; carina on dorsal torulus margin absent; vertex raised in profile, markings absent or present, ornamentation absent, pilosity short, surface unevenly textured.

Thorax: prothorax markings continuous, brown to black, or red, pilosity uniformly distributed, setae pale, or pale and dark admixed, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity dense, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal

costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked strongly in irregular pattern; wing markings on *dcc*.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*, or apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked);

number of protibial spurs: more than two; number of mesotibial spurs: 1; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae long; leg extensively marked.

Abdomen: markings absent, abundant, or sparse; setae long, dark; sternum II without stridulatory organ.

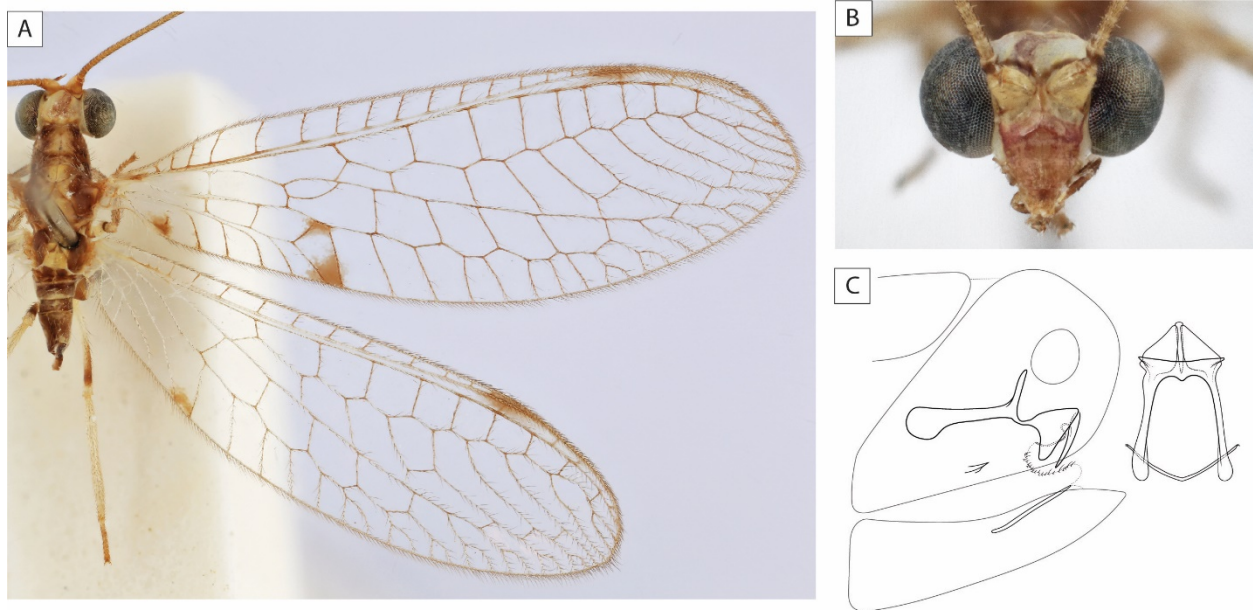
Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, lateral arms simple, not expanded; entoprocessus long, with additional structure, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as thin arch, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi absent or present.

REMARKS: The thin arched shape of the parameres of *Chrysemosa* is unique in Chrysopidae. The genus is closely related to *Suarius*, and both genera are comparatively small and



often brown, have a somewhat elongate sternum VIII+IX in the male, no tignum, and fairly elaborate entoprocessi. They can be distinguished by the presence of the parameres in *Chrysemosa*, and the wings are often not as intensively marked. All species in *Chrysemosa* were formerly in *Suarius*, but Tjeder (1966) erected the genus for all species in which the parameres are present. The larvae of *Chrysemosa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 66.** *Chrysemosa*. A. *Chrysemosa simillima* (Tjeder), fore- and hind wing, dorsal view, photomicrograph. B. *Chrysemosa simillima*, head, frontal view, photomicrograph. C. *Chrysemosa* sp., male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysocerca* Weele 1909

(6 species) figure 40.

*Chrysocerca* Weele 1909: 75. Type species *Chrysocerca jacobsoni* Weele 1909, by original designation and monotypy. Lacroix 1924: 571 [synonymy with *Nineta*], Tjeder 1966: 345 [reinstated as genus].

*Pseudochrysa* Okamoto 1914: 55. Type species: *Pseudochrysa formosa* Okamoto, by monotypy.

Kuwayama 1966: 137 [synonymy under *Chrysocerca*].

DIAGNOSIS: *Chrysocerca* is the only chrysopid genus with the combination of the male ectoprocts strongly elongate, no tignu, and 'v'-shaped parameres, which are longer than the gonarcus.

DISTRIBUTION: Afrotropical, or Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, broad, regular shaped, with basal tooth; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres as wide as long, or shorter; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series diverging, or parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae four in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

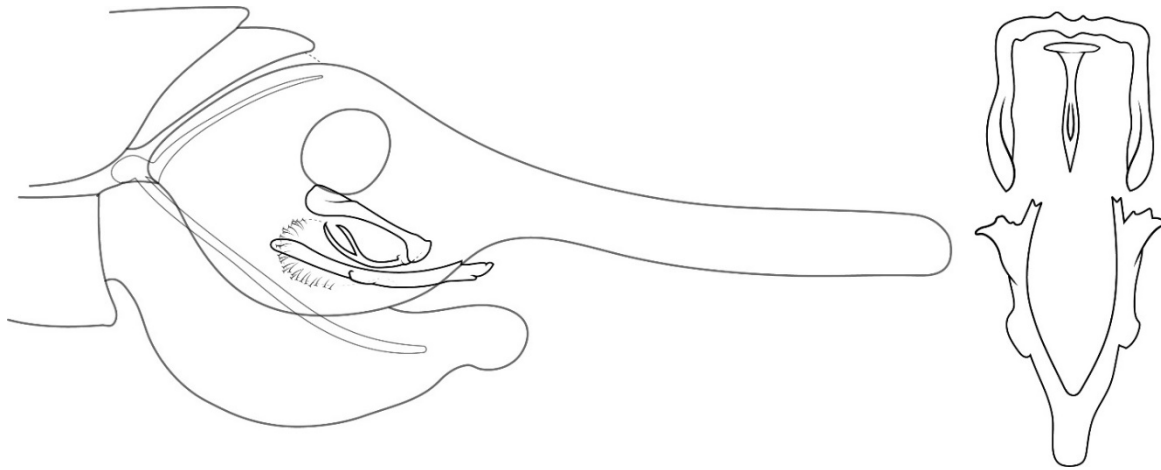
Abdomen: markings absent; setae long, pale; sternum II with or without (e.g. *C. formosa*) stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; subgenitale broader than long.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct with long and narrow apical projection; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sternum VIII and IX fused, elongate, or with ventro-apical lip, without strong apical spines or dense setae; tignum absent; gonarcus medially not fused, membranously separated, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus absent, or minute, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, about as long as lateral arms of gonarcus, mediuncus process present as apical fork in vertical plane; parameres present, arranged as single sclerite, shaped as a 'v', opened towards apex, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *Chrysocerca* is easily identified by the strongly elongate ectoprocts in the male, which can be approximated in other genera (such as *Chrysotropia*, *Nineta*, *Tumeochrysa*, or *Parachrysopiella*), but not to the same extent. The presence of a stridulatory structure on the lateral membrane between tergum and sternum II was reported in New (1989) and Brooks and Barnard

(1990). We were only able to examine *C. formosa*, which does not have this structure, and the species in which it is present is not mentioned in the literature. The larvae of *Chrysocerca* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 67.** *Chrysocerca formosa* (Okamoto), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysopa* Leach 1815

(189 species) figures 1D, H, and see chapter 3.

*Chrysopa* Leach 1815: 138. Type species: *Hemerobius perla* Linnaeus 1758, by subsequent designation by ICZN 1954: 3.

*Aelops* Billberg 1820: 95. Type species: *Hemerobius chrysops* Linnaeus 1758, by subsequent designation by Tjeder 1966: 351. Tjeder 1966: 351 [synonymy under *Chrysopa*].

*Emerobius* Costa 1834: 72. Type species: *Hemerobius chrysops* Linnaeus 1758, by monotypy. Brooks and Barnard 1990: 201 [synonymy under *Chrysopa*].

*Melanops* Doumerc 1861: 192. Type species: *Chrysopa parvula* Doumerc 1861, by monotypy. Leraut 1980: 242 [synonymy under *Chrysopa*].

*Chrysopisca* McLachlan 1875: 23. Type species: *Chrysopisca minuta* McLachlan 1875, by monotypy. Brooks and Barnard 1990: 201 [synonymy under *Chrysopa*].

*Cintameva* Navás 1914c: 214. Type species: *Cintameva venulosa* Navás 1914, by original designation. Smith 1932: 581 [synonymy under *Chrysopa*].

*Minva* Navás 1920b: 288. Type species: *Minva punctata* Navás 1920, by original designation and monotypy. Brooks and Barnard 1990: 201 [synonymy under *Chrysopa*].

*Polyphlebia* Navás 1935: 88. Type species: *Polyphlebia punctata* Navás 1936, by original designation and monotypy. Brooks and Barnard 1990: 201 [synonymy under *Chrysopa*].

*Metachrysopa* Steinmann 1964: 264 [as subgenus of *Chrysopa*]. Type species: *Chrysopa septempunctata* Wesmael 1841, by original designation. Tjeder 1966: 351 [synonymy under *Chrysopa*].

*Nigrochrysopa* Steinmann 1964: 264 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa formosa* Brauer 1850, by original designation. Tjeder 1966: 351].

*Parachrysopa* Séméria 1983: 310. Type species: *Hemerobius pallens* Rambur 1838, by original designation and monotypy. Brooks and Barnard 1990: 201 [synonymy under *Chrysopa*].

*Furcochrysa* De Freitas and Penny 2000: 167. Type species: *Furcochrysa allata* De Freitas and Penny 2000, by original designation. **Syn. nov.**

DIAGNOSIS: *Chrysopa* is the only chrysopid genus with the combination of the flagellar setar arranged in four rings, two gradate series, the ventral apodeme of the male with a dorsal process, no tignum or parameres, and the mediuncus clearly separate from the gonarcus.

DISTRIBUTION: Afrotropical, Hawaii, Nearctic, Neotropical oriental, Palaearctic, or Atlantic Islands.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; maxillary palpus uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented, or straight; mandibles asymmetrical, broad, regular shaped, with basal tooth; frons in profile flat; scape marked apically, basally, completely, dorsally, laterally, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked apically, basally, completely, dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, uniformly dark or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, uniformly brown, with broken band, spots, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, in spots, or in bands, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked or unmarked, predominantly brown to black, pilosity dense, or sparse, setae dark or pale, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity dense, or sparse, setae dark or pale, predominantly long, or predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6, or 0-3; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA basal to origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA basal to 2cua-cup, or meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, scarcely dark, entirely pale, or veins dark basally, pale distally; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*;



ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent, abundant, or predominant; setae long or short, dark or pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, on broad membranous structure; spermatheca average; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular, or with dorsal process; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms simple, not expanded; entoprocessus long, or long, with additional structure, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, larger than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae present in 2 patches; microtholi present.

REMARKS: *Chrysopa* is the largest genus of Chrysopidae, and it is therefore difficult to

group all species under a single diagnosis. Although the characters mentioned above tend to be applicable in the genus, they can be variable, and we therefore advise caution when determining *Chrysopa*. We here synonymize *Furcochrysa* De Freitas and Penny with *Chrysopa*, which resulted within the latter in the most recent phylogeny (see chapter 1). *Furcochrysa* shares most characters with *Chrysopa*, especially the male genitalia, and was erected solely on the basis of forked vein endings of CuA. *Chrysopa* is in strong need of a comprehensive revision based on a phylogenetic analysis. The larvae of numerous species have been described (e.g., Killington 1937, Principi 1947, Tsukaguchi 1978, Monserrat 1982, Gepp 1983, 1984, Canard and Principi 1984, Tsukaguchi 1995, Tauber et al. 2014, and many other) and are debris-carrying or not debris-carrying. The adults are predacious (e.g., Principi and Canard 1984), and large quantities of insect remains were found in their guts (Brooks and Barnard 1990).

Genus *Chrysoperla* Steinmann 1964

(60 species) figure 41.

*Chrysoperla* Steinmann 1964: 260 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa carnea* Stephens 1836, by original designation. Hölzel 1970: 51 [as subgenus of *Anisochrysa* Nakahara], Séméria 1977: 238 [raised to genus].

DIAGNOSIS: *Chrysoperla* is the only chrysopid genus with the combination of a triangular *im* cell without a crossvein, 1rp-m joining M distal to *im*, a tignum and no parameres.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, Hawaii, Nearctic, Neotropical, oriental, Palaearctic, or Atlantic Islands.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth; frons in profile raised laterally; scape marked apically, basally, completely, dorsally, laterally, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked apically, basally, completely, dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length; frons unmarked, uniformly brown or with broken band, spots; carina on dorsal torulus margin absent or present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, continuous, large and discontinuous, fronterolaterally, small spot, in spots, or in bands, brown to black, pilosity denser laterally, or uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity dense, or sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in

costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M distal to *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely dark or entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of

metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

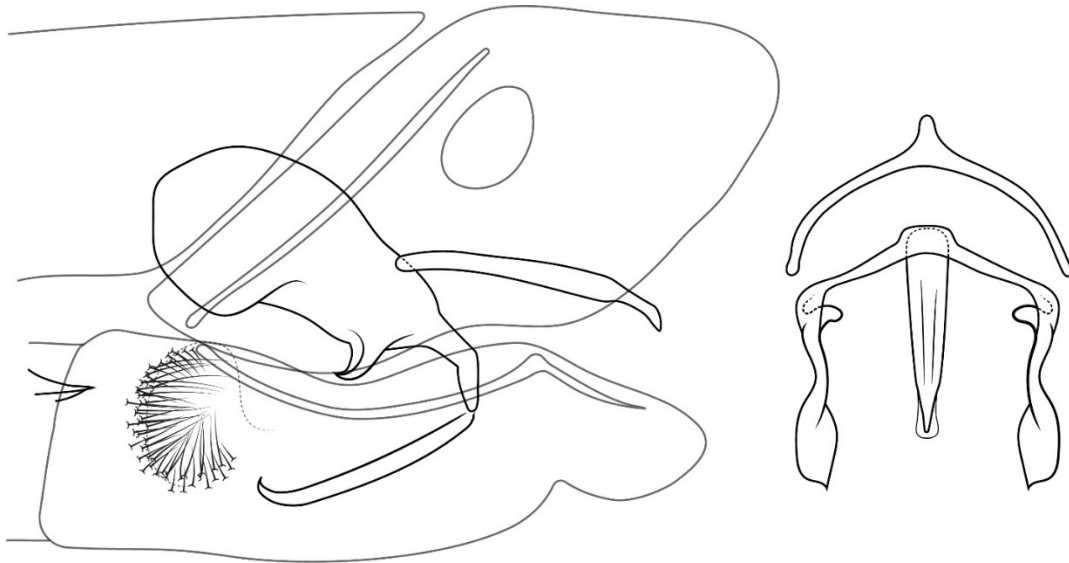
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; subgenitale broader than long, on broad membranous structure; spermatheca average; vela about same size as spermatheca, or smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with ventro-apical lip, without strong apical spines or dense setae; tignum present; gonarcus medially fused, median arch with 2 forward projecting lobes medially, lateral arms apically flat expanded; entoprocessus absent, or minute, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent, or numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *Chrysoperla* is a large genus that occurs worldwide and is frequently used as biological pest control in agriculture. Numerous cryptic species have been described on the basis of substrate-borne vibrational songs that are used for courtship (e.g., Henry 1984, Henry and Wells 1990, Henry et al. 2002, Henry et al. 2014). There is only little morphological variation in the genus, and species are mainly described by coloration patterns. *Chrysoperla* is one of the few genera in which a tignum is present, but no parameres – with *Austrochrysa*, *Atlantochrysa*,

*Plesiochrysa*, and possibly *Nothancyla*. *Peyrimhoffina* is closest related to *Chrysoperla* and resulted within or as sister to the genus. It is possible that *Peyrimhoffina* is an extremely derived species of *Chrysoperla*, but an analysis with further *Chrysoperla* is needed to asses this relationship. The larvae of several species have been described (e.g., Smith 1921, Killington 1937, Toschi 1965, Tjeder 1966, Tauber 1974, Tauber and Tauber 1974, Barnes 1975, Tsukaguchi 1977, Gepp 1983, and Tauber et al. 2014 and many more) and are not debris-carrying. Brooks and Barnard (1990) found no insect remains in the guts of adults, but they mention species in which insect remains were found in the guts (Smith 1922).



**Figure 68.** *Chrysoperla carnea* (Stephens), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Chrysopodes* Navás 1913

(43 species, 2 subgenera)

DIAGNOSIS: *Chrysopodes* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, the palpi not finely pointed apically, two gradate series in the

forewing, the basal most crossvein of the inner gradates meeting PsM, a triangular *im* cell without a crossvein, *c1* shorter than *c2*, the dorsal apodeme of the male with a ventral process, and no tignum or parameres.

Subgenus *Chrysopodes* Navás 1913

(31 species) figure 42.

*Chrysopodes* Navás 1913b: 329. Type species: *Chrysopodes canudasi* Navás 1913, by monotypy.

*Orlandisa* Navás 1914a: 112. Type species: *Orlandisa jubilosa* Navás 1914, by original designation and monotypy. Adams and Penny 1986: 422 [synonymy under *Chrysopodes* Navás].

*Ancylochrysa* Navás 1928: 129. Type species: *Ancylochrysa nevermanni* Navás 1928, by monotypy. Adams and Penny 1986: 422 [synonymy under *Chrysopodes* Navás].

DIAGNOSIS: *Chrysopodes* differs from *Neosuarius* by the combination of the flagellar setae arranged in four rings, the palpi not finely pointed apically, two gradate series in the forewing, the basal most crossvein of the inner gradates meeting PsM, a triangular *im* cell without a crossvein (rarely quadrangular with crossvein), *c1* shorter than *c2*, the dorsal apodeme of the male with a ventral process (in most species), and no tignum or parameres, and a basally rounded and simple tergum IX + ectoproct.

DISTRIBUTION: Neotropical.

Description: body colored pale green.

Head: colored same as body; genal marking red, rarely absent; labial palpus marked on apical 3 palpomeres, marked on apical palpomere, or uniformly pale; maxillary palpus marked on apical palpomere, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, narrow, without basal tooth; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity dense, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present, rarely absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6, or 0-3; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous, or straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same



number in each series; gradate series diverging, or parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate), rarely irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM, rarely PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, marked strongly in irregular pattern, or marked weakly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 0-3, rarely 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long or short; leg unmarked.

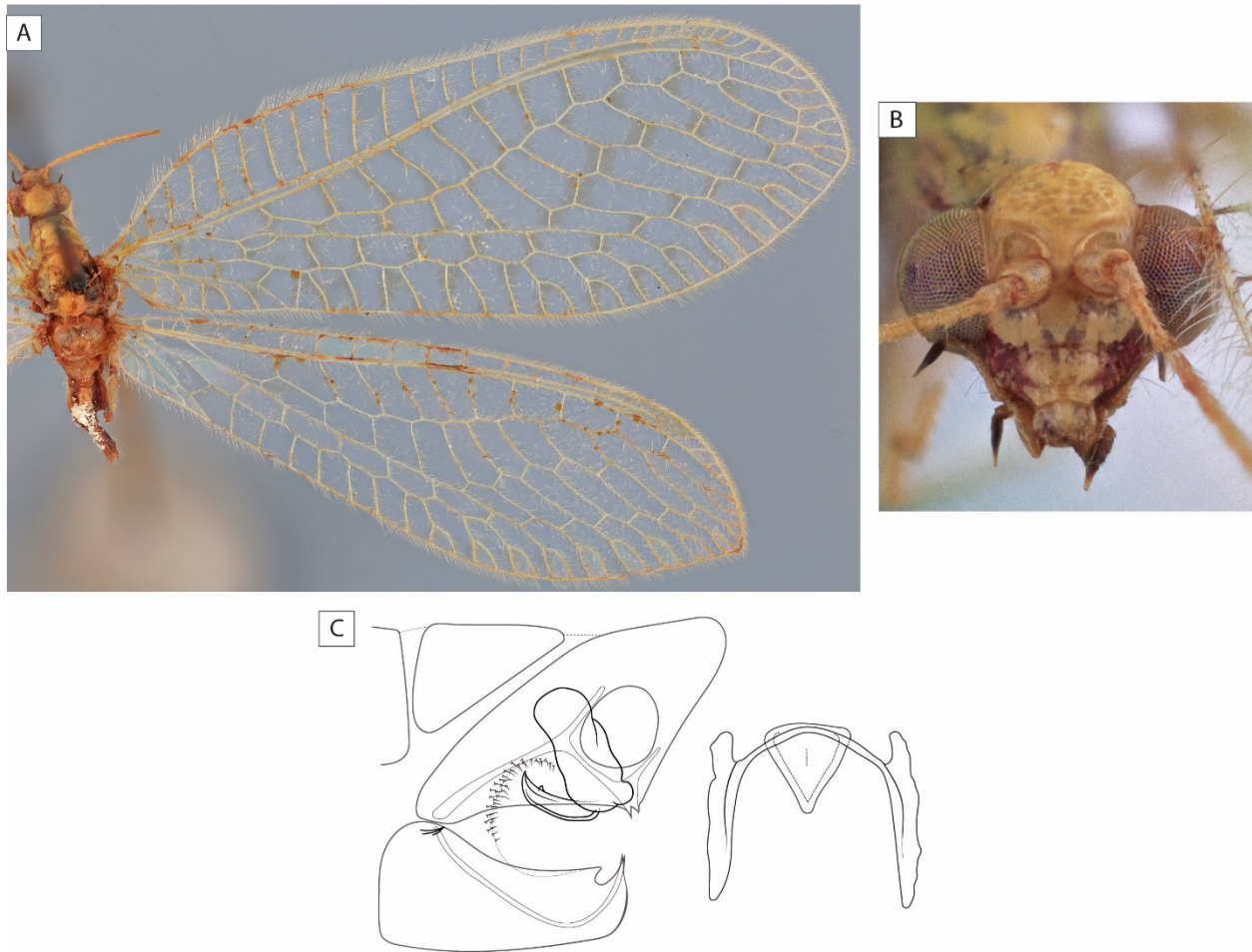
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII apically exerted, pointy, or simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and

sternum absent; subgenitale as long as broad, close to sternum; spermatheca elongate; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process, or with ventral process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with subapical pockets for ectoproct process, tapering apically, and therefore seemingly elongate, or with sub-basal medial pointed expansion, without strong apical spines or dense setae, or with strong apical spines, or with small process along posteromedial margin; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae present in 2 patches; microtholi absent.

Remarks: Brooks and Barnard (1990) described the parameres to be present, and very thin and pointed mandibles in some species of *Chrysopodes*, but the species they based this on is now in the genus *Titanochrysa*. The larvae have been described (Tauber 2003, Silva et al. 2007, Silva et al. 2013, Tauber et al. 2014) and are debris-carrying. *Chrysopodes* can be distinguished from *Neosuarius* by the basally not narrowly expanded tergum IX + ectoproct in the male, and the latter usually has less crossveins in thinner gradates than the outer, otherwise the two subgenera are very similar. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 69.** *Chrysopodes (Chrysopodes) limbata* (Navás). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Subgenus *Neosuarius* Adams and Penny 1987

(12 species)

*Neosuarius* Adams and Penny 1986: 435. Type species: *Chrysopa collaris* Schneider 1851, by original designation. Brooks and Barnard 1990: 212 [as subgenus of *Chrysopodes* Navás].

Diagnosis: *Neosuarius* has the following combination of traits: the flagellar setae arranged

in four rings, the palpi not finely pointed apically, two gradate series in the forewing, the basal most crossvein of the inner gradates meeting PsM, a triangular *im* cell without a crossvein, *c1* shorter than *c2*, the dorsal apodeme of the male with a ventral process, and no tignum or parameres, and a basally expanded and elongate tergum IX + ectoproct.

Distribution: Nearctic, or Neotropical.

Description: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked completely, or entirely pale; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale, predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal

costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area broad; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale, marked strongly in irregular pattern, or marked weakly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale

(unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent, or sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca elongate, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme with ventral process; tergum IX and ectoproct fused; tergum IX with thin expansion towards the abdomen base; ectoproct normally shaped, rounded, or with ventral lobes; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process rarely numerous short setae on apex present; parameres absent; gonosetae absent, rarely sparsely present (<10); gonocristae absent; microtholi absent.

Remarks: Brooks and Barnard (1990) established *Neosuarius* as a subgenus of *Chrysopodes*, and our phylogenetic analysis (see chapter 1) confirms this placement. The two genera can be distinguished by the basally thinly elongate tergum IX + ectoproct in the male and the reduced number of crossveins in the inner gradates of most species of *Neosuarius*. The larvae

of Neosuarius have been described (Tauber et al. 2014) and are debris carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Crassochrysa* Hölzel 1990

(3 species) figure 43.

*Crassochrysa* Hölzel 1990: 285. Type species: *Chrysopa aculeata* Tjeder 1966, by original designation.

DIAGNOSIS: *Crassochrysa* is the only chrysopid genus with the combination of apically not finely pointed palpi, symmetrical and narrow mandibles, with a basal tooth on both sides, and occurring in the Afrotropics.

DISTRIBUTION: Afrotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, narrow, with basal tooth; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with unbroken band; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (*ovate*); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP



forked at *c*<sub>2</sub>; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

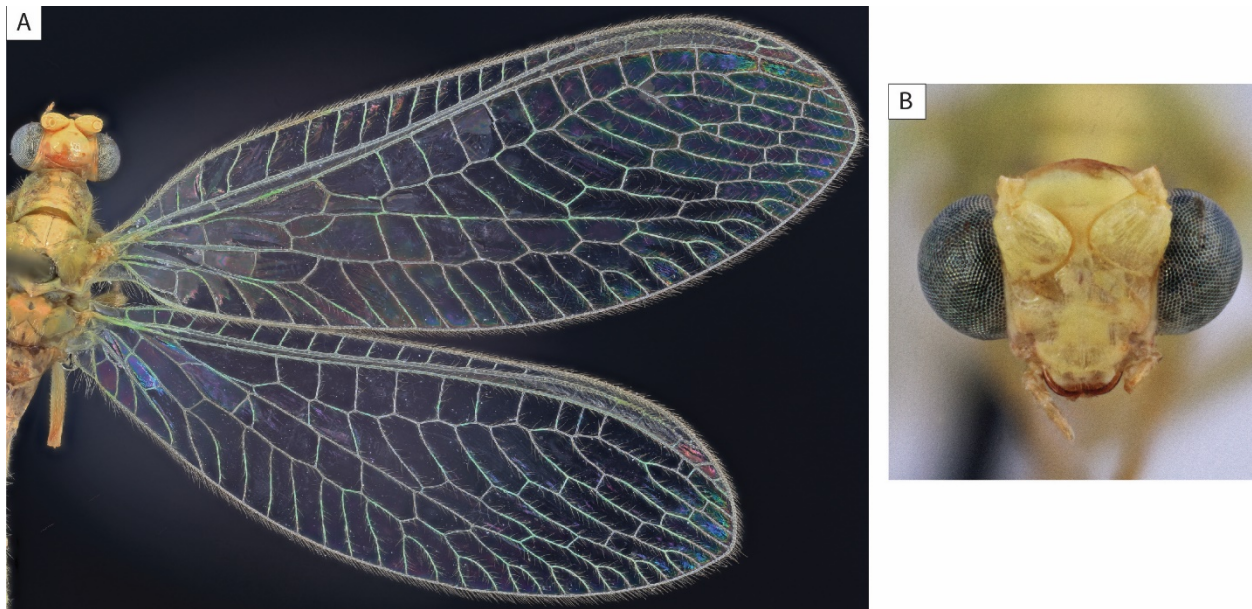
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII with small subapical cone ventrally; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned medially on lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate,

laterally expanded, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent or present, arranged as single sclerite, shaped as single rod, about as long as gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi absent or present.

REMARKS: It is possible that the species with and without parameres are not part of the same genus, as this would be the only chrysopid genus with both character states present. We were only able to study *C. aculeata*, which lacks parameres, but the three species included in *Crassochrysa* should be reexamined. The larvae of *Crassochrysa* are unknown, and the adults are not predacious (Hölzel 1990).



**Figure 70.** *Crassochrysa aculeata* (Tjeder). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Cunctochrysa* Hölzel 1970

(10 species) figure 44.

*Cunctochrysa* Hölzel 1970: 47 [as subgenus of *Anisochrysa* Nakahara]. Type species: *Chrysopa albonineata* Killington 1935, by monotypy. Zeleny 1971: 176 [synonymy under *Suaris* Navás], Tjeder 1972: 23[subgenus of *Chrysopa* Leach], Aspöck et al. 1980: 271 [raised to genus].

DIAGNOSIS: *Cunctochrysa* is the only chrysopid genus with the combination of a mediuncus shaped like an axe head and no parameres.

DISTRIBUTION: Afrotropical, or Palaearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum straight; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, in lateral longitudinal stripe, or in spots, brown to black, pilosity denser laterally, setae pale and dark admixed, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin

absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series or more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale, or marked weakly in irregular pattern; wing markings absent, rarely between PsM and PsC, on *dcc*, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of

crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

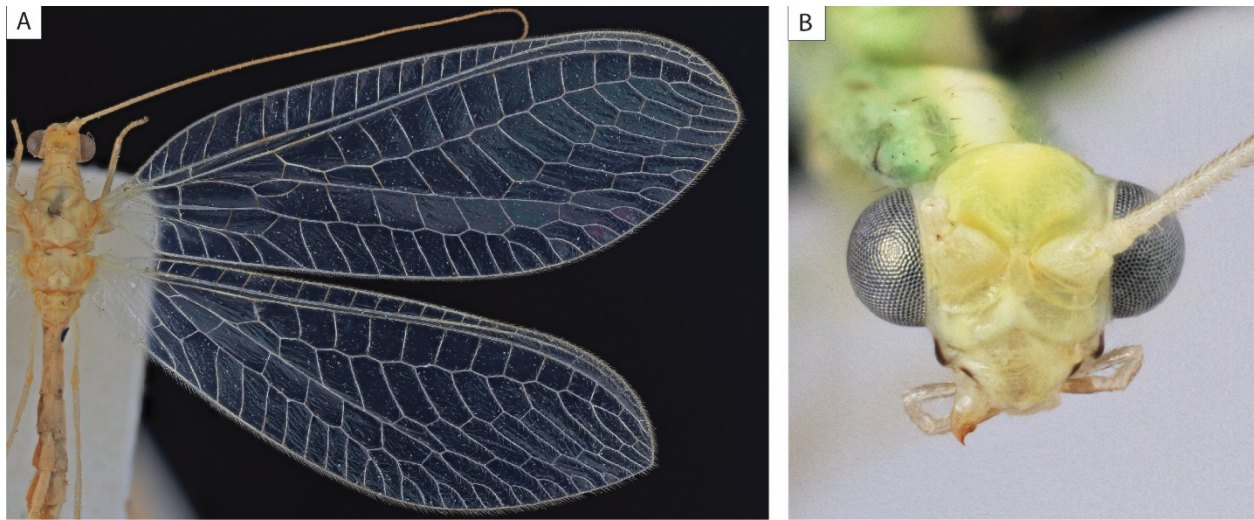
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely dark or entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: tergum IX and ectoproct fused; markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, close to sternum; spermatheca thick, or average; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or shaped like axe head, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent or present.

REMARKS: *Cunctochrysa* is similar to *Pseusomallada*, especially regarding the shape of the mediuncus, but does not have parameres. The two genera are not closely related, and *Cunctochrysa* rather resulted within the *Meleoma*-group in the results of our phylogenetic analysis. Larvae of the genus have been described and are debris-carrying (Killington 1937, Gepp 1983, Tauber et al. 2014). No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 71.** *Cunctochrysa albolineata* Killington. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Eremochrysa* Banks 1903

(18 species, 2 subgenera)

DIAGNOSIS: *Eremochrysa* is the only chrysopid genus with the combination of a single gradate series (outer) in the hind wing, and parameres shaped as a single rod.

REMARKS: *Eremochrysa* is one of the few Chrysopini genera with a yellowish-brown general body color, including other genera of the *Eremochrysa*-group (see chapter 1). As all members of the *Eremochrysa*-group the genus has multiple tibial spurs at least on the meso- and

metathoracic leg. Both subgenera (*Eremochrysa* and *Chrysopiella*) have an additional small sclerite laterally ventral to tergum IX + ectoproct, which is unique in Chrysopidae.

Subgenus *Chrysopiella* Banks 1911

(4 species) figure 45.

*Chrysopiella* Banks 1911: 344. Type species: *Chrysopa sabulosa* Banks 1897, by original designation. Brooks and Barnard 1990: 215 [as subgenus of *Eremochrysa*].

DIAGNOSIS: *Chrysopiella* is the only chrysopid subgenus with the combination of a single gradate series (outer) in fore- and hind wing, and parameres shaped as a single rod.

DISTRIBUTION: Nearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus laterally compressed, or tapered apically; labrum indented; mandibles symmetrical, narrow, with basal tooth, without basal tooth; frons in profile flat; scape marked laterally, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity denser laterally, setae pale and dark admixed, predominantly short; ventrolateral marking on prothorax present; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale and dark admixed, predominantly short; metathorax unmarked, pilosity sparse, setae pale and dark admixed, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 1; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.



Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 1; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; metatibia on inner surface smooth; femoral setae short; leg unmarked.

Abdomen: markings absent; setae short, dark; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; subgenitale as long as broad, on narrow elongate membranous structure; spermatheca average; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; tergum IX with small separate lateral sclerotized area; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sternum VIII and IX fused, elongate, with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with narrow projection medially, lateral arms apically flat expanded; entoprocessus absent, or minute, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as single rod, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *E. (Chrysopiella)* can be distinguished from *E. (Eremochrysa)* by the absence of the inner gradates in the forewing. Both genera have only the outer gradates present in the hind wing, but *E. (Eremochrysa)* has inner gradates in the forewing. Brooks and Barnard (1990) proposed the subgenus status of *Chrysopiella*, which we could confirm in our phylogeny, where it is sister to *Eremochrysa* (see chapter 1). The Larvae of *E. (Chrysopiella)* are unknown and the adults have been described as pollen feeders (Adams and Garland 1981)



**Figure 72.** *Eremochrysa (Chrysopiella)* sp., head, frontal view, photomicrograph.

Subgenus *Eremochrysa* Banks 1903

(14 species) figure 46.

*Eremochrysa* Banks 1903: 158. Type species: *Chrysopa punctinervis* McLachlan 1869, by original designation.

*Lolochrysa* Banks 1950: 59 [as subgenus of *Eremochrysa*]. Type species: *Eremochrysa hageni* Banks 1903, by original designation. Brooks and Barnard 1990: 215 [synonymy under *Eremochrysa*].

DIAGNOSIS: *Eremochrysa* is the only chrysochrysid subgenus with the combination of a single gradate series (outer) in the hind wing, and two in the forewing.

DISTRIBUTION: Nearctic.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking brown; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, narrow; frons in profile flat, or raised laterally; scape marked completely, dorsally, or laterally, less than 1.5x as long as wide; pedicel marked apically, completely, or dorsally; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, or short, surface smooth and glossy.

Thorax: prothorax markings large and discontinuous, brown to black, pilosity uniformly distributed, setae dark or pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked, predominantly brown to black, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; metathorax marked, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula marked or unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple,

straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, four, or three; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series or more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or marked strongly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 1, or two; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 1, two, or zero; number of mesotibial spurs: more than two; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae short; leg unmarked.

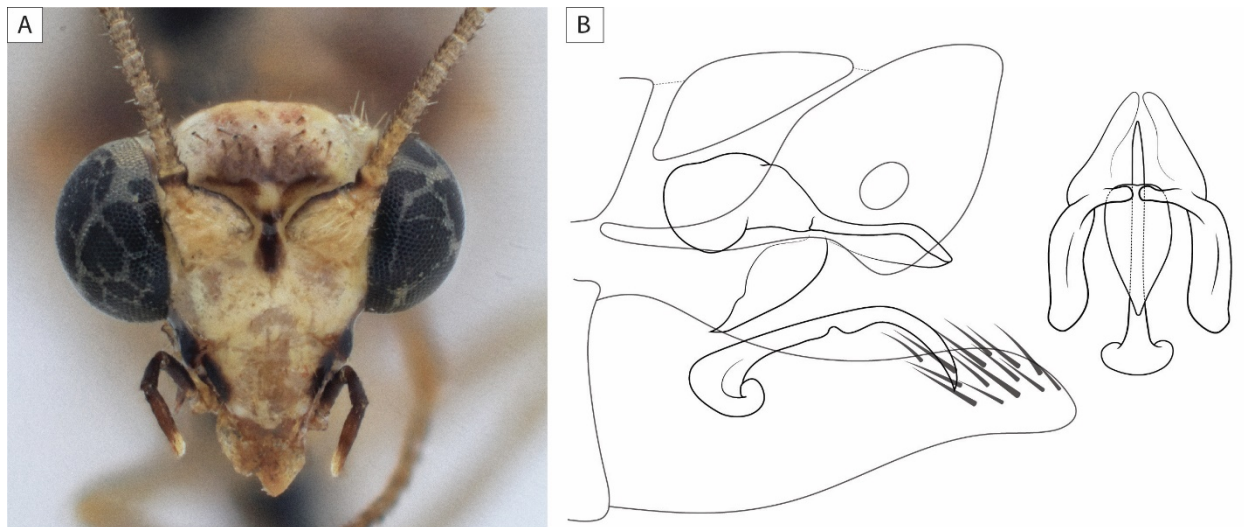
Abdomen: markings abundant; setae short, dark or pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long; spermatheca small, surface smooth; vela smaller than spermatheca; spermathecal duct very short.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; tergum IX with small separate lateral sclerotized area; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, with dense setal patch apically; tignum absent; gonarcus medially fused, median arch with broad medial projection, or with 2 forward projecting lobes medially, lateral arms apically flat expanded; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, larger than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as single rod, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *E. (Eremochrysa)* is similar to *E. (Chrysopiella)*, but can easily be distinguished

by the number of gradates in the forewing. The genus has a very elongate tergum IX + ectoproct in the male as similarly present in *C. (Neosuarius)*. The larvae of *E. (Eremochrysa) punctinervis* (McLachlan) have been described (Smith 1926) and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 73.** *Eremochrysa (Eremochrysa)*. A. *Eremochrysa (Eremochrysa)* sp., head, frontal view, photomicrograph. B. *Eremochrysa (Eremochrysa) fraterna* (Banks), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Glenochrysa* Esben-Petersen 1920

(10 species) figure 47.

*Glenochrysa* Esben-Petersen 1920: 518. Type species: *Glenochrysa typica* Esben-Petersen, by original designation. Tjeder 1966: 410 [as subgenus of *Chrysopa* Leach], New 1980: 32 [reinstated as genus].

DIAGNOSIS: *Glenochrysa* is the only chrysopid genus with the combination of the basal crossvein of the inner gradates not meeting PsM, 1r-m originating on RP, and a narrow basal

expansion of tergum IX + ectoproct of the male. It is also the only genus with a glenofinger.

DISTRIBUTION: Afrotropical, Australasian, Oceanian, or Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical palpomere, or uniformly marked; maxillary palpus uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked completely, or laterally, less than 1.5x as long as wide; pedicel marked laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent or present as T-shaped carina, pilosity short, surface smooth and matte, or unevenly textured; eversible glandular scent gland ( 'glenofinger') present.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, brown to black, pilosity uniformly distributed, setae pale, or pale and dark admixed, predominantly long, or predominantly short, thick long setae patches on pronotum absent or present; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity dense, or sparse, setae pale, or pale and dark admixed, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity dense, or sparse, setae pale, predominantly long, or predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked or unmarked; microtrichia absent except for wing base and anal

lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 3; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*, or joining M distal to *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or scarcely dark; wing markings absent, between PsM and PsC, on *dcc*, on inner gradates, along RS, and on spots in RP sector.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2;



maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

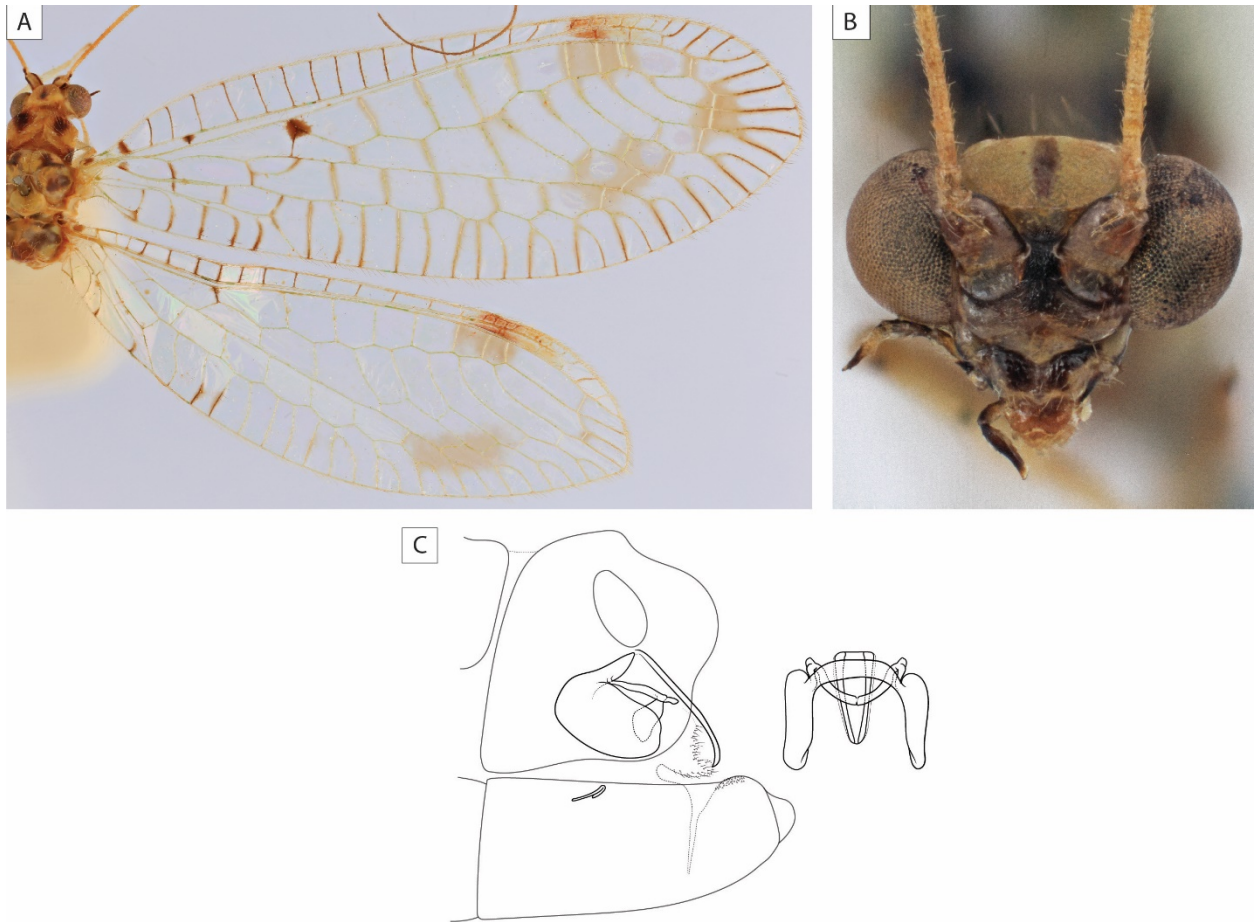
Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg extensively marked or unmarked.

Abdomen: markings absent, predominant, or sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale extended ventrally backwards, close to sternum; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; tergum IX with thin expansion towards the abdomen base; ectoproct apically elongate, or normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with three lobes bearing thick spines, with strong apical spines; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, or long and arching around mediuncus, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent or present apically on sternum IX; microtholi absent.

REMARKS: Most species of *Glenochrysa* have distinct wing markings and often long thick setae on the pro- and mesonotum as well as the posterior wing margin, making this genus very easy recognizable. The parameres were described as present, but small in Brooks and Barnard (1990) and Winterton and Garzón (2015), but we propose that the structure described is rather an enlarged hypandrium internum. It has a membrane medially and there is no second structure present which could be the hypandrium internum (a sclerite present in every chrysopid). The males of *Glenochrysa* have a unique eversible membranous sack anterior to the pronotum ('glenofinger', Duelli 2004). This structure can be inflated and is most likely used to emit semiochemicals (Duelli 2004, Winterton and Garzón 2015). The larvae of *Glenochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 74.** *Glenochrysa*. A. *Glenochrysa* sp., fore- and hind wing, dorsal view, photomicrograph. B. *Glenochrysa conradina* (Navás), head, frontal view, photomicrograph. C. *Glenochrysa minima* Winterton & Garzón-Orduña, male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Himalochrysa* Hölzel 1973

(3 species)

*Himalochrysa* Hölzel 1973b: 367. Type species: *Himalochrysa modesta* Hölzel 1973, by original designation and monotypy.

*Nepalochrysa* Hölzel 1973b: 347 [as subgenus of *Anisochrysa* Nakahara]. Type species: *Anisochrysa* (*Nepalochrysa*) *bhandarensis* Hölzel 1973, by original designation and monotypy. Brooks and Barnard 1990: 220 [synonymy under *Himalochrysa*].

DIAGNOSIS: *Himalochrysa* is the only chrysopterid genus with the combination of a mediuncus with a trifurcate apex (consistent of a single dorsal and paired ventral horns), and either no parameres, or parameres present as a large medially connected and two smaller lateral lobes.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown or red; labial palpus marked on apical palpomere; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, with basal tooth on one side; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark distally, or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, markings absent, ornamentation absent.

Thorax: prothorax markings in lateral longitudinal stripe, or fronterolaterally, small spot, red, setae pale, predominantly short, thick long setae patches on pronotum absent; mesothorax marked or unmarked, predominantly red, predominantly short; metathorax unmarked, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal

crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP absent; number of gradate series: 2, 3, 4, or more; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM, or not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2 or 3; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded;

praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca average; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, lateral arms strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as apical forks in horizontal and vertical plane; parameres absent or present, arranged as single sclerite, shaped as a large medial and smaller lateral lobe, opened towards apex, about as long as gonarcus, positioned ventrally, in sternum IX; gonosetae sparsely present (<10); gonocristae absent; microtholi absent or present.

REMARKS: It is likely that the three species included in *Himalochrysa* are not all of the same genus, due to the differences in number of gradate series, absence or presence of parameres, or microtholi and many more characters. The three species are in need of reexamination. We were not able to place the genus (only *H. modesta* was included) in the phylogeny, because it shares characters of several genus groups. *Himalochrysa* and *Rexa* key out together, but we were not able to determine a closer relationship between these two genera. They can be distinguished by the shape or presence of the parameres. The illustrations of the parameres of *H. modesta* (Hölzel 1973, Brooks and Barnard 1990) resemble those of some *Meleoma* species (such as *M. emucta*), but the

genera are distinct in many other characters. The larvae of *Himalochrysa* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Kostka* Navás 1913

(1 species) figure 48.

*Kostka* Navás 1913b: 319. Type species: *Kostka nacaratus* Navás 1913, by original designation and monotypy.

DIAGNOSIS: *Kostka* is the only chrysopid genus with the combination of a quadrangular *im* cell with a crossvein, few gradate crossveins (connecting ra-rp crossveins) present between RA and RP, and two gradate series, with the inner series not parallel to the outer.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark laterally; antenna longer than forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent, ornamentation absent, pilosity short, surface unevenly textured.

Thorax: prothorax markings in spots, brown to black, pilosity denser laterally, setae pale,

predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) sinuous; gradates in area between RA and RP normally absent, but present between few crossveins; number of gradate series: 2; number of gradate crossveins more in outer series than inner series; gradate series diverging; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark; wing markings on *dcc*, along



RS, and on posterior margin medially.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 0; number of metatibial spurs: 0; metatibia on inner surface smooth; femoral setae long; leg unmarked.

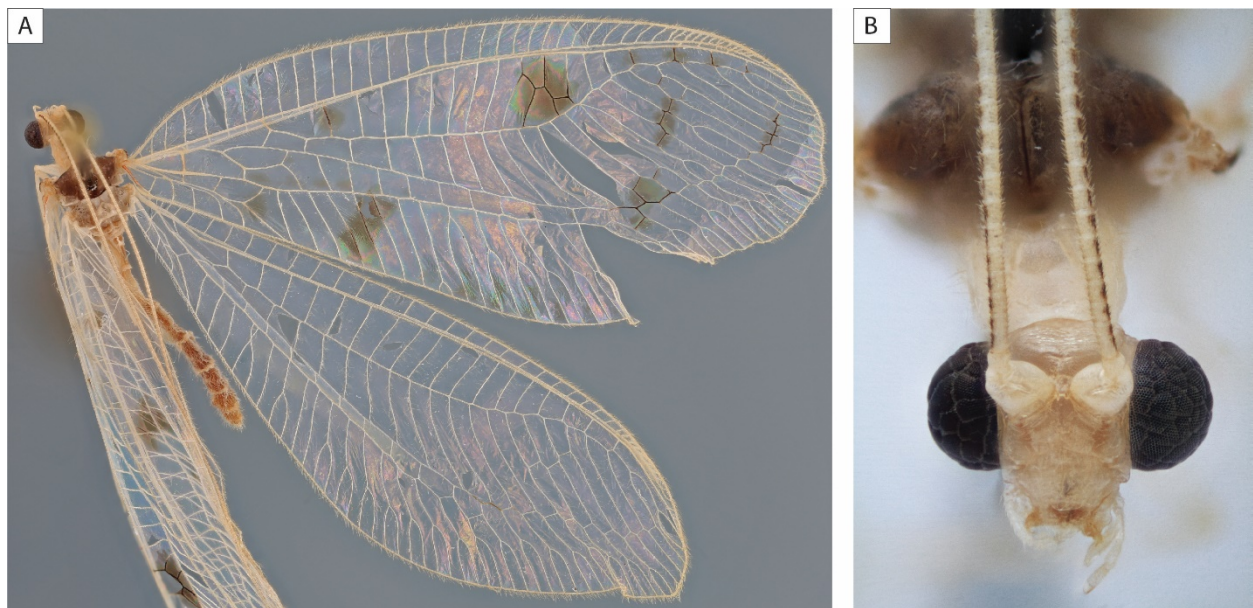
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale longer than broad; spermatheca thin, surface smooth; vela larger than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; ventral apodeme regular; sterna VIII and IX separate, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate and trifurcate apically, about as long as lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae

absent.

REMARKS: *Kostka* is can be easily identified by the two large spots on the pronotum and the markings of the forewing, which is present in this combination in few chrysopids. *Kostka* and *Cacarulla* are the only genera with a quadrangular im cell and gradates between RA and RP. They are much less numerous in *Kostka*, where crossveins are often present only between two or three crossveins, while they can be present along the entire sector in *Cacarulla*. Males of *Kostka* have only eight sterna, which is unique for Chrysopidae. Even with the presence of molecular data (although only one gene), it was not possible to place *Kostka* (see chapter 1), and we cannot suggest a sister genus or close relationships, due to the presence of characters from numerous different clades. The larvae of *Kostka* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 75.** *Kostka nacaratus* Navás. A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Kymachrysa* Tauber and Garland 2014

(2 species)

*Kymachrysa* Tauber and Garland 2014: 88. Type species: *Chrysopa placita* Banks 1908, by original designation.

DIAGNOSIS: *Kymachrysa* is the only chrysopid genus with the combination of strongly curved RP branched between the gradate series, and a basally expanded ventral apodeme in the male (beyond the origin of the dorsal apodeme).

DISTRIBUTION: Nearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown or red; labial palpus marked on apical 3 palpomeres, or uniformly marked; maxillary palpus marked on apical 2 palpomeres, or uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with broken band, spots, or with unbroken band; vertex raised in profile, markings present, ornamentation absent, surface smooth and glossy.

Thorax: prothorax markings diffuse and sparse, red, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale; metathorax unmarked, pilosity sparse, setae pale; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches curved between inner and outer gradates; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); femoral setae short; leg

unmarked.

Abdomen: markings absent; setae short; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale present on apex of sternum; small sclerotized plate between subgenitale and sternum present; subgenitale as long as broad, apparently detached; spermatheca average, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme basally elongate beyond dorsal apodeme; sternum VIII and IX fused, regular; tignum absent; gonarcus medially fused, median arch with 2 forward projecting lobes medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as single rod, about as long as gonarcus, or longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent or present.

REMARKS: *Kymachrysa* was recently described (Tauber and Garland 2014) on the basis of the basally elongate ventral apodeme, which seems to be unique among Chrysopidae. The genus also has curved RP branches, which are prominent here, but can also be found in different extent in other genera (such as *Chrysotropia*, *Mallada*, or *Meleoma*). It has numerous characters consistent with Chrysopini, but resulted within Leucochrysinini in preliminary phylogenetic analysis (although not well supported), with which it has the presence of a praegenitale in common. The larvae of *Kymachrysa* have been described (Tauber et al. 1998, Tauber and Garland 2014) and

been debris-carrying. The feeding habits of the adults are unknown.

Genus *Mallada* Navás 1925

(63 species) figure 49.

*Mallada* Navás 1925a: 24. Type species *Mallada stigmatus* Navás 1925, by monotypy.

*Anisochrysa* Nakahara 1955: 145. Type species: *Anisochrysa paradoxa* Nakahara 1955, by original designation and monotypy. Adams 1959: 25 [synonymy under *Chrysopa* Leach], Tjeder 1966: 416 [as subgenus of *Chrysopa* Leach], Hölzel 1970: 46 [reinstated as genus], Adams 1975: 172 [synonymy under *Mallada*].

DIAGNOSIS: *Mallada* is the only chrysopid genus with the combination of the presence of a tignum, parameres shaped as a single sclerite with two elongate medial lobes, (often partially fringed apically), and a smaller, thin lobe on each side, and a simple terminalia in the male, without a broad sclerotized external structure ventrally of ectoproct apex.

DISTRIBUTION: Australasian, Oceanian, or Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked apically, basally,

completely, dorsally, laterally, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked apically, basally, completely, dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, with broken band, spots, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, in lateral longitudinal stripe, fronterolaterally, small spot, or diffuse and sparse, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, predominantly red, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity sparse, setae dark or pale, predominantly long, or predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 6, or four; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight, or curved between inner and outer gradates; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2 or 3; number of gradate

crossveins approximately same number in each series or more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate), or rarely irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC, or PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, marked strongly in irregular pattern, or marked weakly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2 or 3; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long or short; leg unmarked.

Abdomen: markings absent, or sparse; setae long or short, pale; sternum II without stridulatory organ.



Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or broader than long; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent or present apically, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, elongate, or regular, without strong apical spines or dense setae, or with strong apical spines; tignum present, rarely absent; gonarcus medially fused, median arch with narrow projection medially, or without expansion medially, lateral arms apically flat expanded, or strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus, mediuncus process absent, rarely numerous short setae on apex present; parameres present, arranged as single sclerite, shaped as a structure with two elongate medial lobes, partially fringed apically, and a smaller, thin lobe on each side, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: *Mallada* is a very large genus that is not easily to determine by external features. With the closely related genus *Anomalochrysa* it is unique in the shape of the parameres (figs 29, 46), and the two genera mainly differ in the external, sclerotized plate ventral to the apex of tergum IX + ectoproct in the males of *Anomalochrysa*. It is likely, that the Hawaiian *Anomalochrysa* are a subgenus of *Mallada*, but further analyses are needed to asses this relationship. Since its last

redescription (Brooks and Barnard 1990) many species of *Mallada* have been moved to *Pseudomallada* (now *Apertochrysa*). The two genera are similar, but the parameres are differently shaped. The phylogenetic analysis (see chapter 1) revealed that the two genera are not closely related, with *Mallada* in the *Chrysoperla*-group and *Apertochrysa* in the *Chrysopa*-group. The Austro-Indonesian species group described by Brooks and Barnard (1990) is not monophyletic and includes species of both genera. *Anisochrysa* was synonymized with *Mallada* by Adams (1975), but numerous species that were originally described in this genus are now in *Apertochrysa*, *Chrysoperla* or other smaller genera. The larvae of several *Mallada* species have been described (Terry 1908, Zimmerman 1957, Dessart 1973, Boros 1984, Tauber et al. 2014) and are usually debris carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 76.** *Mallada basalis* (Walker), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Meleoma* Fitch 1855

(28 species) figure 50.

*Meleoma* Fitch 1855: 786. Type species: *Meleoma signoretii* Fitch 1855, by monotypy.

DIAGNOSIS: *Meleoma* is the only chrysopid genus in which a vertex ornamentation in form of an anterodorsal process, often extending on the frons, is present (although not in every species). Apart of this character they can be recognized by the combination of two gradates in the forewing, an elongate sternum VIII+IX, a thin and elongate mediuncus, which is clearly separated from the gonarcus, and parameres shaped as a medial large lobe, partially separated (in some species) and small lateral lobe on each side basally (w-shaped with expanded wings).

DISTRIBUTION: Nearctic, or Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, uniformly marked, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked completely, dorsally, or entirely pale, equal to, or greater than 2x width; pedicel marked apically, completely, or entirely pale; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked, or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation present as anterodorsal processus in male, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings absent, in lateral longitudinal stripe, or fronterolaterally, small spot, red, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches

on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight, or curved between inner and outer gradates; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA basal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple,

unforked; anal lobe rounded, small; wing veins scarcely dark or entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

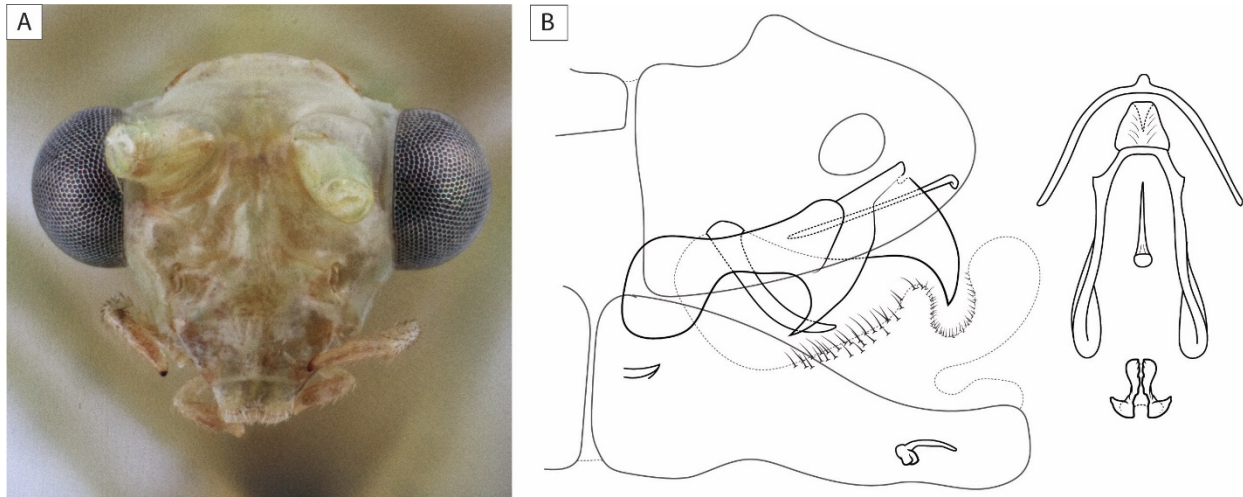
Abdomen: markings absent; setae long, pale; sternum II with or without stridulatory organ; microtholi absent.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, on broad membranous structure; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused, or separate; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, elongate, or with con-like invagination for dorsal structure, without strong apical spines or dense setae; tignum absent or present; gonarcus medially fused, median arch with narrow projection medially, lateral arms apically flat expanded; entoprocessus long, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus

complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, thin, shorter than lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as a medial large lobe, partially separated, and small lateral lobe on each side basally, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent.

REMARKS: *Meleoma* is a very distinctive genus, with many unique characters in the male that are probably associated with courtship. The genus is one of the few genera in which sexual dimorphism exists. This is established by the presence of prominent ornamentations of the vertex anteriorly and the supraantennal frons, a deformed and often in the vertex ornamentation fitting scape, and stridulatory structures on sternum II in many males. The only other genera where stridulatory structures have been found are *Brinckochrysa*, some *Apertochrysa*, and possibly one *Chrysocerca* species. The larvae of several species of *Meleoma* have been described (Putman 1932, 1937, Tauber 1969, Tauber et al. 2014) and are either not or light debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 77.** *Meleoma*. A. *Meleoma signoretii* (Fitch), head, frontal view, photomicrograph. B. *Meleoma emucta* (Fitch), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Nipponochrysa* Tsukaguchi 1995

(1 species)

*Nipponochrysa* Tsukaguchi 1995: 58. Type species: *Nipponochrysa moriutii* Tsukaguchi 1995, by monotypy.

DIAGNOSIS: *Nipponochrysa* is the only chrysopterid genus with the combination of strongly elongate gonocornua (about as long as the lateral arms of the gonarcus), and elongate entoprocessi.

DISTRIBUTION: Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; scape unmarked, less

than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; vertex raised in profile, markings absent, ornamentation absent.

Thorax: prothorax markings absent; ventrolateral marking on prothorax absent; mesothorax unmarked; metathorax unmarked; small expansion on frontal metascutum margin absent.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing



markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; jugal lobe simple.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); leg unmarked.

Abdomen: markings absent, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or extended ventrally backwards, on narrow elongate membranous structure; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with 2 elongate and forward projecting horns medially, lateral arms apically flat expanded; entoprocessus long, with additional structure, secondary process on lateral arms present; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as ventral hook; parameres absent; gonosetae numerous present (>10); gonocristae absent.

REMARKS: The monotypic Japanese genus *Nipponochrysa* can be easily identified by the male genitalia. It resulted within the *Meleoma*-group in the most recent analyses (chapter 1), and

there in a monophylum with *Bornichrysa*, *Atlantochrysa*, *Cunctochrysa* and *Meleoma*. The gonocornua is also pronounced in *Borniochrysa* but not as strong as in *Nipponochrysa*. A sclerotized (often recurved hook) ventral to the mediuncus is present in few genera (*Atlantochrysa*, *Dictyochrysa*, some *Nacarina*, and *Nodochrysa*), but to different extents, and none are closely related to *Nipponochrysa*. The larvae have been described (Tsukaguchi 1995, Tauber et al. 2014) and are not debris-carrying. The adults are presumed to feed on honey dew (Tsukaguchi 1995).

Genus *Parachrysopiella* Brooks and Barnard 1990

(3 species) figure 51.

*Parachrysopiella* Brooks and Barnard 1990: 229. Type species: *Eremochrysa argentina* Banks 1910, by original designation.

DIAGNOSIS: *Parachrysopiella* is the only chrysopid genus with the combination of a single gradate series in the fore- and hind wing, and parameres with four elongate tips (apically bifurcate structure with a sub-basal pointed expansion on each side).

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus uniformly marked; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented, or straight; mandibles symmetrical, narrow, with basal tooth; frons in profile flat; scape marked dorsally, laterally, or medially, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in four rings; flagellar setae as long, or longer than

flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in three longitudinal stripes, brown to black, or red, pilosity uniformly distributed, setae dark, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae dark, predominantly short; metathorax unmarked, pilosity sparse, setae dark, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 1; number of gradate crossveins more in outer series than inner series; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM;

MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*, or longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 1; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: more than two; number of mesotibial spurs: more than two; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae long or short; leg unmarked.

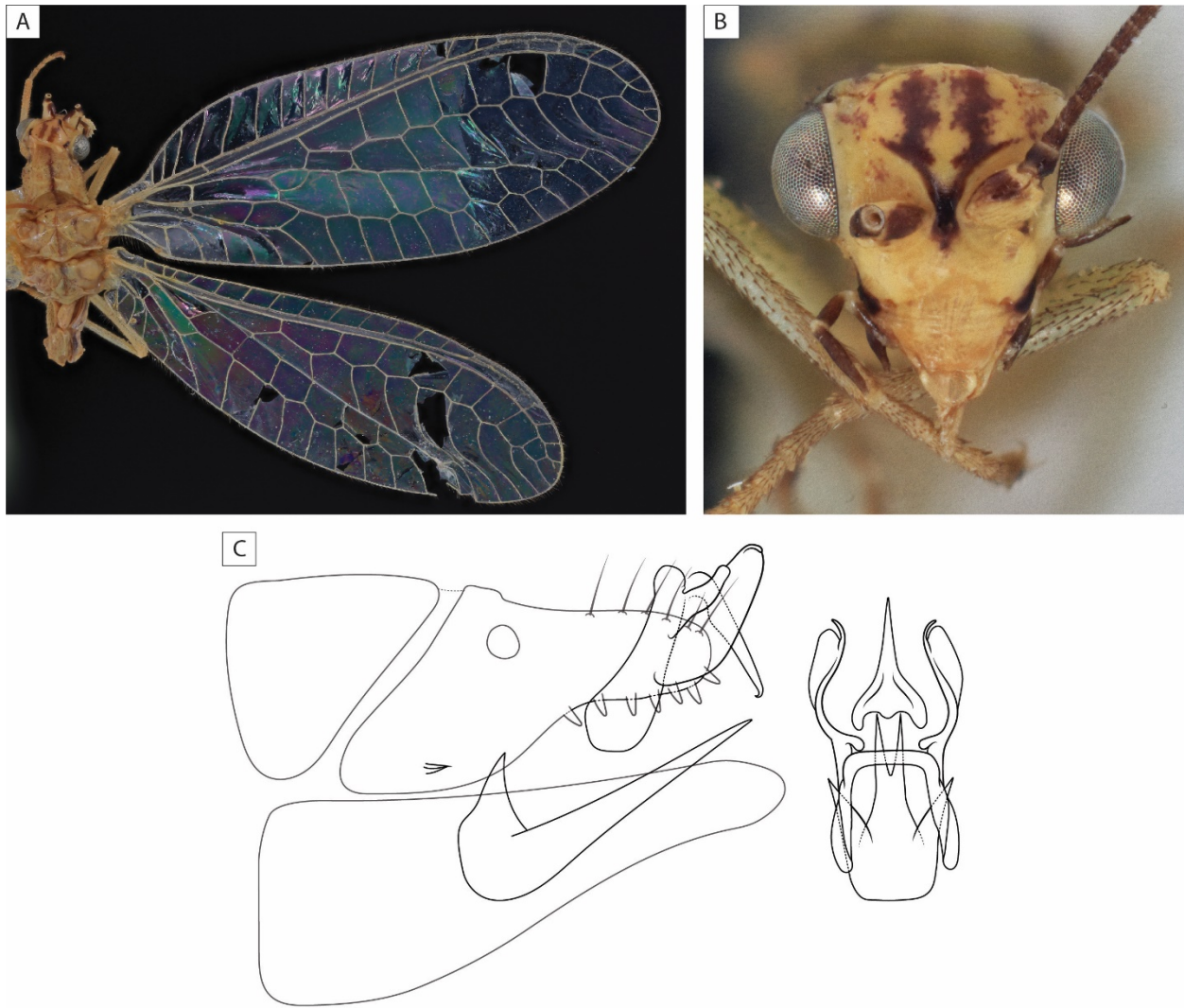
Abdomen: markings absent, or sparse; setae long, dark; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale longer than broad, or extended ventrally backwards, close to sternum; spermatheca average, surface smooth; vela about same size as spermatheca, or larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct apically elongate; dorsal invagination between ectoprocts deep; thick spines on ectoproct

present apicoventrally; ventral apodeme regular; sterna VIII and IX fused, elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus absent, or minute, or long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent or present, arranged as single sclerite, shaped as an apically bifurcate structure with a sub-basal pointed expansion on each side, opened towards apex, longer than gonarcus, positioned ventrally, in sternum IX; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Parachrysopiella* is one of the few Chrysopini with a yellowish brown body color, as *Eremochrysa* or *Suarius*. The genus is easily identifiable due to the strongly reduced wing venation. It is very similar to *Chrysopiella*, but they occur in different regions of the world: *Parachrysopiella* in South America and *Chrysopiella* in North America. The larvae of *Parachrysopiella* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 78.** *Parachrysopiella*. A. *Parachrysopiella talquensis* Penny, fore- and hind wing, dorsal view, photomicrograph. B. *Parachrysopiella argentina* (Banks), head, frontal view, photomicrograph. C. *Parachrysopiella talquensis* Penny, male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Peyerimhoffina* Lacroix 1920

(1 species) figure 1K, 52.

*Peyerimhoffina* Lacroix 1920: 83. Type species: *Peyerimhoffina pudica* Lacroix 1920, by monotypy.

*Tjederina* Hölzel 1970: 48. Type species: *Chrysopa gracilis* Schneider 1951, by original designation and monotypy. Zeleny 1971: 175 [synonymy under *Apertochrysa* Tjeder], Principi 1977: 326 [as subgenus of *Chrysopa* Leach], Aspöck et al. 1980: 261 [reinstated as genus], Brooks and Barnard 1990: 231 [synonymy under *Peyrimhoffina*].

DIAGNOSIS: *Peyrimhoffina* is the only chrysopid genus with the combination of more crossveins in the inner than outer gradates, a regular, rounded sternum VIII+IX, that is not elongate, and the presence of a tignum and parameres.

DISTRIBUTION: Palearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; labrum indented; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, pilosity uniformly distributed, setae dark, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae dark, predominantly long; metathorax unmarked, pilosity sparse, setae dark, predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.



Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

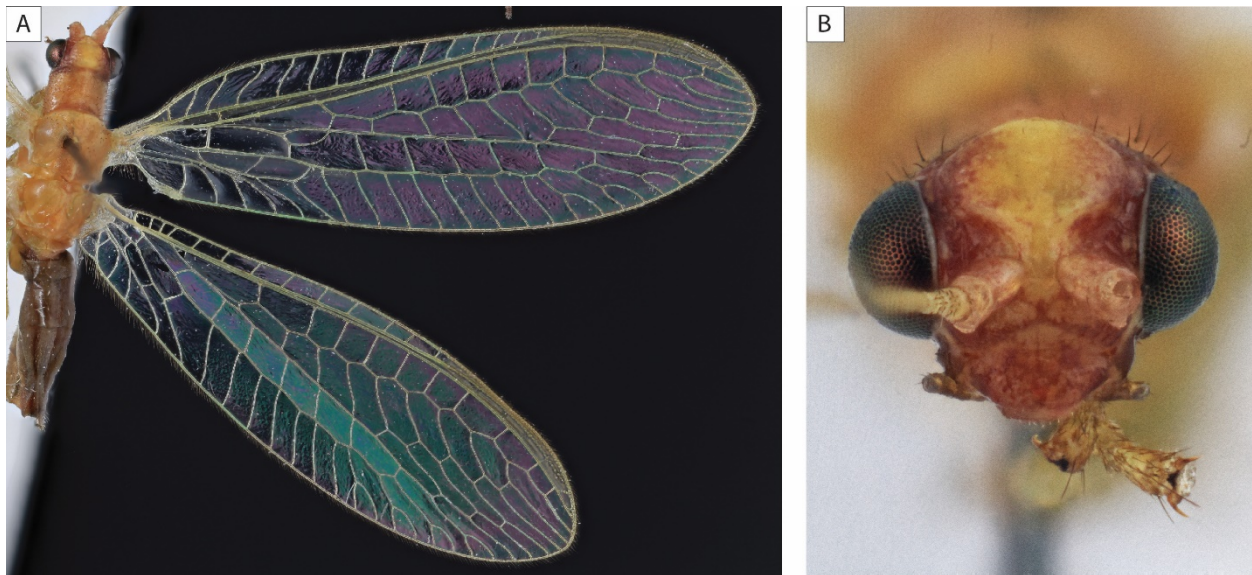
Abdomen: markings absent; setae short, dark; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca thin, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct slightly elongate, prominently tapering towards apicodorsally; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum present; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, about as long as lateral arms of gonarcus, mediuncus process absent; parameres present, arranged as single sclerite, shaped as a narrow 'V', pointed towards apex of abdomen, basally recurved towards lateral, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: *Peyerimhoffina* is easily detected by the shape of the terminalia in the male and female, as well as the reduced number of outer gradate crossveins. The genus is closely related to

*Chrysoperla* and results within the genus in many analyses. Due to the strong differences in the shape of the terminalia and the parameres in *Peyerimhoffina*, we are keeping the the genera separate. The large genus *Chrysoperla* should be subjected to a comprehensive phylogenetic analysis including the monotypic *Peyerimhoffina*. The larvae have been described (Gepp 1983, Tauber et al. 2014) and are not debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 79.** *Peyerimhoffina gracilis* (Schneider). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Plesiochrysa* Adams 1982

(23 species) figure 53.

*Plesiochrysa* Adams 1982a: 28 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa brasiliensis* Schneider 1851, by original designation. Brooks and Barnard 1990: 232 [raised to genus].

DIAGNOSIS: *Plesiochrysa* is the only chrysopid genus with the combination of two gradate series, more crossveins in the outer than inner gradates, a triangular im cell, without a crossvein, a simple, rounded tergum IX + ectoproct, a long and thin mediuncus, and no parameres.

DISTRIBUTION: Australasian, Oceanian, Neotropical, or Oriental.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus marked on apical 2 palpomeres, marked on apical palpomere, or uniformly pale; maxillary palpus marked on apical palpomere, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked dorsally, laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked basally, completely, or entirely pale; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent or present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in lateral longitudinal stripe, in spots, or diffuse and sparse, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly red, pilosity sparse, setae pale, predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark or entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

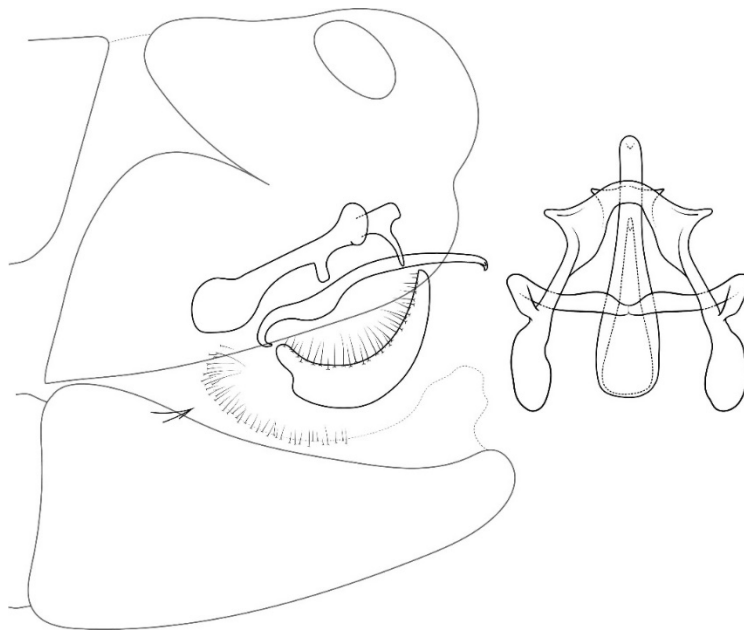
Abdomen: markings absent, or sparse; setae long, pale; sternum II with or without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or broader than long, close to sternum; spermatheca small, surface smooth; vella smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused, or incompletely fused, with suture present; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent; ventral apodeme regular; sternum VIII and IX fused, or incompletely fused, with suture present, regular, or with two pointed lobes bearing thick setae, without strong apical spines or dense setae; tignum absent (old world species) or present (new world species); gonarcus medially fused, median arch with 2 forward projecting horns medially, lateral arms apically flat expanded, or simple, not expanded; entoprocessus absent, long and simple, long and arching around mediuncus, or long, with additional structure, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus clearly separate from gonarcus, or closely associated with gonarcus, with membranous connection, elongate, thin, larger than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent or present as ventral extension with setae (pseudopenis); parameres absent; gonosetae numerous present (>10);

gonocristae absent or present apically on sternum IX; microtholi absent or present.

REMARKS: *Plesiochrysa* is difficult to identify by external characters, and the genus is very heterogenous, but is generally a comparatively large chrysopine. It is the only genus in which a true pseudopenis is present – a long sclerotized structure that is connected to the apex of the mediuncus, although not in all species. The tignum is absent in the old world species, but present in the new world species. Some species have a faint serrated structure laterally on sternum II, which is probably a stridulatory organ, as present in *Brinckochrysa* and few other genera. *Plesiochrysa* is closest related to *Ceratochrysa* and *Chrysopa* (see chapter 1). The larvae have been described (Adams 1959, Mehra 1966, Tauber et al. 2014) and are not debris-carrying. No insect remains were found in the guts of adults, but they have been reported to be predacious (Brooks and Barnard 1990).



**Figure 80.** *Plesiochrysa* sp., male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Rexa* Navás 1920

(2 species) figure 54.

*Rexa* Navás 1920: 289. Type species: *Rexa lordina* Navás 1920, by original designation and monotypy.

*Eurochrysa* Esben-Petersen 1925: 67. Type species: *Chrysopa corsica* Hagen 1864, by original designation. Hölzel 1973: 78 [synonymy under *Rexa*].

DIAGNOSIS: *Rexa* is the only chrysopid genus with the combination of a quadrangular im cell with a crossvein, forked endings of CuA, no tignum, and parameres present.

DISTRIBUTION: Palearctic.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown or red; labial palpus marked on apical 3 palpomeres; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in lateral longitudinal stripe, red, pilosity uniformly distributed, setae dark or pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity dense, or sparse, setae dark or pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly

long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 4, three, or two; number of gradate crossveins approximately same number in each series or more in outer series than inner series; gradate series irregularly arranged, or parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein, or irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC, or PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark or entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 4, three, or



two; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

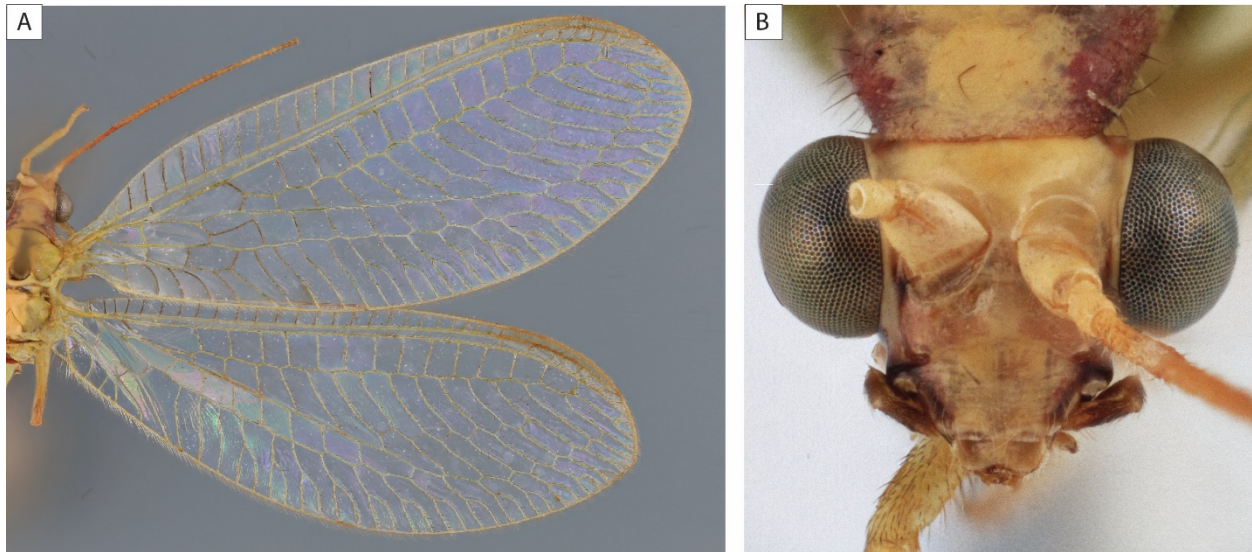
Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale longer than broad, apparently detached; spermatheca thin, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, or without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, or long, with additional structure, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process present as apical forks in horizontal and vertical plane, or present as paired pointed expansions subbasally, dorsally; parameres present, arranged as single sclerite, shaped as an apically bifurcate structure with a sub-basal pointed expansion on each side,

opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent, or sparsely present (<10); gonocristae absent or present apically on sternum IX; microtholi absent.

REMARKS: *Rexa* is a small genus that can easily be distinguished by the quadrangular im cell and the forked vein endings present at the posterior wing margin. Only *Rexa* and *C. (Tumeochrysa)* have forked CuA and MP endings in Chrysopinae, but the two genera are very different in their genitalia. The larvae of *Rexa* have been described (Canard and Labrique 1989, Brooks and Barnard 1990) and are debris carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 81.** *Rexa raddai* (Hölzel). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

Genus *Suarius* Navás 1914

(29 species) figures 1N, 55.

*Suarius* Navás 1914a: 73. Type species: *Suarius walsinghami* Navás 1914, by original designation and monotypy. Tjeder 1966: 372 [as subgenus of *Chrysopa* Leach], Hölzel 1970: 51

[reinstated as genus].

*Vasquezius* Navás 1914a: 75. Type species: *Vasquezius alisteri* Navás, by original designation and monotypy. Hölzel 1980: 169 [synonymy under *Suarius*].

*Prochrysopa* Tjeder 1936: 18. Type species: *Prochrysopa mongolica* Tjeder, by monotypy. Tjeder 1966: 372 [synonymy under *Suarius*], Hölzel 1970: 51 [as subgenus of *Suarius*], Brooks and Barnard 1990: 236 [reinstated synonymy under *Suarius*].

DIAGNOSIS: *Suarius* is the only genus with the combination of two gradate series, a triangular im cell, without a crossvein, more than two tibial spurs on all legs, and no parameres.

DISTRIBUTION: Afrotropical oriental, or Palaearctic.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking brown or red; labial palpus marked on apical 3 palpomeres, or uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented, or straight; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked dorsally, laterally, entirely pale, or ventrally, less than 1.5x as long as wide; pedicel marked laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked; carina on dorsal torulus margin absent; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, in lateral longitudinal stripe, or fronterolaterally, small

spot, brown to black, pilosity uniformly distributed, setae pale, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally with dense, scale-like setae in many species; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series or more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital

cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, marked strongly in irregular pattern, or dark along integumental marking pattern; wing markings absent, on *dcc*, on inner gradates, along RS, and on posterior margin medially.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: more than two; number of mesotibial spurs: more than two; number of metatibial spurs: more than two; metatibia on inner surface smooth; femoral setae long; leg unmarked.

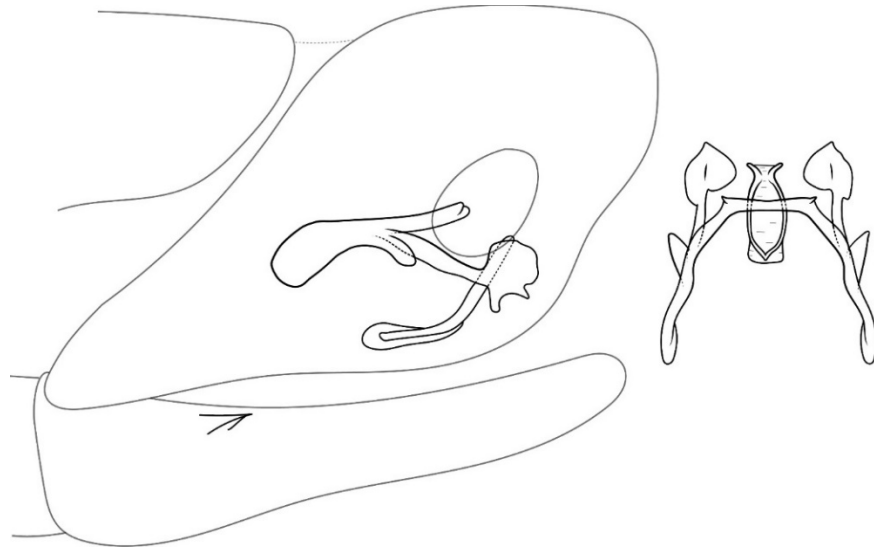
Abdomen: markings absent, abundant, or sparse; setae long or short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale extended ventrally backwards, close to sternum; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, tapering apically, and therefore seemingly elongate, without strong apical spines or dense setae;

tignum absent; gonarcus medially fused, median arch without expansion medially, or with lateral, pointed gonocornua, lateral arms simple, not expanded; entoprocessus long, with additional structure, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms present; mediuncus clearly separate from gonarcus, or closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or with lateral edges sclerotized, medially almost membranously, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi absent.

REMARKS: *Suarius* is one of the few genera in Chrysopini with a yellowish brown body color, as most members of the *Eremochrysa*-group. It also has numerous tibial spurs on all legs, which is rare in Chrysopinae. The males of several species of *Suarius* have thick scales on the dorsal side of R in the hind wing and in some also on the ventral side of R in the forewing. This character is not present in any other genus, and the species in which it can be found used to be gathered in the genus *Prochrysopa*, which Brooks and Barnard (1990) re-synonymized. Brooks and Barnard (1990) noted that the illustration of the wings of the type are not accurate for the genus, as this specimen has an unusual venation for the species. The larvae of *Suarius* have been described (Tauber 1975, Monserrat and Díaz-Aranda 2012, Tauber et al. 2014) and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 82.** *Suaris alisteri* (Navás), male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Titanochrysa* Sosa and de Freitas 2012

(6 species) figure 56, wing figure see chapter 4.

*Titanochrysa* Sosa and de Freitas 2012: 2. Type species: *Titanochrysa circumfusa* (Burmeister 1939), by original designation.

*Cryptochrysa* de Freitas and Penny 2000: 165. Type species: *Cryptochrysa chloros* de Freitas and Penny 2000, by original designation and monotypy. Tauber et al. 2018: 293 [synonymy under *Titanochrysa*]

DIAGNOSIS: *Titanochrysa* is the only chrysopid genus with the combination of labial palpi III-V marked, two gradate series in fore- and hind wing, a simple, rounded tergum IX + ectoproct, no tignum, and parameres shaped as a single rod, and a simple ventral apodeme, not expanded basally.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical palpomere, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles symmetrical, or assymetrical, narrow or broad, without basal tooth, with tooth on both sides, or with tooth on one side; frons in profile raised laterally; scape marked laterally, rarely dorsally, or unmarked, less than 1.5x as long as wide; pedicel marked laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked, or with small spot on parocular area; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy, or unevenly textured.

Thorax: prothorax markings in lateral longitudinal stripe, brown to black, pilosity uniformly distributed, or denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not



fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6, or 0-3; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*, or joining M distal to *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked strongly in irregular pattern, or dark on gradates; wing markings between PsM and PsC, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6, or 0-3; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale longer than broad, or extended ventrally backwards, on broad membranous structure; spermatheca thin or average, surface smooth; vela about same size as spermatheca or larger; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, or tapering apically, and therefore seemingly elongate without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with narrow projection medially, or with strongly sclerotized X-shaped, or V-shaped rods medially, not completely connected to medial arch, or two forward pointing lobes medially, lateral arms apically flat expanded, or simple, not expanded, entoprocessus short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter or larger than lateral arms of gonarcus, mediuncus process present as lateral sclerotized lobes, or setae on apex; thick papillae present ventral of mediuncus of some species; parameres present, arranged as single sclerite, shaped as single rod, basally broad, apically with teeth, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae numerous present (>10); gonocristae absent; microtholi present.

REMARKS: *Titanochrysa* is most easily distinguishable by its coloration, especially of its

dark palpi. De Freitas and Penny (2012) discuss genera that might be closely related in the original description, where *Ceraeochrysa* and *Parachrysiella* have similar external characters, but differ in their genitalia, and *Ungla* is different externally but has similar genitalia. The most recent phylogenetic analysis was not able to place this genus on the basis of morphological characters. The species of *Titanochrysa* have strongly variable mandibles, with all character states present from narrow to broad, and no basal teeth, a tooth on one side or a tooth on both sides. Tauber et al. (2018) recently synonymized the monotypic genus *Cryptochrysa* with *Titanochrysa*. The larvae have been described (Tauber et al. 2012, Tauber et al. 2014) and are debris carrying. The feeding habits of the adults have not been described.



**Figure 83.** *Titanochrysa chloros* (Freitas and Penny), head, frontal view, photomicrograph.

Genus *Ungla* Navás 1914

(25 species) figure 57.

*Ungla* Navás 1914b: 224. Type species: *Ungla annulata* Navás 1914, by original designation and

monotypy. Adams 1975: 169 [synonymy under *Suarius* Navás], Brooks and Barnard 1990: 238 [reinstated as genus].

DIAGNOSIS: *Ungla* is the only chrysopid genus with the combination of broad mandibles, vertex markings present, approximately the same number of crossveins in the outer and inner gradates, *c1* as long or shorter than *c2*, no microtholi in the male, a regular tergum IX + ectoproct, without a narrow basal elongation, a regular ventral apodeme, without a process, no tignum or parameres, and numerous gonosetae present.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical palpomere; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile flat, or raised laterally; scape marked dorsally, or laterally, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, with unbroken band, or with small spot medially on supra-, or intra-antennal frons; carina on dorsal torulus margin absent or present; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and matte, or unevenly textured.

Thorax: prothorax markings in lateral longitudinal stripe, or in spots, brown to black,

pilosity denser laterally, setae dark or pale, predominantly long, or predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae pale, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long, or predominantly short; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight, or sinuous basally; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3 or 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent, or diffuse, weakly defined; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at apex of *mamp1*, or joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to

2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or scarcely dark; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw simple, rarely dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent, or sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum, or on narrow elongate membranous structure; spermatheca thick, or average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded, with ventral lobes, or tapering towards apicoventrally; dorsal invagination between ectoprocts deep, or shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sternum VIII and IX fused, elongate, or tapering apically, and

therefore seemingly elongate, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, or without expansion medially, lateral arms simple, not expanded; entoprocessus long, or short, positioned at the joint of medial arch and lateral arms, or medially on lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae absent; microtholi absent.

REMARKS: *Ungla* has no unambiguous synapomorphies, and can key out with *Glenochrysa* (although most species of that genus are quite distinct). The less distinct species of *Glenochrysa* and *Ungla* can be distinguished by the male genitalia, and the basal most crossvein of the inner gradates meets PsM in *Ungla*, but not in *Glenochrysa*. Additionally, *Ungla* is neotropical and *Glenochrysa* occurs in the Old World. Tauber et al. (2017) stated that the genus is similar to *Neosuarius*, but differs in the male genitalia. *Ungla* is a member of the *Chrysopodes*-group, and was recovered as sister to *Yumachrysa* + *Ceraeochrysa* in the most recent phylogenetic analysis (see chapter 1). *Yumachrysa* and *Ungla* are fairly similar (distinguishable by the genitalia and the long setae on tergum IX + ectoproct in *Yumachrysa*), but parameres are present in *Ceraeochrysa*, and not in the former two. Many species have enlarged spiracles in the abdomen, which is present in few chrysopid taxa. Tauber et al. (2017) provided a comprehensive review of the genus. The larvae of two species have been described (Monserrat and Freitas 2005, Freitas 2007, Reguilón 2010, Tauber et al. 2014), and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 84.** *Ungla argentina* (Navás), head, frontal view, photomicrograph.

Genus *Yumachrysa* Banks 1950

(4 species) figure 58.

*Yumachrysa* Banks 1950: 51 [as subgenus of *Chrysopa* Leach]. Type species: *Chrysopa apache* Banks 1938, by original designation. Tjeder 1966: 372 [synonymy under *Suarius*], Adams and Penny 1986: 121 [raised to genus].

DIAGNOSIS: *Yumachrysa* is the only chrysopid genus with the combination of more crossveins in the outer than inner gradates, a narrow mediuncus that is longer than the lateral arm of the gonarcus, no parameres, and thick, long setae dorsally on the tergum IX + ectoproct, which point towards dorsal.

DISTRIBUTION: Nearctic.



DESCRIPTION: general body colored brown.

Head: colored same as body; genal marking absent; labial palpus marked on apical 3 palpomeres, or uniformly pale; maxillary palpus uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked apically, or completely; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length; frons with broken band, spots; carina on dorsal torulus margin absent; vertex raised in profile, markings present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings large and discontinuous, or in lateral longitudinal stripe, brown to black, or red, pilosity uniformly distributed, setae dark or pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked or unmarked, predominantly brown to black, pilosity sparse, setae dark or pale, predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma absent; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R

ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in outer series than inner series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark or entirely pale; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely dark or entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked, or with markings on femora, tibiae, and tarsi.

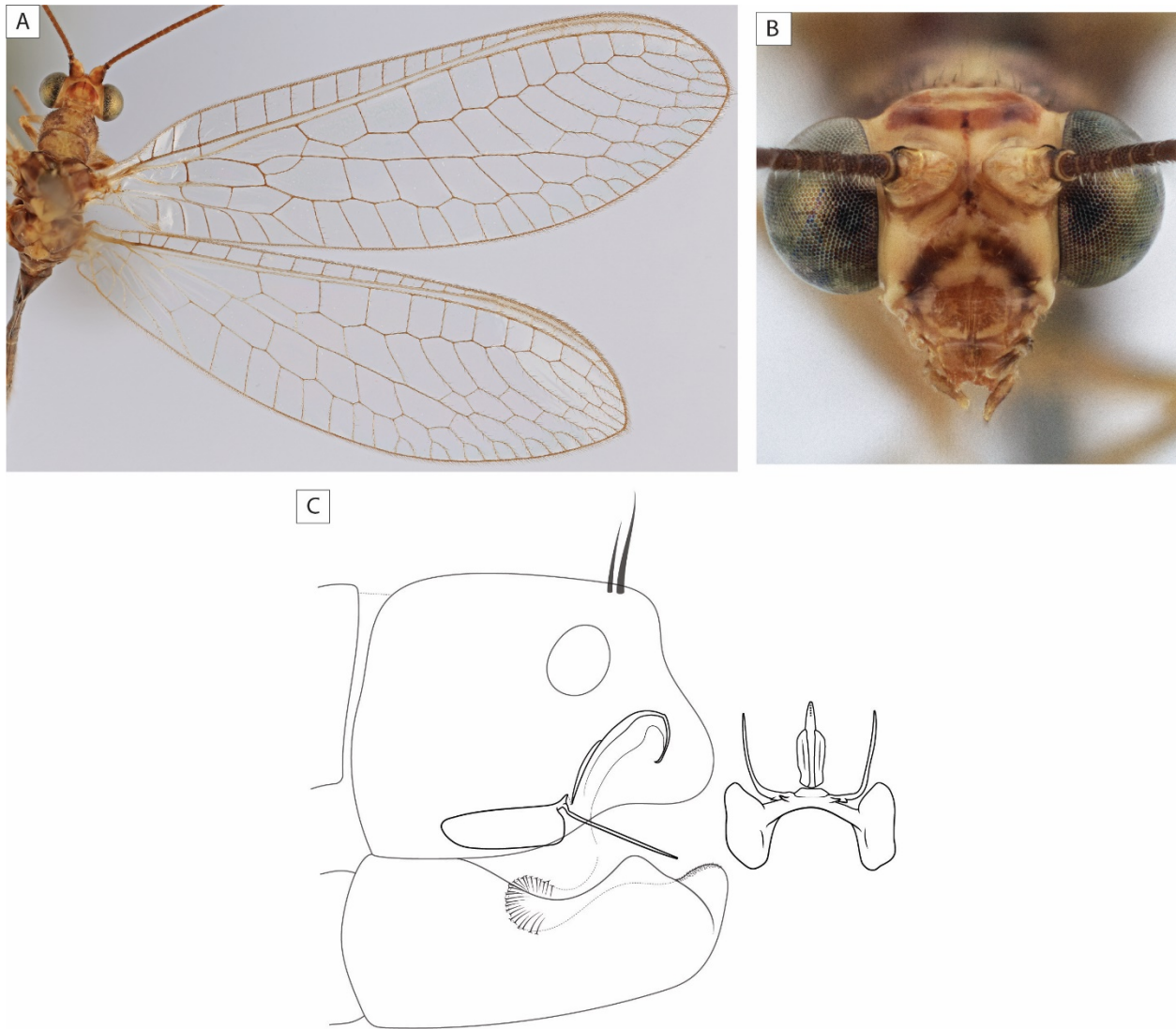
Abdomen: markings absent, or abundant; setae long, dark or pale; sternum II without

stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or extended ventrally backwards, on broad membranous structure; spermatheca small, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct with ventral lobes, or tapering towards apicoventrally; dorsal invagination between ectoprocts deep, patch of long setae present apicodorsally; ventral apodeme regular; sternum VIII and IX fused, regular, or with dorsal projecting horn, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, larger than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae numerous present (>10); gonocristae present apically on sternum IX; microtholi present.

REMARKS: *Yumachrysa* and *Ungla* are fairly similar genera, but can easily be distinguished by the presence of long thick setae on tergum IX + ectoproct in *Yumachrysa*. The two genera are closely related and form a clade along with *Ceraeochrysa*. The larvae of *Yumachrysa* have been described (Tauber 1975, Tauber et al. 2014) and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 85.** *Yumachrysa*. A. *Yumachrysa apache* (Banks), fore- and hind wing, dorsal view, photomicrograph. B. *Yumachrysa apache*, head, frontal view, photomicrograph. C. *Yumachrysa clarivena* (Banks), male genitalia, lateral and dorsal view, schematic line drawing.

Tribe **Leucochrysinini** Adams 1978

(192 species, 8 genera)

Leucochrysinini Adams 1978a: 211. Type genus: *Leucochrysa* McLachlan 1868.

DIAGNOSIS: The tribe Leucochrysinini lacks unambiguous characters in the adult, but most species have fairly large wings with numerous RP branches, are lacking a tignum and parameres (with possible exceptions, see *Leucochrysa* remarks), have no protibial spur, and one meso- and metatibial spur, two long pretarsal setae apically on fifth tarsomere, and many are marked on the mesonotum.

REMARKS: The characters common for Leucochrysinini can be found in this combination in several Ankylopterygini and Chrysopini, and the tribe is mainly defined by larval characters (see Tauber 2007, Tauber et al. 2014).

Genus *Berchmansus* Navás 1913

(2 species)

*Berchmansus* Navás 1913b: 327. Type species: *Berchmansus adumbrates* Navás 1913, by original designation and monotypy.

DIAGNOSIS: *Berchmansus* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, 1r-m originating from R and not RP, and the antenna longer than the forewing.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented;

mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons with broken band, spots; vertex raised in profile, markings present, ornamentation absent.

Thorax: prothorax markings in lateral longitudinal stripe, red, setae pale, predominantly long, thick long setae patches on pronotum absent; mesothorax marked, predominantly brown to black; metathorax marked.

Forewing: microtrichia absent except for wing base and anal lobe; costal area narrow basally and apically, but broadened on basal half; costal setae relatively short; costal crossveins (c-sc) simple, straight; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on R; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua

meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 3; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked strongly in irregular pattern; wing markings along RS, and on posterior margin medially.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsi with tarsomere 5 dark; femoral setae long; leg with markings on femora, tibiae, and tarsi.

Abdomen: markings sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; subgenitale as long as broad, on broad membranous structure; spermatheca average, surface smooth; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; tergum IX with thin expansion towards the abdomen base; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with lateral, pointed gonocornua, lateral arms apically flat expanded; entoprocessus long and arching around

mediuncus, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi present.

REMARKS: *Berchmansus* and *Vieira* (some species) are the only genera in which 1r-m originates from R and not RP, and on this basis they were thought to be closely related. Tauber (2007) transferred two species of *Berchmansus* to *Vieira* on the basis of larval characters. Specimens of this genus are rare and we were not able to examine material, gathering information from Tauber (2007) and Brooks and Barnard (1990). The larvae of *Berchmansus* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Cacarulla* Navás 1910

(1 species) figure 59.

*Cacarulla* Navás 1910b: 479. Type species: *Allochrysa maculipennis* Banks 1910, by original designation and monotypy.

DIAGNOSIS: *Cacarulla* is the only chrysopid species with the combination of the flagellar setae arranged in four rings, and a fully developed gradate series between RA and RP (in the entire area between RA and RP, more than a few crossveins).

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.



Head: colored same as body; genal marking brown; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile flat; scape marked laterally, less than 1.5x as long as wide; pedicel marked apically; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellum uniformly pale; antenna longer than forewing length; frons with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings present, ornamentation absent, pilosity short, surface smooth and glossy.

Thorax: prothorax markings in spots, brown to black, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP present; number of gradate series: 3; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on R; 1rp-ma joining M distal to *mamp1*; additional crossveins rs-m not present

basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 0; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA not fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins longitudinal veins pale, crossveins dark; wing markings between PsM and PsC, on *dcc*, and on inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad; spermatheca small; vela larger than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused;

ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms present; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae absent; microtholi present.

REMARKS: *Cacarulla* is easily distinguished from all Chrysopinae due to the presence of the gradate series between RA and RP. According to our phylogenetic analysis it is closely related to *Leucochrysa* and *Gonzaga*, but further analyses are needed to securely place this striking, large lacewing. The larvae of *Cacarulla* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 86.** *Cacarulla maculipennis* (Banks), head, frontal view, photomicrograph.

Genus *Gonzaga* Navás 1913

(8 species) figure 1969.

*Gonzaga* Navás 1913b: 317. Type species: *Gonzaga torquatus* Navás 1913, by original designation and monotypy. Banks 1915: 624 [synonymy under *Allochrysa* Banks], Banks 1944: 32 [reinstated as valid genus].

DIAGNOSIS: *Gonzaga* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, a well-defined, marked pterostigma, two gradate series in the forewing, parallel to each other, and the inner gradates extended basally parallel to PsM, and with a ventral lobe apically on each tergum IX + ectoproct in the male.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body, or marked brown entirely; genal marking brown; labial palpus uniformly marked; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked completely, less than 1.5x as long as wide; pedicel marked completely; flagellar setal arrangement in four rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons uniformly brown or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation present as T-shaped carina, pilosity absent, surface unevenly textured.

Thorax: prothorax markings absent, or continuous, brown to black, pilosity uniformly

distributed, setae dark, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax present; mesothorax marked, predominantly brown to black, pilosity dense, setae dark, predominantly long; metathorax marked or unmarked, pilosity dense, setae dark, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 6, four, or three; gradates in costal field absent; forked costal crossveins present; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) sinuous, or straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in inner series than outer series, rarely approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM, rarely not basally extended parallel to PsM; basal crossvein of inner gradate series not meeting PsM, rarely meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or

shorter than *c*<sub>2</sub>; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c*<sub>2</sub>; vein 1A forked; vein 2A forked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings between PsM and PsC, on *dcc*, on inner gradates, along RS, and on spots in RP sector.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9, or 10-14; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated, or simple; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

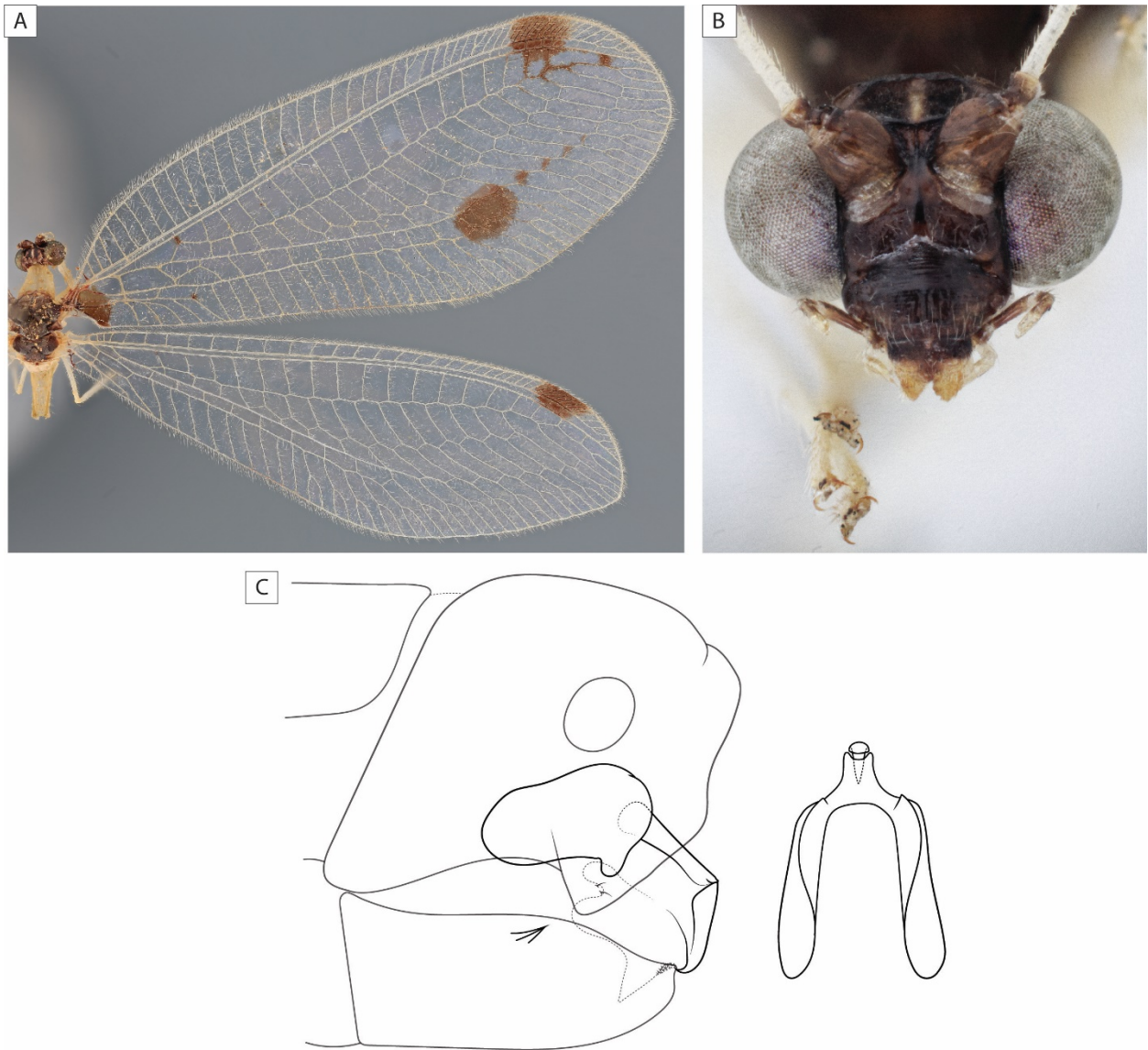
Abdomen: markings abundant; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct not fused, sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum, or on broad sclerotized structure; spermatheca average, surface smooth; vela larger than spermatheca; spermathecal duct long and strongly coiled, or neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct not fused; ectoproct with ventral lobes; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, with con-like invagination for dorsal structure, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, or without expansion medially, lateral arms

strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or elongate, thin, shorter than lateral arms of gonarcus, or about as long as lateral arms of gonarcus, mediuncus process absent or present as lateral sclerotized lobes; parameres absent; gonosetae sparsely present (<10); gonocristae present apically on sternum IX; microtholi present.

REMARKS: *Gonzaga* is similar to *Leucochrysa* and *Nodita*, and can mainly be distinguished by the wing markings, and the ventral pointing lobe on each side of the tergum IX + ectoproct. The genus is closely related to *Leucochrysa* and *Cacarulla*, according to our phylogenetic analysis (see chapter 1), but the supporting characters are few. The larvae of *G. nigriceps* have been described by Tauber et al. (2008) and are debris carrying, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 87.** *Gonzaga nigriceps* (McLachlan). A. Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph. C. Male genitalia, lateral and dorsal view, schematic line drawing.

Genus *Leucochrysa* McLachlan 1868

(37 species)

*Leucochrysa* McLachlan 1868: 208. Type species: *Chrysopa varia* Schneider 1851, by original designation.



*Protochrysopa* Kolbe 1888: 174. Type species: *Chrysopa insularis* Walker 1853, by monotypy.  
McLachlan 1894 [synonymy under *Leucochrysa*].

*Allochrysa* Banks 1903: 143. Type species: *Chrysopa virginica* Fitch 1855, by original designation. Navás 1917 [synonymy under *Leucochrysa*].

DIAGNOSIS: *Leucochrysa* is the only chrysopid species with the combination of the flagellar setae arranged in four rings, two gradate series, a quadrangular *im* cell, with a crossvein present, *c1* as long or shorter than *c2*, usually no wing markings, but the pterostigma, and no tignum or parameres.

DISTRIBUTION: Nearctic, or Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent, brown or red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked completely, laterally, or entirely pale, less than 1.5x as long as wide; pedicel marked completely, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, or uniformly pale; antenna shorter than, or equal to forewing length; frons unmarked, uniformly brown or with broken band, spots; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, in lateral longitudinal stripe, fronterolaterally, small

spot, or in spots, red, pilosity denser laterally, or uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent or present; mesothorax marked or unmarked, predominantly red, pilosity sparse, setae pale, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series basally extending parallel to PsM, or not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to

2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins scarcely dark, entirely pale, or longitudinal veins pale, crossveins dark; wing markings absent, or between PsM and PsC.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings sparse; setae long or short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent or present on apex of sternum; small sclerotized plate between subgenitale and sternum absent or present; subgenitale as long as broad, or extended ventrally backwards, apparently detached, or on narrow elongate membranous structure; spermatheca large, or elongate, surface smooth; vela larger than spermatheca, or smaller than spermatheca; spermathecal duct long and strongly coiled, or long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, or separate, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch

with 2 forward projecting horns medially, or without expansion medially, lateral arms strongly expanded to ear-like structure; entoprocessus absent, or minute; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards, or rotated to over 100°, with lateral arms of gonarcus pointing dorsally; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, or ventrally recurved pointed apex, shorter than lateral arms of gonarcus; parameres absent or possibly rarely present, arranged as two sclerites medially connected membraneously, shaped as small lateral lobes, opened towards apex, shorter than gonarcus, positioned ventrally, in sternum IX; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi present.

REMARKS: *Leucochrysa* and *Nodita* are remarkably similar, but can be differentiated by the shape of the *im* cell. We here exclude the former subgenus *Nodita* from *Leucochrysa* on the basis of our phylogenetic analysis. *Leucochrysa* is most closely related to *Gonzaga* and *Cacarulla*, and a more thorough analysis including more species of *Leucochrysa* is needed to assess these relationships. The parameres are usually absent in Leucochrysini, but we have found small paired structures in our specimen of *L. insularis*, which appear to be small parameres (perhaps vestigial remnants of parameres?). The praegenitale is usually described as absent in Leucochrysini, but there is a structure present at the apex of the female sternum VII in *Leucochrysa*, of which the homologies should be re-examined. The larvae of many species have been described (Jones 1929, Canard and Principi 1984, Mantoanelli et al. 2011, Tauber et al. 2013 and a review in Tauber et al. 2014). No insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Neula* Navás 1917, *nomen inquirendum*

(1 species)

*Neula* Navás 1917: 280. Type species: *Neula mesana* Navás 1917, by original designation and monotypy.

DIAGNOSIS: Impossible at this point (see remarks).

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; flagellum dark basally; antenna longer than forewing length; frons unmarked, markings present.

Thorax: prothorax markings in lateral longitudinal stripe, red.

Forewing: costal area narrow basally; gradates in costal field absent; apical costal area narrow; pterostigma with well-defined marking; RP strongly curved; gradates in area between RA and RP absent; number of gradate series: 3; number of gradate crossveins more in inner series than outer series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; MA and MP rejoining on PsC; 2m-cua originated from MP; anal lobe rounded, small.

Hind wing: number of gradate series: 3.

Legs: pretarsal claw dilated; leg unmarked.

Abdomen: markings absent.

Genitalic characters unknown.

REMARKS: *Neula* is a monotypic genus, with no known specimens; therefore, we can only base this description on the original literature (Navás 1917). Presently, it is not possible to form a diagnosis for the genus due to the lack of information on many characters in the original description. *Neula* is most likely related to, or possibly a synonym of *Lecuoichrysa*, based on the original description and the incomplete drawing of the forewing by Navás (1917). This possibility should be revisited once the type series is located, or new material is discovered. The larvae and gut content of adults of *Neula* are unknown.

Genus *Nodita* Navás 1916 **res. stat.**

(139 species)

*Nodita* Navás 1916: 21. Type species: *Nodita ramosa* Navás 1916, by subsequent designation  
Brooks and Barnard 1990: 249. Brooks and Barnard 1990: 249 [as subgenus of  
*Leucochrysa*].

*Lachlanita* Navás 1929: 369. Type species: *Lachlanita mainerina* Navás 1929. Brooks and  
Barnard 1990: 249 [synonymy under *Nodita*].

DIAGNOSIS: *Nodita* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, straight radial crossveins (ra-rp), two gradate series in the fore- and hind wing, a triangular *im* cell, without a crossvein, *c1* usually as long or shorter than *c2* (slightly longer in some species), usually no wing markings, or very few small markings, a regular dorsal apodeme in the male, no tignum and parameres, absent or short entoprocessi, no or only few gonosetae, and no gonocristae.

DISTRIBUTION: Nearctic, or Neotropical.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking brown or red; labial palpus marked on apical 2 palpomeres, marked on apical 3 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; maxillary palpus marked on apical 2 palpomeres, marked on apical palpomere, uniformly marked, or uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; mandibles asymmetrical, broad, regular shaped, with basal tooth on one side; frons in profile raised laterally; scape marked completely, dorsally, laterally, medially, entirely pale, or ventrally, less than 1.5x as long as wide; pedicel marked dorsally, laterally, or entirely pale; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width, or shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly dark or uniformly pale; antenna longer than forewing length, or shorter than, or equal to forewing length; frons unmarked, or with unbroken band; carina on dorsal torulus margin present; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, in lateral longitudinal stripe, or fronterolaterally, small spot, brown to black, or red, pilosity denser laterally, or uniformly distributed, setae pale, predominantly short, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked or unmarked, predominantly brown to black, or predominantly red, pilosity sparse, setae pale, predominantly long, or predominantly short; metathorax marked or unmarked, pilosity sparse, setae dark or pale, predominantly short; pale medial stripe absent or present; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal

area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked or unmarked; number of maximal c-sc crossveins basal to 1sc-r: 5, or four; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma diffuse, weakly defined, or with well-defined marking; basal subcostal crossvein (1sc-r) present, dark or pale; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM, or not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9, or 10-14; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP, or meets CuA distal to origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*, rarely slightly longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed, or open; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins mostly dark, scarcely dark or dark along integumental marking pattern; wing markings absent, between PsM and PsC, on inner gradates, and along RS.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of



crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch at *mamp1*, or apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae long; leg unmarked.

Abdomen: markings absent, or sparse; setae long or short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent or present on apex of sternum; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, or extended ventrally backwards, apparently detached, or on broad membranous structure; spermatheca elongate, surface smooth; vela smaller than spermatheca; spermathecal duct long and strongly coiled, or neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused or separate, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch with broad medial projection, with 2 forward projecting horns medially, or without expansion medially, lateral arms apically flat expanded, or strongly expanded to ear-like structure; entoprocessus absent, or minute, or short, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous

connection, elongate, laterally expanded, or short, triangular, shorter than lateral arms of gonarcus, mediuncus process absent, or shaped as ventrally recurved tip, forming v-shape in lateral view; parameres absent; gonosetae absent, or sparsely present (<10); gonocristae absent; microtholi absent or present.

REMARKS: *Nodita* is by far the largest genus of Leucochrysinini. We here exclude it from *Leucochrysa* and elevate it to the level of genus, as it was when originally proposed. *Nodita* formed a clade sister to all *Leucochrysa*, *Cacarulla*, and *Gonzaga*, but further analyses including more leucochrysinine genera are needed to assess these relationships. *Nodita* and *Leucochrysa* are extremely similar and can mainly be distinguished by the shape of the *im* cell and larval characters. This genus does not have striking autapomorphies in the adult, and can only be identified by the absence of several characters (see diagnosis). The larvae of several species were described (Smith 1926b, Skorepa and Sharp 1971, Adams 1987, Mantoanelli et al. 2011, and Tauber et al. 2014) and are debris-carrying. No insect remains were found in the guts of adults (Brooks and Barnard 1990).

Genus *Nuvol* Navás 1916

(1 species)

*Nuvol* Navás 1916: 24. Type species: *Nuvol umbrosus* Navás 1916, by original designation and monotypy.

DIAGNOSIS: *Nuvol* is the only chrysopid genus with the unique wing marking, with a large elongate band at the posterior wing margin, a band at the apical wing margin, a band from the base

of RP to the inner gradates (parallel to posterior wing margin), and a band from base of pterostigma to inner gradates. It also has the flagellar setae arranged in four rings, a triangular im cell, without a crossvein, *c1* slightly longer than *c2*, and two gradate series.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored pale green, or yellow.

Head: colored same as body; genal marking red; labial palpus uniformly pale; maxillary palpus uniformly pale; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna longer than forewing length; frons unmarked; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings in lateral longitudinal stripe, red, pilosity uniformly distributed, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae pale, predominantly long; metathorax unmarked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area unmarked; number of maximal c-sc crossveins basal to 1sc-r: 3; gradates in costal field absent; forked costal crossveins absent; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, pale; veins Sc and C not fused; Sc unmodified;

R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins more in outer series than inner series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; *mamp1* irregular (*im* cell present), triangular, without crossvein (ovate); maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsM; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* longer than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings with large elongate markings at posterior wing margin, apical wing margin, from the base of RP to the inner gradates (parallel to posterior wing margin), and from base of pterostigma to inner gradates.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw dilated; tarsi entirely pale (unmarked); femoral setae long; leg unmarked.

Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale as long as broad, close to sternum; spermatheca average, surface smooth; vela about same size as spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: unknown.

REMARKS: *Nuvol* is easily identified by its unique wing markings with three elongate longitudinal markings. The type specimen of *Nuvol* was lost, but Tauber and Sosa (2015) discovered new specimens of the genus and provided a new description. The larvae and gut content of adults of *Nuvol* are unknown.

Genus *Santocellus* Tauber, Tauber, and Albuquerque . 2008

(3 species)

*Santocellus* Tauber et al. 2008: 315. Type species: *Santocellus atlanticis* Tauber et al. 2008, by original designation.

DIAGNOSIS: *Santocellus* is the only chrysopid genus with the combination of the flagellar setae arranged in four rings, two gradate series in the fore- and hind wing, a quadrangular *im* cell, with a crossvein, *c1* as long or shorter than *c2*, no parameres, and apically flat expanded lateral arms of the gonarcus.

DISTRIBUTION: Neotropical.

DESCRIPTION: body colored yellow.

Head: colored same as body; genal marking absent, or red; labial palpus marked on apical 3 palpomeres; maxillary palpus uniformly marked; apical palpus slightly tapered apically, not finely pointed; labrum indented; frons in profile raised laterally; scape marked completely, medially, or entirely pale, less than 1.5x as long as wide; pedicel marked apically, or completely; flagellar setal arrangement in four rings; flagellar setae as long, or longer than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum dark basally, or uniformly pale; antenna longer than forewing length; frons with broken band, spots, or with unbroken band; vertex raised in profile, markings absent or present, ornamentation absent, pilosity absent, surface smooth and glossy.

Thorax: prothorax markings absent, or in spots, brown to black, pilosity denser laterally, setae pale, predominantly long, thick long setae patches on pronotum absent; ventrolateral marking on prothorax absent; mesothorax marked, predominantly brown to black, pilosity sparse, setae pale, predominantly long; metathorax marked, pilosity sparse, setae pale, predominantly long; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula marked; microtrichia absent except for wing base and anal lobe; costal area narrow basally; costal setae relatively short; costal crossveins (c-sc) simple, straight; basal costal area marked; number of maximal c-sc crossveins basal to 1sc-r: 4; gradates in costal field absent; forked costal crossveins absent or present; apical costal area narrow; pterostigma with well-defined marking; basal subcostal crossvein (1sc-r) present, dark; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight, or strongly curved; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each

series; gradate series diverging, or parallel; inner gradate series not basally extended parallel to PsM; basal crossvein of inner gradate series meeting PsM, or not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 0-9; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins dark along integumental marking pattern; wing markings between PsM and PsC, on *dcc*, on inner gradates, along RS, and on posterior margin medially.

Hind wing: sc-r crossveins below pterostigma: 4-6; number of gradate series: 2; number of crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch absent.

Legs: pretarsal claw dilated; tarsal setae two in number; tarsi entirely pale (unmarked); metatibia on inner surface smooth; femoral setae long; leg unmarked, or with band on tibia.

Abdomen: markings sparse; setae long, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; ectoproct with two lobes below gonapophyses, bearing numerous short, very thick setae; gonapophysis with numerous thick pointed setae; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale longer than broad; spermatheca small,

surface smooth; vela smaller than spermatheca; spermathecal duct neither very long nor short, somewhat coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; dorsal invagination between ectoprocts shallow; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, laterally expanded, shorter than lateral arms of gonarcus, mediuncus process absent; parameres absent; gonosetae absent; gonocristae present in 2 patches; microtholi present.

REMARKS: *Santocellus* is exceptionally similar to *Leucochrysa* but differs in the origin of 1rp-ma, which is closer to the origin of RP, and more numerous, as well as larger wing markings than in *Leucochrysa*. The larvae are debris-carrying (Tauber et al. 2008, Tauber et al. 2014). The feeding habits of the adults are unknown.

Tribe **Nothancylini** Garzón et al in rev.

(1 species, 1 genus) figure 61.

Nothancylini Garzón et al in prep. Type genus: *Nothancylla* Navás 1910.

Diagnosis and Remarks: see genus.



Genus *Nothancyla* Navás 1910

(1 species)

*Nothancyla* Navás 1910a: 51. Type species: *Nothancyla verreauxi* Navás 1910, by monotypy.

DIAGNOSIS: *Nothancyla* is the only chrysopid genus with the combination of the flagellar setae arranged in five rings and a tympanal organ present in the forewing. It is also the only genus with the combination of the flagellar setae arranged in five rings, the absence of the basal subcostal crossvein (1sc-r is positioned at pterostigma), PsM continuous with the outer gradates, and the presence of a quadrangular im-cell, with a crossvein.

DISTRIBUTION: Australasia, Oceania.

DESCRIPTION: body colored pale green.

Head: colored same as body; genal marking absent; labial palpus marked on apical 3 palpomeres; maxillary palpus marked on apical palpomere; apical palpus finely pointed; labrum indented; mandibles symmetrical, broad, regular shaped, with basal tooth; frons in profile flat; scape unmarked, less than 1.5x as long as wide; pedicel unmarked; flagellar setal arrangement in five rings; flagellar setae shorter than flagellomere width; flagellomeres at least 1.5x as long as wide; flagellum uniformly pale; antenna shorter than, or equal to forewing length; frons with small spot medially on supra-, or intra-antennal frons; carina on dorsal torulus margin present; vertex raised in profile, markings absent, ornamentation absent, pilosity absent, surface smooth and matte.

Thorax: prothorax markings in one posterolateral spot, brown to black, pilosity denser laterally, setae dark, predominantly long, thick long setae patches on pronotum absent;

ventrolateral marking on prothorax absent; mesothorax unmarked, pilosity sparse, setae dark, predominantly short; metathorax unmarked, pilosity sparse, setae pale, predominantly short; pale medial stripe absent; small expansion on frontal metascutum margin absent.

Forewing: tegula unmarked; microtrichia absent except for wing base and anal lobe; costal area broad basally; costal setae relatively long; costal crossveins (c-sc) simple, straight; basal costal area unmarked; gradates in costal field absent; forked costal crossveins present; apical costal area narrow; pterostigma diffuse, weakly defined; basal subcostal crossvein (1sc-r) absent; veins Sc and C not fused; Sc unmodified; R ventrally unremarkable, with regular setae; number of sc-r crossveins below pterostigma: 4-6; tympanal organ present; RP almost straight; RP branches relatively straight; radial crossveins (ra-rp) straight; gradates in area between RA and RP absent; number of gradate series: 2; number of gradate crossveins approximately same number in each series; gradate series parallel; inner gradate series basally extending parallel to PsM; basal crossvein of inner gradate series not meeting PsM; 1r-m originating on RP; 1rp-ma joining M at *mamp1*; additional crossveins rs-m not present basal to *mamp1*; PsM continuous with outer gradate series; PsM and PsC relatively wide apart; number of crossveins between PsM and PsC: 10-14; *mamp1* irregular (*im* cell present), quadrangular, with crossvein; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3; MA and MP rejoining on PsC; MA and CuA fused; MP and CuA fused; 1m-cua meets CuA at origin of CuP; 2m-cua meets CuA distal to 2cua-cup; 2m-cua originated from MP; cubital cell number: 2; cell *c1* as long, or shorter than *c2*; crossvein 2cua-cup meeting PsC; distal cubital cell (*dcc*) closed; CuP forked at *c2*; vein 1A forked; vein 2A simple, unforked; anal lobe rounded, small; wing veins marked weakly in irregular pattern; wing markings absent.

Hind wing: sc-r crossveins below pterostigma: >7; number of gradate series: 2; number of

crossveins between PsM and PsC: 0-9; maximum number of fused veins on PsM: 2; maximum number of fused veins on PsC: 3, or 4; jugal lobe simple; basal RP branch apical to *mamp1*; ra-rp crossvein basal to the origin of the basal most RP branch present.

Legs: pretarsal claw simple; tarsal setae four in number; tarsi entirely pale (unmarked); number of protibial spurs: 0; number of mesotibial spurs: 1; number of metatibial spurs: 1; metatibia on inner surface smooth; femoral setae short; leg unmarked.

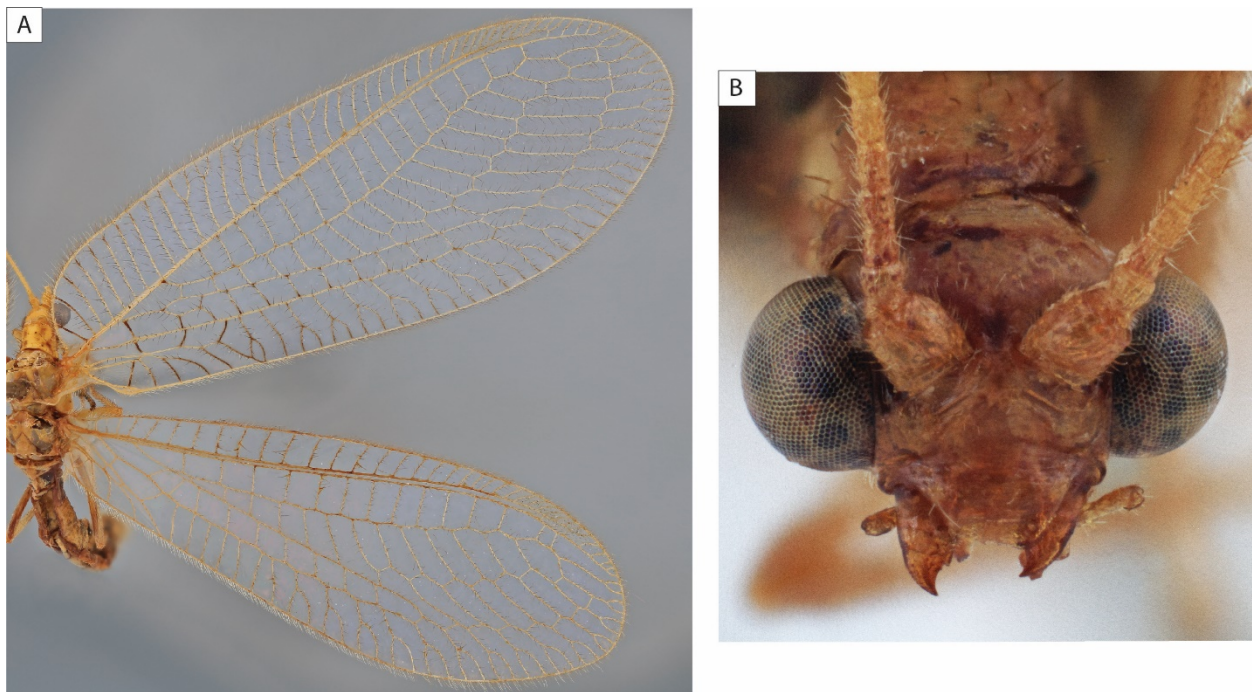
Abdomen: markings absent; setae short, pale; sternum II without stridulatory organ.

Female genitalia: tergum IX and ectoproct fused; sternum VII simple, apically rounded; praegenitale absent; small sclerotized plate between subgenitale and sternum absent; subgenitale broader than long, or extended ventrally backwards, close to sternum; spermatheca thick, surface smooth; vela smaller than spermatheca; spermathecal duct long but not strongly coiled.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct with long and narrow apical projection; dorsal invagination between ectoprocts deep; thick spines on ectoproct absent; ventral apodeme regular; sterna VIII and IX separate, regular, without strong apical spines or dense setae; tignum absent or present; gonarcus medially fused, median arch without expansion medially, lateral arms apically flat expanded; entoprocessus long, positioned at the joint of medial arch and lateral arms, secondary process on lateral arms absent; gonarcus-mediuncus complex in normal position, with lateral arms of gonarcus pointing backwards; mediuncus closely associated with gonarcus, with membranous connection, elongate, thin, about as long as lateral arms of gonarcus; parameres absent; gonosetae absent; gonocristae absent; microtholi absent.

REMARKS: *Nothancyla* is a distinct genus which intermingles characters of all subfamilies,

especially Apochrysinæ and Chrysopinæ. It lacks a basal subcostal crossvein and has forked costal crossveins, characters that occur in Apochrysinæ. In the forewing the presence of an *im* cell is noteworthy (like Chrysopinæ and Nothochrysinæ) and differs from Apochrysinæ where such a cell is never present. The most striking evidence for the placement of the genus is the presence of a tympanal organ. Apochrysinæ were thought to have an elongate tympanal organ (Brooks and Barnard 1990, Winterton and Brooks 2002), but we demonstrate that this character is unique to Chrysopinæ (see chapter 1). We therefore place *Nothancyla* in Chrysopinæ, an assignment which is supported by phylogenetic analyses in which the genus falls as sister to all other Chrysopinæ (see chapter 1). Due to the novel suggestion of the absence of the tympanum in Apochrysinæ we also provide a diagnosis which does not include this character. The larvae of *Nothancyla* are unknown, and no insect remains were found in the guts of adults (Brooks and Barnard 1990).



**Figure 88.** *Nothancyla verreauxi* Navás. A Fore- and hind wing, dorsal view, photomicrograph. B. Head, frontal view, photomicrograph.

## Genera incertae sedis

Genus *Sinochrysa* Yang 1992

(1 species)

*Sinochrysa* Yang 1992: 449. Type species: *Sinochrysa hengduana* 1992, by original designation.

DISTRIBUTION: Oriental.

REMARKS: The original description of this monotypic genus provides little information, as the English translation is very brief and no illustrations are provided, except the terminalia of male and female. In a subsequent publication (Yang 1999) a more detailed English translation as well as a habitus drawing with spread wings is provided. Yang (1999) placed this genus in Nothochrysoidea, probably on the basis of the presence of a pronounced anal lobe (in original description = “forewing with jugal lobe”). The illustration in Yang (1999) shows, that neither an anal lobe in the forewing nor a jugal lobe in the hind wing is present. The second reason to place this genus in Nothochrysoidea was the course of PsM, which is unusual in this taxon, as PsM seems to be broken posterior to *im*. Nonetheless, it is visible in the illustration that PsM is continuous with the outer gradates (especially well visible in the hind wing), and we therefore tend to believe that this genus belongs to Chrysopidae, possibly Belonopterygini given its stout appearance and the presence of long paired parameres in the male genitalia. This genus is a peculiar chrysopid, with numerous unique characters in the wings and its placement should be further investigated once material is available.

Genus *Tibetochrysa* Yang 1988

(1 species)

*Tibetochrysa* Yang 1988: 204. Type species: *Tibetochrysa sinica* Yang 1988, by original designation.

DISTRIBUTION: Oriental.

REMARKS: The original description (and a redescription in Yang et al. 2005) of the monotypic *Tibetochrysa* was not available in English, and the only illustration provided shows the female terminalia. At this time we are unable to place or describe this genus in any of the subfamilies. The ectoproct of the female seems to bear two distinct small horns at the apex, dorsal to the lateral gonapophyses.

Genus *Yunchrysopa* Yang and Wang 1994

(1 species)

*Yunchrysopa* Yang and Wang 1994: 69. Type species: *Yunchrysopa tropica* Yang and Wang 1994, by original designation.

DISTRIBUTION: Oriental.

DESCRIPTION:

Head: Palpi tapering, not finely pointed; mandibles symmetrical, broad, regular shapedd, with basal tooth on both sides; scape less than 1.5x as long as wide; antenna longer than forewing length.

Thorax: prothorax markings in two lateral spots.

Wings: unknown.

Legs: pretarsal claw dilated.

Abdomen: unknown.

Female genitalia: tergum IX and ectoproct fused; sternum VII apically rounded; praegenitale absent; subgenitale longer than broad; spermatheca thin, surface smooth; vela about as large as spermatheca.

Male genitalia: dorsal apodeme regular, without process; tergum IX and ectoproct fused; ectoproct normally shaped, rounded; thick spines on ectoproct absent, patch of long setae absent; ventral apodeme regular; sterna VIII and IX fused, regular, without strong apical spines or dense setae; tignum absent; gonarcus medially fused, median arch without expansion medially, lateral arms simple, not expanded; entoprocessus absent; mediuncus long, laterally expanded (shape uncertain); parameres absent; gonosetae numerous present (>10).

REMARKS: The original description of the monotypic genus *Yunchrysopa* (Yang and Wang 1994) provided a brief English translation and solely noted long antennae and “peculiar male genitalia”. No illustrations are present in the original description, but Yang et al. (2005) provided line drawings of the male and female, but unfortunately not of the wings. Given the male genitalia, as seen in the illustrations, the genus likely belongs in Chrysopinae.

## Conclusion

A revised classification of the neuropteran family Chrysopidae was long overdue given the systematic changes since the last revision (Brooks and Barnard 1990). We based the classification

presented in this chapter on the generic relationships recovered in the most recent phylogenetic analyses (see chapter 1). The traditional segregation of Chrysopidae into the three subfamilies – Apochrysinæ, Chrysopinæ, and Nothochrysinæ – is maintained, albeit with augmented circumscriptions and diagnoses. Chrysopinæ are the largest subfamily, including over 95% of the family’s diversity, and is further split into five tribes: Ankylopterygini, Belonopterygini, Chrysopini, Leucochrysinini, and Nothancylini. Descriptions, diagnoses, remarks, and illustrations are provided for all genera and higher taxa, as well as a dichotomous key to identify all chrysopids to the level of genus. We highlight those genera which are in need of detailed revisions and suggest possible placements of genera for which it was not possible to include in current phylogenetic analyses.

## References

- Adams, P. A. 1956. A new genus and new species of Chrysopidae from the western United States, with remarks on the wing venation of the family (Neuroptera). *Psyche* 63(2): 67-74.
- Adams P. A. 1959. Neuroptera: Myrmeleontidae and Chrysopidae. *Insects of Micronesia* 8:13-33.
- Adams, P. A. 1967. A review of the Mesochrysinæ and Nothochrysinæ (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology* 135(4): 215–238.
- Adams, P. A. 1975. Status of the genera *Ungla* and *Mallada* Navás (Neuroptera: Chrysopidae). *Psyche* 82:167-173.
- Adams, P. A. 1978. Zoogeography of New World Chrysopidae, a progress report. *Folia Entomologica Mexicana* 39-40: 210-211.



- Adams, P. A. 1982a. *Plesiochrysa*, a new subgenus of *Chrysopa* (Neuroptera) (Studies in New World Chrysopidae, Part I). *Neuroptera International* 2:27-32.
- Adams, P. A. 1982b. *Ceraeochrysa*, a new genus of Chrysopinae (Neuroptera) (Studies in New World Chrysopidae, Part II). *Neuroptera International* 2:69-75.
- Adams, P. A. 1987. Studies in Neotropical Chrysopidae (Neuroptera) III. Notes on *Nodita amazonica* Navás and *N. oenops*, n. sp. *Neuroptera International* 4:287-294.
- Adams, P. A., and J. A. Garland. 1981. A new species of *Chrysopiella* Banks from western North America (Neuroptera: Chrysopidae). *Canadian Entomologist* 113:1-4.
- Adams, P.A., and N.D. Penny. 1986. Faunal relations of amazonian Chrysopidae. na. Faunal relations of Amazonian Chrysopidae, in Gepp, J., Aspöck, H., and H. Hölzel, (eds.). *Recent Research in Neuropterology. Proceedings of the 2nd International Symposium on Neuropterology* pp.119-124.
- Adams, P. A., and N. D. Penny. 1992. New genera of Nothochrysininae from South America (Neuroptera: Chrysopidae). *Pan-Pacific Entomologist* 68(3): 216-221.
- Aspöck, H., Aspöck, U., and H. Hölzel. 1980. *Neuropteren Europas*. Goecke & Evers.
- Aspöck, H., Aspöck, U., and H. Hölzel. 2001. *Kommentierter Katalog der Neuropterida (Insecta: Raphidioptera, Megaloptera, Neuroptera) der Westpaläarktis*. *Denisia* 2: 1-606.
- Banks, N. 1903. A revision of the Nearctic Chrysopidae. *Transactions of the American Entomological Society* 29(2): 137-162.
- Banks, N. 1911. Descriptions of new species of North American neuropteroid insects. *Transactions of the American Entomological Society* 37:335-360.

- Banks, N. 1915. New neuropteroid insects, native and exotic. Proceedings of the Academy of Natural Sciences of Philadelphia 66:608-632.
- Banks, N. 1924. Descriptions of new neuropteroid insects. Bulletin of the Museum of Comparative Zoology 65:419-455.
- Banks, N. 1931. Some neuropteroid insects from the Malay Peninsula. Journal of the Federated Malay States Museums 16:377-409.
- Banks, N. 1937. Philippine neuropteroid insects. Philippine Journal of Science 63:125-174.
- Banks, N. 1938a. Further neuropteroid insects from Malaya. Journal of the Federated Malay States Museums 18: 220-235.
- Banks, N. 1938b. New native neuropteroid insects. Psyche 45(1): 72-79.
- Banks, N. 1940. Report on certain groups of neuropteroid insects from Szechwan, China. Proceedings of the United States National Museum.
- Banks, N. 1943. Some interesting Neuroptera from Australia. Proceedings of the New England Zoological Club 22: 99-104.
- Banks, N. 1943. Neuroptera of northern South America. Part III. Chrysopidae. Boletín de Entomología Venezolana 3: 1-34.
- Banks, N. 1950. Notes and descriptions of western Chrysopidae (Neuroptera). Psyche 57:45-67.
- Barnard, P. C., and S. J. Brooks. 1984. The African lacewing genus *Ceratochrysa* (Neuroptera: Chrysopidae): a predator on the cassava mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae). Systematic Entomology 9:359-371.
- Barnes, B. N. 1975. The life history of *Chrysopa zastrowi* Esb. Pet. (Neuroptera: Chrysopidae)

- Billberg, G. J. Enumeratio Insectorum in Museo Gust. Joh. Billberg. Typis Gadelianis, Holmiae pp. 138.
- Boros, C. B. 1984. Descriptions of the larvae of six Australian species of *Chrysopa* Leach, s. l. (Neuroptera: Chrysopidae). Australian Journal of Zoology 32:833-849.
- Brauer, F. 1850. Beschreibung und beobachtung der österreichischen Arten der Gattung *Chrysopa*. Naturwissenschaftliche Abhandlungen, gesammelt und durch subscription herausgegeben von Wilhelm Haidinger 4(4):1-12.
- Brauer, F. 1864. Entomologische Beiträge. B. Zur Kenntnis der Neuropteren. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 17: 27-30.
- Breitkreuz, L., Winterton, S. L., and M. S. Engel. 2015. Revision of the green lacewing subgenus *Ankylopteryx (Sencera)*(Neuroptera, Chrysopidae). ZooKeys 543: 111-127.
- Brooks, S. J. 1983. A new genus of Oriental lacewings (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History (Entomology) 47: 1-26.
- Brooks, S. J. 1984. A redefinition of the Italochrysinini (Chrysopidae), with the description of a new genus from Nigeria. Neuroptera International 3:79-88.
- Brooks, S. J. 1986. A new genus of Ankylopterygini (Chrysopidae). Neuroptera International 4: 35-48.
- Brooks, S. J., and P. C. Barnard. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History, Entomology 59(2): 117–286.
- Canard, M., and H. Labrique. 1989. Bioecologie de la chrysope mediterraneenne *Rexa lordina* Navás (Neuroptera: Chrysopidae) et description de ses stades larvaires. Neuroptera

International 5:151-158.

Canard, M., and M. M. Principi. 1984. Development of Chrysopidae. Pp. 57-75 in Canard, M., Séméria, Y., and New, T. R. (Eds.). *Biology of Chrysopidae* (Vol. 27). Springer.

Costa, O. G. 1834. Cenni zoologici ossia descrizione sommaria delle specie nuove di animali scoperti in diverse contrade del regno nell' anno 1834. Napoli.

Dessart, P. 1973. *Dendrocerus propodealis* sp. n. (Hym. Ceraphronoidea) parasite de *Chrysopa madestes* Banks (Neur. Chrysopidae) en Inde. Bulletin et Annales de la Société Royale Belge d'Entomologie 109:269-276.

Doumerc, A. J. L. 1861. Description d'une nouvelle espèce de Névroptère de la tribu des Hémérobiens. Annales de la Société Entomologique de France 4(1):192.

Duelli, P. 2004. Der Glenofinger, eine spektakuläre prothorakale Drüse bei einer afrotropischen Florfliege (Neuroptera, Chrysopidae). Denisia 13:173-175.

Esben-Petersen, P. 1914. Australian Neuroptera Part I. Proceedings of the Linnean Society of New South Wales 39:635-645.

Esben-Petersen, P. 1917. Australian Neuroptera. Part III. In Proceedings of the Linnean Society of New South Wales 42(1): 203-219.

Esben-Petersen, P. 1918. Neuroptera and Mecoptera, in Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. Arkiv för Zoolgi 11(26): 1-37.

Esben-Petersen, P. 1920. South African Neuroptera. I. Annals of the South African Museum 17:507-521.

Esben-Petersen, P. 1928. Neuroptera, in Insects of Samoa and other Samoan terrestrial Arthropoda

7(3): 89-108.

Fitch, A. 1855. Report [upon the noxious and other insects of the state of New-York]. Transactions of the New York State Agricultural Society 14:705-880.

Fraser, F. C. 1951. A revision of the Madagascar Neuroptera with a key to their identifications and descriptions of new species. I. Osmylidae, Hemerobiidae and Chrysopidae. Naturaliste Malgache 3:15-31.

Fraser, F. C. 1952. New species of Neuroptera in the Museum National d 'Histoire Naturelle, Paris. Revue Française d 'Entomologie 19: 55-64.

Fraser, F. C. 1955. Nouvelles notes sur les Nevropteres de Madagascar. Naturaliste Malgache 7:127-137.

de Freitas, S., and N. D. Penny, Two new genera of Neotropical Chrysopini (Neuroptera: Chrysopidae). Journal of the Kansas Entomological Society 73:164-170.

Garzón–Orduña, I., Winterton, S., Jiang, Y., Breitkreuz, L., Duelli, P., Engel, M., Penny, N., Tauber, C., Mochizuki, A., and X. Liu. A molecular supermatrix approach to green lacewing phylogeny reveals higher–level relationships and a single origin of larval camouflaging behavior (Neuroptera: Chrysopidae). (in review, Molecular Phylogenetics and Evolution).

Gepp, J. 1983. Schlüssel zur Freilanddiagnose mitteleuropäischer Chrysopidenlarven (Neuroptera, Chrysopidae). Mitteilungen des Naturwissenschaftlichen Vereins für Steiermark 113: 101-132.

Gepp, J. 1984. Morphology and anatomy of the preimaginal stages of Chrysopidae: a short survey, pp. 9-19 in Canard, M., Séméria, Y., and New, T. R. (Eds.). Biology of Chrysopidae (Vol.

27). Springer.

Gerstaecker, A. 1863. Ueber einige neue Planipennien aus den familien der Hemerobiiden und Panorpiden. Stettiner Entomologische Zeitung 24:168-188.

Girard, M. J. A. 1862. Indication et discussion d'Un nouveau caractere générique du genre Hemerobius, tribu des Myrméléoniens, ordre des Névropteres et description de deux especes nouvelles de ce genre recueillies par le RP Montrouzier et désignées par Lui sous les noms de Chloromelas et stigma. Annales de la Société Entomologique de France 2: 59-614.

Hagen, H. A. 1866. Hemerobidarum synopsis synonymica. Stettiner Entomologische Zeitung 27: 369-462.

Handlirsch, A. 1908. Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen. W. Engelmann.

Henry, C. S. 1984. The sexual behavior of green lacewings. Pp. 101-110 in Canard, M., Séméria, Y., and New, T. R. (Eds.). Biology of Chrysopidae (Vol. 27). Springer.

Henry, C. S., and M. L. Wells. 1990 .Sexual singing preceding copulation in *Chrysoperla plorabunda* green lacewings: observations in a semi-natural environment (Neuroptera: Chrysopidae). Florida Entomologist 73:331-333.

Henry, C. S., Brooks, S. J. Duelli, P., and J. B. Johnson. 2002. Discovering the true *Chrysoperla carnea* (Insecta: Neuroptera: Chrysopidae) using song analysis, morphology, and ecology. Annals of the Entomological Society of America 95:172-191.

Henry, C. S., Brooks, S. J., Johnson, J. B., Mochizuki, A., and P. Duelli. 2014. A new cryptic species of the *Chrysoperla carnea* group (Neuroptera: Chrysopidae) from western Asia:

- parallel speciation without ecological adaptation. *Systematic Entomology* 39:380-393.
- Hölzel, H. 1967. Die Neuropteren Vorderasiens II. Chrysopidae. Beiträge zur Naturkundlichen Forschung in Südwestdeutschland 26(1): 19-45.
- Hölzel, H. 1970. Zur generischen Klassifikation der paläarktischen Chrysopinae. Eine neue Gattung und zwei neue Untergattungen der Chrysopidae (Planipennia). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* 22: 44-52.
- Hölzel, H. 1973b. Neuroptera aus Nepal: I. Chrysopidae. Ergebnisse des Forschungsunternehmens Nepal Himalaya. *Khumbu Himal* 4(3): 333-388.
- Hölzel, H., Stelzl, M., and P. Ohm. 1990. Chrysopidae (Neuroptera) aus Senegal und Gambia. I: Ankylopterygini. *Neuroptera International* 6(2): 63-73.
- ICZN. 2010. Opinion 2254 (Case 3399) *Dichochrysa* Yang, 1991 (Insecta, Neuroptera): generic name not conserved. *Bulletin of Zoological Nomenclature*, 67(3):261-262.
- Killington, F. J. 1935. *Chrysopa albolineata* nom. nov. for *Chrysopa tenella* Schneid. (Neur.). *Journal of the Society for British Entomology* 1: 87.
- Killington, F. J. 1937. A Monograph Of The British Neuroptera. Vol. II. London, 306 pp.
- Kimmins, D.E. 1939. Some new South African Neuroptera. *Annals and Magazine of Natural History* 10(15):561-579.
- Kimmins, D. E. 1939. The first instar larva of *Nathanica capitata* (Fabr.). *Journal of the Society for British Entomology* 1: 240-241.
- Kimmins, D. E., 1952. Some new Australian Chrysopidae. *Annals and Magazine of Natural*

- History (12)5:69-81.
- Kimmins, D. E. 1952b. A revision of the genera of the Apochrysinæ (Fam. Chrysopidae). *Journal of Natural History* 5(58): 929-944.
- Kolbe, H. J. 1888. Die geographische Verbreitung der Neuroptera und Pseudoneuroptera der Antillen, nebst einer übersicht über die von Herrn Consul Krug auf Portoriko gesammelten Arten. *Archiv für Naturgeschichte*. 54:153-178.
- Kuwayama, S. 1962. A revisional synopsis of the Neuroptera in Japan. *Pacific Insects* 4(2): 325-412.
- Kuwayama, S. 1966. The type specimens of the Neuroptera in the collection of the Entomological Institute, Hokkaido University. *Insecta Matsumurana* 28:133-140.
- Lacroix, J. L. 1920. Faune Névroptérique de l'Algérie et de la Tunisie. II (1) Chrysopide nouveau. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 11:83-84.
- Lacroix, J. L. 1923. Chrysopides nouveaux. *Bulletin de la Société Entomologique de France* 1923: 119-122.
- Leach, W. E. 1815. Entomology., in Brewster, D. (ed.). *Edinburgh Encyclopaedia* Edinburgh 9(1): 57-172.
- Leraut, P. 1980. Liste des Planipennes de France (Neuroptera). *Bulletin de la Société entomologique de France* 85: 237-253.
- Mantoanelli, E., Tauber, C. A., Albuquerque, G. S., and M. J Tauber. 2011. Larvae of four *Leucochrysa* (*Nodita*) species (Neuroptera: Chrysopidae: Leucochrysinini) from Brazil's Atlantic coast. *Annals of the Entomological Society of America* 104:1233-1259.



- MacLachlan, R. 1868. A Monograph of the British Neuroptera-Planipennia. Transactions of the Royal Entomological Society of London 16(2): 145-224.
- MacLachlan, R. 1875. Setchatokrylye (Neuroptera), in Fedchenko, A. P. Travels in Turkestan. Zoogeograficheskiia izsledovania 5(2): 1-60 [titel and journal translated].
- MacLachlan, R. 1888. The Neuroptera of Madeira and the Canary Islands. Journal of the Linnean Society of London, Zoology 16:149-183.
- MacLachlan, R. 1894. On two small collections of Neuroptera from Tachien-lu, in the province of Szechuen, western China, on the frontier of Thibet. Annals and Magazine of Natural History 6(13): 421-436.
- Mehra, B. P. 1966. Biology of *Chrysopa lacciperda* Kimmins. Journal of the Bombay Natural History Society 63:215-218.
- Mochizuki, A., Henry, C. S., and P. Duelli. 2017. *Apertochrysa* (Neuroptera: Chrysopidae): A heterogeneric phantom? Zootaxa 4238(1): 58–72.
- Monserrat, V. J. 1977. Sobre los Neurópteros de las Islas Canarias, I: *Anisochrysa* (*Atlantochrysa*) *atlantica* (MacLachlan, 1882) (Plan. Chrysopidae). Boletín de la Asociación Española de Entomología 1:151-159.
- Monserrat, V. J., and L. M. Díaz-Aranda. 2012. Los estadios larvarios de los crisópidos Ibéricos (Insecta, Neuroptera, Chrysopidae), nuevos elementos sobre la morfología larvaria aplicables a la sistemática de la familia. Graellsia 68:31-158.
- Muma, M. H. 1957. Effects of larval nutrition on the life cycle, size, coloration, and longevity of *Chrysopa lateralis* Guer. Florida Entomologist 40:5-9.
- Nakahara, W. 1915. A Synonymic List of Japanese Chrysopidae, with Descriptions of One New

- Genus and Three New Species. *Annals of the Entomological Society of America* 8(2): 117-123.
- Nakahara, W. 1955. New Chrysopidae from Formosa. *Kontyû* 23:143-147.
- Navás, L. 1910a. Crisópidos (Ins Neur.) nuevos. *Brotéria* 9:38-59.
- Navás, L. 1910b. Crisópidos nuevos ó poco conocidos. *Revista de la real academia de ciencias exactas físicas y naturales de Madrid* 9: 473-480.
- Navás, L., 1911. Nouvelles formes de Chrysopides (Ins. névr.) de France. *Annales de l'Association des Naturalistes de Lavallois-Perret* 17: 12-14.
- Navás, L., 1912. Crisópidos y Hemeróbidos (Ins. Neur.) nuevos o críticos. *Brotéria* 10: 98-113.
- Navás, L. 1913a. Crisópidos Sudamericanos. *Brotéria* 11: 149-168.
- Navás L. 1913b. Les Chrysopides (Ins. Névr.) du Musée de Londres. *Annales de la Société scientifique de Bruxelles* 37: 292-33.
- Navás, L., 1913c. Algunos órganos de la alas de los insectos. In II International Congress of Entomology 2: 178-186.
- Navás, L., 1914a. Les Chrysopides (Ins. Névr.) du Musée de Londres. *Annales de la Société scientifique de Bruxelles* 38(2): 73-114
- Navás, L., 1914b. Neurópteros sudamericanos. Primera [I] serie. *Brotéria (Zoológica)* 12:45-56, 215-234.
- Navás, L., 1914c. Quelques Névroptères recueillis par le Dr. Malcolm Burr en Transcaucasie. *Revue Russe d'Entomologie* 14:211-216.
- Navás, L. 1915. Neurópteros nuevos o poco conocidos (Sexta [VI] serie). *Memorias de la Real*

- Academia de Ciencias y Artes de Barcelona 12(3): 119-136.
- Navás, L. 1916. Neurópteros Sudamericanos. Tercera [III] serie. *Brotéria* 14:14-35.
- Navás, L. 1917. Neue Neuropteren. Dritte [III] serie. *Entomologische Mitteilungen* 6:274-282.
- Navás, L. 1919. Algunos insectos Neurópteros de la República Argentina. Serie tercera [III]. *Revista de la Real Academia de Ciencias Exactas Físicas y Naturales de Madrid*. 17:287-305.
- Navás, L. 1920a. Insectos Sudamericanos (2a serie). *Anales de la Sociedad Científica Argentina* 90:44-51.
- Navás, L. 1920b. A Contribution to the Knowledge of the Neuropteron Insects of Algeria. *Novitates Zoologica* 26: 283-290.
- Navás, L. 1925a. Neurópteros del Museo de Berlin. *Revista de la Academia de Ciencias exactas, físicas, químicas y naturales de Zaragoza* 9: 20-34.
- Navás, L. 1925b. Névroptères nouveaux. *Annales de la Société Scientifique de Bruxelles* 44(1): 566-573.
- Navás, L. 1927b. Insectos de la Somalia Italiana. *Memorie della Società Entomologica Italiana* 6:85-89.
- Navás, L. 1928. Insectos del Museo de Hamburgo. Primera [I] serie. *Boletín de la Sociedad Entomologica de España* 11: 59-138.
- Navás, L. 1929. Insectos exóticos Neurópteros y afines del Museo Civico de Génova. *Annali del Museo Civico di Storia Naturale Giacomo Doria* 53:354-389.
- Navás, L. 1933. Décadas de insectos nuevos. Década 24. *Brotéria (Ciências Naturais)* 29:101-110.

- Navás, L. 1935. Insectos de Berberia. Serie 12. Boletín de la Sociedad Entomologica de España 18:77-100.
- Navás, L. 1936a. Décadas de insectos nuevos. Década 28. Brotéria (Ciências Naturais) 32:161-170.
- Navás, L. 1943. Comunicaciones entomológicas. 18. Insectos de Madagascar. Segunda [II] serie. Revista de la Academia de Ciencias Exactas Fisico-Químicas y Naturales de Zaragoza 18(1): 42-74.
- Needham, J. G. 1909. Notes on the Neuroptera in the collection of the Indian Museum. Records of the Indian Museum 3(12): 185-210.
- New, T. R. 1980. A revision of the Australian Chrysopidae (Insecta: Neuroptera). Australian Journal of Zoology Supplementary Series 28(77): 1-143.
- New, T. R. 1981a. Some early stages of *Dictyochrysa* Esben-Petersen (Neuroptera, Chrysopidae). Neuroptera International 1(3): 136-140.
- New, T. R. 1981b. Aspects of the biology of *Chrysopa edwardsi* Banks (Neuroptera, Chrysopidae) near Melbourne, Australia. Neuroptera International 1:165-174
- New, T. R. 1983. The egg and first instar of *Italoichrysa insignis* (Neuroptera, Chrysopidae). Australian Entomological Magazine 10: 29-32
- New, T. R. 1986a. Some early stages of *Calochrysa* Banks (Neuroptera, Chrysopidae). Australian Entomological Magazine 13: 11-14.
- New, T. R. 1986b. Notes on the larva of *Anomalochrysa* McLachlan (Neuroptera, Chrysopidae). Neuroptera International 4: 31-34.

- New, T. R. 1989. Handbuch der Zoologie, Band/Volume IV Arthropoda: Insecta, Planipennia: lacewings. Walter de Gruyter, Berlin, New York.
- Okamoto, H. 1914. Über die Chrysopiden-Fauna Japans. The journal of the College of Agriculture, Tohoku Imperial University, Sapporo, Japan 6(3): 51-74.
- Oswald, J. D. 1987. *Hypochochrysa* Hagen, 1866 (Chrysopidae) and *Stenorrhachus* Mel., 1886 (Nemopteridae) are valid names in the Neuroptera. Neuroptera International 4: 225-229.
- Oswald, J. D. 2008. Opinion 2254 (Case 3399) *Dichochochrysa* Yang, 1991 (Insecta, Neuroptera): generic name not conserved. The Bulletin of Zoological Nomenclature 65(3):178-182.
- Oswald, J. D. 2018. Neuropterida Species of the World. Version 5.0. <http://lacewing.tamu.edu/SpeciesCatalog/Main>. Last accessed on April 07 2018.
- Perkins, R. C. 1913. Review of Neuroptera, in Fauna Hawaiiensis being the land-fauna of the Hawaiian Islands, D. Sharp, ed. Cambridge University Press pp. 1-16.
- Principi, M. M. 1946. Contributi allo studio dei Neurotteri italiani. IV. *Nothochrysa italica* Rossi. Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna. 15: 85-102.
- Principi, M. M. 1956. Contributi allo studio dei Neurotteri Italiani. V. Ricerche su *Chrysopa formosa* Brauer e su alcuni suoi parassiti. Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna 16:134-175.
- Principi, M. M. 1977. Contributi allo studio dei Neurotteri Italiani. XXI. La morfologia addominale ed il suo valore per la discriminazione generica nell'ambito delle Chrysopinae. Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna 31:325-360
- Principi, M. M., and M. Canard. 1984. Feeding habits. Pp. 76-92 in Canard, M., Séméria, Y., and New, T. R. (Eds.). Biology of Chrysopidae (Vol. 27). Springer.

- Putman, W. L. 1932. Chrysopids as a factor in the natural control of the oriental fruit moth. Canadian Entomologist 64:121-126. (D)15:29-37.
- Putman, W. L. 1937. Biological notes on the Chrysopidae. Canadian Journal of Research
- Schneider, W. G., 1851. Symbolae ad monographiam generis Chrysopae, Laech. Hirt.
- Séméria, Y. 1977. Discussion de la validite taxonomique du sous-genre *Chrysoperla* Steinmann (Planipennia, Chrysopidae). Nouvelle Revue d'Entomologie 7:235-238.
- Séméria, Y. 1983. Deux genres jumeaux de Chrysopinae: *Chrysopa* Leach et *Parachrysopa* nov. gen. (Planipennia, Chrysopidae).
- Silva, P. S., Albuquerque, G. S., Tauber, C. A., and M. J. Tauber. 2007. Life history of a widespread Neotropical predator, *Chrysopodes (Chrysopodes) lineafrons* (Neuroptera: Chrysopidae). Biological Control 41:33-41.
- Silva, P. S., Tauber, C. A., Albuquerque, G. S., and M. J. Tauber. 2013. Larvae of five horticulturally important species of *Chrysopodes* (Neuroptera, Chrysopidae): shared generic features, descriptions and keys. ZooKeys 262:39-92.
- Skorepa, A. C., and A. J. Sharp. 1971. Lichens in "packets" of lacewing larva (Chrysopidae). Bryologist 74:363-364.
- Sosa, F., and C. A. Tauber. 2017. The genus *Vieira* Navás (Neuroptera: Chrysopidae): a new species, a key to the species, and new geographic records. Zootaxa 4258(1): 43-59.
- Smith, R. C. 1921. A study of the biology of the Chrysopidae. Annals of the Entomological Society of America 14:27-35.
- Smith, R. C. 1922. The biology of the Chrysopidae. Memoirs of the Cornell University

- Agricultural Experiment Station 58:1287-1372.
- Smith, R. C. 1926a. The life history and habits of *Eremochrysa punctinervis* McLachlan (Neuroptera). Bulletin of the Brooklyn Entomological Society 21:48-52.
- Smith, R. C. 1926b. The trash-carrying habit of certain lace wing larvae. Scientific Monthly, New York 23:265-267.
- Smith, R. C. 1932. The Chrysopidae (Neuroptera) of Canada. Annals of the Entomological Society of America 25:579-601.
- Sosa, F., and S. de Freitas. 2002. A new genus of Neotropical Chrysopini (Neuroptera: Chrysopidae). Zootaxa 3351:1-18.
- Steinmann, H. 1964. The *Chrysopa* species (Neuroptera) of Hungary. Annales Historico-Naturales Musei Nationalis Hungarici 56:257-266
- Tjeder, B. 1941. Some remarks on "The generic names of the British Neuroptera". Entomologisk Tidskrift 62: 24-31.
- Tjeder, B. 1966. Neuroptera–Planipennia. The Lace–wings of Southern Africa. 5. Family Chrysopidae. South African Animal Life 12: 228–534.
- Tauber, C. A. 1969. Taxonomy and biology of the lacewing genus *Meleoma* (Neuroptera: Chrysopidae). University of California Publications in Entomology 58(7): 1-94.
- Tauber, C. A. 1975. Larval characteristics and taxonomic position of the lacewing genus *Suarius*. Annals of the Entomological Society of America 68:695-700.
- Tauber, C. A. 2003. Generic characteristics of Chrysopodes (Neuroptera: Chrysopidae), with new larval descriptions and a review of species from the United States and Canada. Annals of

- the Entomological Society of America 96:472-490.
- Tauber, C. A. 2004. A systematic review of the genus *Leucochrysa* (Neuroptera: Chrysopidae) in the United States. *Annals of the Entomological Society of America* 97(6): 1129-1158.
- Tauber, C. A. 2007. Review of *Berchmansus* and *Vieira* and description of two new species of *Leucochrysa* (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America* 100(2): 10-138.
- Tauber, C. A., and J. A. Garland. 2014. *Kymachrysa*, a new genus of Nearctic green lacewings (Neuroptera, Chrysopidae, Chrysopini). *ZooKeys* 437:87-108.
- Tauber, C. A., and T. de León. 2001. Systematics of green lacewings (Neuroptera: Chrysopidae): larvae of *Ceraeochrysa* from Mexico. *Annals of the Entomological Society of America* 94:197-209.
- Tauber, C. A., de León, T., López-Arroyo, J. I., and M. J. Tauber. 1998. *Ceraeochrysa placita* (Neuroptera: Chrysopidae): generic characteristics of larvae, larval descriptions, and life cycle. *Annals of the Entomological Society of America* 91:608-618.
- Tauber, C. A., de León, T., Penny, N. D., and M. J. Tauber. 2000. The genus *Ceraeochrysa* (Neuroptera: Chrysopidae) of America North of Mexico: larvae, adults, and comparative biology. *Annals of the Entomological Society of America* 93:1195-1221.
- Tauber, C. A., and F. J. Sosa. 2015. Rediscovery of *Nuvol umbrosus* Navás (Neuroptera, Chrysopidae, Leucochrysinini): a redescription and discussion. *Zookeys* 519:141-153.
- Tauber, C. A., Sosa, F., and A. Contreras-Ramos. 2018. *Cryptochrysa* Freitas & Penny, a generic homonym, replaced by *Titanochrysa* Sosa & Freitas (Neuroptera: Chrysopidae). *Zootaxa*,



4375(2): 287-295.

Tauber, M. J., and C. A. Tauber. 1978. Thermal accumulations, diapause, and oviposition in a conifer-inhabiting predator, *Chrysopa harrisii* (Neuroptera). *Canadian Entomologist* 106:969-978.

Tauber, M. J., and C. A. Tauber. 2015. Phenological responses of *Pseudomallada* (Neuroptera: Chrysopidae): comparative data from three Nearctic species and interspecific hybrids. *European Journal of Entomology* 112:49-62.

Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2006. *Berchmansus elegans* (Neuroptera: Chrysopidae): larval and adult characteristics and new tribal affiliation. *European Journal of Entomology* 103(1): 221.

Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2008. A new genus and species of green lacewings from Brazil (Neuroptera: Chrysopidae: Leucochrysiini). *Annals of the Entomological Society of America* 101:314-326.

Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2014. Debris-carrying in larval Chrysopidae: unraveling its evolutionary history. *Annals of the Entomological Society of America* 107(2): 295–314.

Tauber, C. A., Albuquerque, G. S., and M. J. Tauber. 2014. Revision of the Neotropical green lacewing genus *Ungla* (Neuroptera, Chrysopidae). *ZooKeys* 674:1-188.

Terry, F. W. 1905. Leaf-hoppers and their natural enemies. (Pt. V. Forficulidae, Syrphidae, and Hemerobiidae). *Bulletin Hawaiian Sugar Planters' Association Experiment Station (Entomological Series)*, 1(5): 163-181.

Terry, F.W. 1908. Notes on the life-history of an endemic hemerobiid (*Nesomicromus vagus*

- Perk.). Proceedings of the Hawaiian Entomological Society 1:174-175.
- Tjeder, B. 1936. Schwedisch-chinesische wissenschaftliche expedition nach den nordwestlichen provinzen Chinas, unter leitung von Dr. Sven Hedin und Prof. Sü Ping-chang. Insekten gesammelt vom schwedischen arzt der expedition Dr. David Hummel 1927-1930. 62. Neuroptera. Arkiv för Zoologi 29A(8):1-36
- Tjeder, B. 1966. Neuroptera–Planipennia. The Lace–wings of Southern Africa. 5. Family Chrysopidae. South African Animal Life 12: 228–534.
- Toschi, C. 1965. The taxonomy, life histories, and mating behavior of the green lacewings of Strawberry Canyon (Neuroptera: Chrysopidae). Hilgardia 36(11):391-433.
- Tsukaguchi, S. 1979. Taxonomic notes on *Brinckochrysa kintoki* (Okamoto) (Neuroptera: Chrysopidae). Kontyû 47:358-366.
- Tsukaguchi, S. 1978. Descriptions of the larvae of *Chrysopa* Leach (Neuroptera, Chrysopidae) of Japan. Kontyû 46:99-122.
- Tsukaguchi, S. 1985. A check list of published species of Japanese Chrysopidae (Neuroptera). Kontyû 53:503-506.
- Tsukaguchi, S. 1995. Chrysopidae of Japan: (Insecta, Neuroptera). Yutaka Insatsu, Osaka, Japan.
- Weber, N. A. 1942. A neuropterous myrmecophile, *Nadiva valida* Erichs. Psyche 49: 1-3.
- van der Weele, H. W., and E. Jacobson 1909. Mecoptera and Planipennia of Insulinde, with biological notes. Notes from the Leyden Museum 31:1-100.
- Winterton, S. L. 1995. A new genus and species of Apochrysinæ (Neuroptera: Chrysopidae) from Australia, with a checklist of Australian Chrysopidae. Austral Entomology, 34(2): 139-

145.

- Winterton, S. L., and S. J. Brooks. 2002. Phylogeny of the apochry sine green lacewings (Neuroptera: Chrysopidae: Apochry sineae). *Annals of the Entomological Society of America* 95(1): 16–28.
- Winterton, S. L., and I. J. Garzón-Orduña. 2015. A new species of *Glenochrysa* Esben-Petersen from Australia (Neuroptera, Chrysopidae). *ZooKeys* 541:79-85.
- Yang, C. K. 1988. Neuroptera: Osmylidae, Dilaridae, Hemero biidae, Chrysopidae, Mantispidae, Myrmeleontidae, Ascalaphidae, Corydalidae, pp. 193-216, in Huang, F. S., Wang, P. Y., Yin, W. Y., Yu, P. Y, Lee, T. S., Yang, C. K., and X. J. Wang (eds.), *Insects of Mt. Namjagbarwa region of Xizang*. Science Press, Beijing.
- Yang, C. K. 1992. Neuroptera. pp. 438-454, in Chen, S. (ed.). *Hengduan shan qu kun chong* [=Insects of the Hengduan Mountains Region]. Vol. 1. Ke xue chu ban she [=Science Press], Beijing, China.
- Yang, C. K., and X. X. Wang. 1994. The golden eyes of Yunnan with descriptions of some new genus and species (Neuroptera: Chrysopidae). *Journal of Yunnan Agricultural University* 9(2):65-74.
- Yang, C. K., Yang, X. K., and X. K. Wang. 1999. Chrysopidae, in Huang, B.K. (ed). *Fujian kun chong zhi* [=Fauna of Insects Fujian Province of China]. 3: 106-131, 159-163.
- Yang, X. K. 1991. *Dichochrysa* nom. nov. for *Navásius* Yang et Yang 1990 (Neuroptera: Chrysopidae) nec. Esben-Petersen 1936 (Neuroptera: Myrmeleonidae). P. 150, in Zhang, Guang-xue (ed.). *Scientific Treatise on Systematic and Evolutionary Zoology*. Vol. 1. Popular Science Press, Beijing, China.

Yang, X. K., Yang, C. K., and W. Z. Li. 2005. Neuroptera, Chrysopidae. Fauna Sinica. Insecta vol. 39. Science Press, Beijing.

Zelený, J. 1971. Green lace-wings of Czechoslovakia (Neuroptera, Chrysopidae). Acta Entomologica Bohemoslovaca 68:167-184.

Zimmerman E. C. 1957. Ephemeroptera, Neuroptera, Trichoptera. Insects of Hawaii: a manual of the insects of the Hawaiian Islands, including an enumeration of the species and notes on their origin, distribution, hosts, parasites, etc. University of Hawaii Press, Honolulu, Hawaii 6: 1-209.

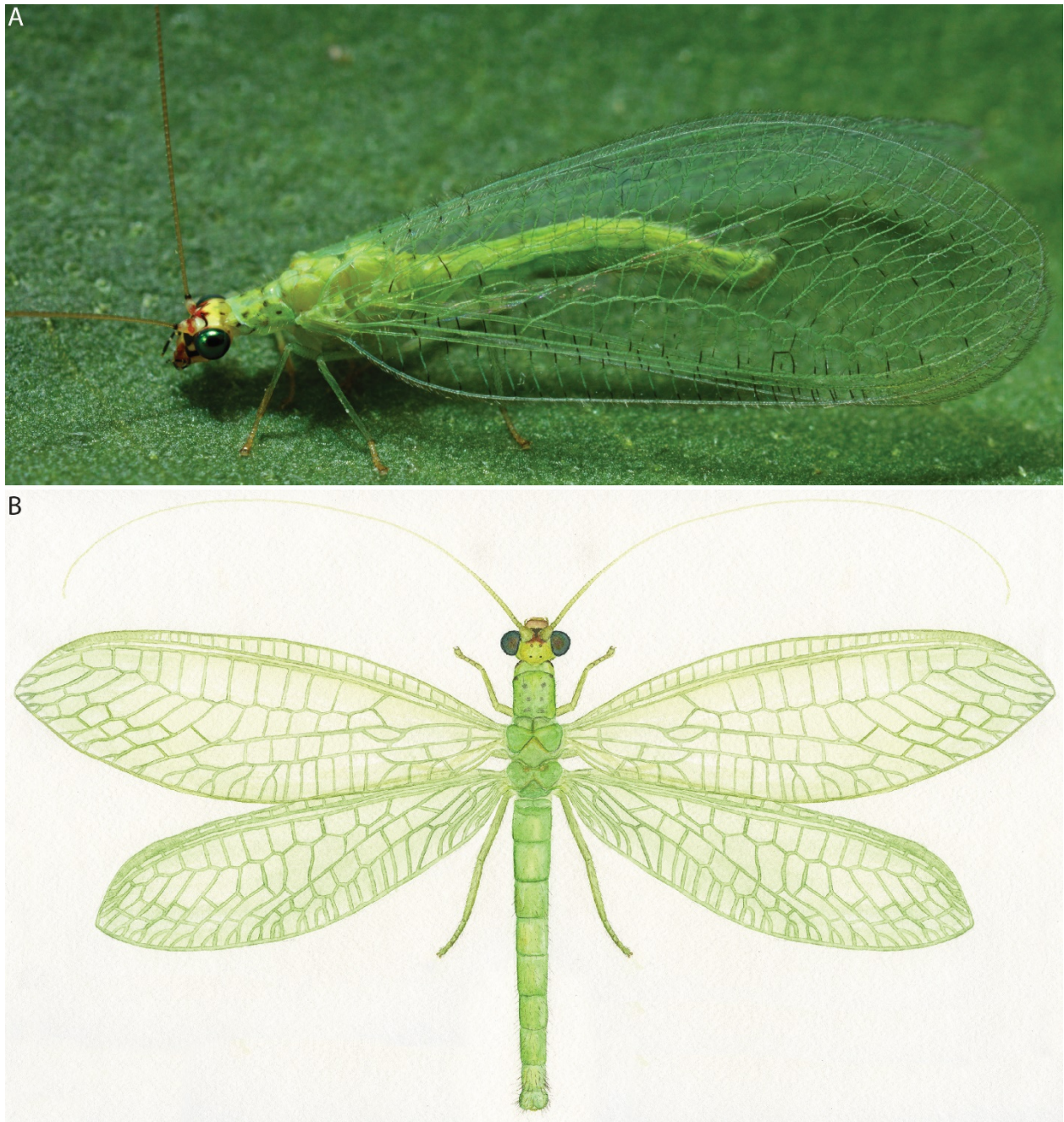
## Chapter 3

Morphology of *Chrysopa oculata* as an exemplar  
for the family Chrysopidae (Neuroptera)

## Introduction

The morphology of Chrysopidae has mostly been discussed in the frame of species descriptions, generic revisions, and identification keys. Although Chrysopidae are not known as a morphologically variable insect family, they show much diversity when studied in more detail. With variations especially in the wing venation and male genitalia there is a great, often hidden, morphological disparity in the family. As such, the wings can be large, broad and with numerous fine veins (e.g., Apochrysinæ, and most Leucochrysinini and Ankylopterygini), or small and with few veins as in many Nothochrysinæ or some Chrysopini with strongly reduced wing venation (e.g., *Parachrysopiella* Brooks and Barnard, *Eremochrysa* Banks). Additionally, fusions of the veins, as further discussed in Chapter 4, contribute to the great diversity in wing characters. The male genitalia vary in the structure of the individual sclerites and even in the composition of the sclerites, with quite simple genitalia in Apochrysinæ, to the most complex genitalia in highly derived Chrysopini such as *Pseudomallada* Tsukaguchi or *Meleoma* Fitch. The characters of the head, thorax, legs, and external abdominal sclerites have rarely been discussed in detail and, hitherto, formal clarification of homologies and standardization of the terms were lacking.

The aim of this chapter is the detailed description and discussion of all adult external morphological characters, as well as the internal male and female genitalic characters of one species. This will allow future studies to rely on a consistent terminology and a simplified identification of morphological structures, with the aid of detailed descriptions and illustrations. As an exemplar for Chrysopidae we chose a species of the genus *Chrysopa* Leach.



**Figure 89.** Habitus of *Chrysopa oculata*. A. Photomicrograph of living individual, male. B: Drawing of dorsal habitus, male, watercolor.

*Chrysopa* was described by Leach in 1815 and is the type genus for Chrysopidae, the latter of which was established by Schneider (1851) as the group “Chrysopina” within the family Hemerobiidae. The genus *Chrysopa* has undergone numerous changes in composition, with an

abundance of synonyms and splitting off additional genera throughout the last century and a half (Brooks and Barnard 1990, and see chapter 2). Overall, the generalized morphology of the genus led to it becoming a “waste-basket” taxon, basically incorporating all of those generalized chrysopines that did not fit in otherwise more distinctive genera. The genus *Chrysopa* is a derived member of the Chrysopini and its morphology (especially external) is typical for the tribe as a whole, which mostly varies in coloration and male genitalic characters as well as some wing venation features. *Chrysopa* is a common, species-rich genus, with about 55 currently recognized species, and a Holarctic distribution (Aspöck et al. 1980, Garland 1985, Brooks and Barnard 1990, Penny et al. 2000). Given the general morphological consistency in most traits across the group, the morphological account presented herein can easily be adapted to other species of the genus.

For this study, the species *Chrysopa oculata* (Say) was selected because of its accessibility, its comparatively simple identification, and the ease with which most characters can be viewed due to its coloration (fig. 1). *Chrysopa oculata* is one of the most common lacewings in the American Midwest, distributed throughout the Nearctic, and can easily be determined by the coloration of its head (Bickley and McLeod 1956, Penny et al. 2000). The coloration varies in intensity and has lead researchers to describe numerous subspecies and varieties (e.g., Fitch 1855, Burmeister 1939, Banks 1911, Smith 1932, Bram and Bickley 1963), which have subsequently been synonymized (e.g., Penny et al. 2000, Brooks and Barnard 1990). In the original description, Say (1839) considered *C. oculata* the analogue of the European *Chrysopa perla* (Linnaeus), owing to its pronounced head coloration and the odor it emits. The species can be found throughout summer and is especially active around sunset and the early night hours. It is a field-inhabiting species that also often occurs at the periphery of forests or bushes (Henry 1982, Principi and Canard 1984). The female lays stalked, spread out (not in clusters as other chrysopids) eggs (fig.



2A) on leaves of grass, shrubs, or small trees, often close to potential prey. The first instar (fig. 2B) hatches after about 4–6 days and immediately starts feeding on small soft-bodied insects – mostly aphids (Principi and Canard 1984), but *C. oculata* has also been reported to prey on numerous other insects, such as small hemipteran nymphs, moth larvae, or even conspecific larvae (Garland 1985), and we observed that the larvae prey on most any insect whose size permits them to be easily captured by the lacewing. This predatory behavior and general association with aphids has given chrysopid larvae the common name aphid-lions or aphidlions or even aphid-wolves. The larvae are non-trash carrying (naked), which is associated with a faster and more aggressive predatory behavior, but possess long dorsal setae (Weed 1897, Tauber et al. 2014). As in all other chrysopids, *C. oculata* has three instars (the development of which takes about two weeks in total), and the third instar spins a globular silken cocoon in which it develops into the prepupa (fig. 2D) (Principi and Canard 1984). The mobile prepupa hatches from the cocoon after about two weeks and almost immediately sheds its pupal skin to eclose as an adult. There are up to three generations per summer and the last generation overwinters as prepupae in the cocoon (Henry 1982).



**Figure 90.** *Chrysopa oculata*, immature states, photomicrographs. A. Egg (ca. 5 days old), lateral view. B: First instar, immediately after hatching, lateral view. C: Second instar, dorsal view. D: Prepupa, immediately after hatching from cocoon, lateral view.

The adults of *C. oculata* are carnivorous, feeding on the same prey as their larvae, a trait not common among Chrysopidae (Canard and Principi 1984). When irritated, males and females release a strong odor which, due to its main component (skatole), is similar to the smell of feces (Blum et al. 1973); a trait that has resulted in such green lacewings sometimes being known commonly as “stinkflies” in North America. Due to its widespread distribution in the Nearctic, *C. oculata* has been the subject of numerous studies considering its biology and anatomy. Multiple redescriptions, including identification keys, were provided by Banks (1903), Smith (1932), Bickley and McLeod (1956), Bram and Bickley (1963) and Penny et al. (2000). Hwang and

Bickley (1961) provided an outstanding treatment of the internal and external morphology of its reproductive system. The first notes on the biology of *C. oculata* were presented by Weed (1897) and Henry (1982), Bickley (1952) provided an overview in the inheritance of variation in coloration, and Canard and Principi (1984) and Garland (1985) added detailed descriptions of the species' life history.

A solid understanding of general morphology and the proper homology and accurate identification of characters, recognized by a standard terminology, are critical for further analyses. Indeed, given the specialized and complex morphologies of most insect lineages, strong foundations establishing basic morphological terminologies that are rooted in crucial homology assessments are often lacking although certainly needed. Historical terminologies of convenience which crop up within each insect lineage are often inconsistently applied and sometimes imply improper homologies, or misidentify important sclerites, particularly among genitalic sclerites and it is therefore important to address these nomenclatures. Careful morphological accounts have done much to advance their respective subjects (e.g., Michener 1944, Krishna et al. 2013, Brannoch et al. 2017, among many others). Modern efforts to establish online ontologies for individual insect orders or even across all Hexapoda are the 21<sup>st</sup> Century equivalent of basic comparative morphological treatments. For insect wings, the groundbreaking works of Needham and Comstock (1898a, 1898b, 1898c, 1898d, 1898e, 1898f, 1898g, 1898h, 1899a, 1899b, 1899c, and the summary in Comstock 1918) laid the basis for morphological study of insect wings. They explored the development, function, and homologies all pertinent wing characters and noted the shared and unique aspects of each order. Although their classification is now mostly outdated, their morphological treatment and proposed nomenclature is still widely used, sometimes with little or no necessary augmentation during the last century. The most comprehensive comparative

morphological accounts, covering the entirety of insect anatomy, are those of Snodgrass (1935) and Matusda (1965, 1970, 1976), and while some more modern works have appeared all lack the depth and detail provided by these authors.

Morphological treatments of Chrysopidae are scarce, with Comstock (1918) still accounting for one of the most detailed works, but the family has often been represented as a component of early attempts to establish groundplan patterns for insects. In fact, historically Neuroptera (with Chrysopidae often cited owing to the easy access to material) were mistakenly believed to retain many plesiomorphies for Pterygota and thereby often served as a proxy for ancestral insect morphology, especially in terms of wing venation (e.g., Latreille 1807, 1817, Stephens 1835, Westwood 1839, 1840, Rambur 1842, Comstock 1918).

Killington (1937) revised neuropteran morphology with detailed drawings and descriptions focused around Hemerobiidae, with discussions about differences relative to other families, the latter of which were accompanied by informative illustrations. He described the morphology of Chrysopidae in detail and provided figures – which for the wing venation were particularly excellent. His work is the only work, aside from Comstock (1918) that inferred the correct actual venation pattern from the pupal wing pad.

Historically, patterns of coloration and wing venation were the only diagnostic characters employed (Barnard 1984), but Tjeder (1966) steered focus toward the male genitalia as a useful tool for species and generic delimitation, presenting this material in his revision of South African Chrysopidae. Similarly, Aspöck et al. (1980) revised the neuropteran fauna of Europe, including Chrysopidae, and New (1980) revised the Australian representatives of the family, both including detailed morphological descriptions and illustrations. Barnard (1984) summarized the characters that were commonly used for chrysopid taxonomy by reviewing the work on chrysopid

morphology up to that date, from authors such as R. Smith (1932), M. Principi (1977), P. Adams (1967), F. Killington (1937), C. Henry (1980), B. Tjeder (1966), C. and T. Tauber (1969), T. New (1980), and H. and U. Aspöck and H. Hölzel (1980). A comparative morphology of Neuroptera, including Chrysopidae, was conducted as part of general review of the order by New (1989). Chrysopidae have been included in several comparative treatments of individual character complexes of Neuroptera or broader insect taxa. The wing base was discussed by several authors (Hörnschemeyer 1998, 2002, Zhao et al. 2014), the anatomy of Chrysopidae by Bitsch (1984), the male genitalia by Aspöck and Aspöck (2008), the wings by Breitkreuz et al. (2017, see chapter 4), and some character complexes of individual species, such as the reproductive system of *C. oculata* (Hwang and Bickley 1961), have been described in detail. In the comprehensive generic revision by Brooks and Barnard (1990) – a benchmark in the history of chrysopid research and the foundation for subsequent investigators – the morphology of adult Chrysopidae was briefly defined before discussing variations observed among the genera. Publications, which focus on individual genera, species, or regions, especially authored by T. New, B. Tjeder, C. and M. Tauber, M. Principi, N. Penny, and S. Tsukaguchi discuss morphological traits, sometimes with exceptional detail (e.g., Principi 1954, Tjeder 1966, New 1980, Penny 1996, Tauber et al. 2006, Tauber 2017, Tsukaguchi 1995, among many others). Despite this considerable effort, there remains inconsistency in the application of terms, particularly among genital sclerites, and characters not historically employed in taxonomic descriptions of species have been ignored. As such, a general encyclopedia for chrysopid morphology remains to be established.

This contribution provides a detailed description of all external morphological characters of an adult chrysopid, *C. oculata*. Additionally, each character is illustrated in the form of Photomicrographs or schematic line drawings and defined in the glossary. A comprehensive

treatment, which includes characters beyond those that are taxonomically informative for species circumscription was lacking and we hope that this work can be used as a proxy for other Chrysopidae. Large numbers of the morphological features retain the plesiomorphic states for *Chrysopa*, Chrysopini, Chrysopinae, or even higher taxonomic groups. As such, general components of the thorax, legs, and external abdominal sclerites tend to vary comparatively little from the conditions observed among other Neuroptera, Neuropterida, or even Holometabola (Brooks and Barnard 1990, Mastuda 1965, 1970, 1976, New 1989, Grimaldi and Engel 2005). This chapter focuses on the morphology of one species, but descriptions of the differences between chrysopid taxa can be found in the framework of the generic revision (chapter 2), and discussions of character evolution for numerous traits in Chrysopidae in the phylogenetic analysis (chapter 1).

## Material and Methods

This study is based on male and female adults of *Chrysopa oculata* (Say 1839) from Kansas. Material was collected by sweeping in tall grass and on bushes, especially during dusk throughout the months of June–August in areas southeast of Lawrence, KS. The identification of the species was determined by reference to Penny (2000). The specimens were fixed through freezing or exposure to cyanide, and the females were kept in tubes overnight to lay eggs. Larvae hatched after two days and were reared in small plastic containers with aphids as a food source up to the third instar, and then spun their cocoon after 2–3 weeks, pupated, and eclosed after 1–2 weeks. Adults were mounted or dissected while still fresh to obtain photographs that most closely approximate the appearance of the character states in living individuals. Dissections for staining were initially cleared in micro-tubes filled with a 10% KOH solution, in a ca. 70° water bath, for about 30–60 minutes. The clearing reaction was stopped by placing the dissections in distilled

water and adding a drop of acetylic acid. Following clearing, dissections were washed again in distilled water and then placed in 85% ethanol for the addition of stain. Chlorozol black dissolved in 85% alcohol was inserted to or placed on the dissection with the help of a fine syringe. Depending on the dissection, staining took between 10–60 minutes, after which is the preparation was placed in glycerin for further examination and storage. A total of 30 specimens were prepared in this manner, with 18 males and 12 females. Vouchers of the specimens, in the form of undissected mounted adults and slide-mounted cleared and stained dissections, are deposited in the collection of the Division of Entomology, University of Kansas Biodiversity Institute.

In general, morphological nomenclature is adapted from Comstock (1918), Killington (1936), Matsuda (1965, 1970, 1976), and Brooks and Barnard (1990). Specimens were examined with a Nikon SMZ 1500 stereomicroscope. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, stacked in Zerene Stacker, and then arranged in Adobe Photoshop and Illustrator CC2017. For the Photomicrographs, dissections were placed on a slide with glycerin and covered by a thin glass plate to prevent the dissection from moving and to correct for light distortion due to the curvature of the glycerin surface. Line drawings were produced in Adobe Illustrator CC2017 on the basis of photographs of wings from representative species.

**Format:** The descriptions and illustrations of the morphological characters are arranged from anterior to posterior, and focus on the external sclerites, except for the genitalia. In each section the morphology of characters of specific body regions of *C. oculata* is described in detail and important variations across the family are discussed in their proper position within the text. For a more comprehensive comparative morphology of the genera of Chrysopidae refer to chapter 2. The line drawings are as close to the natural state as possible, to allow researchers to identify

structures easily. For some body regions in which the identification of the sclerites is more complicated (such as the lateral thorax and male genitalia), additional schematic drawings are provided. Additionally, a glossary with definitions of the morphological characters is given.

## Morphology

### General appearance

*Chrysopa oculata* is a typical Nearctic green lacewing with a light green body and some dark brown and red markings on the head and thorax (fig. 1). It measures about 1.5 cm ( $\pm$  2 mm) from the apex of the head to the apex of the wings, when the wings are folded over the body, and without the wings (head to apex of abdomen) it is about 1.0 cm ( $\pm$  1 mm) long. There is no significant size difference between males and females, but, when alive, females seem slightly larger, due to the often slightly expanded abdomen. Specimens reared in the lab were up to three mm smaller than individuals caught in the wild, probably due to the food source and small size of the container in which they were reared. As in all insects, the body is organized into three tagmata – head, thorax, and abdomen – and each tagma has its associated appendages, such the mouthparts, legs, wings, and genitalia. The body is almost entirely covered in micropilosity and the longer setae are variously arranged in denser areas throughout the body.

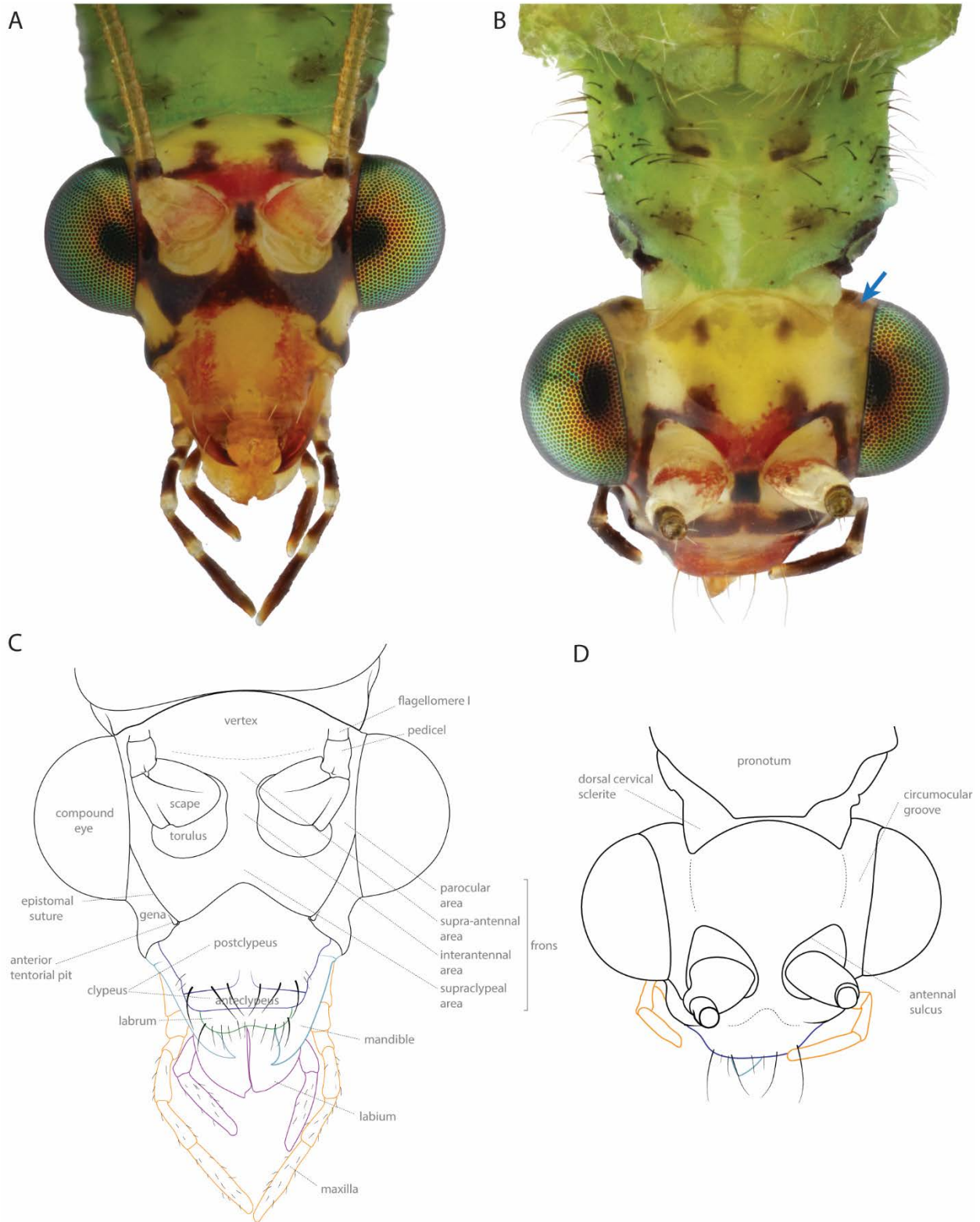
### Head

#### General shape

The head is prognathous, slightly elongate, and somewhat dorsoventrally flattened (figs. 3–4). This is the general head shape of most Chrysopidae, but some have a more rounded head. In



lateral view the compound eyes occupy about one half of the length of the head. The head bears numerous appendages, that all have a sensory input or gustatory function: antenna, clypeus, labrum, mandible, maxilla, labium, and even the compound eyes. Few genera (*Meleoma* and *Glenochrysa* Esben-Petersen) have projecting ornamentations on the vertex or supra-antennal frons that can include large grooves to encompass the scape.

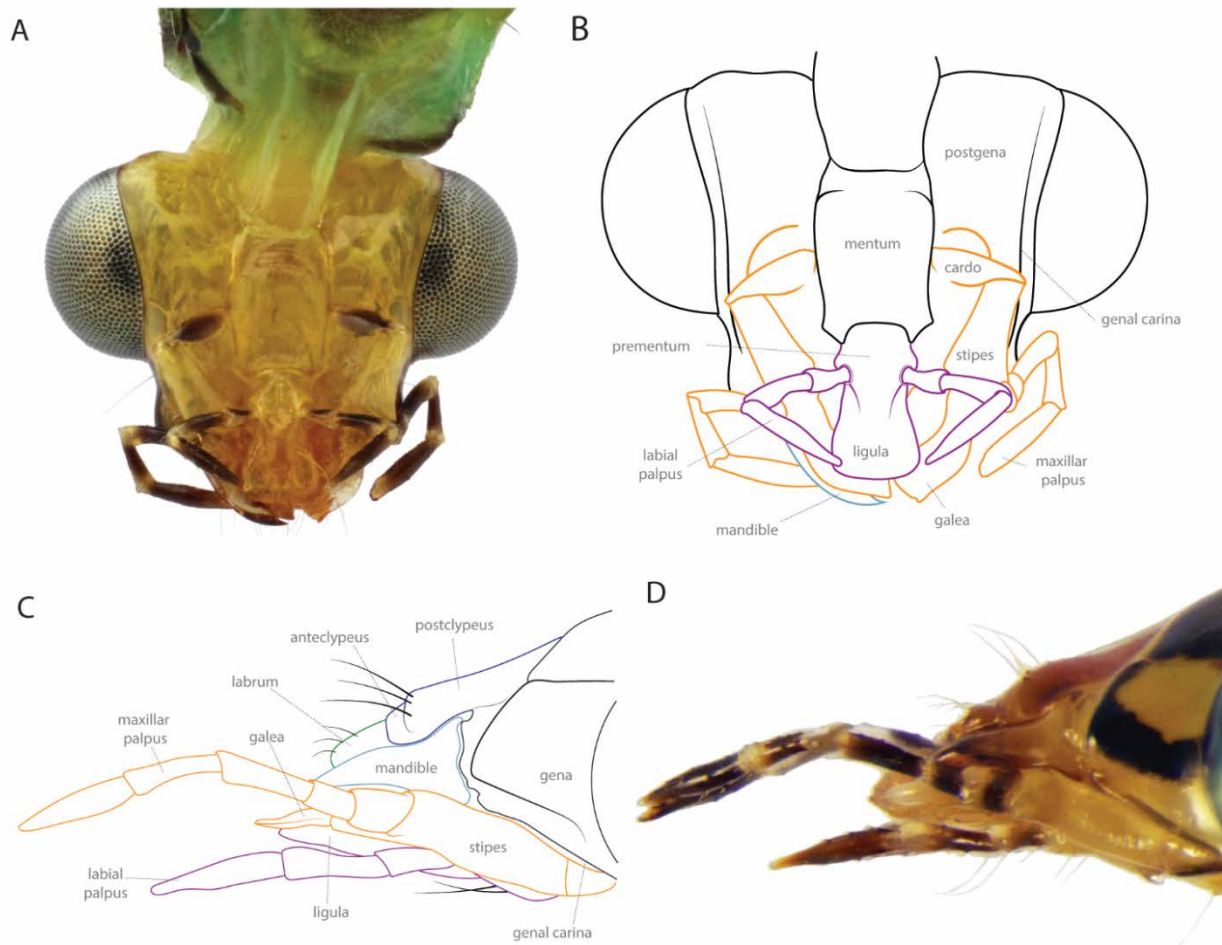


**Figure 91.** *Chrysopa oculata*, head. A–B Photomicrographs, C–D line drawings. A, C: dorso-frontal view. B, D: dorsal view, blue arrow indicating ill-defined margin between vertex and postgena. Dark blue: clypeus; green: labrum; light blue: mandible; violet: labium; orange: maxilla.

## Antenna

The **antenna** is shorter than the forewing and reaches to about two thirds of its length (~1.1 cm) in living individuals (fig. 1). The **torulus** is oval and larger than the diameter of the scape (fig. 3). In *C. oculata* it is easily detectible because it is unmarked, and therefore stands out from the surrounding integument of the frons and vertex, which is marked red and brown. The **antennal sulcus** is posteriorly present as a faint line, only visible in the right light setting, such as an oblique light, producing a small shadow of the sulcus. The **scape** (fig. 5A) is about as long as broad, basally oval, and the basal half is weakly marked with red (on all sides in some specimens, only dorsally in others). The scape and pedicel have a sclerotized articulation, which is positioned medioventrally and can be observed in living individual, due to a small invagination at the base of the pedicel and a sulcus on both scape and pedicel. The **pedicel** is smaller than the scape, slightly longer than wide, minutely hourglass-shaped, and marked with a broad brown ring on the apical half. The **flagellum** is entirely pale and consists of about 90 ( $\pm$  10) flagellomeres (fig. 1B). Each flagellomere is about twice as long as wide (fig. 5B), although the basal-most flagellomeres tend to be slightly shorter than the more apical ones. A flagellomere bears four circular rows of setae, which are dark, pointed towards the flagellar apex, and about as long as the flagellomere is wide. Subapically there are several longer setae that arise at a 90 degree angle from the flagellomere.

The coloration and dimensions of all antennal parts vary within Chrysopidae. The dimensions of the antenna in *C. oculata* are average for Chrysopinae. The state of four flagellar setal rings can be found exclusively in Chrysopinae, with only one exception (*Nothancyla* Navás, which is sister to all other Chrysopinae and has the presumably plesiomorphic five setal rings), whereas Nothochrysiniae and Apochrysiniae have five or six rings.



**Figure 92.** *Chrysopa oculata*, head details. A, D Photomicrographs, B, C line drawings. A, B: ventral view. C, D: lateral view. Dark blue: clypeus; green: labrum; light blue: mandible; violet: labium; orange: maxilla.

## Frons

The frons is bordered laterally by the inner margin of the compound eye and the gena, basally by the vertex, and apically by the basal clypeal margin, which is also the epistomal sulcus (fig. 3B). It is often strongly marked, as in *C. oculata*, and there are no setae present (fig. 3B). It is generally subdivided into four regions (fig. 2D), which can be loosely defined by reference points, but are not clearly delimited and are applied rather for orientation than forming distinct structures. The area above the toruli but below the vertex is the **supra-antennal** area, which is marked red in *C. oculata*. The **interantennal** area describes the space between the two toruli, and

has a distinct dark brown spot in *C. oculata*. The **parocular** area is delimited by the inner margin of the compound eye and the torulus and is usually slightly concave in Chrysopidae. The **supraclypeal** area is the entire region of the frons that is below the toruli and above the clypeus, but lateroventrally is margined by the gena. In *C. oculata* it is marked almost entirely with a continuous dark brown band. The apical margin is shaped as a rounded W in dorsal view (figs. 3A, B), and flat in lateral view (not bulging) (fig. 4D), and is completely smooth in *C. oculata*. Many Chrysopidae have a slightly inflated frons, in which the lower margin, bordering the clypeus and gena, is clearly visible due to the flat clypeus and raised frons. The coloration of the frons can vary greatly in Chrysopidae, from entirely pale, to spotted or entirely marked.

## Gena

The lateral and lower integument of the head is a loosely defined region, which can be divided in gena (figs. 3A, B, 4C, D) and postgena (figs. 4C, B). These two parts are divided by the **genal carina** (fig. 4B), which is a thin carina, originating at the posterior mandibular articulation and runs parallel to the posterior ocular margin, while thinning towards the base of the head and is present in most Neuroptera. The **gena** is margined by the epistomal sulcus (figs. 3A, B), where it meets the clypeus, the mandible base (figs. 4C, D), the ventral margin of the compound eye, and the genal carina. In *C. oculata* it is marked with a dark longitudinal band, and a thin transverse band at the base of the mandible, but the markings vary in color and intensity across Chrysopidae. The **postgena** is the integumental space between the genal carina, the posterior compound eye margin, the vertex, cervix, and maxilla. Its margin with the vertex is not clearly demarked, and we define it as a straight line between the slightly pointed upper tangent of the compound eye and the cervix. This line has diffuse dark brown markings in *C. oculata* (fig. 3G, see blue arrow). Gena

and postgena are comparatively consistent within Chrysopidae and vary only little in size and dimensions, in congruence with general head dimension.

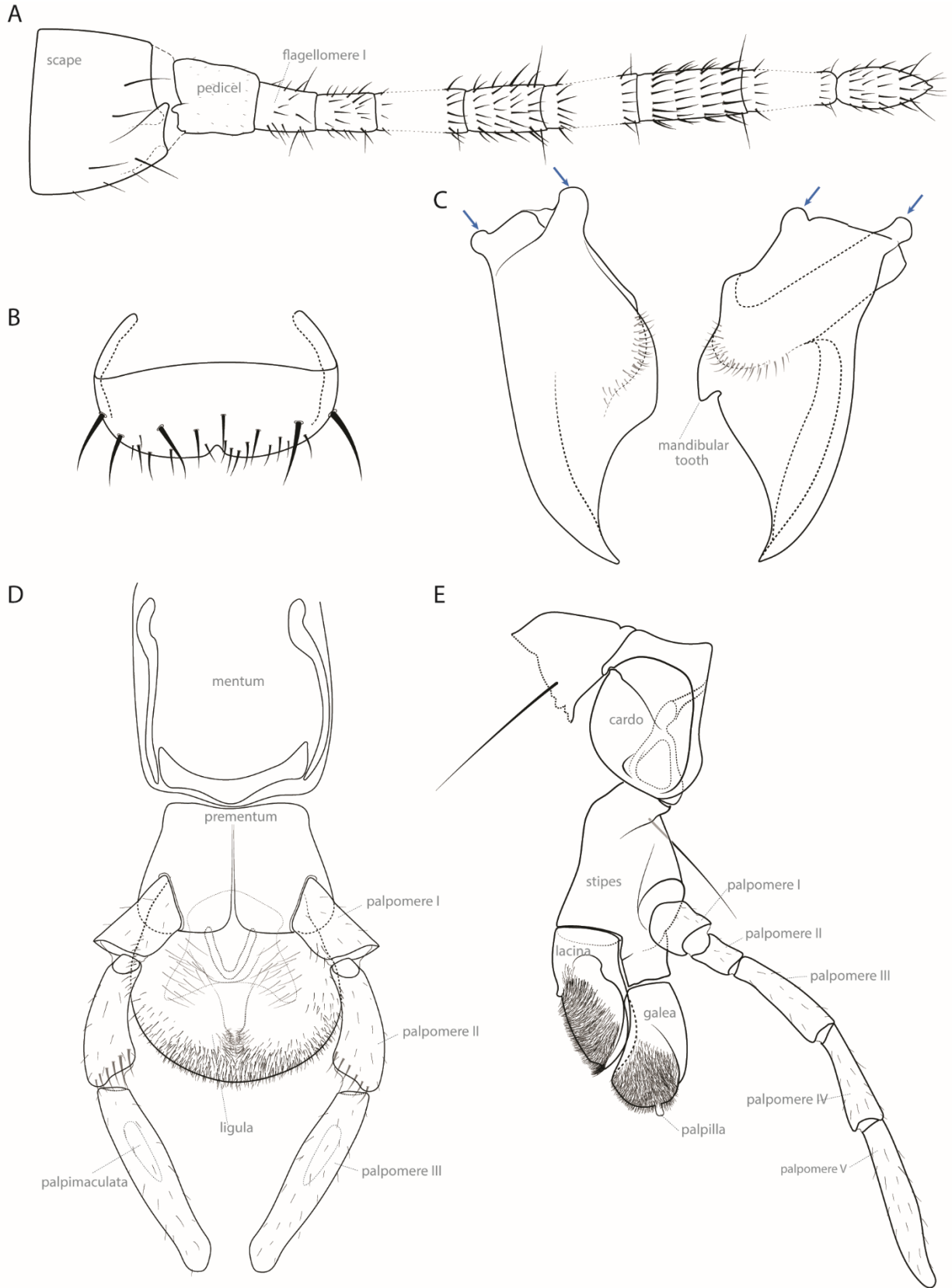
## Vertex

The **vertex** is the dorsal space of the head, above and between the upper tangent of the compound eyes, which is margined posteriorly by the occipital sulcus (visible only in dissection, the compound eyes, and the supra-antennal area of the frons (figs. 2B, E)). It is slightly raised in *C. oculata*, which is typical for Chrysopidae in which the shape of the vertex can vary from flat to strongly raised. The integument is smooth and polished, without wrinkles or any other coarse surface sculpturing. The raised shape of the vertex is due to a broad groove (**circumocular groove**) around the compound eyes, visible especially in frontal view. The vertex is marked red around the toruli and the brown markings vary between specimens from two brown spots on each side dorsally (a total of four spots) to unmarked.

## Clypeus

The **clypeus** (figs. 3A, B, 4C, D) of *C. oculata* is superficially difficult to delimit from the frons, because the epistomal sulcus, which defines the boundary between the lower frons (supraclypeal area) and clypeus, is faint. The basal margin of the clypeus borders the frons, the lateral margin the gena, and the apical margin is broadly truncate and not indented or emarginate. Embedded within the epistomal sulcus, at the point where the frons, clypeus, and gena meet is the anterior tentorial pit. The upper clypeal margin (= the frontoclypeal portion of the epistomal sulcus) is medially angled (ca. 90°) and as such pointed towards, but not reaching, the interantennal area of the frons. The widest point of the clypeus is medially, where the line between the mandibular base of each side is about as long as the length of the clypeus. The surface sculpture of the clypeal integument is smooth and polished. The clypeus has diffuse red lateral markings in

most specimens and additional small brown lateral markings in others. It can be divided by an ill-defined **anteclypeus**, which is a comparatively less-sclerotized, narrow area along the apical margin, and the **postclypeus** (fig. 3B). This dorsal part of the clypeus bears setae and coloration, which are not present on the anteclypeus. In dissected and stained specimens, the anteclypeus appears as a membranous area. There are six (three on each side) thick prominent pale setae apically on the postclypeus, in a row parallel to the apical clypeal margin (in a few specimens there are four or eight setae). The general shape of the clypeus varies little within Chrysopidae, but the coloration can vary from unmarked to entirely red or brown and a different number of setae may be present on the apical margin of the postclypeus.





**Figure 93.** *Chrysopa oculata*, head appendages, line drawings. A. Antenna, ventral view. B: Labrum, dorsal view. C: Mandibles, blue arrows indicating articulation points, gray setae on ventral side of mandible, dorsal view. D: Labium, ventral view, gray setae on dorsal side. E: Right maxilla, ventral view.

## Labrum

The visible part of the **labrum** is slightly narrower than the clypeus and about four to five times shorter than wide (figs. 3A, B). Its apical margin is medially concave, leading to a wide and rounded W-shape (fig. 5B). The surface sculpture of the integument is smooth and polished and there are no markings. The apical margin bears a row of thick pale setae which insert subapically, and are parallel to the apical labral margin amongst shorter, thinner setae. These thick setae vary in number, but usually there are four or five present on each side. The shape of the labrum is consistent within Chrysopidae, varying mainly in the depth of the medial concavity (which can also be influenced by the age of the individual, and due to wear on the mouthparts).

## Mandible

The **mandible** has two points of articulation with the gena (figs. 4C, 5C, see blue arrows). In *C. oculata* the mandibles are broad and asymmetrical, meaning that each has a similar size and both are pointed with a single tip, but one (left side) bears the **mandibular tooth** basally (fig. 5C). The outer margin is slightly convex and enforced by a grade on the ventral surface, while the inner margin is strongly concave, with two sharp edges. Along the inner base of the sclerotized part of the mandible is a small elongate patch of about 30 short setae. From the outer anterior articulation to the tip, the mandible is about three times as long as wide. Mandibles of Chrysopidae can vary in dimensions (especially width), and whether they are symmetrical (tooth present or absent on both mandibles) to asymmetrical (tooth only present on one mandible).

## Maxilla

The labium and maxilla are the most complex components of the mouthparts, positioned ventrally, and each consists of several parts. The **maxillae** are paired structures and not fused medially as is the labium. Each maxilla is composed of five podites: cardo, stipes, lacinia, galea, and maxillary palpus (fig. 5D). The **cardo** articulates with the postgena. It is about as long as broad in *C. oculata* and gives rise to the stipes. The **stipes** is about twice as long as broad, comparatively flat in lateral view, has a few long setae subbasally, and bears the palpus, the lacinia, and the galea. The **maxillary palpus** is connected to the stipes by the palpifer, a slightly exerted and rounded structure of the stipes. There are five palpomeres in all chrysopids. Palpomere I is about as long as wide, and broader than all other palpomeres. Palpomere II is short as well, being only slightly longer than wide. Palpomeres III–V are at least three times as long as broad, and palpomere V tapers apically in lateral view, but is rounded and slightly truncate in dorsal or ventral view. Each palpomere bears sparse short setae, which sit on minute expansions of the integument. The galea and lacina are attached to the stipes apically. The **galea** is the external process of these two and originates from the apical-most point of the stipes. It is rounded apicolaterally, but has a small, but prominent rounded palpilla, and it bears numerous fine setae. The interior surface is concavely rounded to accommodate the exterior surface of the lacinia. The **lacinia** is the interior-most structure of the maxilla and is sickle-shaped apically. Its exterior surface is convex, strongly sclerotized, and runs along the concave interior of the galea. It has a large field of fine dense setae that point towards the interior surface, with some long setae at the base of the field and a thicker brush-like area at the apical-most point of the lacinia. The maxilla mainly varies in its coloration among Chrysopidae.

## Labium

The medially fused **labium** is the posterior-most mouthpart appendage, of which only the palpus is paired (fig. 5E). It is divided in four main parts: mentum, prementum, ligula, and palpus. The labium is homologous to the second maxillae of Crustacea, and the various components are serially homologous to the sclerites of the maxilla. Thus, the paired primary components of the maxilla have fused equivalents in the labium: mentum = cardo, prementum = stipes, ligula (= fused glossa and paraglossae) = galea and lacinia, and the palpi. The **mentum**, is long and flat, rounded-rectangular shaped in ventral view, and can be easily mistaken as a part of the ventral head integument (fig. 4A). Posteriorly it borders portions of the cervix, and laterally the postgena and the cardo of the maxilla in ventral view. The **prementum** is apically connected to the ligula, and apically bilobed, opening towards the apex where each lobe forms a palpifer bearing a palpus. The **labial palpus** consists of three palpomeres, as in all other Chrysopidae, and its general shape does not vary much within the family. Palpomere I inserts on the prementum to an ovate palpifer and is only slightly longer than broad. Palpomere II is about twice as long as broad and wider towards its apex. It bears a row of thick setae apically on the ventral surface. Palpomere III is the longest of the three labial palpomeres and, as is the case for maxillary palpomere V, is dorsoventrally flattened and slightly truncate apically. The three palpomeres are connected by membranous articulations. Palpomere III has a dorsolateral ovate impression subbasally (palpimaculata), which is present in most Neuroptera and could be associated with a sensory function (New 1989). There are small setae present on minute expansions of the integument throughout the palpus. The **ligula** is a rounded non-paired lobe, resulting from fusion of the glossa (medial) and paraglossae (lateral), and which bears numerous fine and small setae along its apical margin and some thicker setae on the ventral surface. It is basally connected to the apical margin of the prementum.

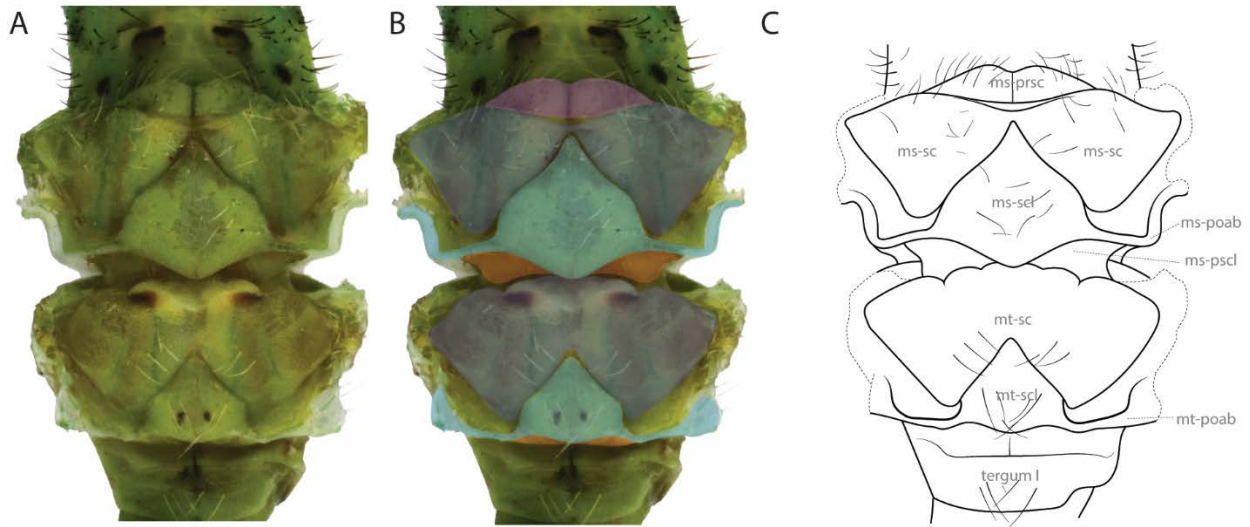
## Eyes

The **compound eyes** are large and round, reaching about half the length of the head in frontal view (fig. 3A). A single compound eye is about half as wide as the frons in frontal view. They are iridescent in living individuals and turn dark brown when fixed. *Chrysopa oculata*, as all green lacewings and most Neuroptera, do not have ocelli, instead their vertex is smooth without traces of ocellar structures (in some other members of Neuroptera, such as Dilaridae and Osmylidae, there are raised tubercles and ocelli or ocellar-like structures; Coniopterygidae were once believed to have ocelli but instead have a raised, dome-like structure on the vertex (New 1989)).

## Thorax

The thorax of most Neuroptera varies little in its general composition and as such the traits present in *C. oculata* can be simply adopted for other Chrysopidae. The thorax consists of three segments – prothorax, mesothorax, and metathorax – and each segment has its set of respective appendages (figs. 6–12). Each has a pair of legs (fore-, mid, and hind legs), while the pterothoracic segments (meso- and metathorax) have a pair of wings (fore and hind wing). Whereas the prothorax is rather simple in its elements, both meso- and metathorax are more complicated, with multiple elements in their dorsal, pleural, and ventral elements (as a result of the presence of the wings and associated muscles) rendering the identification of sclerites more complicated. The generalized set of structures of the meso- and metathorax is as follows: the notum consists of prescutum, scutum, and scutellum, and the pleuron consists of episternum and epimeron, which can be divided into the dorsal anepisternum/anepimeron and the ventral katepisternum/katepimeron. The coxa is strongly integrated with the thorax, and the meron can seem incorporated into the epimeron in dissections. The whole thorax is covered in dense pale

micropilosity and scattered long setae are present, which are pale except for numerous dark setae on the dorsal prothorax. The general shape of the thoracic sclerites does not vary within Chrysopidae, but the coloration and setation can vary strongly.

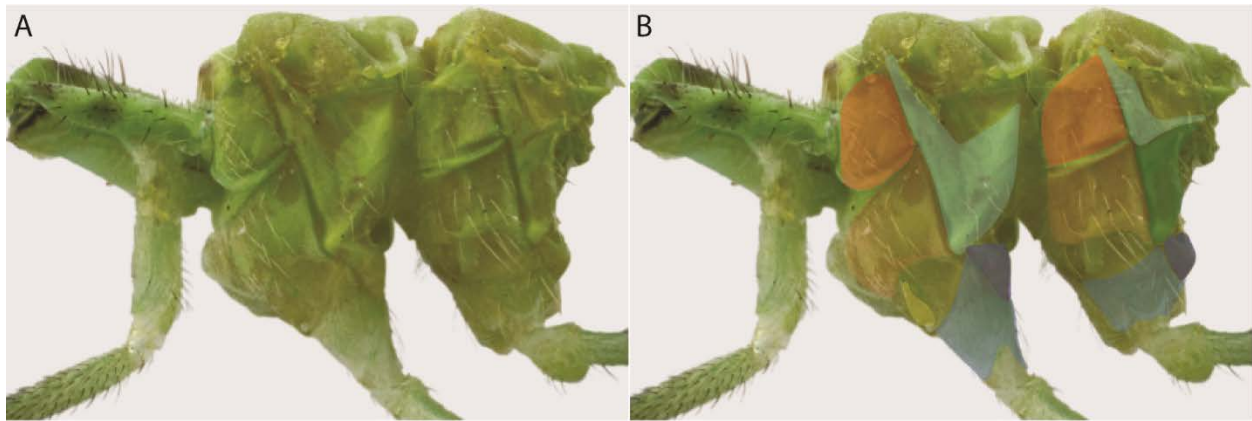


**Figure 94.** *Chrysopa oculata*, thorax, dorsal view. A. Photomicrograph. B Photomicrograph with sclerites indicated by color; pink: prescutum; dark blue: scutum; light blue: scutellum; orange: postscutellum. C: Line drawing; ms-poab: mesonotal postalar bridge; ms-prsc: mesoprescutum; ms-pscl: mesopostscutellum; ms-sc: mesoscutum; ms-scl: mesoscutellum; mt-poab: metanotal postalar bridge; mt-prsc: metaprescutum; mt-pscl: metapostscutellum; mt-sc: metascutum; mt-scl: metascutellum.

## Thoracic body

The **prothorax** has a single dorsal element – the pronotum – which covers that “segment” completely and extends slightly ventral, covering the sides partially (figs. 7-8). The pronotum of *C. oculata* is marked with three small brown spots on each side (varying in size between specimens). It bears numerous thick dark setae, which are more abundant laterally, and some scatters thinner clear setae amidst fine micropilosity. It is about as long as wide, the lateral margins are straight and the frontal margin is tapering towards the anterior, but truncate medially. The Prothorax is connected to the head through the cervix and the dorsal cervical sclerite extends in pointed edges, abutting the vertex, which are pale at the apex and marked with a small brown spot

at the junction with the pronotum (figs. 3C, D). The propleuron is a single, mostly membranous structure and not separated into different sclerites as in meso- and metathorax. The prosternum is unmarked and covered in micropilosity and scarce long clear setae. The most prominent structure on the pronotum is the procoxa, which is the first part of the foreleg. Different as in the meso- and metathorax, the coxa inserts simply in the propleuron, and is not surrounded by specific sclerites. The spiracle, which is a small round opening of a trachea and has a respiratory function, is positioned in the membranous area between pro- and mesothorax.



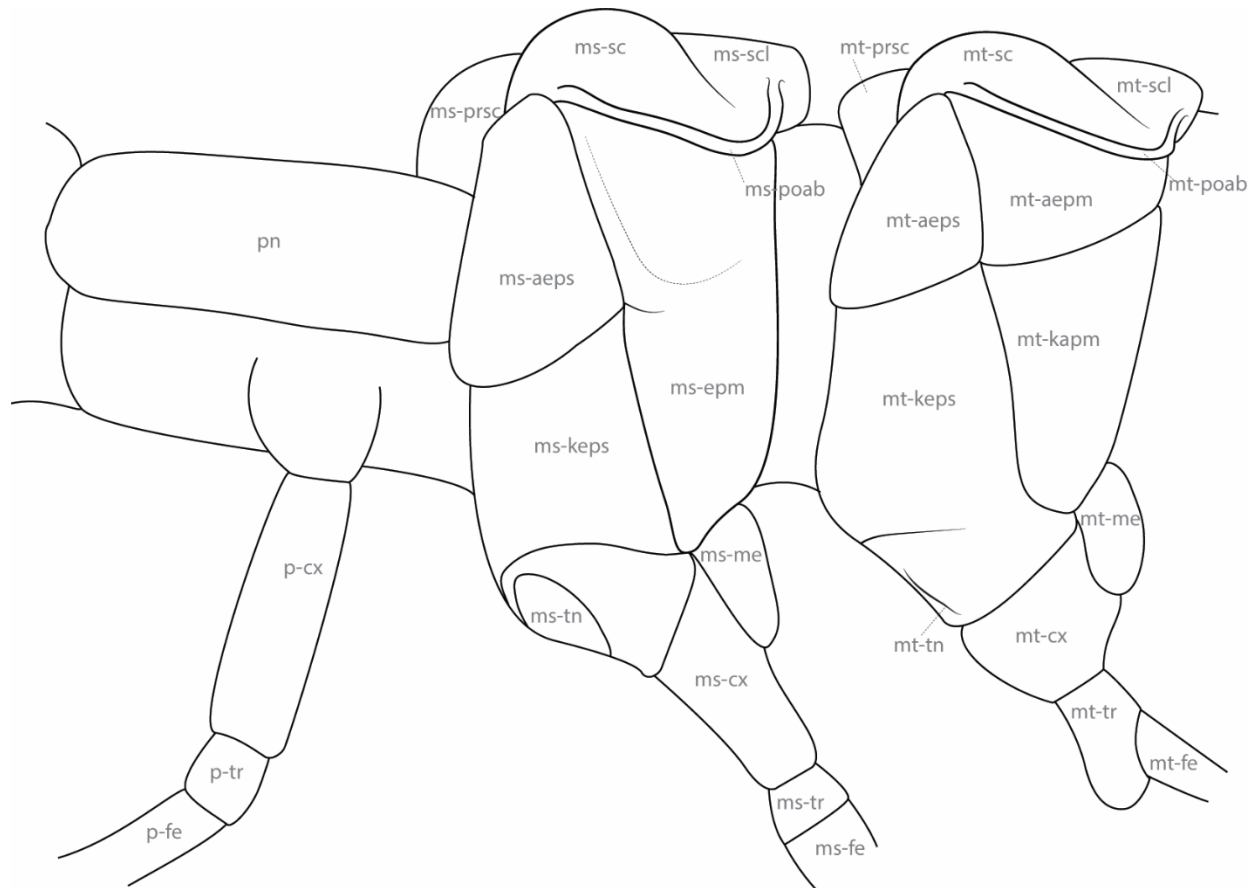
**Figure 95.** *Chrysopa oculata*, thorax, with fore- and hind wing removed, lateral view. A. Photomicrograph. B Photomicrograph with sclerites indicated by color; dark orange: anepisternum; light orange: katepisternum; yellow: trochantin; light green: epimeron/anepimeron; dark green: katepimeron; dark blue: meron; light blue: coxa. C: Line drawing.

The **Mesonotum** is the largest part of the dorsal thorax (fig. 6). It is divided in mesoprescutum (ms-psc), mesoscutum (ms-sc) and mesoscutellum (ms-scl). The **mesoprescutum** overlaps the pronotum slightly in dorsal view with the rounded anterior mesoscutal lobe, and has an anterior medial impression, leading to the deep medial mesoprescutellar suture that divides the two sides. It is unmarked and bears multiple long pale setae which are pointing towards anterior. The mesoscutal furrow is prominent, especially due to the inflated mesoscutum. Each side of the **mesoscutum** has a slightly rounded anterior margin and the two sides have a narrow connection medially. The lateral margin is slightly expanded towards the wing base, where it loosely connects with the anterior margin of the forewing, and its posterior margin is tapering towards the apex. This apical tapering on each side results in a deep W-shape of the entire posterior margin of the mesoscutum. The interio-posterior margin is formed by the mesoscuto-mesoscutellar suture, which borders the mesoscutellum. The mesoscutum is unmarked and bears long pale setae on the anterior half. The **mesoscutellum** is roughly diamond shaped, expanding medioanteriorly, reaching the narrow connection between the two mesoscutum sides, and medioposteriorly, where it slightly overlaps the metascutum in dorsal view. Its lateral expansions form connections to the posterior margin of the forewing (**mesonotal postalar bridge** (ms-poab)). The postalar bridge is extended straight laterally and bent anteriorly towards the wing base in a 90° angle. There are few long pale setae present medially on the mesoscutellum. The mesopostnotum is inconspicuous and only laterally visible in dorsal view. The **mesopleuron** has three most prominent parts (figs. 7, 8): the mesoanepisternum (ms-aeps), mesokatepisternum (ms-keps) (combined to mesoepisternum (ms-eps)) and the mesoepimeron (ms-epm), which dominate the small mesopreepisternum (ms-peps),

and mesotrochantin (ms-tn). The two episternal parts are separated from the singular epimeron by the long, oblique angled, deep mesopleural sulcus (ms-plS). It runs from the pleural wing process (PWP) to the coxa. Where the mesoanepisternum and mesokatepisternum meet the mesopleural sulcus there is a small bridge like structure connecting mesoepisternum and mesoepimeron over the suture. The **mesoanepisternum** is bordering the pronotum anteriorly, the mesoprescutum, the mesoscutum and the wing base dorsally, the mesoepimeron posteriorly and the mesokatepisternum ventrally. Mesoanepisternum and mesokatepisternum are separated by the mesonotal transepisternal suture (ms-tesS), which arises from the mesopleural sulcus in an angle that is slightly more than 90 in the mesoanepisternum and about 60 in the mesokatepisternum. The **mesokatepisternum** borders the mesoepimeron posteriorly, the ms-st anterioventrally and the mesotrochantin and mesocoxa ventrally. It extends ventrally along the lateral margin of the mesopreepisternum, enveloping the mesotrochantin and mesocoxa. It meets the most ventral point of the mesopleural sulcus in a small extension, together with a dorsal extension of the mesocoxa, an anterior extension of the mesomeron and a ventral extension of the mesoepimeron, forming a small bulge. The **mesoepimeron** is as wide as the wing base and its ventral most extension meets the dorsal margin of the mesocoxa at the mesopleural sulcus. The posterior margin is curved from the wing base (at the mesonotal post alar bridge) to the mesocoxa, and borders the dorsal margin of the mesomeron. The mesoepimeron is broadly V shaped, but the margin between the sclerite and the membranous integument below the wing base is not prominent. There is no mesonotal transepimeral suture that defines a dorsal and ventral mesoepimeron as in the metanotum. The **mesotrochantin**, which is positioned between mesokatepisternum and the mesocoxa, and is barely visible, and can only be detected in a dissected specimen. It is narrowly ovate and has a small articulation with the mesocoxa. The mesokatepisternum is narrowly extended ventrally, and the



membranous part around the mesotrochantin separates it from the mesocoxa, so that these two structures are not meeting. The spiracle is positioned in the dorsolateral membranous area between meso- and metathorax.



**Figure 96.** *Chrysopa oculata*, thorax, lateral view, simplified schematic line drawing; p-cx: procoxa; p-fe: profemur; pn: pronotum; p-tr: protrochanter; ms-aeps: mesoanepisternum; ms-cx: mesocoxa; ms-epm: mesoepimeron; ms-fe: mesofemur; ms-keps: mesokatepisternum; ms-me: mesomeron; ms-poab: mesonotal postalar bridge; ms-prsc: mesoprescutum; ms-sc: mesoscutum; ms-scl: mesoscutellum; ms-tn: mesotrochantin; ms-tr: mesotrochanter; mt-aepm: metaanepimeron; mt-aeps: metaanepisternum; mt-cx: metacoxa; mt-fe: metafemur; mt-kepm: metakatepimeron; mt-keps: metakatepisternum; mt-me: metameron; mt-poab: metanotal postalar bridge; mt-prsc: metaprescutum; mt-sc: metascutum; mt-scl: metascutellum; mt-tn: metatrochantin; mt-tr: metatrochanter.

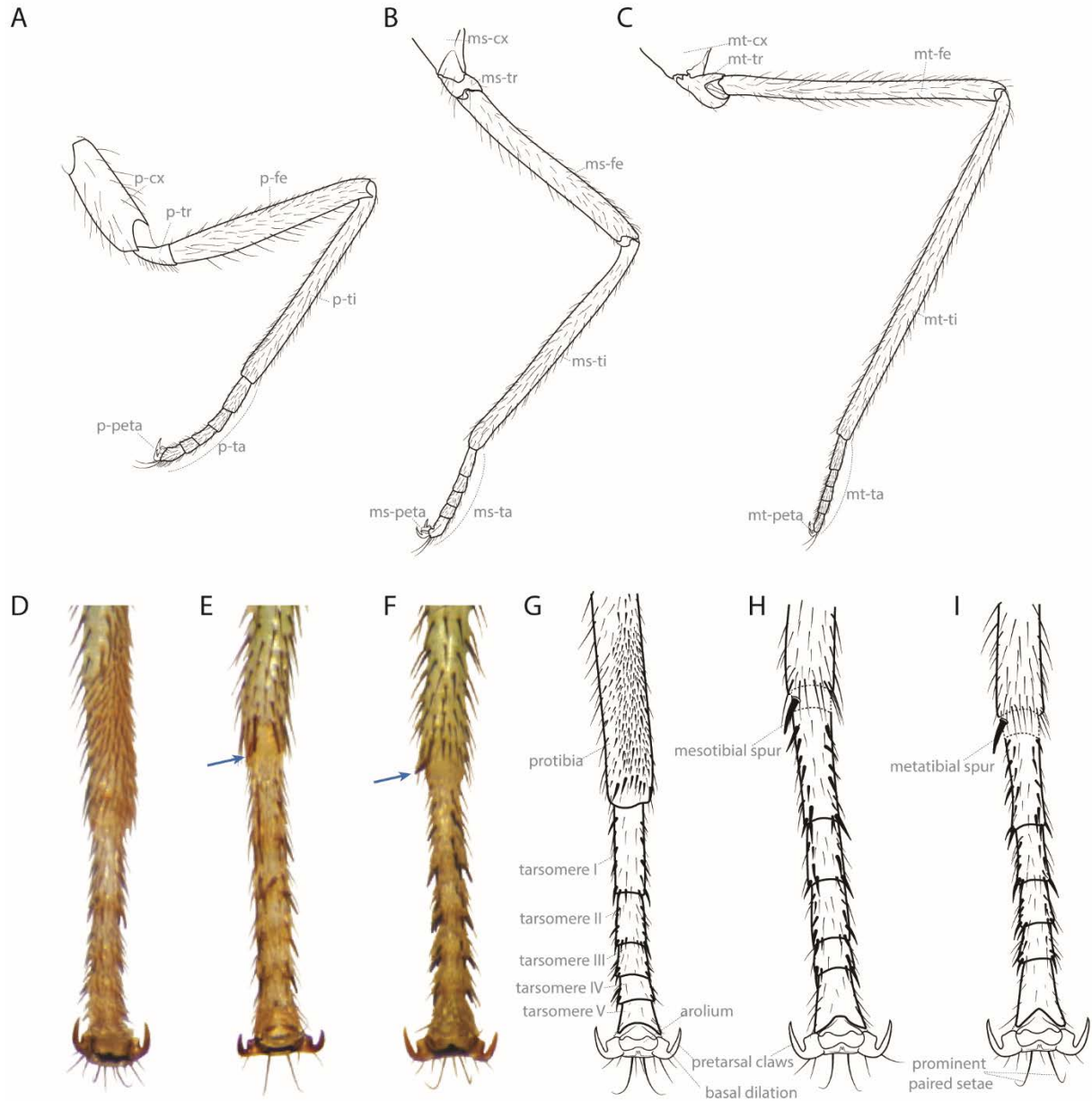
The **Metanotum** is similar to the mesanotum, but does not have a defined prescutellum (fig. 6). The **metascutum** (mt-sc) is anteriorly expanded in three shallow lobes. The medial lobe is inconspicuous and mostly hidden by the overlapping mesoscutellum. The lobe of each side bears

a prominent field of dense, fine microsetae and is marked with a brown spot. This velvety patch of microsetae is associated with the folding of the wings over the body, through a corresponding field of microsetae between the third anal vein and the posterior wing margin of the forewing. They are present in all Neuroptera and have been speculated to be part of a stridulatory system, but are most likely only a locking device (Eichele and Villiger 1974, Henry 1980, New 1989). The anterior margin of the metascutum tapers towards posteriolateral where it meets the wing base. The posterior margin of the entire metascutum is W-shaped, medially divided by the anterior margin of the metascutellum and the posterior lobes are pointed apically. There are very few long pale setae present medially. The **metascutellum** (mt-scl) is shaped like the mesoscutellum except for the posterior margin, which is less expanded towards posterior. It bears a small submedial brown marking and very few long pale setae. The metanotal post alar bridge (mt-poab) is less angled than in the mesonotum. The metapostnotum is small and inconspicuous. The **Metapleuron** is very similar to the mesopleuron, and differs to the latter especially in regards to the epimeron (figs. 7, 8). The **metaepimeron** is divided in a dorsal and ventral part by the metanotal transepimeral suture (mt-temS). The **metaanepimeron** (mt-aepm) is slightly shorter but broader than the **metakatepimeron** (mt-kepm), and forms a triangle between wing base, the metapleural suture (mt-plS), and the metanotal transepimeral suture. As in the mesonotum, mt-aepm and metaanepisternum are connected by a small bridge like structure that stretches over the metapleural sulcus. The metaepisternum is divided into **metaanepisternum** (mt-aeps) and **metakatepisternum** (mt-keps), as in the mesonotum, and shaped very similarly. The metatrochantin is smaller than the mesotrochantin, as is the membranous area surrounding it. The dorsal margin of the metacoxa is less pointed than the mesocoxa. There is a spiracle in the

membranous area between the metanotum and tergum I, positioned posterior-ventrally of the metanotal post alar bridge in lateral view.

## Legs

Like all insects, Chrysopidae have a set of prothoracic, mesothoracic, and metathoracic legs, each with six podites (fig. 9): coxa (cx), trochanter (tr), femur (fe), tibia (ti), tarsus (ta), and pretarsus (peta). Apart from coloration, the legs of Chrysopidae vary little, and few characteristics are of taxonomic value. They are usually elongate, the setae can be short and dark to long and pale, the pretarsal claws can be dilated or simple, and the metacoxa is always inflated ventrally. A few taxa have a stridulatory structure on the metafemur, which is associated with ridges on sternum II, sternum III, or the pleural membrane in that region (e.g., *Brinckochrysa* Tjeder, *Meleoma*, *Chrysocerca* Weele) (New 1989, Brooks and Barnard 1990). Whereas other Neuroptera have irregular setae apically on tarsomere V, most Chrysopidae have two or four long medial setae. The number of setae seems to be distinctive for higher taxa, and as such, they are absent in Nothochrysinæ, two setae are present in most Chrysopinæ, and four setae are present in most apochrysinæ, *Nothancylla*, and the enigmatic chrysopine genus *Kostka* Navás. Additionally, the presence and number of spurs at the apex of the pro-, meso-, and metatibiae are distinctive among higher taxonomic groups across the family. Most Chrysopinæ have no spurs on the protibia, and one on each on the meso- and metatibiae, except for a clade including *Parachrysopiella*, *Eremochrysa*, *Chrysemosa* Brooks and Barnard, and *Suarius* Navás, which have one or multiple spurs on the protibia and multiple spurs on both meso- and metatibiae. Apochrysinæ lack tibial spurs on all legs and the number per leg varies in Nothochrysinæ, with all states present from lacking spurs to multiple spurs on each leg, and the “1-2-2” state in *Nothochrysa* McLachlan, which is otherwise typical for Chrysopinæ.



**Figure 97.** *Chrysopa oculata*, legs. A–C: Photomicrographs, latero-frontal view. D–E: Tarsus, photomicrographs, ventral view. G–H: Tarsus, line drawings, ventral view. A, D, G: Prothoracic leg. B, E, F: Mesothoracic leg. C, F, I: Metathoracic leg. Blue arrows indicate tibial spur; ms-cx: mesocoxa; ms-fe: mesofemur; ms-peta: mesopretarsus; ms-ta: mesotarsus; ms-ti: mesotibia; ms-tr: mesotrochanter; mt-cx: metacoxa; mt-fe: metafemur; mt-peta: metapretarsus; mt-ta: metatarsus; mt-ti: metatibia; mt-tr: metatrochanter; p-cx: procoxa; p-fe: profemur; p-peta: propretarsus; p-ta: protarsus; p-ti: protibia; p-tr: protrochanter.

The **prothoracic leg** (figs. 9A, D, G) is entirely unmarked and inserts lateroventrally on the prothorax where the coxa articulates with the propleuron (fig. 7C). The **procoxa** (p-cx) is

thinner than the meso- and metacoxae, about twice as long as broad. The **protrochanter** (p-tr) is cylindrical and about as long as wide. **Profemur** (p-fe) and **protibia** (p-ti) are both thin and long, with the latter being only slightly longer and the former being slightly thicker. The setae on the profemur and protibia are dark and slightly longer on the profemur, especially basally. At the articulation of these two podites, the profemur bears two small lateral extensions, that overlap the base of the protibia, which has a small medial expansion towards the profemur. The protibia has a dense field of short, comparatively pale setae apically on the inner surface (figs. 9D, G), which is common in other insects and associated with the cleaning of the head and antenna. There is no tibial spur on the protibia of *C. oculata*, which is the most common state in Chrysopidae. Instead there are several thick setae present at the apical margin of the protibia. The **protarsus** (p-ta) is divided into five tarsomeres (the generally plesiomorphic condition for the insectan tarsus), of which the basal-most tarsomere (= basitarsus) is the longest. Each **tarsomere** has several thick setae lateroventrally, forming two longitudinal rows along the protarsus. Tarsomere V (= distitarsus) bears long, thin setae dorsally, including two prominent long setae, which insert submedially and reach far beyond the apex of the fifth tarsomere and the pretarsal claws. The **pretarsus** (peta) consists of the unguitactor plate (which is operated by muscles originating in the tibia and inserting on an elongate internal apodeme or “tendon” arising from the base of the unguitactor plate), which articulates basally to the apex of the distitarsus; the paired ungues (= claws); and the arolium. The **arolium** is positioned between the pretarsal claws, dorsally sclerotized, and the aroliar pad is inflated in living individuals. The pretarsal claws are strongly dilated, which is common in green lacewings, but simple, non-dilated pretarsal claws can also be found in many groups. Whether the pretarsal claw is dilated or simple can vary even within a genus, but not among individuals within a species.

The **mesothoracic leg** (figs. 9 B, E, H) differs from the prothoracic leg, in the following: The **mesocoxa** (ms-cx) is longer than the procoxa, and has a dorsal expansion, which meets the mesopleural sulcus (fig. 7C). It is clearly separated into coxa and meron, which is not evident in the procoxa. Many Neuroptera have a distinct meron on the meso- and metathoracic appendages, which, especially in living individuals, can be seen as a prominent sclerite but otherwise can be slightly crumpled when dried. The **mesomeron** (ms-me) is ovate with the dorsal margin slightly expanding towards the anterior and there meeting the ventral extension of the mesokatepisternum. Its anterior and ventral margin is bordered by the dorso-lateral margin of the mesocoxa. The articulation between mesocoxa and mesotrochanter as well as between mesotrochanter and mesofemur is more heavily sclerotized than in the same points of articulation in the foreleg. The mesocoxa is roughly diamond shape in lateral view, with its dorsal margin expanding towards the ventral extension of the mesoepimeron. Anteriorly it is adjacent to the mesotrochantin and the membranous area between mesokatepisternum and mesocoxa. The distal margin is slightly bilobed anteriorly, articulating with the mesotrochanter and there is a large and rounded membranous triangular area dorsad that articulation. The **mesotrochanter** (ms-tr) is small and invaginated, leading to a V-shaped dorsal basal margin. The distal margin has a less pronounced invagination and articulates with the mesofemur. While the metatrochanter is strongly inflated ventrally, the mesotrochanter is unmodified. There is no dense patch of short setae apically on the **mesotibia** (ms-ti), instead it is uniformly covered in long dark setae. The mesotibia has a single spur apically on the ventral surface, which is the predominant state in Chrysopinae.

The **metathoracic leg** (figs. 9C, F, I) is shaped similar to the mesothoracic leg, except for the following: The **metacoxa** (mt-cx) is shorter than the mesocoxa, but about as broad. The articulation of coxa and trochanter are similar between the meso- and metathorax, but the

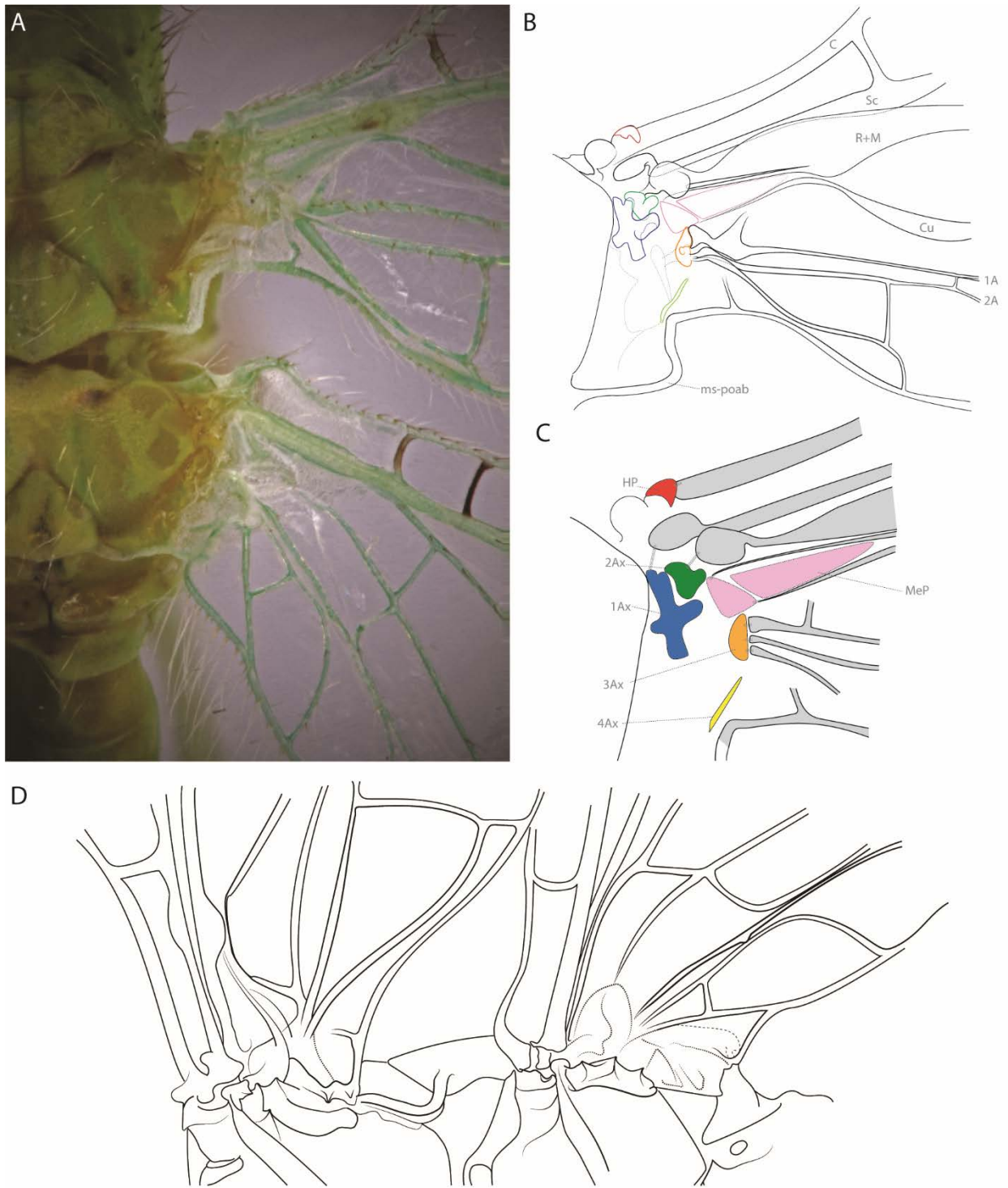
metafemur and metatrochanter have a more complex articulation. The **metatrochanter** (mt-tr) has a larger membranous area and a small elongate sclerotized structure within this membrane, which is basally connected to the metatrochanter and apically articulating with the metafemur. The metatrochanter is inflated towards its apex, especially on ventrally, leading to a lopsided-pear shape in lateral view.

## Wings

The **wing base** (fig. 10) is complex and due to many fusions and losses it is difficult to decipher the identity of each structure. Neoptera developed a folding mechanism that allows them to fold their wings backwards along and over the posterior thorax and abdomen. The combination of this mechanism and the need for functionality and strength for flying lead to an elaborate complex of axillary sclerites that are situated in the membrane at the articulation of the wing with the thorax, and around the notal and pleural wing processes. All winged insects have two axillary sclerites plesiomorphically, and there is an additional third sclerite and a medial plate in Neoptera (Comstock 1918, Matsumuda 1970, Grimaldi and Engel 2005). Each sclerite in the wing base is associated with a specific longitudinal vein of the wing. In the generalized insect wing the **humeral plate** (HP) is associated with the costa (C), the **first axillary sclerite** (1Ax) with the subcosta (Sc), the **second axillary sclerite** (2Ax) with the radius (R), the **medial plate** (MeP) with the media (M) and cubitus (Cu), and the **third axillary sclerite** (3Ax) with the anal veins. These sclerites have been strongly modified in derived insect groups, and sclerotizations of the vein bases often obscure the identification of the axillary sclerites. Neuropterida have a relatively broad 1Ax, ventral to which the pleural wing process (PWP) sits, their 2Ax is normally small and triangular, 3Ax is often fragmented in multiple small parts, and some of these can be reduced, and they have a small elongate additional sclerite between 3Ax and the posterior notal process (PNP), which is

the **fourth axillary sclerite** (4Ax) (Hörnschemeyer 1998, 2002, Zhao et al. 2014). The wing base of the two wings are similar but not identical (fig. 10A). The sclerotized bases of Sc and R are quite elaborate in the hind wing and render the identification of the shapes and exact position of 1Ax and 2Ax complicated.



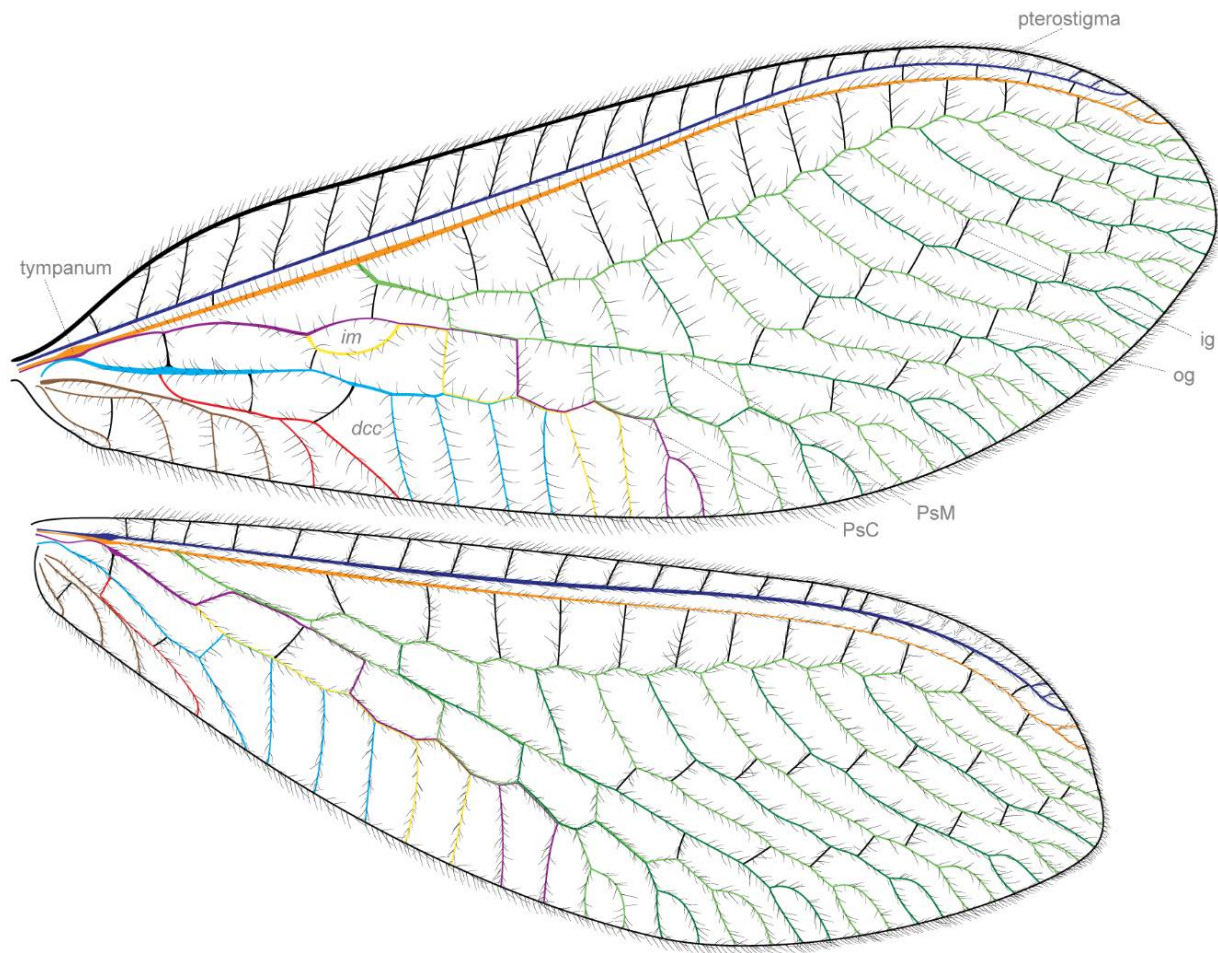


**Figure 98.** *Chrysopa oculata*, wingbase. A. Photomicrograph, meso- and metanotum, and wing base of fore- and hind wing, dorsal view. B: Line drawing of forewing base, dorsal view. C: Simplified schematic line drawing of forewing base, dorsal view. D: Line drawing of upper meso- and metapleuron, and wing base of fore- and hind wing, ventro-lateral view. 1A: first anal vein; 2A: second anal vein; 3A: third anal vein; 1Ax: first axillary sclerite (blue); 2Ax: second axillary sclerite (green); 3Ax: third axillary sclerite

(orange); 4Ax: fourth axillary sclerite (yellow); C: costa; Cu: Cubitus; HP: humeral plate; M: media; MeP: medial plate; ms-poab: mesonotal postalar bridge; R: radius; Sc: subcosta.

The paths of the veins can be determined with the help of the paths of the tracheae. The chrysopid wing is characterized by the formation of **pseudoveins**, in which several longitudinal and (less frequently) crossveins fuse to form an apparent single vein (fig. 11). In the forewing, the **pseudomedia** (PsM) is formed by abscissae of RP branches, MA, MP, and some crossveins, and the **pseudocubitus** (PsC) is formed by abscissae of RP branches, MA, MP, and CuA. In the hind wing MA is not involved in PsM, but instead the main vein of RP. A more detailed comparison of the venation in the three subfamilies, a discussion of differences between actual and apparent wing venation, as well as a discussion of the homologies of the veins is provided in chapter 4. The present chapter will only discuss the wing venation of *C. oculata* and direct the reader to chapters two and four for a comprehensive discussion of the great variety in the wing venation of Chrysopidae.

The wings of *C. oculata* are typical for Chrysopinae, with a wing venation and general shape that can be found in the majority of species. The veins are predominantly light green, with some dark brown crossveins or apparent crossveins, especially in the basal half of the wing. The formation of pseudoveins, the shape of the intermediate cell (*im* or *mamp1*) and the numbers of crossveins that form the inner and outer gradates in fore- and hind wings are the most common states in Chrysopidae. Even more so than in the forewing, there is very little variation in the venation patterns of the hind wing.



**Figure 99.** *Chrysopa oculata*, fore- and hind wing, line drawing, venation based on tracheation pattern; *dcc*: distal cubital cell; *ig*: inner gradates; *im*: intermediate cell; *og*: outer gradates; *PsC*: pseudocubitus; *PsM*: pseudomedia; dark blue: subcosta (*Sc*); orange: radius anterior (*RA*); green: radius posterior (*RP*); violet: media anterior (*MA*); yellow: media posterior (*MP*); light blue: cubitus anterior (*CuP*); red: cubitus posterior (*CuP*); brown: anal veins (*A*).

## Forewing

As most chrysopids, *C. oculata* has slightly elongate and rounded forewings, with a basal third that is significantly thinner than the apical third (figs. 1, 11). The thickness of the veins varies on the wing, with some areas in the basal third of the wing enlarged (e.g., tympanal organ, *CuA*). The coloration of the wing integument is minimal in *C. oculata*, with possible sparse spotting close to the vein junctions. There is a constant pattern of long setae along the veins and the wing margin on the entire wing.

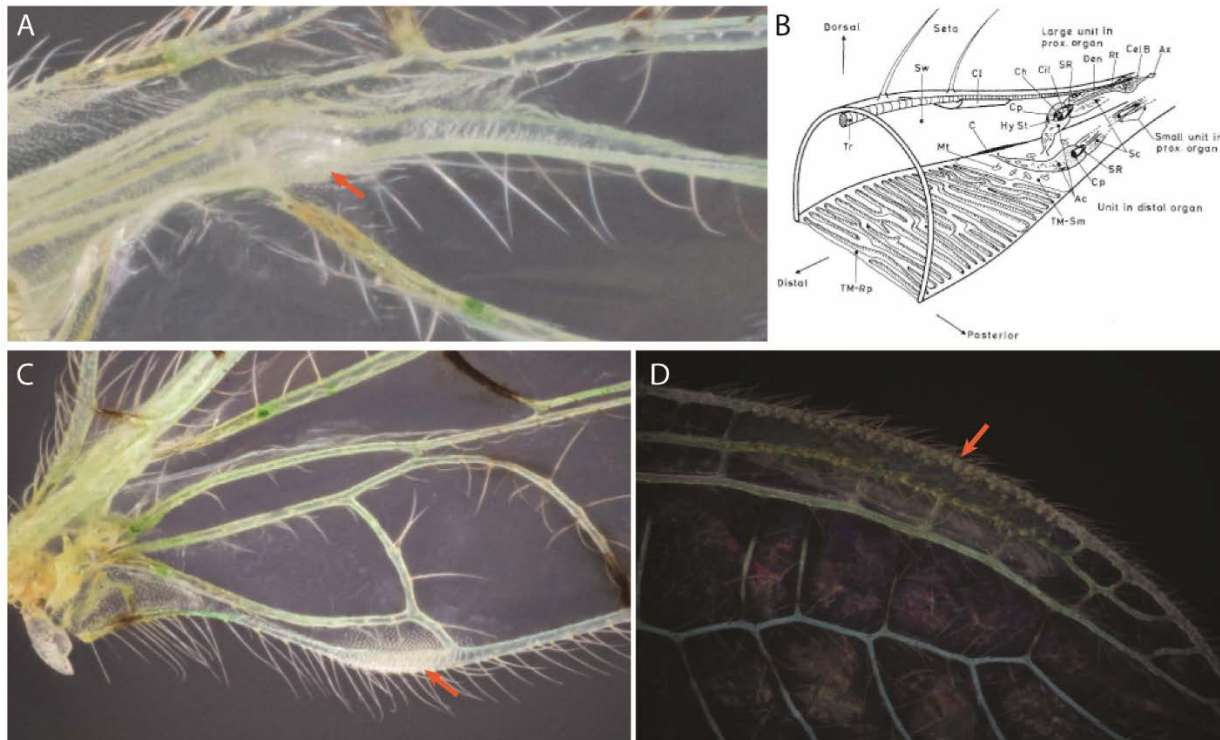
The **costa** is clearly recognizable in the basal half of the wing and thinning out in the apical half, but bears setae along the whole wing margin. **Subcosta** and radius (or anterior radius) are parallel, and fairly straight for most of the wing span. There are around 20–25 crossveins between the costa and subcosta proximal to the pterostigma, which are all straight and not subdivided. The **pterostigma** is unmarked and the crossveins are fading, but the setae remain (fig. 12D). The subcosta has two to four terminal twigs. The first crossvein between subcosta and radius (1sc-r or bsx) is present basally on the wing, which is a synapomorphy for all Chrysopinae and Nothochrysinæ, except reversed in *Nothancyla*. In *C. oculata* there are three to four c-sc present basal to 1sc-r. At the level of the pterostigma, there are four or five additional sc-r crossveins. The **radius** is sub-basally fused with the media and enlarged to form the tympanal organ. This organ is present in all Chrysopinae, has been associated with the detection of ultrasonic sound (Miller and McLeod 1966), likely of bat echolocation (Miller 1984), and was studied in detail for *Chrysoperla carnea* Stephens by Miller (1970). It is formed by the inflated radius and the ventrally fused media. It contains two chordotonal organs with scoloporous sensilla, a large hollow space, a rippled ventral membrane of the vein, and the trachea of R and M (Erhardt 1916, Miller 1970, 1984) (fig. 12B). A detailed study of the tympanum of *C. oculata* has not been conducted and it is assumed that its structure is similar to that described by Miller (1970) for *C. carnea*. Although it has not been studied in detail, the tympanum is easy to identify in all Chrysopinae due to the swelling of R and the rippled membrane (fig. 12A). Posterior to the tympanal organ the radius is split into the **radius anterior** (RA) and **radius posterior** (RP). The anterior radius (RA) is fairly straight and simply terminates in three to four twigs, but the posterior radius (RP), which splits off RA in the anterior third of the wing, has numerous long branches and crossveins between them. As such, RP dominates most of the apical two-thirds of the wing. In most specimens it has 12

branches ( $\pm 1$ ), of which the basal four are part of the fused pseudoveins. The crossveins between RA and RP are straight and, as in most Chrysopidae, there is no crossvein present basal to the origin of the basal-most RP branch. Most RP branches have forked terminals. Apical to the pseudoveins there are two rows of crossveins between the individual RP branches, which form the **inner** and **outer gradates**. In *C. oculata* the number of inner and outer gradate crossveins are about the same, with around eight in each row. The distance between inner and outer gradates increases gradually from apical to basal. PsM is continuous with the outer gradates, and the basal-most inner gradate meets this pseudovein, meaning that this crossvein connects the basal-most RP branch, which is not involved in PsM, with the apical-most RP branch, which is involved in PsM, after it joins PsM. This varies among Chrysopidae, with the basal inner gradate often not meeting PsM, but connecting the two RP branches. The only true crossvein, without tracheation, that originates on the main RP vein is 1rp-ma, and is positioned basal to the basal-most RP branch on RP, and within the *im* cell on MA. There are about eight “crossveins” between PsM and PsC in *C. oculata*, although the number can slightly vary due to the number of RP branches involved in PsM and PsC. The first two crossveins are actual crossveins, meaning that there are no tracheae running through the veins. They connect M and CuA (1m-cua), as well as MA and CuA (1ma-cua). The third apparent crossvein that connects PsM and PsC is actually MP, which leaves PsM to join PsC, the fourth is MA and the fifth to seventh are branches of RP. The last vein between PsM and PsC is a true crossvein, which is the case in most Chrysopidae, and can appear as a part of the outer gradates, depending on its orientation. The **media** joins R close to the wing base and is there part of the tympanal organ. Posterior to the tympanal organ and anterior to RP, M splits off R and forms the first part of the PsM. The basal abscissae are composed by M, which then splits into MA and MP, forming the intermediate cell (*im* or *mamp1*). In *C. oculata*, and most other Chrysopinae, MP

then rejoins MA on the PsM, leading to an ovate triangular shape of *im*. MA is fused with RP for the length of one abscissa on PsM and for the length of two abscissae on PsC. With MP it is fused for the length of one abscissa on PsM, right after MP rejoins MA and therefore closing the *im* cell, and on PsC for the length of four abscissae. It is fused with CuA for one abscissa on PsC. MP diverges from PsM directly basal to the origin of the basal-most RP branch. MA and MP always have two terminal twigs meeting the wing margin, but MA can terminate in a single fork or, like MP, in two individual veins, splitting off PsC. The **cubitus** arches basally towards the area of the tympanal organ, but does not meet the fused R and M. It splits into CuA and CuP, more basal on the wing relative to other sectors. The anterior and posterior branches split closely before the 1m-cua crossvein. CuP immediately arches toward the posterior wing apex, as it is prominent in Neuroptera, and terminates in two veins, which are split basally to 2cua-cup. CuA has four terminal veins meeting the wing margin in *C. oculata*, which is also the state for the vast majority of Chrysopidae. These four branches all originate on PsC and are never forked. CuA is partially fused with MA for three abscissae and with MP for one abscissa of PsC. There are two crossveins between CuA and CuP, which lead to the formation of the two cubital cells. These are about the same length in *C. oculata*, which is the case for most Chrysopinae, and especially Chrysopini. The distal cubital cell (dcc) is formed by the apical-most abscissa of CuP, the crossvein 2cua-cup, an abscissa of CuA, and the basal-most terminal of CuA, as well as the wing margin. The three **anal veins** are the posterior-most veins in the chrysopid wing, and not fused with veins of any other sector. Only 1A is forked apically, while 2A and 3A are simple, although both or neither can be forked in Apochrysininae or Nothochrysininae. There is a short crossvein between CuP and 1A (1cup-1a), which can seem as though these two longitudinal veins are fused at this point, and between 2A and 3A there is a long crossvein. The minutely expanded basal wing margin and 3A enclose a



field of dense microsetae (fig. 12C), where 3A meets the wing margin, which is present in all Neuroptera (New 1989). This field is associated with a patch of dense microsetation on the metascutum, where it serves as a locking mechanism to hold the wings abutted to the body (Henry 1980). A stridulatory function has been suggested (Riek 1967, New 1989, Eichele and Villiger 1974), but this hypothesis was not confirmed by tests for high frequency sound production in Chrysopidae (Henry 1980).



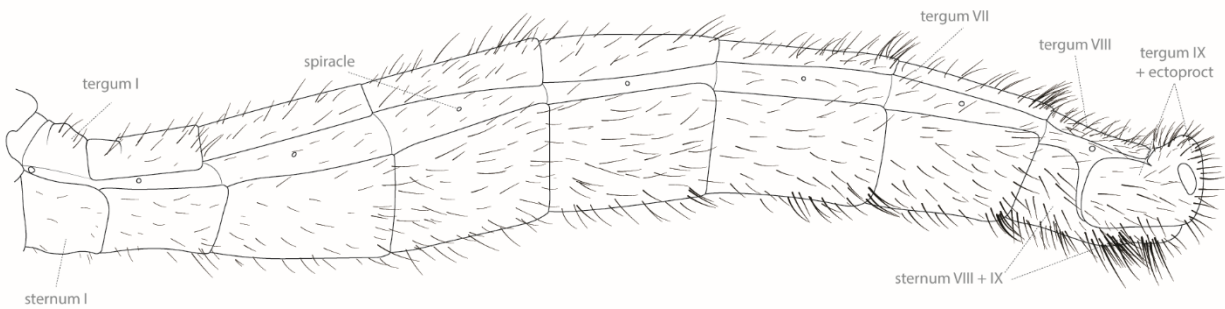
**Figure 100.** Wing details. A, C, D: *Chrysopa oculata*, photomicrographs. A. Subbasal area of forewing, ventral view, arrow indicating tympanal organ. B: *Chrysoperla carnea* (Stephens), schematic line drawing of tympanal organ detail from Miller 1970 (Ac: attachment cell; Ax: axon of the large unit with dilation; C: anterior-ventral cuticular ridge; CelB: cell body and nucleus of the bipolar neuron of the large unit; Ch: channel within the cap of the large unit; CI: cuticular invagination; Cil: “cilium”; Cp: cap; Den: dendrite of the bipolar neuron of the large unit; H: hypodermis; HySt: hyaline structure on the top of the cap of the large unit; Mt, microtrichia; Rt: “ciliary root;” Sc: sclopale cells; SR: scolopale rod; Sw: swelling in the radial vein; TM-Rp: rippled portion of the tympanic membrane; Tr: trachea). C: Basal area of forewing, ventral view, arrow indicating the field of microtrichia between 3A and posterior wing margin. D: Apical area of forewing, dorsal view, arrow indicating pterostigma.

## Hind wing

The hind wing is apically slightly more pointed than the forewing, and the wing venation pattern is similar with some important exceptions (figs. 1, 11). The subcosta and radius are slightly enlarged basal to the first costal crossvein, but there is no tympanal organ present. There is no subcostal crossvein (c-sc) present basally on the wing, and there may be one fewer crossvein between Sc and R below the pterostigma than in the forewing. R has about the same number of branches as in the forewing or only one or two fewer and the number of gradate crossveins is equally similar. RA and RP split more basally than in the forewing and the main RP vein fuses with MA where the crossvein 1rp-ma would be in the forewing. The bases of the pseudoveins are formed by different components than in the forewing and there is a general trend of longitudinal veins zig-zagging. PsM is basally formed by RP, where it splits off RA, and shortly after fuses with MA for one abscissa. PsM is then formed by MA and branches of RP, and MP is never involved. As in the forewing, the basal-most four branches of RP form more than half of PsM. MA is part of PsM for two abscissae and leaves it after fusing with the first RP branch. The base of PsC is not formed by Cu, as it is in the forewing, but by M. At the divergence of MA and MP, the latter remains on PsC, where it fuses with CuA after one abscissa, then with MA, and on its last abscissa with the basal-most branch of RP. There are about seven apparent crossveins between PsM and PsC, of which only the second and last are actual crossveins, without tracheae. The first apparent crossvein is actually MA joining RP in PsM, and the third is MA rejoining MP on PsC. The fourth to sixth crossveins are formed by branches of RP leaving PsM and joining PsC. The cubitus splits into CuA and CuP on the level of 1m-cu, and whereas CuP has only a single terminal, CuA has four terminals, as in the forewing. The main difference to the forewing is, that in the hindwing the second apparent crossvein between the M and Cu sectors is formed by CuA, where it joins MP on PsC. Although the basal-most terminal of CuA simply diverges to the wing margin,



the apical three terminals branch off from PsC. Because of the different path of CuA, *dcc* is formed completely by abscissae of this longitudinal vein in the hind wing, namely the two basal-most terminals and the wing margin. The three anal veins are simple, and not forked, and there is no microsetal patch on the small jugal lobe. The described venation pattern of the hind wing is extremely conserved within Chrysopidae, and where differences occur they are mainly found in the number of RP branches and their crossveins.



**Figure 101.** *Chrysopa oculata*, male abdomen, line drawing, lateral view.

## Abdomen

### External sclerites

The abdomen is the most uniform tagma among Chrysopidae, when not considering the terminalia (fig. 13). The abdomen of *C. oculata* is unmarked and bears dense pale setation among microsetation, which covers the entire integument. Both sexes have nine externally visible terga and males have nine sterna, whereas females have only seven. The anterior margin of the first tergum is connected to the metathorax, and the tergum is divided into two loosely defined parts (anterior and posterior) in dorsal view, due to a transverse fold of the integument (easily visible in dissected specimens). Terga and sterna are separated by broad membranous pleural areas, in which the spiracles are positioned medially on each segment. Terga I–VIII are uniform and each about

1.5 times as long as broad in dorsal view, and the same is the case with sterna I–VII in ventral view. In *C. oculata* tergum IX is fused with an additional tergum-like structure in both sexes, the **ectoproct** (figs. 14A, 15D, E), and sterna VIII and IX are fused in the male (figs. 15D, E), which is the case in most Chrysopidae. Tergum IX + ectoproct bears the **callus cerci**, which is a round field of long sensory setae and consists of 15–20 trichobothria in *C. oculata*. The external **female terminalia** are quite simple (figs. 14A, B), which is often the case in Chrysopidae, but some modifications can also be found. Sternum VII is rounded and not apically expanded or impressed. Tergum VIII is smaller than tergum VII, and the fused tergum IX + ectoproct reaches sternum VII. Apical to tergum IX + ectoproct females have an additional, paired, and weakly sclerotized element, called the **lateral gonapophyses**, which surround the opening for the genitalia, and are kidney shaped in lateral view. The **male terminalia** are slightly more complex than the female, but overall simple in comparison to the elaborate terminalia of many chrysopid taxa. Tergum IX + ectoproct is rounded apically, as is the fused sternum VIII + IX (figs. 15D, E). The fused sternum VIII + IX is basally as broad as sternum VII and tapers apically. The margin between the two fused sclerites is not visible in undissected specimens, but can be detected in stained dissections due to the absence of microtholi on sternum IX (figs. 15F, G, gray arrows). **Microtholi** are dense glandular openings on the integument of male sterna III–VIII in *C. oculata*, and are present in many but not all chrysopid taxa. They are easily detected in dissected and stained male abdomens, as small, dense clear spots (figs. 15F, G). These microtholi can be present on varying sets of sterna and terga throughout Chrysopinae. A striking feature in most species of the genus *Chrysopa*, and also in *C. oculata*, are the prominent and pointed dorsal and ventral apodemes. These structures are strongly sclerotized longitudinal thickenings of the integument, which are positioned lateromedially on tergum IX + ectoproct and along the dorsal lateral margin of sternum VIII + IX.

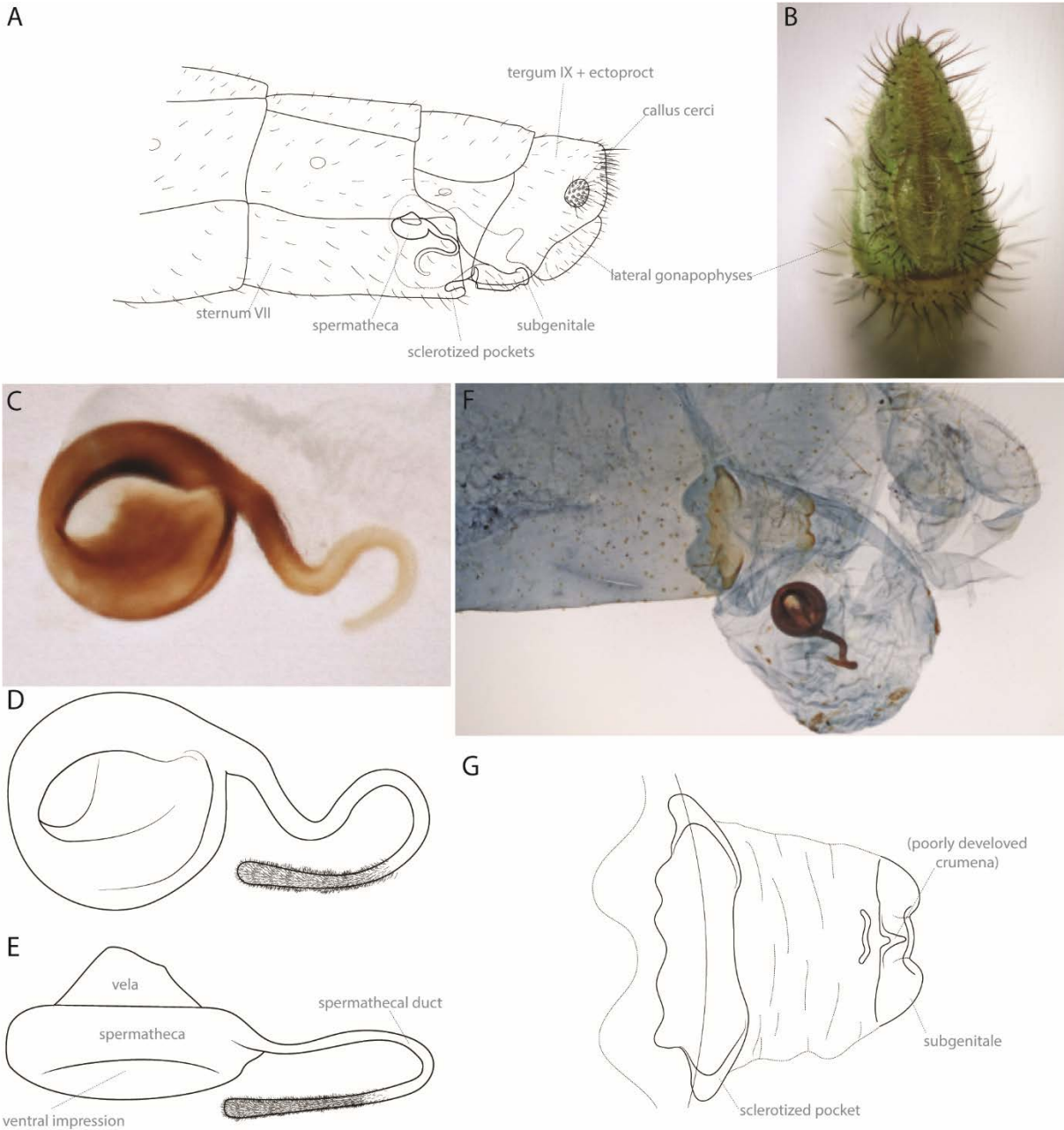
The **dorsal apodeme** is curved, and does not penetrate the membrane apically, but rather fades at the level of the callus cerci. The ventral apodeme is parallel to the upper margin of sternum IX, slightly curved, and penetrates the membrane apically, terminating in an upwards pointing tip. Sternum IX fades out apically, into a weakly sclerotized membrane, that bears a large patch of thick, strongly sclerotized **gonocristae** on each side (fig. 15G). The gonocristae point towards the interior of the terminalia and could have a barb function. These patches are typical for the genus *Chrysopa*, but often not visible in living individuals because the membranous sack they are positioned on is usually folded inwards.

## Genitalia

### Female genitalia

The female genitalic complex is exceedingly less complicated than the male's genitalia (fig. 14A). There are two sclerotized parts in *C. oculata*: the spermatheca complex and the subgenitale complex. The **subgenitale** is located in different positions throughout the family Chrysopidae, with variation between a placement adjacent to sternum VIII, on a separate sclerite, or on a membranous broad expansion. The latter condition is the case for *C. oculata*, in which this membranous area is sclerotized at the base, forming an inward-pointing pocket on each side (figs. 14F, G). The subgenitale is slightly broader than long and bilobed, where the two lobes are separated by a small flat medial area. There is small longitudinal, pointed expansion medially within the subgenitale (which can be recurved in many Chrysopidae = **crumena**) and a thin transverse, slightly W-shaped sclerotized structure basal to it. In lateral view, the apical part of the subgenitale is rounded and slightly expanded ventrally. The subgenitale connects interiorly to a wrinkled membranous sack, which, when exerted (by manually pulling out the sack, see fig. 14F), contains the spermathecal complex (figs. 14C, D, E). This complex has three parts: the

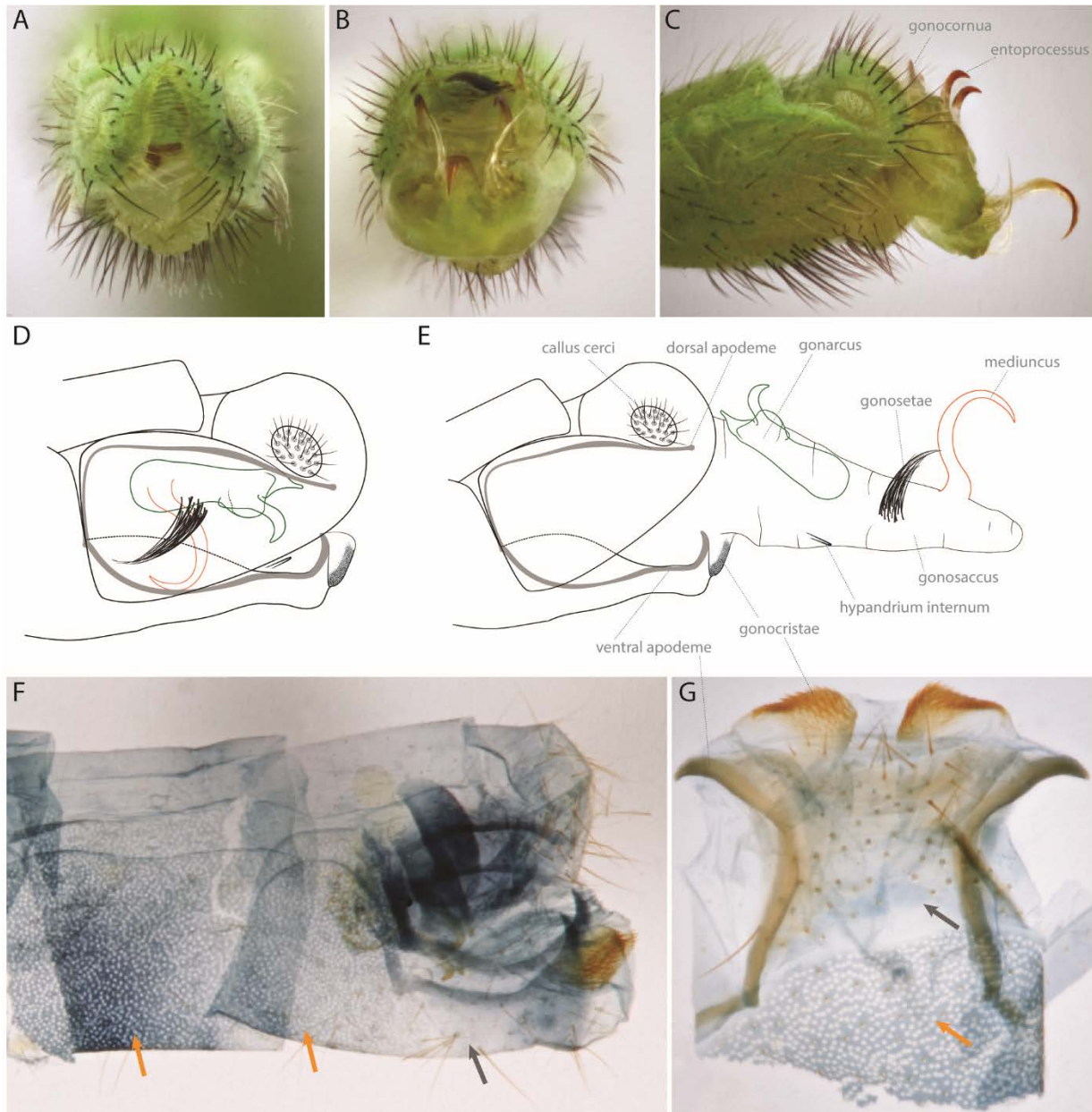
spermatheca, the vela, and the spermathecal duct, all of these are fairly conserved in Chrysopidae, particularly when comparing them to the vast variety of male genitalia, but dimensions of each element can vary. The **spermatheca** of *C. oculata* is round and slightly flattened in lateral view, with a smooth surface and a ventral invagination, leading to a doughnut-like shape, which is the most common state in the family. It is strongly sclerotized and therefore easily detected in dissections, even without staining. Dorsally, there is a medial expansion, the **vela**, which is triangular in lateral view and in *C. oculata* slightly smaller than the spermatheca. It is somewhat pointed to the opposite direction of the spermathecal duct. In other Chrysopidae the vela can be up to twice as long as the spermatheca or minute, so that it is barely discernible. The vela has a long thin slit on one side, which opens into the bursa copulatrix. This membranous sack is not visible in cleared dissections, but the reproductive organs of *C. oculata* have been illustrated in detail by Hwang and Bickley (1961). On one side, the spermatheca forms a long and thin expanded **spermathecal duct**. It is basally sclerotized and apically membranous, but covered in fine setae. The spermathecal duct is short and barely curled in *C. oculata* and most Chrysopini. It can be strongly elongate and curled in Apochrysinæ or Leucochrysinini, and varies from short and thickened to elongate but not strongly curled in Nothochrysinæ.



**Figure 102.** *Chrysopa oculata*, female genitalia. A. schematic line drawing, apex of female abdomen, lateral view. B: Photomicrograph, apex of female abdomen, caudal view. C: Photomicrograph, spermathecal complex, ventral view. D: Schematic line drawing, spermathecal complex, ventral view. E: Schematic line drawing, spermathecal complex, lateral view. F: Photomicrograph, cleared and stained terminalia, ventral view. G: Schematic line drawing, subgenitale and apex of sternum VII, ventral view.

### Male genitalia

The **male genitalia** are exceedingly more complex than the female genitalia and vary greatly within Chrysopidae. As in most chrysopids, *C. oculata* is equipped with the standard set of male genitalic structures: the gonarcus and the mediuncus, but is missing two structures that are found in some chrysopid taxa: the **tignum**, which is an arch-like sclerotized structure dorsal of the gonarcus (present in some higher Chrysopini), and **parameres**, which are ventral sclerotized structures from the sternum (present in most Belonopterygini and various Chrysopini). After thorough study of the genitalic structures in Chrysopidae and closely related families we propose the homology of the parameres and the gonapsis, where the gonapsis is simply a fused pair of parameres. For a detailed review on this character see chapters 1 and 2.



**Figure 103.** *Chrysopa oculata*, male terminalia. A. Photomicrograph, apex of male abdomen, caudal view. B: Photomicrograph, caudal view, genitalia partially exposed. C: Photomicrograph, apex of male abdomen, lateral view, genitalia exposed. D: Schematic line drawing, lateral view, genitalia in resting position. E: Schematic line drawing, lateral view, gonosaccus completely exerted. F: Photomicrograph, cleared and stained male terminalia, lateral view. G: Photomicrograph, cleared and stained sternum VIII + IX, ventral view; orange arrows indicate sterna with microtholi present, gray arrows indicate sternum IX (fused with VIII) with microtholi absent.

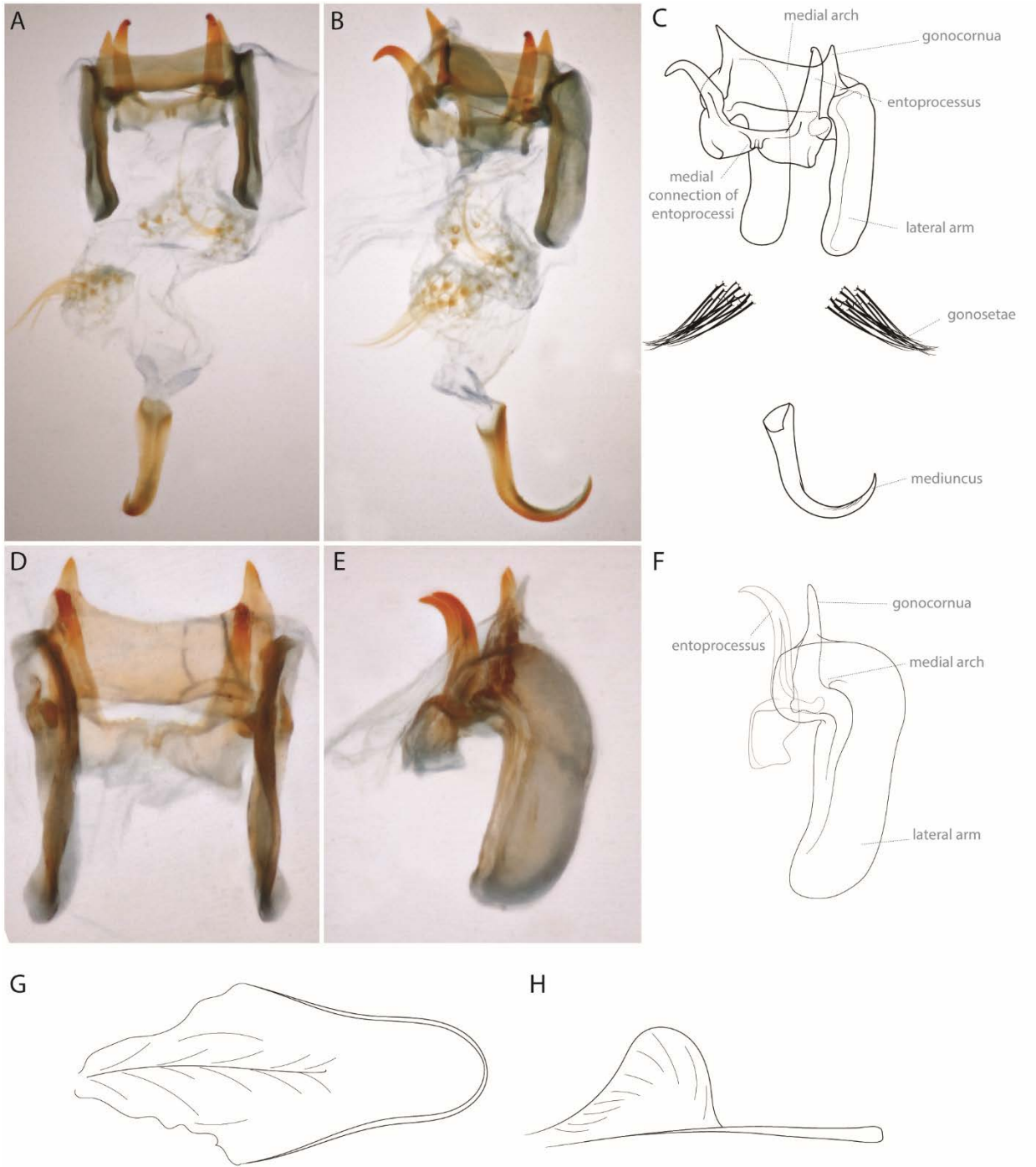
All genitalic structures are positioned on the **gonosaccus** (fig. 15E), and, while normally laying within the terminalia (fig. 15D), are exerted during copulation or manually by pulling gently

on the elongate mediuncus, which is often exposed. The gonarcus complex, which includes the gonarcus, the entoprocessi (see below), and the mediuncus of *C. oculata* has become strongly derived from the presumably primitive arch and loosely associated triangle in lower chrysopids. The **gonarcus** can be divided in three parts: the two lateral arms and the medial arch between these arms (figs. 16A–F). The **lateral arms of the gonarcus** of *C. oculata* are elongate and throughout broad in lateral view. The part adjoining the **medial arch** is ventrally expanded towards the entoprocessus, resulting in a small ear-shaped structure, and the dorsal margin is strongly rounded. The lateral arms are apically rounded and slightly curved inwards, leading to a broad spoon-like shape. The medial arch is strongly flattened and therefore about as broad as the lateral arms. It is latero-frontally expanded, forming a horn on each side (**gonocornua**), pointing towards the apex of the abdomen, and the bases of these horns are connected by a straight line. Any medially expanded structure of the gonarcus has historically been called a gonocornua, but several non-homologous characteristics have been summarized under this term. We here define the gonocornua as a frontal expansion of the medial arch and not of the lateral arm. The **entoprocessus** of *C. oculata*, with its medial fusion, is not typical for Chrysopidae, which is normally a simple elongate expansion of the lateral arm. The base of the entoprocessus is connected to the ear-shaped ventral expansion at the anterior end of the lateral arm of the gonarcus. It is expanded frontally into a large horn, which is about half as long as the lateral arm of the gonarcus and apically curved ventrally, and apicomediaally to a thin arch, where the two entoprocessi fuse. The entire structure of the fused entoprocessi is ventral to the medial arch of the gonarcus, and parallel to its posterior margin. The third part of the gonarcus complex is the **mediuncus**, which is greatly derived in *Chrysopa*, as it is completely detached and far removed from the gonarcus. Due to this position it has previously been described as a “pseudopenis”, but this term is reserved for an elongate structure that is present



in addition to the mediuncus at its apex (e.g., some *Plesiochrysa* Adams). Adams (1969) proposed that the arcessus (closely attached to the median arch of gonarcus), “pseudopenis”, and mediuncus are homologous but such a proposal has not been adopted in subsequent studies and these distinct terms are still in use. We propose the universal implementation of the term *mediuncus*, which is most broadly used in Neuroptera, because the previously employed terms simply describe different positions of a homologous structure. The mediuncus of *C. oculata* is about as long as the lateral arm of the gonarcus, tapering apically, and recurved, with the tip pointing ventrally. Regardless of its detached position and elongate form, the mediuncus of *Chrysopa* can be homologized with the mediuncus of other Chrysopidae and is not a separate structure. In order to determine whether a structure ventral to the gonarcus is the mediuncus or an elaborate, medially fused entoprocessus, the position of attachment has to be considered. An entoprocessus is associated with the lateral arm of the gonarcus (usually ventrally on the anterior half) and either completely fused with it or articulating, but never disconnected. A mediuncus is never connected to the lateral arm, but instead associated with the median arch of the gonarcus, with which it is membranously connected, although (as in *C. oculata*) often far distal to the median arch that it is seemingly disconnected. The membrane of the gonosaccus attaches to the gonarcus dorsally on the median arch, then connects the ventral median arch to the dorsomedial margin of the fused entoprocessi, and then runs from the ventral-most part of the entoprocessus to the mediuncus. This results in the exposed horns of the gonocornua and entoprocessus when the gonosaccus is exerted (figs. 15C, E). In *C. oculata* there are paired fields of about 15 long, curved setae between the gonarcus and the mediuncus, which are classified as **gonosetae**, due to their position on the gonosaccus. The **hypandrium internum** (figs. 16G, H), which is present in all Neuroptera, can be difficult to detect in *C. oculata*, as it is positioned more apically than in most Chrysopidae. It is a thin U-shaped arch,

about one third of the length of the mediuncus, weakly sclerotized and associated with the gonopore. The area between the two arms of the arch is covered with a membrane, which is medially elevated, to a faint expansion, shaped like a keel. The shape of the hypandrium internum does not vary much in Chrysopidae, except for the size and whether it is U- or V-shaped.



**Figure 104.** *Chrysopa oculata*, male genitalia. A. Photomicrograph, cleared and stained gonarcus complex, ventral view. B: Photomicrograph, cleared and stained gonarcus complex, latero-ventral view. C Line drawing, gonarcus complex, latero-ventral view. D: Photomicrograph, cleared and stained gonarcus and entoprocessi, dorsal view. E: Photomicrograph, cleared and stained gonarcus and entoprocessi, lateral view. F: Line drawing, gonarcus and entoprocessi, dorsal view. G: Line drawing, hypandrium internum, lateral view. H: Line drawing, hypandrium internum, lateral view.

## Glossary

Provided below is a glossary of the morphological terms as applied herein for structures across Chrysopidae. For each term a definition is provided; where applicable, an abbreviation; the plural of the term; a figure reference; whether it is present in only males (♂) or females (♀); and whether the structure is paired or unpaired in Chrysopidae. All characters of the lateral thorax (pro-, meso-, and metapleura), wings, and legs are universally paired and therefore not explicitly noted here.

**Abscissa** – pl. abscissae. A section of a longitudinal vein between connecting veins or crossveins.

**Acumen** – [♂, unpaired] small frontomedian expansion of the tignum.

**Anal lobe** – posterior most sector of the forewing, enlarged posterior to the anal veins, and pointed in some Chrysopidae (especially Nothochrysinae); figs. 11, 12C.

**Anal veins (A)** – longitudinal veins 1A, 2A, and 3A, posterior to CuP, associated with the third axillary sclerite (3Ax); figs. 9B, C, 11, 12C.

**Anepimeron (aepm)** – pl. anepimera. Postero-dorsal sclerite of metapleuron; figs 7–8.

**Anepisternum (aeps)** – pl. anepisterna. Anterio-dorsal sclerite of meso- and metapleuron; figs 7–8.

**Anteclypeus** – [unpaired] apical portion of clypeus, band-shaped area at apical clypeal margin delimited basally from the postclypeus by a thin transversal impression; figs. 3A, B.

**Antenna** – [paired] segmental appendage of the head functioning as a sensory organ and composed of three highly modified podites: scape, pedicel (bearing internally the Johnston's organ), and flagellum (itself subdivided into a variable number of flagellomeres).

**Antennal sulcus** – pl. sulci. Sulcus around the torulus; forming a thin carina dorsally in some Chrysopidae; fig. 3D.

**Arcessus** – {♂, term outdated} term was used for a mediuncus closely attached to medial arch of gonarcus; see *mediuncus*.

**Arolium** – pl. arolia. Inflated membranous sack of pretarsus at apex of unguitactor plate and medial to the ungues (= claws); fig. 10.

**Banksian cells** – {term outdated} cells formed by RP, branches of RP, and the PsM.

**Basal subcostal crossvein** – first crossvein between Sc and R (1sc-r), which is positioned basal to the origin of RP in most extant Chrysopidae, except Apochrysinæ; fig. 11.

**Bursa copulatrix** – [♀, unpaired], pl. bursa copulatrices. The copulatory pouch forming the primary element of the female genital chamber.

**Callus cercus** – [paired], pl. cerci. Round patch of long sensory setae positioned laterally on the ectoproct; figs. 14A, 15D, E.

**Cardo** – [paired], pl. cardines. Basal-most part of the maxilla which articulates to the head capsule; fig. 5E.

**Circumocular groove** – [paired] broad groove on vertex and the parocular area of the frons, around the compound eyes, visible especially in frontal view.

**Clypeus** – [unpaired] apical-most sclerite of the head capsule, adjoining the frons and covering the labrum as well as the mouth opening; figs. 3–4.

**Compound eye** – [paired], pl. compound eyes. Cluster of individual visual components (ommatidia) with individual facets with corneas, and collectively forming the primary visual sensory organs.

**Costa (C)** – anterior-most longitudinal vein of the wings, forming the anterior wing margin and fading towards apex; proximally associated with the humeral plate.

**Coxa** (cx) – pl. coxae. Basal-most podite of the hexapod leg, articulating with the thorax basally and with the trochanter apically; composed of basicoxa and meron; fig. 7.

**Crossvein** – a frequently small vein element, often transverse to the long axis of the wing, connecting two longitudinal veins and not internally traversed by a trachea.

**Crumena** – [♀, unpaired] small ventral dimple basally on subgenitale, in some taxa with an expanded tip, pointing towards the base.

**Cubitus** (Cu) – longitudinal vein posterior to M and anterior to A, associated with the medial plate. Split into the cubitus anterior (CuA) and cubitus posterior (CuP); figs. 10, 11.

**Distal cubital cell** (*dcc*) – diamond-shaped cell that is formed by different elements of the cubitus in the two wings. Forewing: CuP, CuA, distal-most crossvein between these two longitudinal veins and (in most Chrysopidae) the wing margin; hind wing: formed by CuP and the wing margin; fig. 11.

**Dorsal apodeme** – [♂, paired], pl. dorsal apodemes. Sclerotization of the anterolateral margin of tergum IX in the male abdomen (can be expanded ventrally in some Chrysopidae, forming a pointed tip); fig. 15D–F.

**Ectoproct** – [paired or unpaired], pl. ectoprocts. Apical-most external dorsal sclerite (remnant of tergum X) of the male and female abdomen, which is fused with tergum IX in most Chrysopidae, and generally surrounds the anus; figs. 14A, C, 15C–F.

**Entoprocessus** – [♂, paired], pl. entoprocessi. Attachment of the lateral arm of the gonarcus, usually pointing ventrally, varying from absent, a small tip, to large arching structures with additional appendages; figs. 16A–F.

**Epimeron** (epm) – pl. epimera. Posterior half of the meso- and metapleuron. Divided in katepimeron (kepm) and anepimeron (aepm) in metanotum; figs. 7, 8.

**Epistomal sulcus** – pl. epistomal sulci. The sulcus uniting the anterior ends of the subgenal sulci across the face, including within its path the anterior tentorial pits and internally marked by an epistomal costa.

**Femur** (fe) – pl. femora. Third podite from base of the hexapod leg, articulating basally with the trochanter and apically with the tibia; figs. 9A–C.

**Flagellar seta** – pl. flagellar setae. Seta present on flagellomeres, arranged in series of four, five, or six rings in Chrysopidae; fig. 5A.

**Flagellomere** – pl. flagellomeres. Single article of the subdivided antennal flagellum; fig. 5A.

**Flagellum** – [paired], pl. flagella. Apical podite and largest section of the insectan antenna, and subdivided into numerous flagellomeres; fig. 5A.

**Forewing** – [paired] anterior wing, articulating with the mesothorax; figs. 1B, 11.

**Frons** – [unpaired] frontal part of the integument of the head, between compound eyes, vertex, gena, and clypeus, divided in supra-antennal, interantennal, parocular, and supraclypeal area; fig. 3.

**Galea** – [paired], pl. galeae. Outer apical-most part of the maxilla, bordering the lacinia (inner apical-most component) and basally articulating with the stipes. The medial surface is covered in fine setae; fig. 5D.

**Gena** – [paired], pl. genae. Lateral part of the integument of the head, between compound eye, frons, clypeus, mandibular base, and postgena; figs. 3A, B, 4.

**Genal carina** – [paired], pl. genal carinae. Longitudinal carina along the margin of the gena and postgena and parallel to the posterior margin of the compound eye; figs. 4A, B.

**Gonapsis** – {♂, term outdated} formerly used to describe the medially fused ventral sclerite of the male genitalia; see *parameres*.

**Gonarcus** – [♂, unpaired] Arching structure of the internal male genitalia, broadly U-shaped with a median arch and a lateral arm on each side. Medially attaching to mediuncus; lateral arms with entoprocessus in most taxa.

**Gonocornua** – [♂, paired], pl. gonocornuae. Lateral horn on median arch of gonarcus; figs. 16A–F.

**Gonocristae** – [♂] strongly sclerotized teeth associated with the male genitalia, often in two patches, apically on sternum XI; fig. 15G.

**Gonosaccus** – [♂, unpaired] membranous sack on which the interior male genitalia are positioned; fig. 15C, E.

**Gonosetae** – [♂] setae positioned on gonosaccus, mostly in a paired patch, lateral, or lateroventral of mediuncus; figs. 15C–E.

**Hindwing** – [paired] posterior wing, articulating with the metathorax; figs. 1B, 11.

**Hypandrium internum** – [♂, unpaired] small sclerite at the gonoporus, V- or U-shaped with a keel on the membrane between the lateral arms; present in all Neuroptera and homologous to sternum X; figs. 16G, H.

**Katepimeron** (kepm) – postero-ventral sclerite of metapleuron; figs 7–8.

**Katepisternum** (keps) – antero-ventral sclerite of meso- and metapleuron; figs 7–8.

**Inner gradates** (ig) – row of crossveins between the RP branches, positioned anterior to the outer gradates and posterior to the main RP vein; fig. 11.

**Intermedial cell** (*im*) – first cell between the MA and MP (*mamp1*), in most Chrysopidae formed as an intermedial cell, that comprises only a part of the space between the PsM and PsC, and can vary in shape from triangular and quadrangular, when crossvein is involved, or ovate, when the cell is entirely formed by MA and MP, which fuse posterior to the cell; fig. 11.

**Jugal lobe** – posterior most section of the hind wing, enlarged and pointed posterior to the anal veins in some Chrysopidae (especially Nothochrysinæ).

**Labial palpus** – [paired], pl. labial palpi. Tactile and mobile part of the labium, originating laterally on the prementum and composed of three palpomeres; fig. 5E.

**Labium** – [unpaired] ventral-most appendage of the mouthparts, adjoining the cervix and the postgena, composed of the mentum, prementum, ligula, and labial palpus; figs. 4A, B, 5E.

**Labrum** – [unpaired] dorsal, W-shaped mouthpart sclerite apicoventral to the clypeus, dorsal to the mouth opening; figs. 3A, B, 5B.

**Lacina** – [paired] medioapical part of the maxilla, articulating with the stipes; the medial facing side is covered in fine setae and it bears a palpilla apically; fig. 5D.

**Lateral gonapophysis** – [paired], pl. lateral gonapochyses. Proximal, lateral process of ovipositor (vestigial in most Neuroptera) valves, likely formed of fused first and second gonapophyses of insectan groundplan and which plesiomorphically formed functional ovipositor (e.g., Archaeognatha, Zygentoma), and formed in Neuroptera as proximal processes from sternum IX.

**Ligula** – [unpaired] medioapical part of the labium, originating on the prementum and formed of fused glossa and paraglossae; fig. 5E.

**Longitudinal vein** – wing vein that originates from the wing base, where it connects to a basal articulatory sclerite, or from the apical splitting of a portion of such a vein, always bearing internally a trachea, and generally running along long axis of wing. Multiple longitudinal veins can fuse to pseudoveins, in which several tracheae are present; fig. 11.

**Mandible** – [paired], pl. mandibles. Most heavily sclerotized and anterior appendage of the mouthparts, broadly sickle-shaped, pointed apically and asymmetrical in most Chrysopidae, with a basal tooth on one mandible; figs. 3A, B, 4C, D, 5C.

**Maxilla** – [paired], pl. maxillae. Medial appendage of mouthparts, anterior and dorsal to labium, abutting the latter and the postgena, composed of cardo, stipes, lacina, galea, and maxillary palpus; figs. 4A, B, 5D.

**Maxillary palpus** – [paired], pl. maxillary palpi. Tactile and mobile part of the maxilla originating laterally on the stipes and composed of five palpomeres; fig. 5D.

**Media anterior (MA)** – longitudinal vein posterior to R and anterior to Cu, associated with the medial plate. Split into the media anterior (MA) and media posterior (MP); fig. 11.

**Median plate** – {♂, term outdated} flat expansion of the median arch of the gonarcus.

**Mentum** – [unpaired] basal-most part of the labium, articulating laterally with the head capsule, posteriorly connecting to cervical sclerite and membrane, and laterally bordering the postgena and anteriorly the base of the maxilla; figs. 4A, B, 5E.



**Merion** (me) – postero-dorsal subdivision of the coxa, ventral to the epimeron, apparent as a thoracic sclerite in Neuroptera; not reaching the trochanter; figs. 7, 8.

**Mesothorax** – [unpaired] second and medial thoracic segment, bearing the mid-leg and forewing; figs. 6–8.

**Metathorax** – [unpaired] third and posterior-most thoracic segment, bearing the hind leg and hind wing; figs. 6–8.

**Microtholi** – [♂] small circular dimples in the integument of the male abdomen, probably with a glandular function; best visible in a cleared and stained specimen, as small clear spots in the stained integument; figs. 15F, G.

**Notum** – dorsal surface of thorax; fig. 6.

**Outer gradates** (og) – row of crossveins between the RP branches, positioned posterior to the inner gradates and anterior (and most often parallel) to the wing margin; fig.11.

**Palpomere** – individual article of the labial or maxillary palpus; figs. 5D, E.

**Parameres** – [♂, paired/unpaired] ventral-most structure of the male genitalia; paired or fused sclerites. Homologous to medially fused parameres in Chrysopini formerly termed gonapsis (see character discussion in Chapter 1).

**Pedicel** – [paired] antennal podite between scape and flagellum, internally bearing the Johnston's organ; fig. 5A.

**Pleuron** – lateral surface of thorax, forming side-wall of thorax; figs. 7, 8.

**Pleural sulcus** (pS) – dorsoventral sulcus on meso- and metapleura, separating episternum (anterior) and epimeron (posterior), dorsally terminating in the pleural wing process; figs. 7, 8.

**Pleural wing process** – rounded expansion of the pleural sulcus, with an articulation to the first axillary sclerite; fig. 10D.

**Postalar bridge** (poab) – [paired] membranous connection between the scutellum and the posterior wing margin, present on meso- and metanota; figs. 6, 10A.

**Postclypeus** – [unpaired] basal portion of the clypeus, connecting to frons and gena, bearing long setae apically, and delimited apically from the ante clypeus by a thin transversal impression; figs. 3A, B.

**Postgena** – [paired] ventral part of the integument of the head, between compound eye, vertex, cervical sclerite, maxilla, labium, and gena; figs. 4A, B.

**Praegenitale** – [♀, unpaired] sclerotized part of the integumental region between sternum VII and subgenitale, or in some Chrysopinae dislocated within sternum VII; mainly present in Belonopterygini and Leucochrysinini.

**Premmentum** – [unpaired] sclerite of labium, bearing the lacina and labial palpus, basally bordering the mentum; figs. 4A, B, 5E.

**Prescutum** (prsc) – [unpaired] anterior-most sclerite of mesonotum between pronotum and mesoscutum, in metanotum structure is fused with metascutum and is not recognized as an individual sclerite; fig. 6.

**Pretarsus** (peta) – apical most podite of the hexapod leg, basally articulating with the tarsus, and bearing two pretarsal claws as well as the arolium.

**Pretarsal claw** – paired claws (ungues) at the apex of the leg, one of three primary components of the pretarsus, which is the podite apical to tarsus; owing to the overall reduction of the pretarsus, the pretarsal claws seem to originate from the fifth tarsomere but, articulate, like the arolium, to the unguitractor plate (which itself is small and slightly covered by the apex of the distitarsus); claws can be basally dilated or simple in Chrysopidae; fig. 9.

**Prothorax** – [unpaired] anterior thoracic segment, bearing the foreleg; fig. 3C, 6–8.

**Pseudocubitus** (PsC) –p present in the fore- and hind wing posterior to PsM and anterior to the anal veins; in the fore- and hind wing of Chrysopidae, CuA, MA, MP, and several RP sectors are usually involved; fig. 11.

**Pseudomedia** (PsM) – pseudovein present in the fore- and hind wing posterior to R and anterior to PsM; in the forewing of Chrysopidae MP, several RP sectors, and crossveins are usually involved, as well as MA in taxa where the *im* cell is ovate; in the hindwing, MP and several RP sectors are involved; fig. 11.

**Pseudopenis** – [♂, unpaired] apical attachment of the mediuncus, present in few Chrysopini. Term was previously used for a far detached, elongate mediuncus.

**Pseudovein** – apparent as a longitudinal vein, but the result of several fused veins, and therefore containing multiple tracheae; different veins can be involved in individual abscissae of the pseudovein; fig. 11.

**Pterostigma** – slightly more sclerotized region of the wing integument, apically between Sc and the wing margin; can be strongly marked in some Chrysopidae or weakly marked to unmarked in others; usually there are only ill-defined costal crossveins at the pterostigma; fig. 12D.

**Radius anterior** (RA) – longitudinal vein posterior to Sc and anterior to M, associated with the second axillary sclerite; divided into the radius anterior (RA) and radius posterior (RP), which has numerous long, zig-zagged branches in Chrysopidae, forming the majority of the wing; fig. 11.

**Scape** – [paired] basal most segment of the antenna, its base is articulating with the frons in the torulus, and with the pedicel via a small sclerotized articulation apically; fig. 5A.

**Scutellum** (scl) – [unpaired] posterior most sclerite of meso- and metanotum, connecting to the posterior wing margin through the poab; fig. 6.

**Scutum** (sc) – [unpaired] medial sclerite of meso- and metanotum, comprising the largest part of the notum of each "segment"; V-shaped on each side and connected medially; metascutum bearing two patches of dense microsetae frontomedially, locking the forewings on the back of the insect; fig. 6.

**Spermathecal duct** – [♀, unpaired] elongate tube, connected to the spermatheca, basally sclerotized, apically membranous and fringed, varying from basally thickened and short to strongly elongate and coiled.

**Spermatheca** – [♀, unpaired] receptacle for the receipt and storage of sperm in the female genitalia.

**Sternum** – [unpaired] ventral thoracic or abdominal segment, strongly reduced in metathorax and in chrysopid male there are nine abdominal sterna present externally, in female seven externally; fig. 13.

**Stipes** – [paired] part of the maxilla, originating on cardo, and apically bearing the lacinia, galea, and maxillary palpus; figs. 4A, B, 5D.

**Subcosta** (Sc) – longitudinal vein posterior to C and anterior to R, associated with the first axillary sclerite; fig. 11.

**Subgenitale** – [♀, unpaired] sternum VIII of the female abdomen, which is strongly reduced and in most Chrysopidae positioned on membrane, detached from sternum VII; figs. 14A, F, G.

**Tarsomere** – individual element of the subdivided tarsus; five tarsomeres present in all legs; fig. 9.

**Tarsus** – (ta), pl. tarsi. Next to apical podite of the hexapod leg, basally articulating with the tibia, composed of five tarsomeres, and apically articulating with the pretarsus; fig. 9.

**Tergum** – [unpaired] dorsal sclerite of the abdomen; nine present in Chrysopidae; fig. 13.

**Tibia** – (ti) fourth podite of the hexapod leg, basally articulating with the femur, apically with the tarsus; fig. 9.

**Tibial spur** – thick, elongate spine at the apex of the tibia, positioned in the membranous region anterior to the articulation with the tarsus; in Chrysopidae there is usually one present on each of the meso- and metatibiae, but they can also rarely be absent or multiple spurs present on all tibiae; figs. 9E, F, H, I.

**Tignum** – [unpaired] arched sclerite dorsal to the gonarcus, present in some Chrysopini; fig. 13.

**Torus** – [paired], pl. toruli. Antennal socket, medially on frons, membranous articulation point of frons and antenna; fig. 3.

**Transepimeral sulcus** (tepmS) – transverse sulcus separating katepimeron and anepimeron in metanotum; figs. 7, 8.

**Transepisternal sulcus** (tpeS) – transverse sulcus separating katepisternum and anepisternum in meso- and metanotum; figs. 7, 8.

**Trochanter** (tr) – second podite of the hexapod leg, articulating basally with the coxa and apically with the femur, usually much shorter than either; figs. 7–9.

**Trochantin** (tn) – small sclerite ventral to the katepisternum, articulating with the coxa, reduced dramatically in many higher insects, and only scarcely present in Chrysopidae (stronger developed in mesothorax than metathorax); figs. 7, 8.

**Tympanal organ** – enlarged region of the R and basally fused M, forming an acoustic sensory organ to detect high frequency wave lengths (probably only for bats, see Henry 1980, Miller 1984); figs. 12A, B.

**Vela** – [♀, unpaired] weakly sclerotized triangular lobe dorsally on spermatheca, with an opening to the bursa copulatrix; figs. 14C–E.

**Ventral apodeme** – [♂] sclerotization of the dorsal margin of sternum VII + IX of the male abdomen, can be expanded dorsally forming a pointed tip; figs. 15D–G.

**Vertex** – [unpaired] dorsal part of the integument of the head, between compound eye, frons, postgena, and cervix; fig. 3.

## Conclusion

With this work we hope to contribute to the understanding of chrysopid morphology, by providing the most comprehensive morphological study of a species to date. Apart from describing the taxonomically valuable characters, we included those which are historically not usually described in detail (e.g., meso- and metanota). Future research on representatives of the other subfamilies and tribes, i.e., Nothochrysinæ, Apochrysinæ, Belonopterygini, and Ankylopterygini, as well as enigmatic genera such as *Nothancyla* or *Kostka*, would be beneficial. Most importantly, we have attempted to provide a standard terminology and definitions for particular sclerites,

indicating proper homologies not only with other Chrysopidae but more broadly across Neuroptera. This will ideally allow for more precise comparisons between taxa and the definition of characters for investigations into the evolution and functional morphology of these elements.

## References

- Adams, P. A. 1967. A review of the Mesochrysinæ and Nothochrysinæ (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology* 135(4): 215–238.
- Adams, P. A. 1969. New species and synonymy in the genus *Meleoma* (Neuroptera, Chrysopidae), with a discussion of genitalic homologies. *Postilla* 136: 1–18.
- Aspöck, H., Aspöck, U., and H. Hölzel. 1980. *Neuropteren Europas*. Goecke & Evers.
- Banks, N. 1903. A revision of the Nearctic Chrysopidae. *Transactions of the American Entomological Society (1890–)* 29(2): 137–162.
- Banks, N. 1911. Descriptions of new species of North American neuropteroid insects. *Transactions of the American Entomological Society (1890–)* 37(4): 335–360.
- Barnard, P. C. 1984. Adult morphology related to classification. *Biology of Chrysopidae*, in Canard, M., Séméria, Y., & New, T. R. (Eds.). *Biology of chrysopidae* (Vol. 27). Springer.
- Bickley, W. E. 1952. Inheritance of some varietal characters in *Chrysopa oculata* Say (Neuroptera: Chrysopidae). *Psyche* 59(2): 41–46.
- Bickley, W. E., and E. G. MacLeod. 1956. A synopsis of the Nearctic Chrysopidae with a key to the genera (Neuroptera). *Proc. Entomol. Soc. Wash* 58(4): 177–202.
- Bitsch, J. 1984. Anatomy of adult Chrysopidae, in Canard, M., Séméria, Y., & New, T. R. (Eds.). *Biology of chrysopidae* (Vol. 27). Springer.
- Blum, M. S., Wallace, J. B., and H. M. Fales. 1973. Skatole and tridecene: Identification and possible role in a chrysopid secretion. *Insect Biochemistry* 3(12): 353–357.

- Bram, R. A. and W. E. Bickley. 1963. Green lacewings of the genus *Chrysopa* in Maryland (Neuroptera: Chrysopidae).
- Brannoch, S. K., Wieland, F., Rivera, J., Klass, K. D., Béthoux, O., and G. J. Svenson. 2017. Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). *ZooKeys*. 696:1–100
- Breitkreuz, L. C., Winterton, S. L., and M. S. Engel. 2017. Wing Tracheation in Chrysopidae and Other Neuropterida (Insecta): A Resolution of the Confusion about Vein Fusion. *American Museum Novitates* (3890): 1–44.
- Brooks, S. J. and P. C. Barnard. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History, Entomology* 59 (2): 117–286.
- Burmeister, H. 1839. *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie, Zweite Abtheilung, Kaukefe, Gymnognatha, (Zweite Hälfte; vulgo Neuroptera)*. Berlin.
- Comstock, J. H. 1918. *The wings of insects*. Ithaca: Comstock Publishing Company, xviii+[i]+430 pp., +10 pls.
- Comstock, J. H., and J. G. Needham. 1898a. The wings of insects [Chapter 1: an introduction to the study of the homologies of the wing veins]. *American Naturalist* 32 (373): 43–48.
- Comstock, J. H., and J. G. Needham. 1898b. The wings of insects [Chapter 2: the venation of a typical insect wing]. *American Naturalist* 32 (374): 81–89.
- Comstock, J. H., and J. G. Needham. 1898c. The wings of insects [Chapter 3: the specialization of wings by reduction]. *American Naturalist* 32 (376): 231–257. [covers parts 1 (introduction), 2 (Plecoptera), 3 (Psocoptera), 4 (Hemiptera: Auchenorrhyncha), 5 (Hemiptera: Heteroptera), 6 (Lepidoptera), and 7 (Trichoptera)]
- Comstock, J. H., and J. G. Needham. 1898d. The wings of insects [Chapter 3 (continued)]. *American Naturalist* 32 (377): 335–340. [covers part 8 (Diptera)]

- Comstock, J. H., and J. G. Needham. 1898e. The wings of insects [Chapter 3 (continued)]. *American Naturalist* 32 (378): 413–424. [covers parts 9 and 10 (Hymenoptera), and part 11 (Embiodea)]
- Comstock, J. H., and J. G. Needham. 1898f. The wings of insects [Chapter 3 (concluded)]. *American Naturalist* 32 (380): 561–565. [covers part 12 (Coleoptera)]
- Comstock, J. H., and J. G. Needham. 1898g. The wings of insects [Chapter 4: The specialization of wings by addition]. *American Naturalist* 32 (382): 769–777. [covers parts 1 (accessory veins) and 2 (suppression of branching)]
- Comstock, J. H., and J. G. Needham. 1898h. The wings of insects [Chapter 4 (continued)]. *American Naturalist* 32 (384): 903–911. [covers part 3 (Odonata)]
- Comstock, J. H., and J. G. Needham. 1899a. The wings of insects [Chapter 4 (continued)]. *American Naturalist* 33 (386): 117–126. [covers part 4 (Ephemeroptera)]
- Comstock, J. H., and J. G. Needham. 1899b. The wings of insects [Chapter 4 (concluded)]. *American Naturalist* 33 (391): 573–582. [covers parts 5 (Orthoptera) and 6 (conclusion)]
- Comstock, J. H., and J. G. Needham. 1899c. The wings of insects [Chapter 5: the development of wings]. *American Naturalist* 33 (395): 845–860. [covers parts 1 (position and growth), 2 (origin of tracheae), 3 (hypodermis), and 4 (tracheae and hypodermis)]
- Eichele, G. and W. Villiger. 1974. Untersuchungen an den stridulationsorganen der florfliege, *Chrysopa carnea* (St.) (Neuroptera: Chrysopidae). *International Journal of Insect Morphology and Embryology* 3(1): 41–46.
- Erhardt, E. 1916. Zur Kenntnis der Innervierung und der Sinnesorgane der Flügel von Insekten. *Zoologische Jahrbücher (Abteilung für Anatomie und Ontogenie)* 39:293–334.
- Garland, J. A. 1985. Identification of Chrysopidae in Canada, with bionomic notes (Neuroptera). *The Canadian Entomologist* 117(6): 737–762.
- Grimaldi, D., and M. S. Engel. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press, xv + 755 pp.



- Henry, C. S. 1980. The importance of low-frequency, substrate-borne sounds in lacewing communication (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America* 73(6): 617–621.
- Henry, C. S. 1982. Reproductive and calling behavior in two closely related, sympatric lacewing species, *Chrysopa oculata* and *C. chi* (Neuroptera: Chrysopidae) [Acoustical communication, USA]. *Proceedings–Entomological Society of Washington (USA)*.
- Hörnschemeyer, T. 1998. Morphologie und Evolution des Flügelenks der Coleoptera und Neuropterida. *Bonner Zoologische Monographien*, 43. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Hörnschemeyer, T. 2002. Phylogenetic significance of the wing-base of the Holometabola (Insecta). *Zoologica Scripta* 31(1): 17–29.
- Hwang, J. C. and W. E. Bickley. 1961. The reproductive system of *Chrysopa oculata* (Neuroptera: Chrysopidae). *Annals of the Entomological Society of America* 54(3): 422–429.
- Killington, F. J. 1937. *A Monograph Of The British Neuroptera*. Vol. II. London, 306 pp.
- Krishna, K., Grimaldi, D. A., Krishna, V., and M. S. Engel. 2013. *Treatise on the Isoptera of the world*. (Bulletin of the American Museum of Natural History, no. 377).
- Leach, W. E. 1815. Entomolgy. In Brewster, D. (ed.). *Edinburgh Encyclopaedia*. 9(1): 57–172. Edinburgh.
- Latreille, P. A. 1807. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata* [vol. 3]. Parisiis et Argentorati [Paris and Strasbourg]: A. Koenig, 258 pp.
- Latreille, P. A. 1817 [1816]. Les crustacés, les arachnides et les insectes. In G. Cuvier, *Le règne animal distribué d'après son organisation: pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée*. Avec figures, dessinées d'après nature [vol. 3]: 1–653. Paris: Déterville, xxix + 653 pp.
- Matsuda, R. 1965. Morphology and evolution of the insect head. *Memoirs of the American Entomological Institute*, 4:1–334.

- Matsuda, R. 1970. Morphology and evolution of the insect thorax. The Memoirs of the Entomological Society of Canada 102(76), 5–431.
- Matsuda, R. 1976. Morphology and Evolution of the Insect Abdomen: With Special Reference to Developmental Patterns and their Bearings upon Systematics. Pergamon Press, 533 pp.
- Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the AMNH 82(6).
- Miller, L. A. and E. G. Macleod. 1966. Ultrasonic Sensitivity: A Tympanal Receptor in the Green Lace Wing *Chrysopa carnea*. Science 154(3751): 891–893.
- Miller, L. A. 1970. Structure of the green lacewing tympanal organ (*Chrysopa carnea*, Neuroptera). Journal of Morphology 131(4): 359–382.
- Miller, L. A. 1984. Hearing in Green Lacewings and their Responses to the Cries of Bats, in Canard, M., Séméria, Y., & New, T. R. (Eds.). Biology of chrysopidae (Vol. 27). Springer.
- New, T. R. 1980. A revision of the Australian Chrysopidae (Insecta: Neuroptera). Australian Journal of Zoology Supplementary Series 28(77): 1–143.
- New, T. R. 1989. Handbuch der Zoologie, Band/Volume IV Arthropoda: Insecta, Planipennia: lacewings. Walter de Gruyter, Berlin, New York.
- Penny, N. D. 1996. A Revision of *Parachrysopiella* (Neuroptera: Chrysopidae). Journal of the Kansas Entomological Society 69(3): 222–233.
- Penny, N. D., Tauber, C. A., and C. A. Teresa de Leon. 2000. A new species of *Chrysopa* from western North America with a key to North American species (Neuroptera: Chrysopidae). Annals of the Entomological Society of America 93(4), 776–784.
- Principi, M. M. 1954. Contributi allo studio dei Neurotteri Italiani. XI. *Chrysopa viridana* SCHN. Bollettino dell'Istituto di Entomologia della Università degli Studi di Bologna 20: 359–376.
- Principi, M. M., and M. Canard. 1984. Feeding habits, in Canard, M., Séméria, Y., and New, T. R. (Eds.). Biology of Chrysopidae (Vol. 27). Springer.

- Rambur, J. P. 1842. Histoire naturelle des insectes. Néuroptères. Paris: Roret, xvii +[i] + 534 pp., +12 pls.
- Riek, E. F. 1967. Structures of unknown, possibly stridulatory, function on the wings and body of Neuroptera; with an appendix on other endopterygote orders. Australian Journal of Zoology 15(2): 337–348.
- Say, T. 1839. Descriptions of New North American Insects, and Observations on Some Already Described. By Thomas Say. Continued from Vol. IV., NS, p. 470. Transactions of the American Philosophical Society 6: 155–190.
- Schneider, W. G. 1851. Symbolae ad monographiam generis Chrysopae. Editio minor. Ferdinandum Hirt, Vratislaviae
- Smith, R. C. 1932. The Chrysopidae (Neuroptera) of Canada. Annals of the Entomological Society of America 25(3): 579–601.
- Snodgrass, R. E. 1935. Principles of insect morphology. McGraw–Hill Book: London.
- Stephens, J. F. 1835. Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable [Mandibulata, vol. 6]. London: Baldwin and Cradock, 240 pp., + pls. xxviii–xxxiv.
- Tauber, C. A. 1969. Taxonomy and biology of the lacewing genus *Meleoma* (Neuroptera: Chrysopidae). University of California Publications in Entomology 58, 94pp.
- Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2006. *Berchmansus elegans* (Neuroptera: Chrysopidae): larval and adult characteristics and new tribal affiliation. European Journal of Entomology 103(1): 221.
- Tauber, C. A., Tauber, M. J., and G. S. Albuquerque. 2014. Debris–carrying in larval Chrysopidae: unraveling its evolutionary history. Annals of the Entomological Society of America 107(2): 295–314.
- Tjeder, B. 1966. Neuroptera–Planipennia. The Lace–wings of Southern Africa. 5. Family Chrysopidae. South African Animal Life 12: 228–534.

- Tsukaguchi, S. 1995. Chrysopidae of Japan: (Insecta, Neuroptera). Yutaka Insatsu, Osaka, Japan.
- Weed, C. M. 1897. The Golden-Eye or Lace-Wing Fly. *The American Naturalist* 31(366): 500–502.
- Westwood, J. O. 1839. An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families [vol. 1]. London: Longman, Orme, Brown, Green, and Longmans, xii + 462 pp.
- Westwood, J. O. 1840. An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families [vol. 2]. London: Longman, Orme, Brown, Green, and Longmans, xi + 587 + [i] + 158 pp.
- Zhao, C., Liu, X., and D. Yang. 2014. Wing base structural data support the sister relationship of Megaloptera and Neuroptera (Insecta: Neuropterida). *PLoS One* 9(12): e114695.

## Chapter 4

Wing Tracheation in Chrysopidae and Other Neuropterida (Insecta):

A Resolution of the Confusion about Vein Fusion<sup>1</sup>

---

<sup>1</sup> Breitzkreuz, L. C., Winterton, S. L., & Engel, M. S. (2017). Wing Tracheation in Chrysopidae and Other Neuropterida (Insecta): A Resolution of the Confusion about Vein Fusion. *American Museum Novitates* (3890), 1-44.

## Abstract

The wings of insects are one of their most prominent features and embody numerous characters and modifications congruent with the variety of their lifestyles. However, despite their evolutionary relevance, homology statements and nomenclature of wing structures remain understudied and sometimes confusing. Early studies on wing venation homologies often assumed Neuropterida (the superorder comprising the orders Raphidioptera, Megaloptera, and Neuroptera: snakeflies, alderflies and dobsonflies, and lacewings) to be ancient among Pterygota, and therefore relied on their pattern of venation for determining groundplans for insect wing venation schemata and those assumptions reciprocally influenced the interpretation of lacewing wings. However, Neuropterida are in fact derived among flying insects and thus a reconsideration of their wings is crucial. The identification of the actual wing venation of Neuropterida is rendered difficult by fusions and losses, but these features provide systematic and taxonomically informative characters for the classification of the different clades within the group. In the present study, we review the homology statements of wing venation among Neuropterida, with an emphasis on Chrysopidae (green lacewings), the family in which the highest degree of vein fusion is manifest. The wing venation of each order is reviewed according to tracheation, and colored schemata of the actual wing venation are provided as well as detailed illustrations of the tracheation in select families. According to the results of our study of vein tracheation, new homology statements and a revised nomenclature for veins and cells are proposed.

## Introduction

One of the most conspicuous traits among the majority of insects are their wings. The winged insects (Pterygota) comprise over 98% of hexapod diversity (Grimaldi and Engel, 2005; Engel, 2015), and their wings have allowed them to disperse effectively, locate resources, and evade predators. In addition, wings have been coopted into numerous alternative functions, ranging from protection and thermoregulation to concealment and communication, or in numerous instances have been lost outright (Grimaldi and Engel, 2005; Engel et al., 2013). Wings and flight appeared first among the insects (Engel et al., 2013), and extend deep into the early history of the class, with evidence of pterygotes in the earliest Devonian (Engel and Grimaldi, 2004). Given their comparatively flat form and durability, wings preserve well and it is therefore not surprising that the fossil record of insects is largely comprised of the remains of wings. Yet, despite their seeming simplicity, wings have left many entomologists exasperated in many regards, not the least of which has been in deducing their evolutionary origin. With their often easily discerned pattern of veins, crossveins, and markings extending through the main body of the wing, it is easy to understand why considerable attention has been given to vein homology and function. While many have sought a record of pterygote evolutionary history written out in the venation of wings (e.g., Brauer, 1885; Handlirsch, 1906, 1907, 1908; Comstock, 1918; Martynov, 1924, 1925, 1938), clear homologies and patterns have at times vexed even the most distinguished of morphologists.

The wing venation of insects has been a matter of contention and controversy for well over a century (e.g., Hagen, 1870; Adolf, 1879; Brauer, 1885; Redtenbacher, 1886; Brauer and Redtenbacher, 1888; Comstock, 1918; Lameere, 1922, 1923; Martynov, 1924, 1930; Needham, 1935; Hamilton, 1972a), and while many fundamental elements have been established an equal or greater number of details remain fiercely debated (e.g., Béthoux and Nel, 2001, 2002; Kukulová-Peck and Lawrence, 2004; Rasnitsyn, 2007; Béthoux, 2008; Engel et al., 2013; Prokop et al.,

2017). In more recent history, confusion over vein homologies, combined with perceptions of either putative lability or overconservatism within a given lineage, has led some researchers to discount the systematic value of wings in favor of genitalic structures. Characters of female and particularly male genitalia are certainly effective for species-level identification, or recognition of groups of related species (e.g., Aspöck, 1986), but this does not preclude valuable information from wings. In fact, wings remain an important source of character data for estimating relationships among insects at various levels of interest.

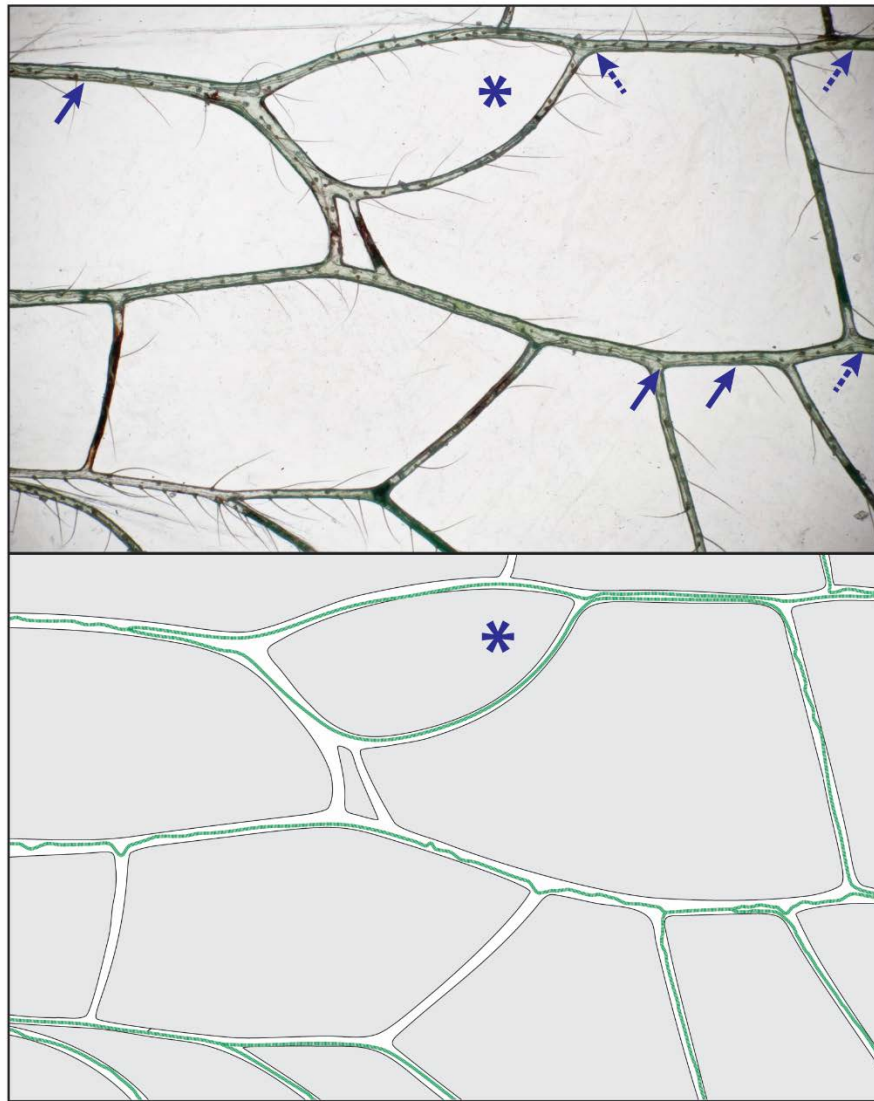
In many insect lineages there is a disjunction between the actual venation (including fusions and losses) and what is visible across the wing, the result of total or partial fusion, or even loss of particular vein sections. It is this ambiguity between the actual and apparent venation that has resulted in difficulties in interpreting vein homology and many subsequent controversial interpretations. Apparent venation refers to the simple pattern observed macroscopically, whereas actual venation, according to one hypothesis, should take into consideration the paths and trajectories of the tracheae that form these veins internally (e.g., Needham, 1903). The use of tracheal trajectories as a proxy for actual venation has stimulated discussion about the validity and extensibility of using tracheation for homology determinations (Ross, 1936; Fraser, 1938; Fennah, 1944; Whitten, 1962; Carpenter, 1966), and there are reasons why tracheae are not perfectly concurrent with the final, observed venation in a developing wing. While the complete notion of a one-to-one correspondence between tracheae and veins in the origin of wings may not be settled, nor do their courses match those of veins in every instance, some broad patterns exist and should therefore not be dismissed. Tracheae extend only through the longitudinal veins and thus provide evidence for fusion otherwise rendered hidden by the apparent venation (e.g., Fraser, 1943; Béthoux, 2005; Béthoux and Wieland, 2009).



Patterns of tracheation in insect wings, particularly by looking through various stages of wing development, were once broadly explored (e.g., Comstock and Needham, 1898a, 1898b, 1898c, 1898d, 1898e, 1898f, 1898g, 1898h, 1899a, 1899b, 1899c; Comstock, 1918; Withycombe, 1922). Such work subsequently fell out of fashion and was dismissed cavalierly primarily because a few cases blocked a comprehensive explanation for all taxa owing to tracheal capture or differences between pupal wing pads and the adult wing (e.g., Fraser, 1938; Holdsworth, 1942; Fennah, 1944; Whitten, 1962; Wootton, 1965; Carpenter, 1966). It is true that the “pre-tracheation” hypothesis (Needham, 1903, 1935; Comstock, 1918) incorrectly asserts that the tracheae form first and separate the layers in the developing wing, and thereby do not actually form the final veins, and instead run through the vein lacunae. Nevertheless, the course of the tracheae may serve as a reliable marker for ascertaining vein identities as there remains in many taxa a correlation between tracheae and the final veins. Indeed, the pattern of tracheation in many lineages largely reflects the course of sectors of the wing, and therefore remains an important body of evidence for establishing elements of vein homology, albeit not the sole source. The tracheae are particularly useful in locating sections where the longitudinal veins have changed course, with segments (abscissae) appearing like crossveins in places, and fused. In such locations, the two original tracheae can be found adjoining within the course of a single “apparent” vein (thus, demonstrating fusion at that point) (e.g., see fig. 1). As with most patterns in evolution, there are often exceptions, and universal statements require a list of examples where they do not hold; even Comstock (1918) alluded to such exceptions for tracheation. Tracheation certainly points to an exceptional case, and some of the rancor directed at Needham’s “pre-tracheation hypothesis” was unwarranted. Accordingly, in those cases where there is considerable confusion over the identity of particular vein elements,

recourse to tracheation may serve as an important indicator of the original homology, especially when placed in the context of other forms of evidence.

The insect superorder Neuropterida comprises the familiar lacewings, antlions, owlflies, dobsonflies, hellgrammites, snakeflies, etc. Among the hyperdiverse Holometabola, extant neuropteridan diversity seems meager, with fewer than 6500 species collectively. Nonetheless, they have some of the most spectacular wings, whose mesh of veins makes their general moniker of “lacewing” very appropriate. This netted threadwork of veins, however, has been equally frustrating to study. Vein fusion has fueled confusion relative to the “apparent” versus “actual” pattern of the sectors in the neuropteridan wing. Early entomologists assumed those wings with a large number and latticework of veins to be primitive, and therefore used “Neuroptera” as a proxy for ancestral wing venation (Redtenbacher, 1886; Comstock, 1918). At the time, the order included many unrelated insect groups such those today classified as Odonata, Ephemeroptera, Plecoptera, Embiodea, Isoptera, Psocoptera, Mecoptera, and even Trichoptera, all gathered together as “Neuroptera” (e.g., Latreille, 1807, 1817; Stephens, 1835; Westwood, 1839, 1840; Rambur, 1842). In fact, the neuropterous orders as we understand them today include only Megaloptera, Raphidioptera, and Neuroptera sensu stricto (the latter sometimes referred to as Planipennia) and, as members of the derived Holometabola, Neuropterida are phylogenetically distant from the ancestral pterygote and its general wing traits. Nonetheless, lacewings have been integral in the historical development of systems of vein nomenclature and homology, and especially the green lacewings (Chrysopidae). Naturally, establishing correct vein identities in chrysopids is important for the systematics of this family, and also for interpreting those patterns present in other neuropteran lineages, given that early work on Chrysopidae served as the basis for historical interpretations across Neuroptera.



**Figure 105.** Photomicrograph and line drawing of *Chrysopa nigricornis* Burmeister show detail of mamp1 (first intermedial cell, indicated by asterisk) and surrounding area, illustrating the dissimilarity between apparent and actual venation, ventral view. Solid arrows indicate points of tracheal division, dashed arrows indicate fusions of veins with multiple tracheae present; course of tracheae indicated by green lines.

In an attempt to resolve controversies regarding vein identities in the wings of chrysopids and homologies for use in phylogenetic studies of the family, we employed corroborating evidence from tracheation across the entire Neuropterida. We have examined a selection of chrysopids representing the spectrum of extant diversity, as well as representatives of nearly all neuropterous families and orders so as to place the pattern found in Chrysopidae within a broader context. By

adopting the use of tracheation, we do not imply anything regarding wing origins as it relates to the defunct “exite” or “gill hypothesis” for overall wing homology, that is, wings as serial homologs with abdominal gills found in some crown-group naiads (e.g., Landois, 1871; Wigglesworth, 1976; Kukulová-Peck, 1978, 1983, 1991), which is in opposition to the “paranotal hypothesis” (e.g., Müller, 1873a, 1873b, 1875; Crampton, 1916; Hamilton, 1971, 1972a; Wootton, 1976; Rasnitsyn, 1981). Instead, wings have been more recently determined to be of largely notal origin with the incorporation of subcoxal elements to form an articulation at the base, also known as the dual model hypothesis (e.g., Grimaldi and Engel, 2005; Niwa et al., 2010; Engel et al., 2013; Prokop et al., 2017). In this context, the tracheae of the wing represent nothing more than similar tracheation of any body structure. We resurrect tracheation as a method for investigating wing vein identities, as an additional line of evidence. What general consequences this might have for the interpretation of venation across all Pterygota, particularly the early diverging lineages of Ephemeroptera, Triplosoptera, Palaeodictyoptera, and Odonoptera, is beyond the scope of the present work. Similarly, we fully recognize that there are instances where tracheae may be more labile and misleading and should not be adopted wholeheartedly in the absence of other evidence. Nonetheless, we do provide some potential implications our findings have regarding the controversial fate of the media anterior (MA) in Neuroptera.

## Wings

Comprehensive reviews of insect wing structures and venation have been published over the centuries and are not repeated here. For pertinent reviews of these subjects, we direct the reader to Snodgrass (1909, 1935), Hamilton (1971, 1972a, 1972b, 1972c), Wootton (1979, 1992), Brodsky (1994), and Engel et al. (2013). Nonetheless, some details are useful to mention.

The insect wing is formed by an outgrowth of the body at the juncture of the meso- and metathoracic nota and the upper portion of their corresponding pleura. For Holometabola, wings develop from imaginal discs in the larva, forming in the pupal wing pads; in hemimetabolous insects the wing pads develop externally in nymphal stages. The wing initially extends outward as a thin, flat body cavity forming two layers (upper and lower) of the wing body sac. These membranes lay down the cuticle and elongate, tubular cavities (lacunae) form between them. Finally, tracheae enter the lacunae and provide the wing with nutrients. In the adult vein these often sclerotized lacunae are visible as the veins with the tracheae detectable within them.

When the wing is outstretched, three major regions can be described: the remigium takes up the majority of the wing's surface and encompasses the space with the most sectors (costa to cubitus) anterior to the claval furrow, whereas the anal and jugal areas often take up only a small portion of the posterior wing surface, especially in more derived insect lineages. The remigium is separated into two parts by the median-flexion line, which, as for all other principle folds, runs from base to apex. The claval furrow separates the remigium and anal area, while the jugal fold separates the latter from the jugum, which often forms a small lobe (jugal lobe). The anal area can be divided by an anal fold.

Winged insects are typically divided into paleopterous and neopterous forms. Paleopterous wings have different articulatory sclerites, ranging from the comparatively simple wing base of Odonatoptera (with two axillary sclerites) to the complex system of plates in the Ephemeropterida (Matsuda, 1970). These orders can only bring their wings together over the body, fully extended, but not folded flat over the abdomen and abutting the body. The exception is the extinct Diaphanopteroidea, which evolved a mechanism of neopterous folding, convergent with Neoptera

(Grimaldi and Engel, 2005). Neoptera have a distinctive arrangement of three axillary sclerites and median plate, the form of the third axillary sclerite being critical to the folding of the wings.

The main features in a wing are the series of longitudinal sectors, or principal veins. These are, from anterior to posterior, denoted in the Comstock and Needham (1898a, 1898b, 1898c, 1898d, 1898e, 1898f, 1898g, 1898h, 1899a, 1899b, 1899c) tradition as: costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A) (this original nomenclature was set forth by Redtenbacher, 1886). These sectors are formed of hollow spaces through which run extensions of the tracheal system (originally consisting of a single trachea per sector), and they are often modified through ramified branching, fusion with other sectors, or simple loss of one or more sections. These alterations reflect the interplay between historical patterns resulting from inherited transformations (i.e., phylogenetic inertia), and organization imposed by the flight mechanics peculiar to the species under investigation (i.e., functional constraints). Crossveins often occur between the longitudinal sectors, which are hollow and do not contain portions of the wing tracheae (or at most have minute, tapering portions of tracheoles). This permits comparatively easy identification of true crossveins relative to the principal sectors, even when the latter are considerably modified (e.g., Tillyard, 1916; Comstock, 1918; Withycombe, 1922). Crossveins are usually denoted by the two longitudinal sectors (or portions of those sectors) they connect, and then numbered from proximal to apical. Due to the association of each longitudinal vein with a different axillary element in the wing base, we can determine that, for example, R in one order is the same as R in another order, and thus underpinning our hypothesis of comparative homology at any taxonomic level. Therefore it follows that the costa is associated with the humeral plate, the subcosta with the first axillary sclerite, the radius with the second, media and cubitus with the median plate, and the anal veins with the third axillary sclerite. In the radius, media and cubitus

there is a distinction between anterior and posterior, which can be simple branching and size differential. Different ways of naming these sectors were proposed by Kukalová-Peck (1991) and Béthoux and Nel (2001, 2002) ( $\alpha$  and  $\beta$  branches) (table 1). For this study, we define the anterior and posterior branches as the branches resulting from the first split of a longitudinal vein. In the case of Hemerobiidae and Ithonidae, where multiple R branches are present we cannot make a certain assessment as to whether RA or RP is bearing the multiple branches. Historically, the determination of anterior and posterior branches was decided by examining corrugation or pleating, but in higher taxa this feature is often lost. We here assume that the bifurcation points are homologous to the observed conditions in extinct taxa in which corrugation can be observed.

**Table 1.** Comparison of systems of insect wing vein nomenclature as it applies to Neuropterida.

present work		Kukalová-Peck (1991)		Béthoux (2005)		Comstock (1918)	
C		C		C		C	
Sc		Sc		ScP		Sc	
R	RA	R+MA	RA	R	RA	R	RA
	RP		RP+MA		RP/RS		RS
M	MA	M	MP1+2	M	MA	M	MA
	MP		MP3+4		MP		MP
Cu	CuA	Cu	CuA	Cu	CuA	Cu	CuA
	CuP		CuP		CuP		CuP
A	A1	A	AA1	A	AA1	A	A1
	A2		AA2		$\alpha$ AA2		A2
	A3		AA3		$\beta$ AA2		A3
	A4		AP		$\gamma$ AA2		A4
	...		...		...		...
J		J		J		J	

Although there is a standardized way of naming veins, there is no universal nomenclature that covers the spaces between them, or cells. The names that are applied to cells are quite heterogeneous, and vary depending on the order and author. Sometimes cell nomenclature is based on their relative position to other markers, such as the submarginal cells in most Hymenoptera, or

in relation to the bounding veins. In Chrysopidae there are named cells that are of importance, such as the intramedian (*im*) or the distal cubital (*dcc*) cells (fig. 16A) (e.g., Brooks and Barnard, 1990).

Entomologists working on different lineages of Pterygota sometimes use subtle modifications of the Comstock-Needham-Redtenbacher vein nomenclature, but overall the fundamentals of the present system differ little from that established by Comstock and Needham. Kukalová-Peck and colleagues (1978, 1983, 1991, 1997, 2008, 2009; Kukalová-Peck and Richardson, 1983; Riek and Kukalová-Peck, 1984; Kukalová-Peck and Brauckmann, 1992; Haas and Kukalová-Peck, 2001; Kukalová-Peck and Lawrence, 2004; Kukalová-Peck et al., 2009) have provided the most extensive recent revision of the Comstock-Needham system as well as other hexapod appendicular structures, attempting to incorporate considerable, albeit controversial (Béthoux and Briggs, 2008; Béthoux et al., 2008), evidence from paleontological data. The Kukalová-Peck venational modification effectively considers all the longitudinal sectors to have been paired in the ancestral insect wing, and relies on an archetype with some hypothetical veins not present in any modern or fossil wing (refer to Discussion, below). This system considers each sector to have had an anterior and posterior ramus, giving costa anterior, costa posterior, subcosta anterior, subcosta posterior, and so forth. There may be some merit to ScA and ScP in some taxa, such as in Palaeodictyoptera, Odonata, and even Symphyta; however, this would require a much more extensive study across pterygotes. In Neuroptera C and Sc do not bifurcate, but all other sectors split into an anterior and posterior branch subbasally. Most neuropteran families show no to little fusion of longitudinal veins, but there are several autapomorphies in the wing venation, including fusions, with the highest degree of fusion present in Chrysopidae (refer to Results, below).



## Wing Venation of Chrysopidae

Comstock (1918), summarizing his series of earlier papers with Needham, utilized the tracheation of pupal wing pads to explore vein identities across insects, and this work remains the most extensive of its kind. In that work, the forewing venation of *Chrysopa nigricornis* Burmeister was discussed, and with the same pattern of venation as that presented here. Comstock (1918) summarized information for all currently recognized families of Neuropterida and made some general conclusions about wing venation patterns, and suggested an extensive fusion in the chrysopid fore- and hind wing. In fact, the wings of Chrysopidae display the greatest degree of fusion among Neuroptera; as such, there is much difficulty in identifying the actual course of the longitudinal veins and especially of RP, MA, and MP. This difficulty results from the formation of pseudoveins in the fore- and hind wing, which appear to be single veins but are actually the product of several fused longitudinal and crossveins. Later, Tillyard (1916) undertook a similar investigation of developing pupal wings across Neuropterida, and based on this he suggested some slight modifications to interpretation of chrysopid wing venation. While his overall scheme was similar to that of Comstock (1918), not all of the veins across the remigium (i.e., each vein from proximal origin to wing margin termination) were accounted for in Tillyard's discussion. He concluded that there is less fusion in the chrysopid wing than Comstock had proposed. Eight decades would pass before the subject would be revisited in any considerable detail. Adams (1996) revived the tracheation approach and revised the homology of neuropteran wing venation, particularly basing his conclusions on the venation established by Comstock, as well as Tillyard's illustrations of pupal wings. Adams' interpretation of the chrysopid wing did not contain an inordinate degree of fusion between veins and, like Tillyard's before him, did not account for all the longitudinal veins (i.e., not every vein could be traced from its proximal origin to its termination at the wing margin).

Despite more than a century of concerted effort investigating neuropteran wing venation, the latticework of chrysopid wing veins remained a complicated matter to be unraveled. When examining many of the individual sections of veins, particularly those near the base and posterior margin and seemingly composed of the abscissae of RP, MA, MP, and CuA, it remains confusing at any given point which vein elements are involved. Accordingly, the cells with their borders demarcated by these vein elements are unclear, particularly as one compares increasingly divergent wings. The present contribution is an attempt to revisit this important topic of establishing vein homologies. Aside from the usual means of ascertaining vein identity (e.g., position, connection, axillary sclerite articulation), we employ tracheation in mature wings as corroborating evidence and in the tradition of Comstock, Needham, Tillyard, and Adams.

We differentiate between *apparent* and *actual* wing venation. By apparent wing venation we mean the perceived venation without considering tracheae. In the actual wing venation, the longitudinal veins are defined by the paths of the tracheae. As an example, in Chrysopidae the apparent venation would include the pseudoveins such as PsM (pseudomedial) and PsC (pseudocubital) (sensu Adams, 1996; Brooks and Barnard, 1990; fig. 16A), whereas the actual venation is based on the longitudinal veins forming these composite structures (fig. 16B).

Longitudinal veins are represented by capital letters, crossveins and cells by lowercase letters. The abbreviation for crossveins is a combination of the two longitudinal veins that are connected by said crossvein and its number (numbered from proximal to apical). For example, if we address the second crossvein between MP and CuA, the abbreviation is 2mp-cua. Cells are described by italicized abbreviations without hyphenation (e.g., *im* or *mamp1*) (see Discussion for detailed description of vein and cell nomenclature, below).

## Material and Methods

Tracheae are best visible when examining the ventral surface of the wing under high magnification and with transmitted light. Preferably, eclosed (nonteneral) adult pinned specimens with spread wings were examined to observe the entire wing and wing base. There is no special preparation necessary, rendering this process noninvasive and allowing observation of tracheae even in rare material. The wings of a few Neuroptera do not allow the easy examination of tracheae, either because they are too small or the veins are too thickly sclerotized or infuscate to see through (without removal and clearing), but overall such wings did not show any obvious abnormalities. Tracheae are visible in most, but not every specimen, possibly due to the method of fixation. Aside from other evidence, such as corrugation or pleating, especially in fossils, we mainly rely on adult tracheation for the determination of the actual venation pattern. In Neuroptera there are currently no documented cases in which the pupal and adult tracheation were not identical (e.g., Tillyard, 1916), and in all examined species we could not find discrepancies.

We examined at least two genera of each extant neuropteridan family, except for Coniopterygidae, Rhachiberothidae, and Nevrorthidae, where no or insufficient material was available. For these families we extracted information from the literature. We attempted to sample putatively basal groups for each family, but were limited by availability of suitably preserved material (i.e., wings spread, tracheation visible). Material examined is deposited in the collection of the California State Collection of Arthropods, Sacramento, California, and the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas. The presentation of taxa is loosely organized around those relationships recovered by Winterton et al. (2010, 2017), at least in the sense of not recognizing suborders Nevrorthiformia, Hemerobiiformia, and Myrmeleontiformia within Neuroptera. Instead, we use a series of monophyletic superfamilies but not in an order that matches their pattern of branching from the base of Neuroptera based on the

classification proposed recently by Engel et al. (2018). The current numbers of species of the families and subfamilies were extracted from the Lacewing Digital Library (Oswald, 2017). Wings were examined with Nikon SMZ 1500 and Olympus SZX7 stereomicroscopes, using transmitted light. Line drawings were produced in Adobe Illustrator CC2015 on the basis of photographs of wings from representative species. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens as well as an Olympus DP72 digital camera attached to an Olympus SZX16 stereomicroscope, and then arranged in Adobe Photoshop and Illustrator CC2015. Abbreviations for wing veins and cells are provided in the legend to figure 2.

## Results

In the wings of Neuropterida, “actual” and “apparent” patterns of venation are not always identical. Tracheae are present within the longitudinal veins of all insect wings. These tracheae are visible in the adult wing and follow the same paths as those in the pupal wing pads of Neuropterida, among the taxa we examined. Tracing the tracheae allows for the determination of these “actual” longitudinal sectors, and it is possible to determine points of fusion between these due to the presence of multiple tracheae (fig. 1) within a single vein abscissa. In addition, the precise points of ramification of particular tracheal stems can be observed (fig. 1), and this branching gives rise to the broader fields of particular vein systems (e.g., the medial field encompasses the space between the various branches of the medial stem). Crossveins can appear superficially identical to longitudinal veins but differ by the lack of tracheae running through them; though minute tracheoles can enter, they rarely persist. This distinction has proven useful in detecting the actual pattern of venation in the various families of Neuropterida.

## Lineages of Neuropterida

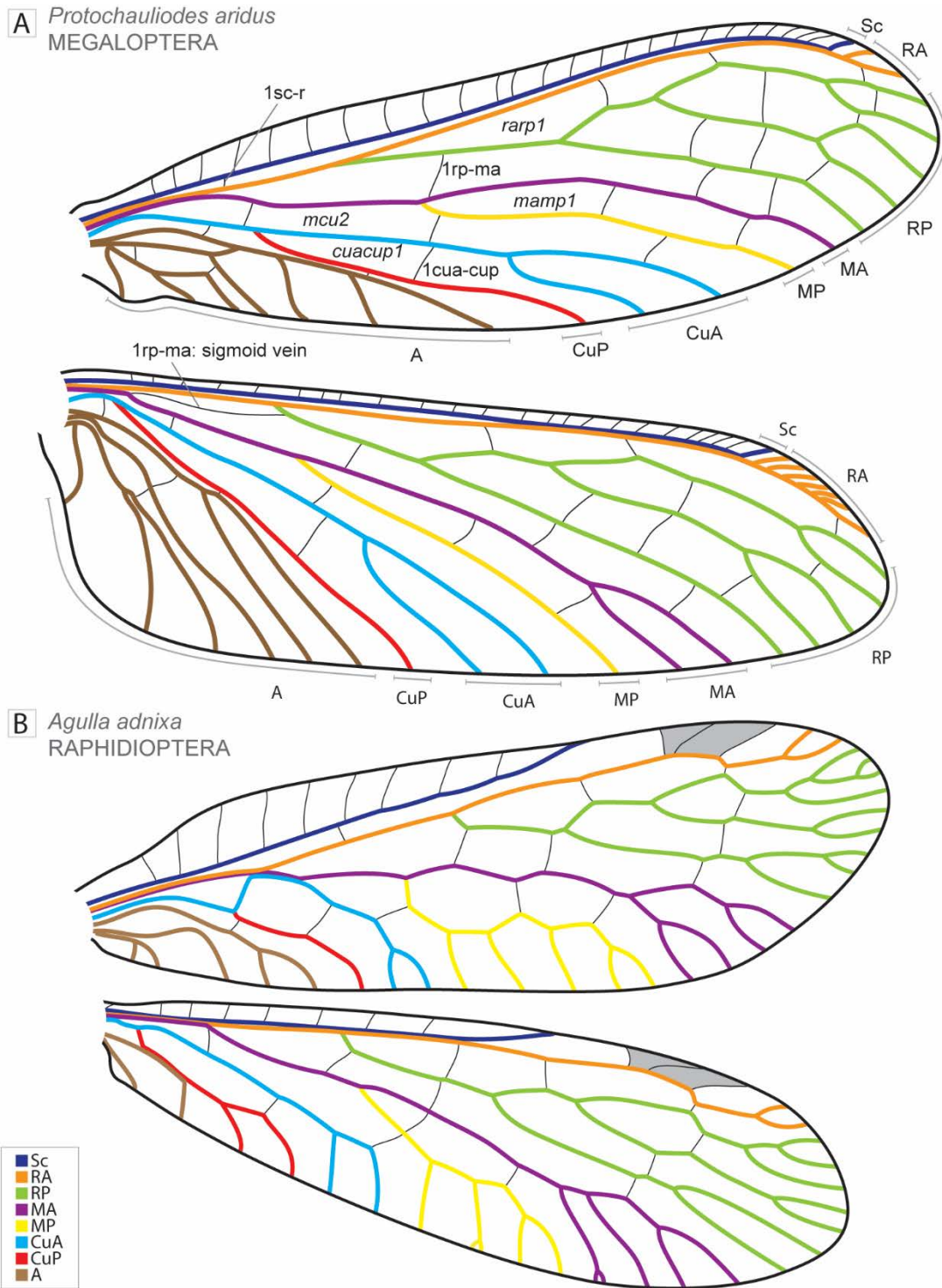
As noted earlier, the wings of many Neuropterida are comparatively simple, possessing few or no fusions among the sectors. In several families the apparent and actual patterns of venation are identical and the identity of the longitudinal veins can be determined easily without reliance on extra evidence such as tracheation. In such cases, the usual sectors can be identified by their proximal connections to individual axillary sclerites in the wing base and articulation. Each family has a unique pattern of wing venation, and some have clear autapomorphies in vein fusion, recognizable through the study of tracheae as described here.

## Order Megaloptera (Figure 2A)

Megaloptera comprise 373 species in two distinct lineages—the large dobsonflies, fishflies, and hellgrammites of Corydalidae (295 species), and the diminutive alderflies of Sialidae (78 species). The megalopteran wing is slightly elongate, there are no differences between the apparent and actual venation, and the general pattern of tracheation present in corydalids is identical to that observed in Sialidae. As in Psychopsidae, Hemerobiidae, Nevrothidae, and many Osmylidae there are no tracheal fusions in the fore- or hind wing. The longitudinal veins extend across the length of the remigium without considerable changes to their courses over this distance, and RP does not occupy a disproportionately large area of the wing. The “sigmoid vein” of the corydalid hind wing (and other neuropteridan hind wings with such a crossvein) has been a subject of discussion for the last century (e.g., Martynov, 1928; Tillyard, 1932; Carpenter, 1940). In the hind wing, the first crossvein between R and M (1r-m, 1rp-m, or 1rp-ma, depending on the lineage) can be straight or sigmoid shaped. When it is arched (as in fig. 8), the crossvein is usually elongate and more longitudinal in orientation (rather than transverse), and has traditionally been dubbed the

sigmoid vein. The presence of a sigmoid vein has been used as evidence for a possible fusion of MA into R or RP (Martynov, 1928). Within this line of argumentation, the sigmoid vein is considered a vestige of MA. This means that MA's proximal origin from the stem of M is revealed by the sigmoid vein and in those taxa where this crossvein is more transverse and short, it has taken on a more typical crossveinlike appearance as part of its reduction and attachment to R or RP. The absence of tracheation in the sigmoid vein was dismissed as it was assumed that the tracheae of R and MA were proximally fused beyond recognition in extant taxa, and therefore secondarily lost in this abscissa of MA. While this is a possibility, the argument relies on a combination of absence of evidence, ad hoc supposition of complete fusion, and the peculiar reappearance of the MA trachea in the portion of its branch beyond the purported RP+MA fusion (i.e., present in the apical sector of MA beyond the sigmoid vein and after it re-separates from RP as the posteriormost branch of the radial field). The presence of the sigmoid vein (i.e., the more elongate, longitudinal, proximal crossvein between R and MA, RP and MA, or RP and M) serves as some of the primary evidence for proximal fusion of R or RP and MA, along with a reversal in corrugation (see Discussion, below). In addition, in megalopteran wings the costal crossveins are simple (not forked), there is no recurved humeral vein (i.e., first costal crossvein, which is curved toward the wing base in some families and is often pectinately forked), and trichosors (i.e., short veinlets without tracheation on the wing margin that are typical of many Neuroptera) are lacking. The pterostigma varies from absent to marked.

Species examined: *Protochauliodes aridus* Maddux (fig. 2A); other species examined but not figured: *P. cascadius* Evans, *Sialis nevadensis* Davis, and *Sialis* sp.



**Figure 106.** Line drawings of forewings and hind wings of Megaloptera and Raphidioptera. A. *Protochauliodes aridus* Maddux (Megaloptera), longitudinal veins: Sc (subcosta; dark blue), RA (radius anterior; orange), RP (radius posterior; green), MA (media anterior; purple), MP (media posterior; yellow), CuA (cubitus anterior; light blue), CuP (cubitus posterior; red), A (anal; brown); crossveins: 1rp-ma (first crossvein between RP and MA), 1cua-cup (first crossvein between CuA and CuP); cells: rarp1 (first interradial cell); mamp1 (first intermedial cell), mcu2 (second medial cell). B. *Agulla adnixa* (Hagen) (Raphidioptera).

## Order Raphidioptera (Figure 2B)

Modern snakeflies comprise approximately 248 species in two comparatively similar families, Raphidiidae and Inocelliidae, that differ in the presence or absence of pterostigmal crossveins among other traits. The snakefly wing is neither strongly elongate nor rounded. Unique to Raphidioptera is a subbasal fusion of M and CuA (fig. 1B), which in its form is not present in any other Neuropterida. CuA arches anteriorly to join M, taking on a form that makes it look like the first apparent crossvein between M and CuA. CuA then shortly diverges from M. In snakefly wings R and M in the forewing are proximally fused, or nearly so, sometimes appearing as a single vein proximally, a feature also present in Sisyridae, most Chrysopidae, and Mantispoidea (i.e., Berothidae, Rhachiberothidae, and Mantispidae). In Raphidioptera this fusion is present in the fore- and hind wing; however, the individual tracheae representing R and M are distinct within the fused vein at its base. Accordingly, this fusion is not so derived as to be obscured by complete fusion of their tracheal stems. The costal crossveins are simple, a recurved humeral vein is absent, trichosors are absent, and in the hind wing crossvein 1r-m is simple. The pterostigma is strongly marked in most taxa.

Species examined: *Agulla adnixa* (Hagen) (fig. 2B); other species examined but not figured: *Agulla* sp.

## Order Neuroptera Superfamily Myrmeleontoidea Family Psychopsidae (Figure 3)

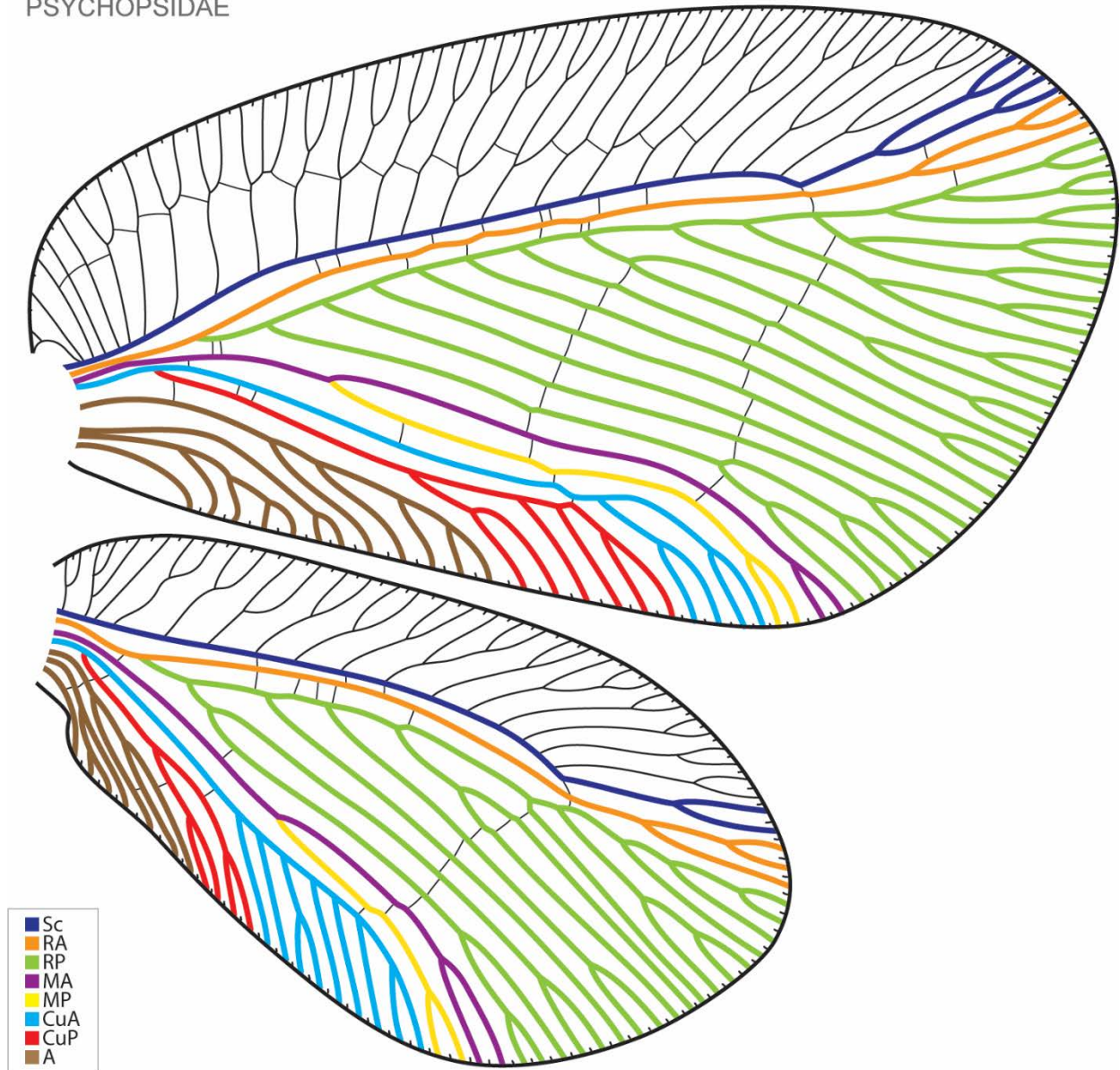
Silky lacewings are a small group with about 26 extant species in five genera; they have a disparate, relict distribution in the Oriental, Australasian, and southern Afrotropical regions



(Oswald, 1993; Bakkes et al., 2017). The large, broad wings of Psychopsidae are characterized by a dominant costal and radial sector, but all longitudinal veins are tracheated in correspondence with the branching pattern. No fusions are detectable in the fore- or hind wing. Apart from some Apochrysinæ and Myrmeleontidae, psychopsid wings are the only Neuropterida with a gradate series in the costal field (fig. 3). Crossvein 1r-m of the hind wing is simple and not sigmoidal in shape (i.e., not forming a so-called sigmoid or sigmoidal vein). The costal crossveins are forked, sometimes dichotomously; a distinct, recurved humeral vein is present; and trichosors are present along the entire wing margin (fig. 3). The pterostigma is inconspicuous in most taxa and weakly marked in few.

Species examined: *Psychopsis insolens* McLachlan (fig. 3); other species examined but not figured: *Psychopsis illidgei* Froggatt, *P. barnardi* Tillyard, *P. elegans* (Guérin-Méneville), *P. gracilis* Tillyard, *P. mimica* Newman, and *Zygophlebius leoninus* Navás.

PSYCHOPSIDAE



**Figure 107.** Line drawings of forewing and hind wing of *Psychopsis insolens* McLachlan (Psychopsidae); see figure 2 for explanation of abbreviations.

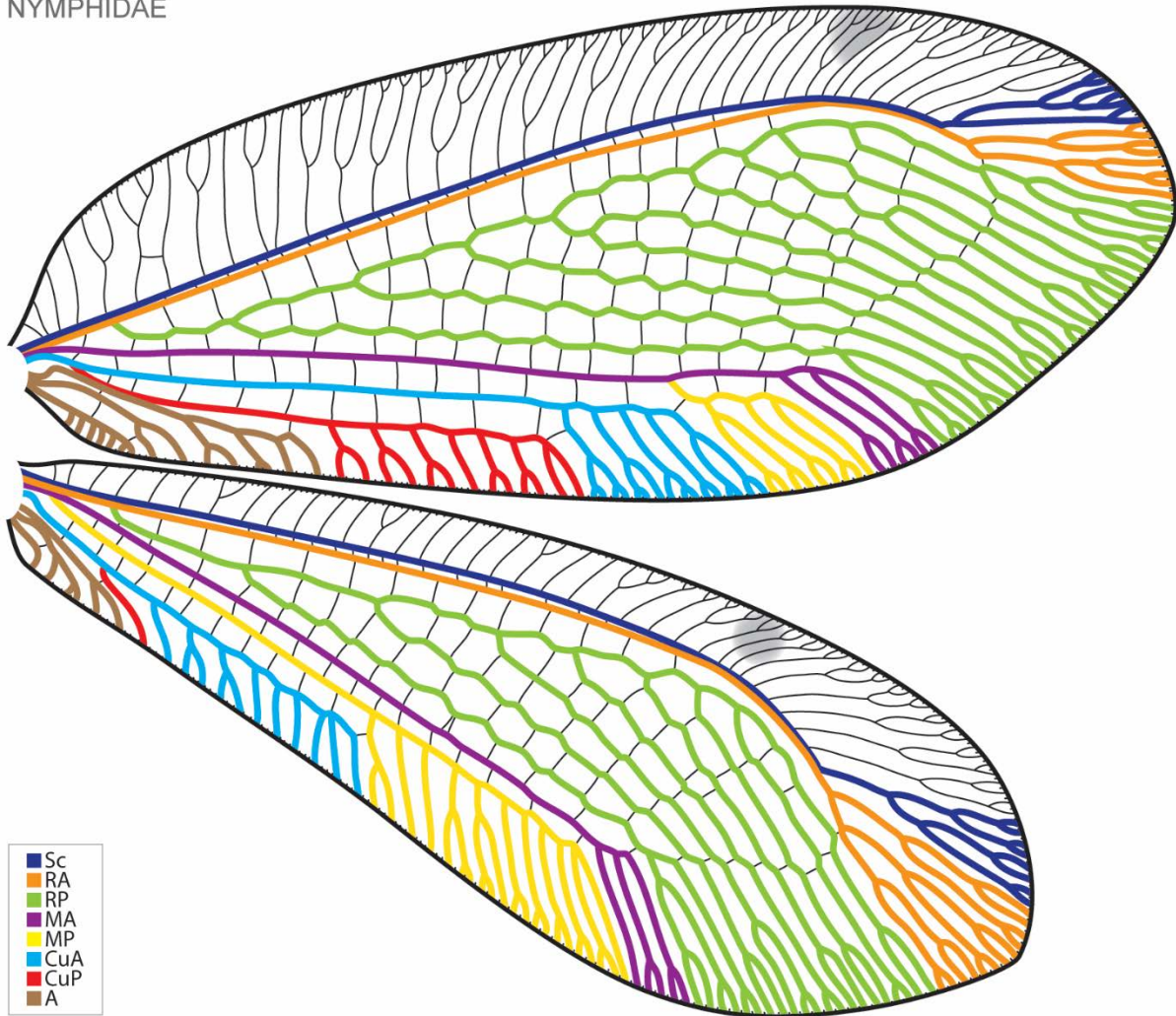
**Family Nymphidae**  
(Figure 4)

Split-footed lacewings are a small group and comprise 35 modern species endemic to Australasia. Nymphids have elongate to ovoid wings with a rather conservative pattern of wing venation with little secondary fusion, so the tracheae reflect the apparent venation. In the forewing, MP diverges from MA apically on the wing further than in any other Neuroptera except some

Osmylidae. Indeed, overall similarities between wings of distantly related Nymphidae and Osmylidae have led some authors to misplace fossil taxa in either family (e.g., Myskowiak et al., 2015). Nymphidae often have a large RP field with numerous crossveins forming a prominent reticulation (fig. 4), although this is known from other families as well. The only fusion present is Sc and RA at the level of the pterostigma. Crossvein 1rp-ma of the hind wing is short and not sigmoidal. The costal crossveins are forked, a recurved humeral vein is absent, and trichosors are present along the entire margin. The pterostigma is small, but present. A notable apomorphy for Nymphidae is the presence of thyridiate crossveins in the Sc-RA space. These crossveins originate on Sc but do not reach RA and are abbreviated presumably due to crossing the flexion line between the two longitudinal veins (Oswald, 1998; Shi et al., 2015).

SPECIES EXAMINED: *Myiodactylus osmyloides* Brauer (fig. 4); other species examined but not figured: *Osmylops armatus* (McLachlan), *O. ectoarticulatus* Oswald, *Nesydrion nigrinerve* Esben-Petersen, and *Nymphes myrmeleonoides* Leach.

## NYMPHIDAE



**Figure 108.** Line drawings of forewing and hind wing of *Myiodactylus osmyloides* Brauer (Nymphidae); see figure 2 for explanation of abbreviations.

## Family Nemopteridae (Figure 5)

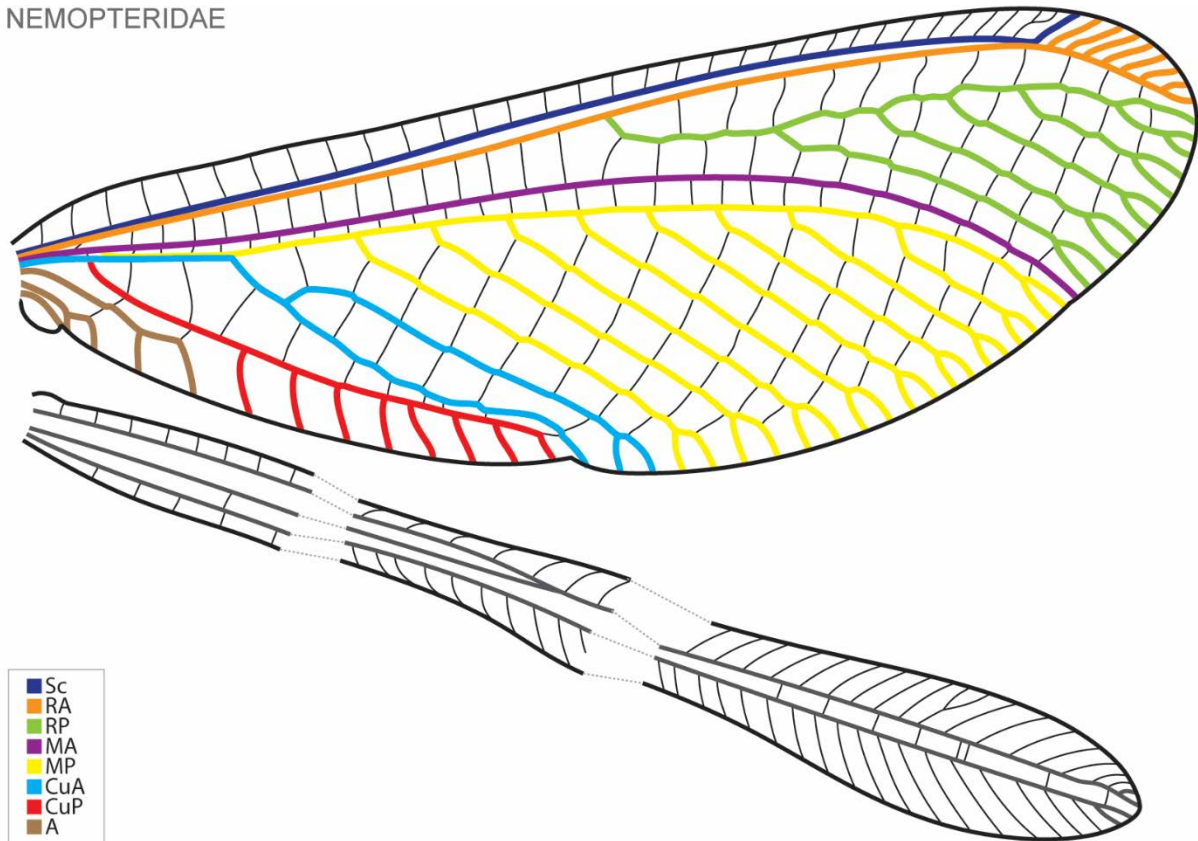
Spoon-wings and thread-wing lacewings comprise 146 extant species in two subfamilies, Crocinae and Nemopterinae, distributed in most biogeographical regions except the Nearctic. Nemopteridae have ovoid forewings, but are unique in their extremely elongate, petiolate hind wings; concomitantly the hind-wing venation is greatly reduced (fig. 4). In the forewing there is only one major fusion of the longitudinal veins, whereby MP originates basally and then almost immediately merges with CuA for a short distance (MP+CuA usually has a length bordering 4–5

ma-mp[+cua] crossveins) (fig. 5). The forewing RP originates near the middle of the wing, while MA is unbranched and comparatively unremarkable. By contrast, after its separation from CuA, MP produces a series of pectinate branches, creating a wide MP field along the posterior wing margin. Once MP and CuA diverge again, CuP has one principle fork. CuP has multiple marginal branches. The hind wing of Nemopteridae is greatly elongate and there is uncertainty about the identity of the veins. Three major longitudinal veins are present of which Sc can be identified easily, but the constitution of the two posterior veins cannot be assessed by examining the tracheation. These two veins are most likely a result of several fusions containing parts of R, M, and Cu. Due to the extensive amount of fusion in most of the hind wing further detailed examination of the wing venation, tracheation, and development is needed to determine homology. The costal crossveins are simple, there is no recurved humeral vein, and trichosors are lacking. The pterostigma is very small, but present.

Species examined: Undetermined genus (fig. 5, forewing), *Nemoptera sinuata* Olivier (fig. 5, hind wing); other species examined but not figured: *Halter halteratus* (Forskål), *Nemia costalis* (Westwood), and *Nemoptera coa* (Linneaus).



## NEMOPTERIDAE



**Figure 109.** Line drawings of undetermined nemopterine genus (forewing) and *Nemoptera sinuata* Olivier (hind wing) (Nemopteridae); see figure 2 for explanation of abbreviations.

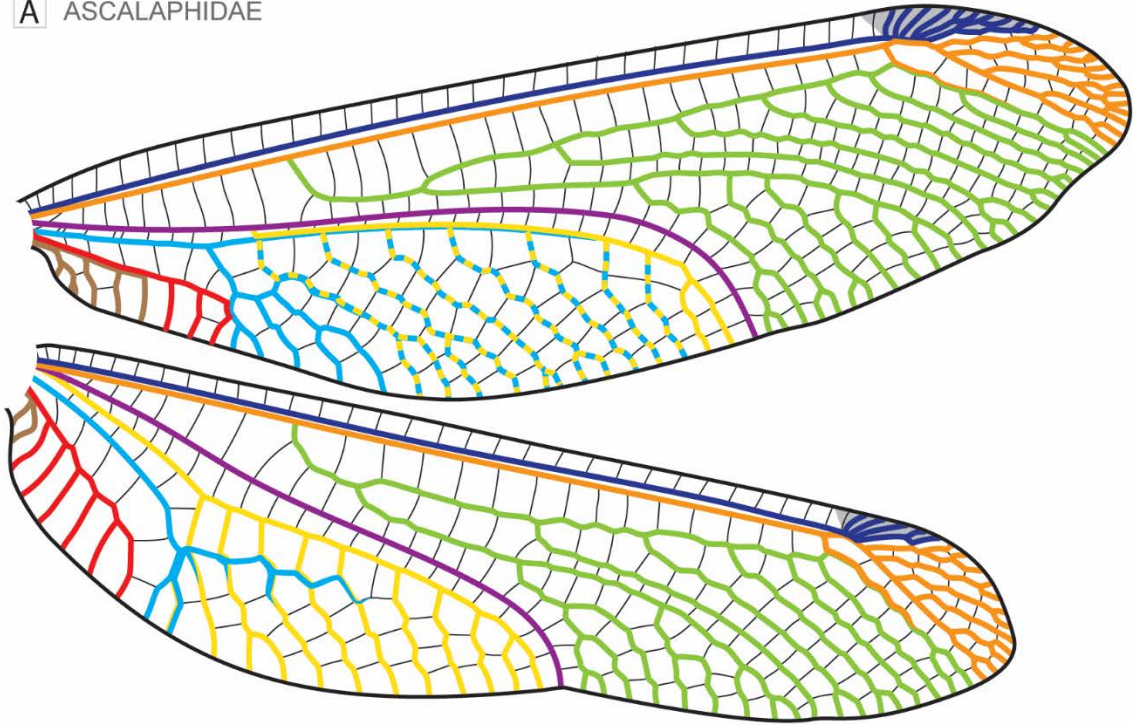
## Family Ascalaphidae (Figure 6A)

Owlflies comprise 431 extant species in three subfamilies, two of which are distributed worldwide. Ascalaphid wings are elongate and the forewing is characterized by a complete intermingling of MP and the anterior branch of CuA, thus forming an elongate MP+CuA. In the forewing MP diverges from MA, and is present as an apparent transverse crossvein; it then immediately fuses with CuA just apical to the first fork in CuA (fig. 6A). Two intermingled tracheae extend to the wing margin in MP+CuA and the branches originating from this sector can variably be assigned to MP or CuA; that is, the origin of the individual branch trachea are often visible and can confidently be assigned to either MP or CuA. Thus, in any given ascalaphid wing a particular branch of MP+CuA may either originate from the trachea of MP or from that of CuA,

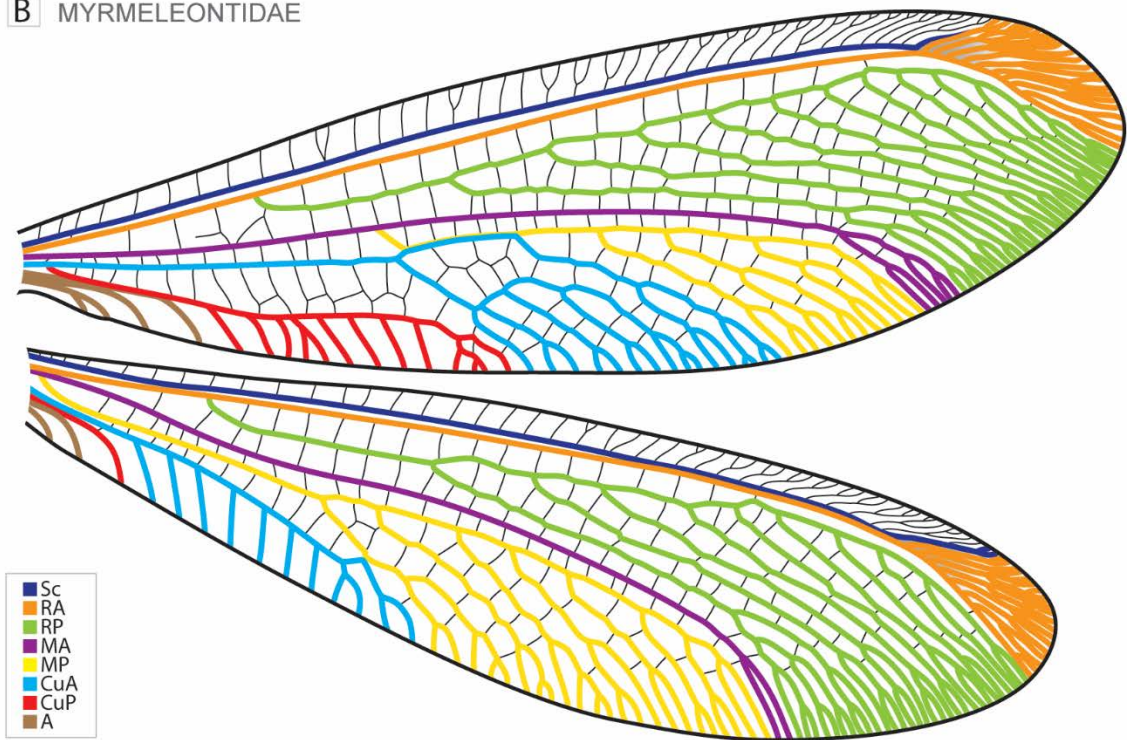
without a consistent pattern (hence the dotted pattern of colors used in figure 6A). As far as we have been able to observe, this is the most significant derivation in tracheation pattern among the lineages of Neuroptera. Otherwise, the apparent venation is similar to the closely related Myrmeleontidae, although the latter lack the overlapping and intermingled tracheae of MP+CuA. Like nemopterids, Ascalaphidae often have a simple MA, without branches, and this, along with the close association of MP+CuA, might be apomorphic for the Nemopteridae + (Ascalaphidae + Myrmeleontidae) clade. In the hind wing MP and CuA overlap only briefly in the marginal area and first MP branches (fig. 6A). The costal crossveins are simple, there is no recurved humeral vein, trichosors are lacking, and in the hind wing crossvein 1rp-ma is slightly curved. The pterostigma varies between almost unmarked to strongly marked.

Species examined: *Acheron trux* (Walker) (fig. 6A); other species examined but not figured: *Ascalobyas microcerus* (Rambur), *Libelloides italicus* (Fabricius), *Ululodes arizonensis* Banks, *U. bicolor* (Banks), and *Ululodes* sp.

A ASCALAPHIDAE



B MYRMELEONTIDAE



**Figure 110.** Line drawings of forewings and hind wings of an antlion and owlfly. A. *Acheron trux* (Walker) (Ascalaphidae). B. Undetermined species of Dendroleontini (Myrmeleontidae). See figure 2 for explanation of abbreviations.

Family Myrmeleontidae  
(Figure 6B)



Antlions are the largest group in Neuroptera with 1659 species and numerous subfamilies, although the classification is far from natural, with rampant paraphyly likely. The wings of Myrmeleontidae are elongate and similar to those of Ascalaphidae but lack the extended fusion of MP and CuA present in the latter family. They appear to represent an intermediate between the plesiomorphic basal fusion of MP+CuP in Nemopteridae and the more distal intermingling found in Ascalaphidae. As in Ascalaphidae, MP and CuA do come together, at the base of MP, but then separate and extend to the wing margin forming separate medial posterior and cubital anterior fields. Similar to some Psychopsidae and Apochrysinæ, representatives of Myrmeleontidae can have a gradate series present in the costal field (e.g., *Acanthaclisis* Rambur). The crossvein 1r<sub>pm</sub> of the hind wing is simple and not sigmoidal, and in all wings the costal crossveins can be at times forked, there is no recurved humeral vein, and trichosors are lacking. The pterostigma is marked in most taxa; often it is small and not clearly bordered.

Species examined: Dendroleontini undetermined (fig. 6B); other species examined but not figured: *Brachynemurus abdominalis* (Say), *Dendroleon* sp., *Distaleon* sp., *Froggattisca* sp., *Heleoclisis* sp., *Palpares* sp., and *Stilbopteryx* sp.

## Superfamily Ithonoidea

### Family Ithonidae

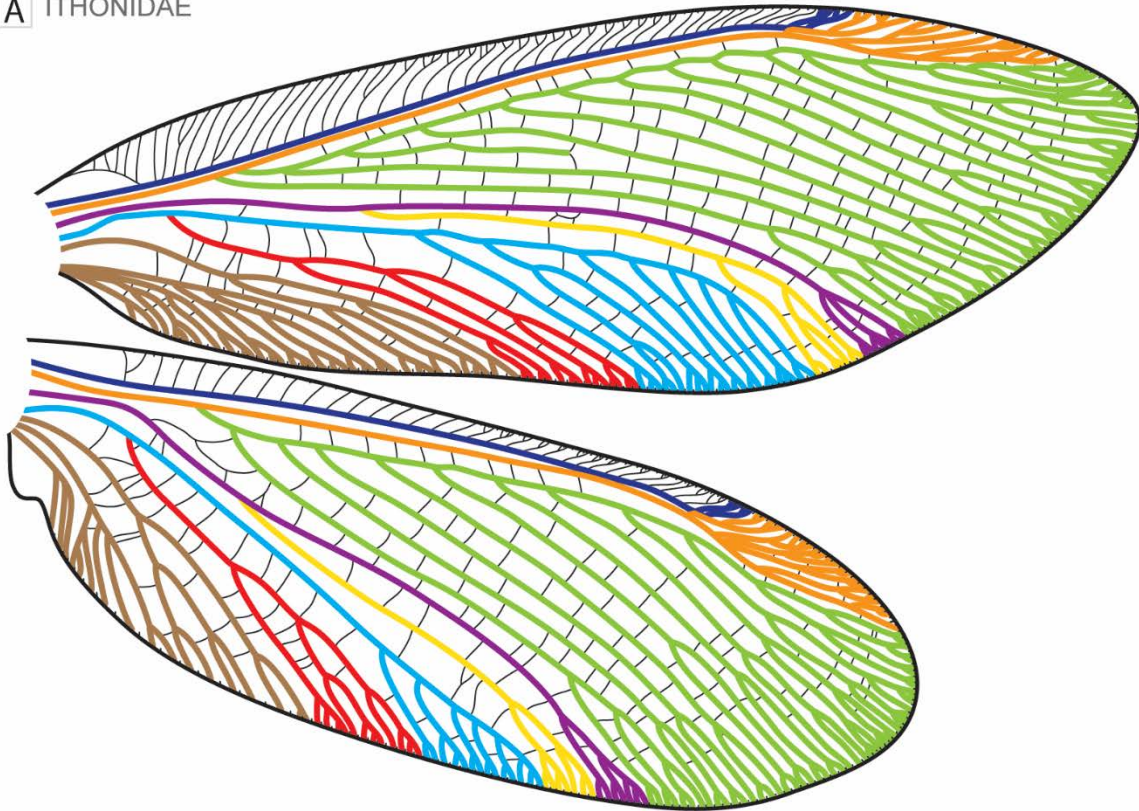
(Figures 7A, 8)

The moth lacewings and giant lacewings comprise 39 species in two main genus groups. The family now incorporates the families Polystoechotidae and Rapismatidae (Winterton and Makarkin, 2010). Ithonid wings are variable in shape from elongate-ovoid, falcate to slightly pointed apically, but in general they are broad with reticulated venation; in one genus (*Adamsiana* Penny) the female is apterous. They are characterized by the presence of up to three radial sectors

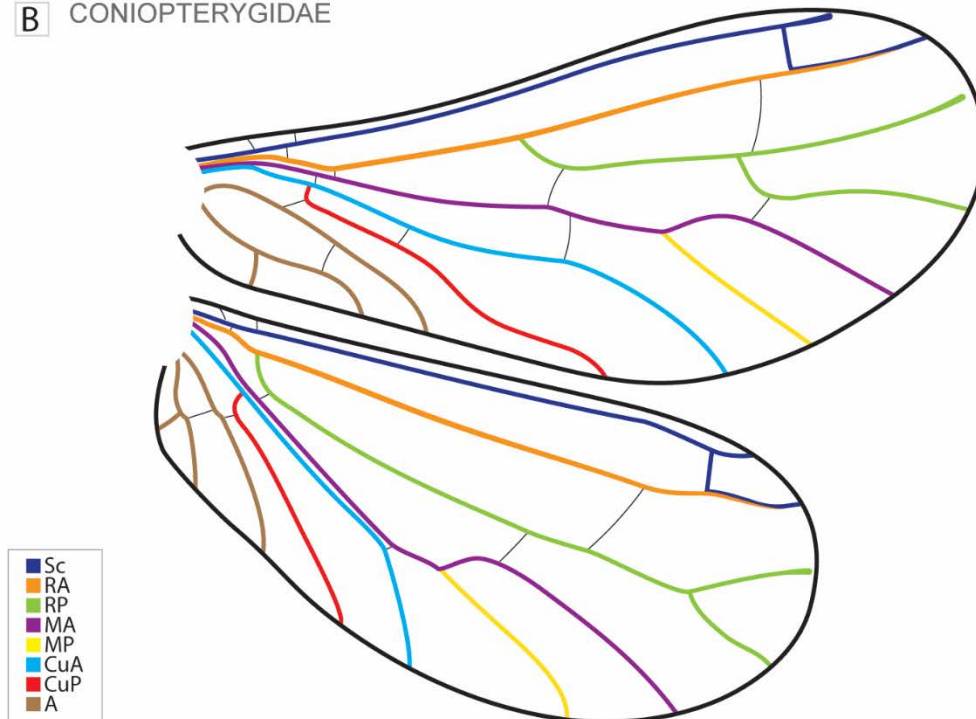
(RP) in the forewing (although most commonly one) and in which the distalmost sector is more greatly developed than the basal sectors (fig. 7A). The only other Neuropterida with multiple origins to RP are Hemerobiidae. There is little fusion present among the veins except the subapical fusion of Sc and RA. In comparison to Coniopterygidae, in which a branch of Sc joins RA through the apparent crossvein, the ithonid vein fusion is due to a branch of RA joining Sc through an apparent crossvein below the area of the pterostigma. The hind wing 1rp-m is sigmoidal. Costal crossveins can be forked, particularly in the apical half of the wing; trichosors are present on the margins, and a recurved humeral vein is present (fig. 8). The pterostigma is inconspicuous.

Species examined: *Ithone fulva* Tillyard (figs. 7A, 8); other species examined but not figured: *Fontecilla graphicus* Navás, *Oliarces clara* Banks, *Platystoechotes lineatus* Carpenter, *Polystoechotes punctata* (Fabricius), and *Rapisma cryptunum* Barnard and New.

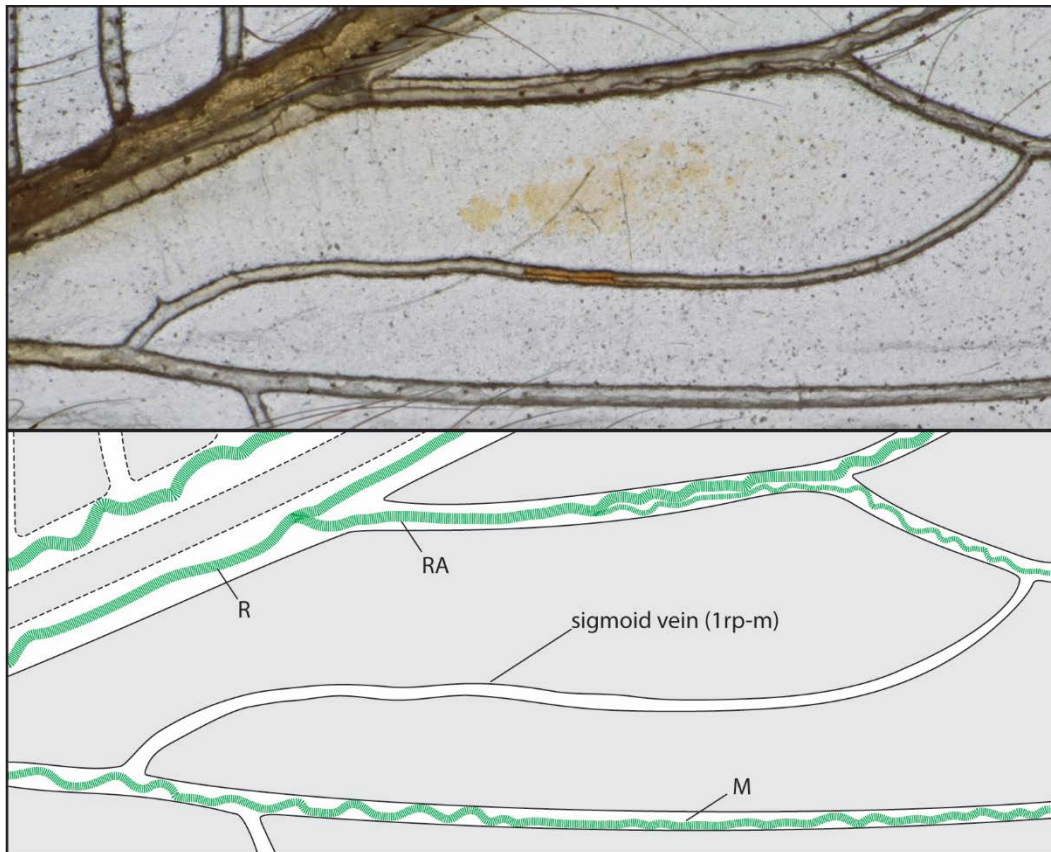
A ITHONIDAE



B CONIOPTERYGIDAE



**Figure 111.** Line drawings of forewings and hind wings of a moth lacewing and dustywing. A. *Ithone fulva* Tillyard (Ithonidae). B. *Aleuropteryx juniperi* (Ohm), re-drawn from Meinander (1972) (Coniopterygidae). See figure 2 for explanation of abbreviations.



**Figure 112.** Photomicrograph (above) and line drawing (below) of the proximal radial and medial sector of the hind wing of *Ithone fulva* Tillyard (Ithonidae), showing the elongate 1rp-m (sigmoid vein) in ventral view. Tracheae demarcated in green.

Superfamily Coniopterygoidea  
 Family Coniopterygidae  
 (Figure 7B)

Dustywings comprise 571 extant species in three subfamilies, two of which are cosmopolitan in distribution. They are particularly distinctive for the presence of a whitish wax layer on the wings and body, as well as a generally reduced venation relative to all other Neuropterida. The wing shape is typically ovoid, although some species have the hind wing greatly reduced. Owing to their exceptionally small size, we were not able to observe tracheation in specimens available to us. Based on studies by Withycombe (1922), it appears that the actual wing venation does not vary dramatically from the apparent venation. There are apparently no fusions present in the fore- or hind wing, except for the partial overlap of  $Sc_2$  and RA. Withycombe

(1922) examined the pupal tracheation of Coniopterygidae and noted the apical descent of a second branch of Sc ( $Sc_2$ ) into the path of RA. At this point RA terminates or partially overlaps the base of the apical  $Sc_2$  abscissa, but it is  $Sc_2$  that terminates at the wing margin, despite appearing as RA. This condition would be analogous to the fusion in Ithonidae, but there the latter RA joins Sc through an apparent crossvein. The branches of the longitudinal veins are often simple apically, although forking does occur in various genera, and some of the Cretaceous dustywings have additional branching not known to occur within the modern fauna (in MA) (Meinander, 1975; Grimaldi, 2000; Engel, 2002, 2016). Otherwise, the generally simple venation is a seemingly unique trait within Neuropterida. The costal crossveins are simple or lacking entirely, no humeral vein is present, trichosors are lacking, and in the hind wing crossvein 1r-m is simple and not sigmoidal. The pterostigma is inconspicuous.

Species examined: *Aleuropteryx juniperi* (Ohm) (redrawn from Meinander, 1972) (fig. 7B).

## Superfamily Osmyloidea

### Family Osmylidae

(Figure 9)

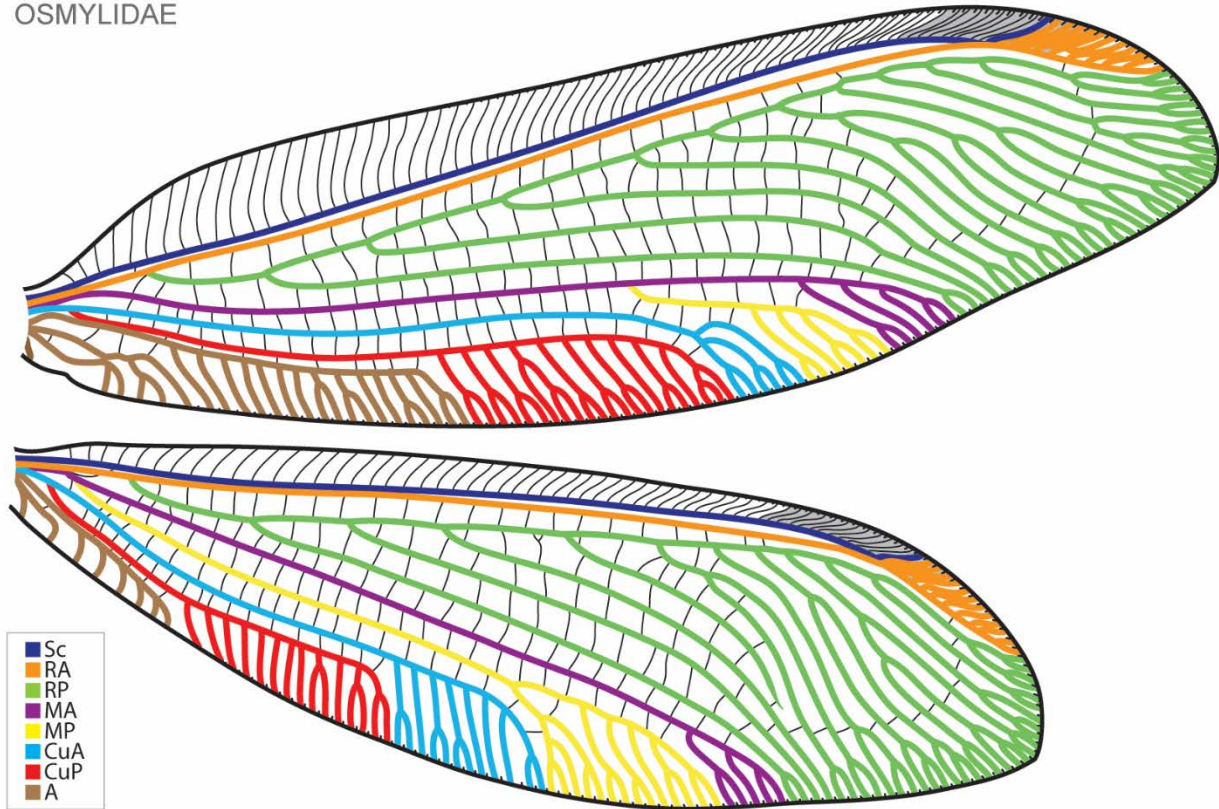
Lance lacewings comprise 212 species in 30 genera. Osmylid wings vary from short and ovoid to elongate and falcate. They are characterized by the distal separation of MA and MP in the forewing, a trait only present elsewhere in Nymphidae. The separation in Osmylidae is not always as easy to see as in the species illustrated here (fig. 9), where MP and CuA are not fused. In some Osmylidae (e.g., *Stenosmylus* McLachlan) fusion of MP and CuA occurs in the distal part of the wing, and some authors have suggested an apparent absence of MP in the forewing (e.g., Shi et al., 2012, Cousin and Béthoux, 2016). Winterton et al. (2017) showed that while MA-CuA fusion

does occur in some derived osmylid species of Stenosmylinae, the absence of MP in the osmylid hind wing was in fact based on incorrect interpretation of incomplete published figures, and examination of species revealed that MP is in fact small but present. When tracing the tracheation it is possible to detect the split of the two medial sectors and the fusion of MP with CuA. Examination of representatives of additional Osmylidae genera is required to fully elucidate the extent of wing vein fusion in this heterogeneous family. As in many other Neuroptera, Osmylidae have numerous crossveins in the radial field and have only a single origin to RP. The RP field is enlarged in Osmylidae and numerous crossveins are present (especially in the proximal two-thirds of the wing). Crossvein 1r-m of the hind wing can be curved in some taxa but is simple in most. The costal crossveins can be forked, a recurved humeral vein is absent and trichosors are present on either part or the entire margin. The pterostigma is weakly marked in most taxa.

Species examined: *Oedosmylus* sp. (fig. 9); other species examined but not figured: *Australysmus* sp., *Eidoporismus pulchellus* Esben-Petersen, *Gryposmylus pubicosta* (Walker), *Kempynus acutus* New, *K. maculatus* New, *Lysmus harmandinus* Navás, *O. latipennis* Kimmins, *Stenosmylus stenopterus* McLachlan, *S. tenuis* (Walker), and *Thyridosmylus paralangii* Wang, Winterton, and Liu.



## OSMYLIDAE



**Figure 113.** Line drawings of forewing and hind wing of *Oedosmylus* sp. (Osmylidae). See figure 2 for explanation of abbreviations.

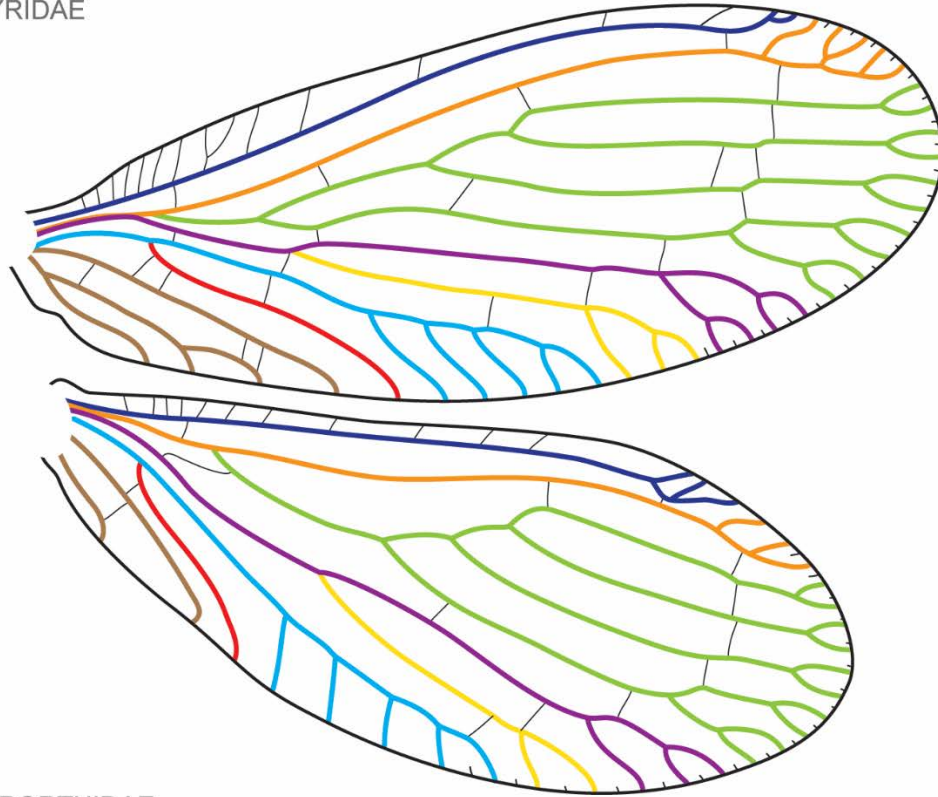
## Family Sisyridae (Figure 10A)

Spongillaflyies comprise 71 species in four genera, with two genera largely cosmopolitan. The small sisyrid wings are rounded and tracheae are rarely visible, and when discernible are often so only in the base of the wing. Therefore, we could not confirm all details of the actual venation, but it seemingly does not vary from the apparent pattern. As in the wings of Raphidioptera, Mantispoidea (Berothidae, Rhachiberothidae, and Mantispidae) and most Chrysopidae R and M are fused at the base. We assume that the veins are fused but not the individual tracheae, as in all other taxa where this character is present. The costal crossveins can be forked, a recurved humeral vein is absent, trichosors are present on the apical margin, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma is inconspicuous.

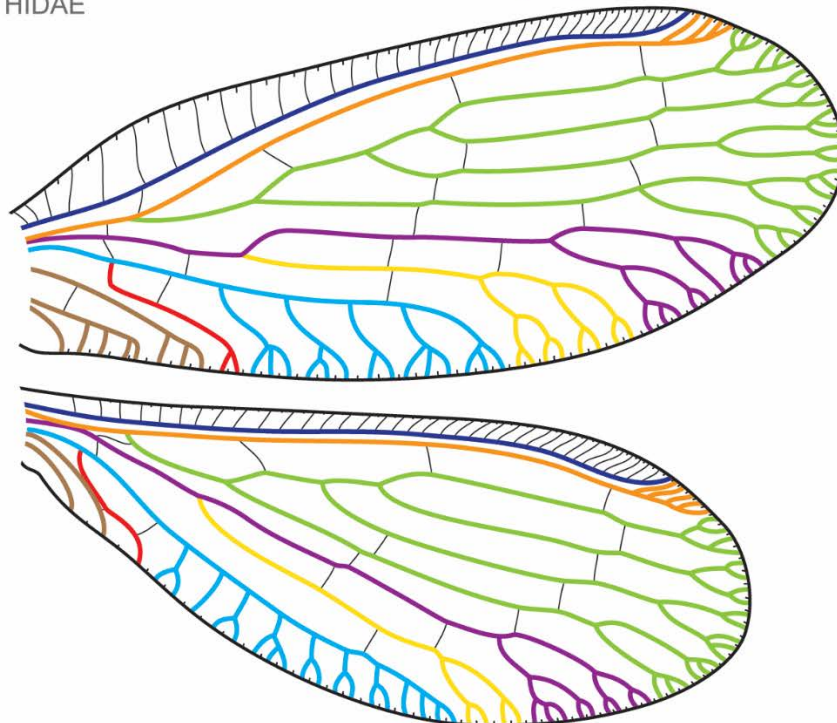
Species examined: *Sisyra* “*flavicornis*” (redrawn and modified from Comstock, 1918; likely a misnomer for *S. fuscata* [Fabricius]) (fig. 10A); other species examined but not figured: *Climacia ariolaris* (Hagen).



A SISYRIDAE



B NEVRORTHIDAE



**Figure 114.** Line drawings of forewings and hind wings of a spongillafly and aquatic lacewing. A. *Sisyra* “*flavicornis*” (redrawn and modified from Comstock, 1918; likely a misnomer for *S. fuscata* [Fabricius]) (Sisyridae). B. *Nevrorthus reconditus* (Montserrat and Gavira) (redrawn from Montserrat and Gavira, 2014) (Nevrorthidae). See figure 2 for explanation of abbreviations.

## Family Nevrorthidae (Figure 10B)

Nevrorthidae are one of the smallest families of Neuroptera, with only 19 extant species in four genera. Suitably preserved specimens of Nevrorthidae were not available for this study, but based on the wing images of Montserrat and Gavira (2014) (fig. 10B) we can assume that the actual venation does not vary from the apparent venation. The rounded wings of Nevrorthidae are very similar to Sisyridae and yet also show some similarities with closely related Osmylidae, belying their intermediate phylogenetic position between the two families. There are no fusions present in the fore- or hind wing, as is the case in Megaloptera, Psychopsidae, most Osmylidae, and Hemerobiidae. Nevrorthidae lack the basal fusion of R and M. The costal crossveins are simple, a recurved humeral vein is lacking, trichosors are present on the entire margin, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma is inconspicuous.

Species examined: *Nevrorthus reconditus* (Montserrat and Gavira) (redrawn and modified from Montserrat and Gavira, 2014) (fig. 10B).

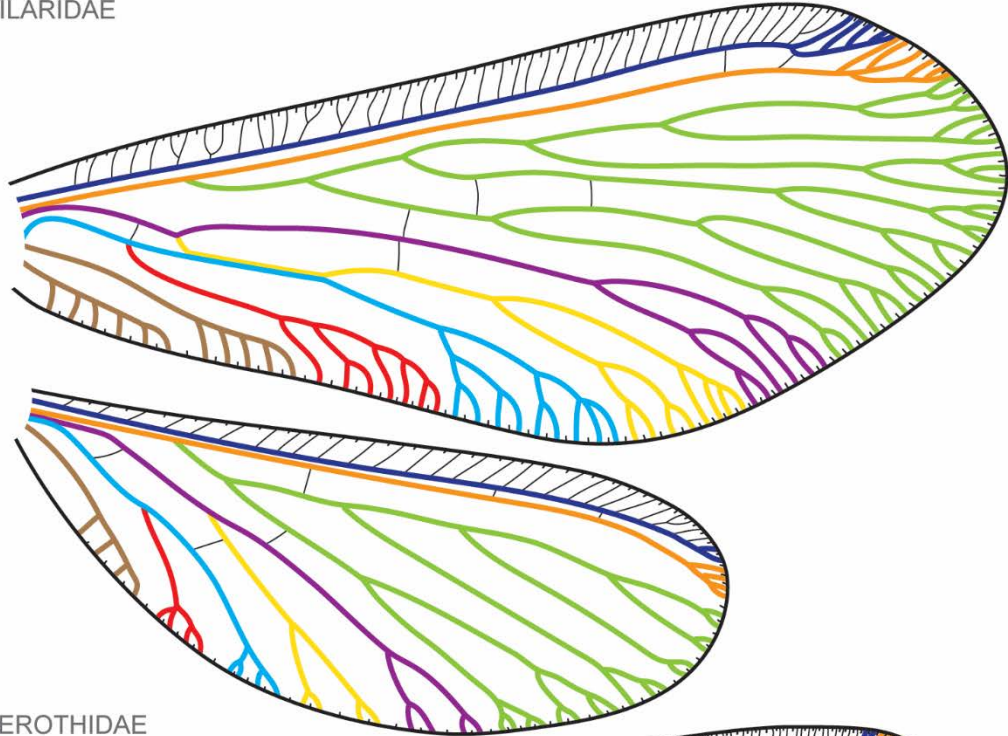
## Superfamily Dilaroidea Family Dilaridae (Figure 11A)

Pleasing lacewings comprise 77 species in six genera (Liu et al., 2017). Dilarid wings are short and rounded and in some taxa the hind wing is reduced. The forewings have only a single discernible fusion, which is the partial merging of MP and CuA (fig. 11A), a condition clearly convergent with that of Nemopteridae, Ascalaphidae, and Myrmeleontidae. Shortly after its divergence from MA, MP joins CuA and they then diverge roughly around the wing's midpoint. The costal crossveins can be forked, there is no humeral vein, trichosors are present on the entire

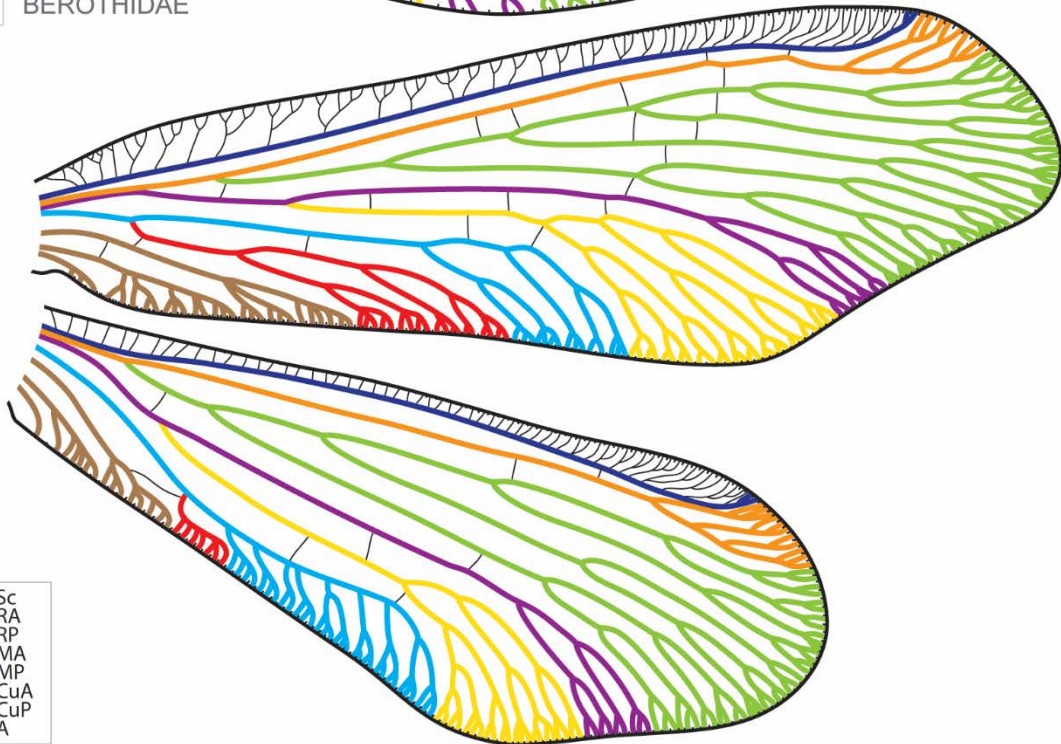
margin, and in the hind wing crossvein 1rp-m varies from simple to sigmoidal. The pterostigma is inconspicuous.

Species examined: *Nallachus americanus* (McLachlan) (hind wing redrawn from Carpenter, 1940) (fig. 11A); other species examined in literature but not figured: *Dilar* sp.

A DILARIDAE



B BEROTHIDAE



■	Sc
■	RA
■	RP
■	MA
■	MP
■	CuA
■	CuP
■	A

**Figure 115.** Line drawings of forewings and hind wings of a pleasing lacewing and a beaded lacewing. A. *Nallachius americanus* (McLachlan) (hind wing redrawn from Carpenter, 1940) (Dilaridae). B. *Trichoma* sp. (Berothidae). See figure 2 for explanation of abbreviations.

## Superfamily Mantispoidea

### Family Berothidae

#### Figure 11B

Beaded lacewings comprise 113 species in 25 genera. Berothid wings vary from short and rounded to elongate and even falcate, and in some taxa the hind wing is reduced. As in Raphidioptera, Sisyridae, Mantispidae, Rhachiberothidae, and most Chrysopidae, R and M are fused at the base in the forewing, with both tracheae evident within the composite vein. In each of the aforementioned taxa, M diverges from R basal to the origin of RP. Aside from this area of basal fusion, all other tracheae follow the apparent wing venation. The costal crossveins are forked, trichosors are present on the entire margin, a recurved humeral vein is present, and in the hind wing crossvein 1rp-m is simple and not sigmoidal. The pterostigma varies from inconspicuous to marked.

Species examined: *Trichoma* sp. (fig. 11B); other species examined but not figured: *Naizema mendozina* (Esben-Petersen), *Stenobiella variola* Winterton, and *Trichoma gracilipenne* Tillyard.

### Family Rhachiberothidae

#### (Figure 12A)

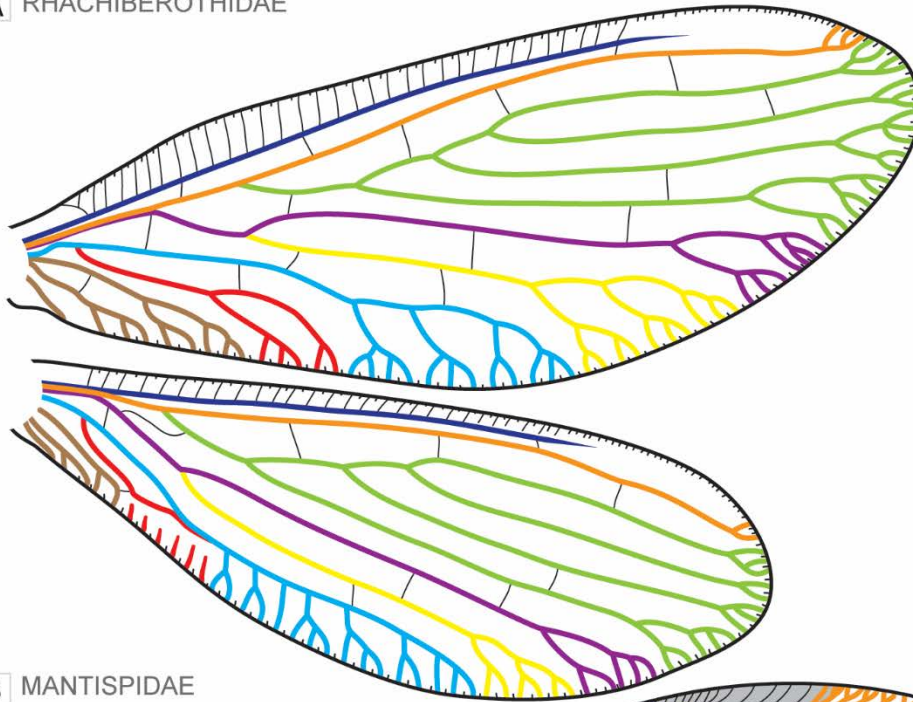
Thorny, or raptor, lacewings are a small group of 13 species in three genera, and their modern diversity is restricted to sub-Saharan Africa. Rhachiberothids have rounded wings, although rarely narrowly elongate in one species. Due to their small size, the tracheae are not visible in many species (often only at the wing base). Consequently, we were unable to confirm details for Rhachiberothidae but assume that the actual wing venation does not vary from the apparent venation in most details, as is the case for the closely related Berothidae. As in Raphidioptera, Sisyridae, Berothidae, most Chrysopidae, and Mantispidae, the bases of R and M

are fused in the forewing. There is an apical fusion of CuA and CuP in the hind wing, thereby forming a cubital loop (fig. 12A). The costal crossveins are simple, trichosors are present on the entire margin, a recurved humeral vein is present, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma varies from inconspicuous to marked.

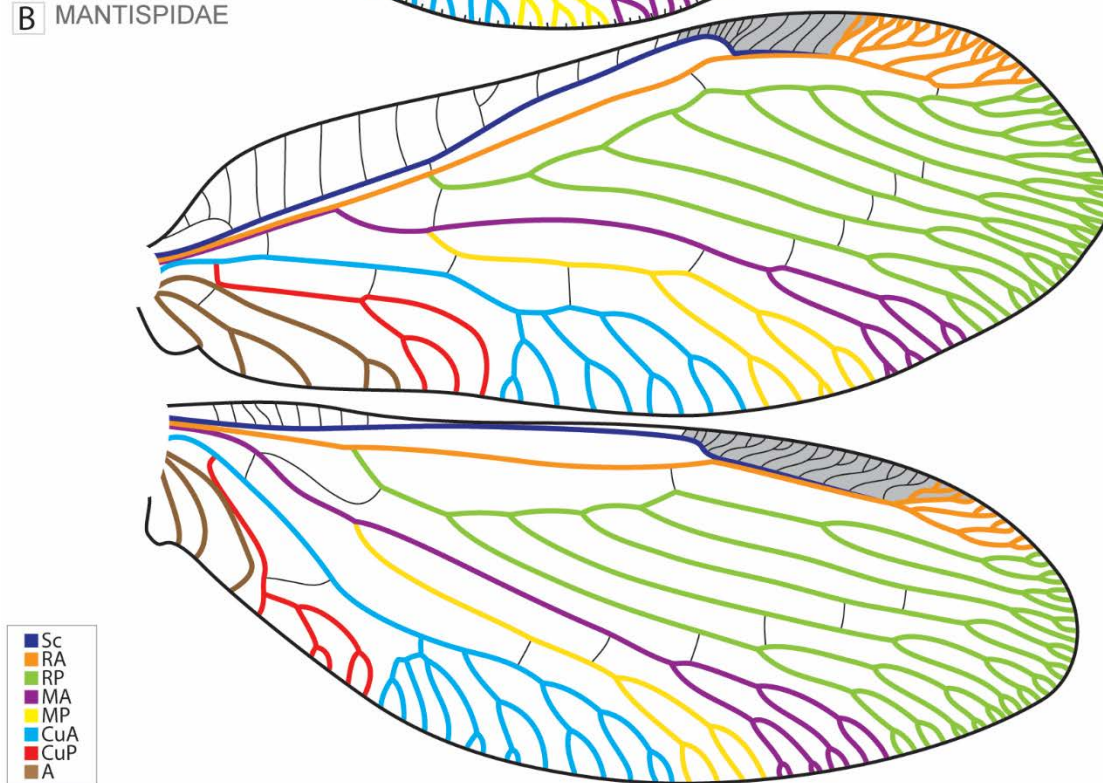
Species examined: *Mucroberotha* sp. (fig. 12A).



A RHACHIBEROTHIDAE



B MANTISPIDAE



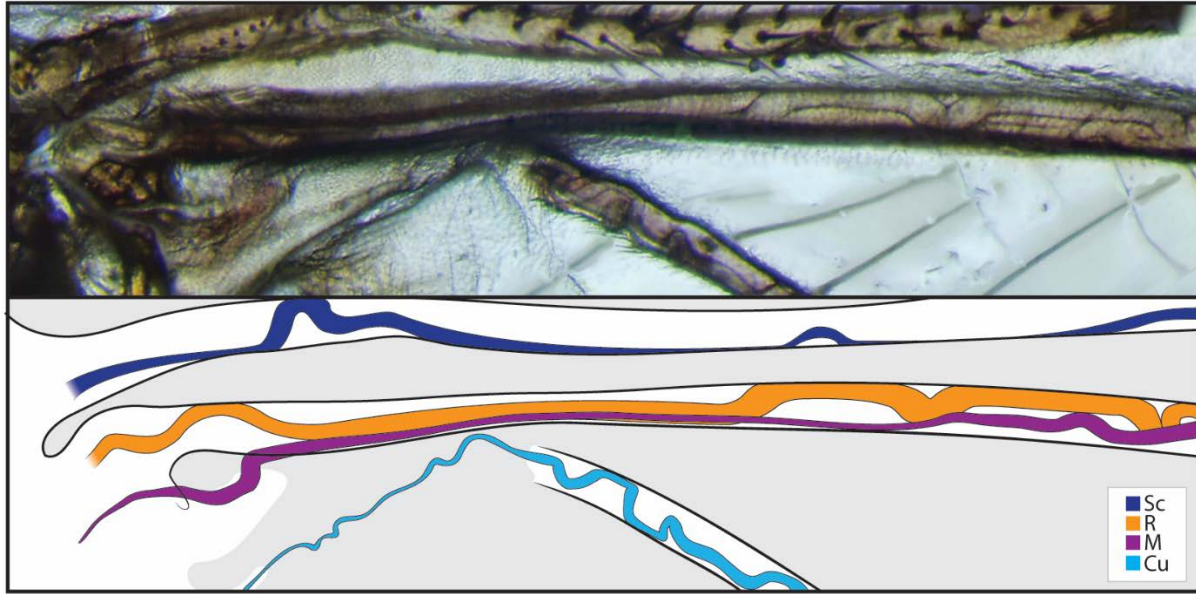
**Figure 116.** Line drawings of forewings and hind wings of a thorny lacewing and a mantispid lacewing. A. *Mucroberotha* sp. (Rhachiberothidae). B. *Plega* sp. (Mantispidae). See figure 2 for explanation of abbreviations.

Family Mantispidae  
(Figure 12B)

Mantidflies are a large group of 395 species in 44 genera. Mantispid wings are rounded and slightly elongate and there are some fossil taxa in which the hind wing is shortened or even absent. R and M are fused at their base, as is also the case in Raphidioptera, Sisyridae, Berothidae, most Chrysopidae, and Rhachiberothidae. Apart of this one area of fusion, and a short fusion of Sc and RA below the pterostigma in some mantispids, all other tracheae follow the apparent wing venation. Some genera of Mantispidae (e.g., *Climaciella* Enderlein) have an additional abscissa of R and M fused in the forewing, which results in the formation of a small cell where M rejoins R. Shortly after this second fusion, M diverges from R and descends toward the wing margin. This second point of fusion has at times served as further evidence for the notion of complete fusion of MA with R, but this does not seem to hold when considering the tracheation (see Discussion, below). The costal crossveins can be forked, a recurved humeral vein may be present, trichosors are present on the apical margin, and in the hind wing crossvein 1rp-m is strongly sigmoidal. The pterostigma varies from weakly to strongly marked.

Species examined: *Plega* sp. (fig. 12B); other species examined but not figured: *Dicromantispa* sp., *Ditaxis biseriata* (Westwood), *Drepanicus chrysopinus* Brauer, *Climaciella* sp., and *Gerstaeckerella* sp.





**Figure 117.** Photomicrograph and line drawing of the wing base of *Plega* sp. (Mantispidae), showing the basal fusion of R and M, ventral view.

## Superfamily Chrysopoidea

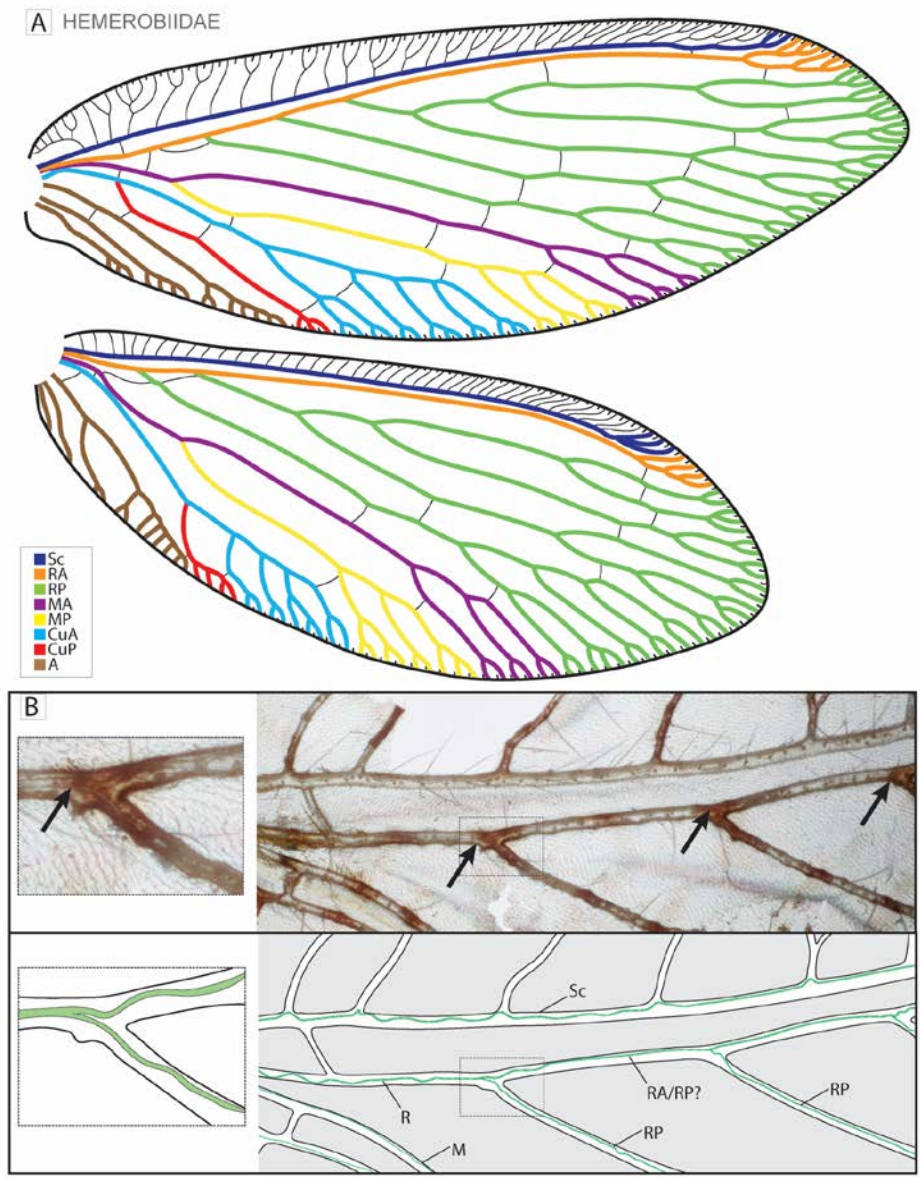
### Family Hemerobiidae

(Figure 14)

Brown lacewings are a large group of 591 species in 28 genera. The shape of hemerobiid wings is highly variable with short, elongate, rounded and falcate forms present and in some taxa the hind wing is reduced. The wing is characterized by the presence of multiple radial sectors, a character state approached only by the occurrence of up to three radial sectors in Ithonidae. Whether this is a duplication of RA or RP branches is uncertain, but the tracheation does not imply a difference between the multiple R branches. It was suggested that the multiple R sectors of Hemerobiidae are an argument in favor of MA basally fusing with R. The basalmost abscissa of R bears a single trachea and each split of the R branches is clearly detectable, with a trachea of equal size (fig. 14B), and therefore does not favor this view. As in Megaloptera, Psychopsidae, Nevrorthidae, and many Osmylidae, there are no fusions present in the fore- or hind wing. The costal crossveins are largely forked, trichosors are present along the entire or only apical margin,

a recurved humeral vein is present and in the hind wing the crossvein 1rp-m is sigmoidal. The pterostigma varies from inconspicuous to marked.

Species examined: *Hemerobius* sp. (fig. 14A), *Micromus posticus* (Walker) (fig. 14B); other species examined but not figured: *Notiobiella* sp. and *Symphorobius* sp.



**Figure 118.** Forewings and hind wings of brown lacewings (Hemerobiidae). A. Line drawings of forewing and hind wing of *Hemerobius* sp. B. Photomicrograph and line drawing of detail of multiple radial sectors of *Micromus posticus* (Walker) in ventral view; tracheae in green. See figure 2 for explanation of abbreviations.

## Family Chrysopidae

(Figures 1, 15–20)

Green lacewings are the second largest family in Neuropterida, comprising 1415 species in three subfamilies. Most chrysopid wings are rounded to slightly elongate, although there are taxa with very broad wings. The venation of the chrysopid wing is one of the most variable and derived within Neuroptera, and the extent of fusion in the forewing and hind wing is unique among Neuropterida. Extensive fusion led to the formation of a pseudomedial (PsM) and pseudocubital (PsC) veins (fig. 16A), which appear as single longitudinal veins, but actually are composites of several longitudinal veins, and for some abscissae also of crossveins, even from different sectors. Due to this extreme fusion it is important to consider both the longitudinal sectors as well as crossveins in further detail. PsM is formed by RP and MA, although these are not completely fused or neither are present over the entire course of PsM. MA always forms a principal component of PsM, whereas MP is integrated into PsM for only one or two abscissa when a triangular intramedian (*im*) cell is present (figs. 1, 16B, 17A). PsC is formed by abscissae of RP, MA, MP, and even CuA. The amount of overlap between the longitudinal veins in PsC and PsM varies between the three subfamilies of Chrysopidae (below).

Fusion of these longitudinal veins progresses gradually from a relatively small degree in Nothochrysinæ to greater complexity among the more derived Chrysopinæ. As such, many nothochrysinæ lack some of those fusions leading to the formation of PsM and PsC (fig. 15A), whereas Apochrysinæ and Chrysopinæ display highly developed pseudoveins (figs. 15B, 16).

There is a general pattern to chrysopid, and especially chrysopine, wing venation. While C and Sc are simple with one branch each and no fusions, R, M, and Cu each have an anterior and posterior branch and are involved in several fusions. The number of RP branches varies greatly

across each lineage, while wings have two MA, two MP, four CuA and two CuP branches. In rare cases, one or more of the longitudinal veins lack one of their branches. Because this general pattern is relatively consistent, it is possible to “estimate” the actual wing venation with the proposed system by simply looking at any given chrysopid wing, even in the absence of the tracheation. All RP branches can be traced from the origin of RP to the margin, and by tracing these branches one by one from the most distal RP branch back to the RP stem, it becomes apparent where along the margin the first branch of MA appears (i.e., the next marginal branch toward the base of the wing proximal to the posteriormost branch of RP). In the great majority of chrysopids this technique leads to a correct determination of the wing venation and each vein is accounted for from its origin to the wing margin.

Certain crossveins are always present in similar positions. In the forewing the first vein originating from RP is always a crossvein (often 1rp-m or 1rp-ma). This initial radial-medial crossvein descends most commonly from RP and only rarely from R (in which case it is 1r-m) (e.g., *Berchmansus* Navás), and joins M slightly proximal to, slightly apical to, or bordering the *im* cell. Two crossveins are present at the base of the forewing between M and Cu (1m-cu or 1m-cua and 2m-cua or 2mp-cua; figs. 15–17), although in some the second crossvein appears forked as it is actually borne by MP where the sector diverges from and then reattaches to MA (fig. 17C). In chrysopids the apparent third crossvein between what is then PsM and PsC is not a crossvein at all but instead MP. The course of MP determines the shape of the *im* cell, with three principal shapes:

1. Triangular, with a crossvein forming one of the cells boundaries (here dubbed pseudotriangular); MP originates apical of 2m-cua and the boundaries of the triangular cell are

formed by MA, MP, and 1ma-mp (fig. 17B). In this shape, common in primitive nothochrysinids, MA and MP first fuse in PsC.

2. Triangular without a crossvein forming a portion of the cell (fig. 17A); MP originates proximal to 2m-cua, which is positioned against the *im* cell (and is therefore more properly an mp-cua crossvein); MP first fuses with MA in PsM at the apex of the *im* cell, hence its triangular form and is bounded completely by abscissae of M (here dubbed eutriangular).

3. Quadrangular; MP originates proximal to 2m-cua and is connected to CuA by that crossvein (thus properly an mp-cu crossvein); MA and MP are connected by a crossvein (1ma-mp) and first fuse on PsC; the *im* cell is composed of MA, 1ma-mp, and two abscissae of MP. Of course, there are instances where the *im* cell is absent (fig. 17C).

There are always two crossveins between CuA and CuP, except for a few apochrysinid wings, in which more crossveins are present. CuP diverges from CuA at a position at or near to 1m-cu, and immediately curves toward the wing apex, rendering CuP one of the veins easiest to detect, even in chrysopid wings with a complex pattern of venation. The traditional *dcc* cell is formed by the posteriormost branch of CuA, the anteriormost branch of CuP, and 2cua-cup (fig. 16A).

Although the forewing pattern varies across the subfamilies, the general pattern of tracheation in the hind wing is the same across these lineages. It is characterized by the partial fusion of MA with RP as well as MP with CuA (figs. 15, 16B, 17). MA and RP are fused shortly after RP diverges from R. Within this short fusion of RP and MA both tracheae are clearly visible. By comparison with the forewing, there is only one crossvein between M and Cu, and the apparent second crossvein is actually CuA arching forward to join MP. Both PsM and PsC are present but not as pronounced as in the forewing. MA and MP diverge relatively basal and always rejoin in

P<sub>s</sub>C. CuP is rarely branched. An *im* cell is absent in the hind wing and the cell that appears as the traditional *dcc* is not formed by CuA and CuP, as in the forewing, but solely by abscissae of CuA.

In most chrysopids the costal crossveins are simple, but in some species they are forked, trichosors are always absent, a recurved humeral vein is absent, and in the hind wing the crossvein 1r<sub>p</sub>-m is simple and not sigmoidal. The pterostigma varies from inconspicuous to marked.

### Subfamily Nothochrysoidea

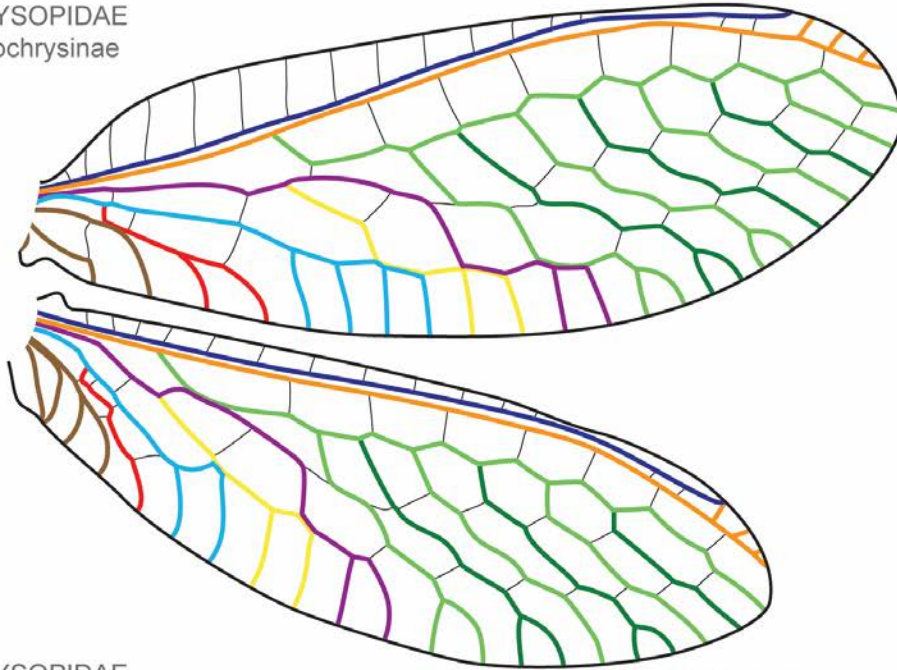
(Figures 15A, 17B, 18)

Nothochrysoidea comprise 19 species in seven genera with a circumtemperate distribution. The wing venation of this subfamily is the least derived within Chrysopidae. *Nothochrysa* McLachlan are the only nothochrysoidea with a strongly developed P<sub>s</sub>M and P<sub>s</sub>C, and therefore more greatly resemble the other chrysopid subfamilies (e.g., Brooks and Barnard, 1990). The remaining nothochrysoidea genera have a less developed venation in which there is little to no overlap of veins in the pseudoveins, rendering them less prominent (fig. 15A). The *im* cell is always present and is either pseudotriangular (fig. 17B) or quadrangular. A tympanal organ (see below) is absent in all Nothochrysoidea (fig. 18).

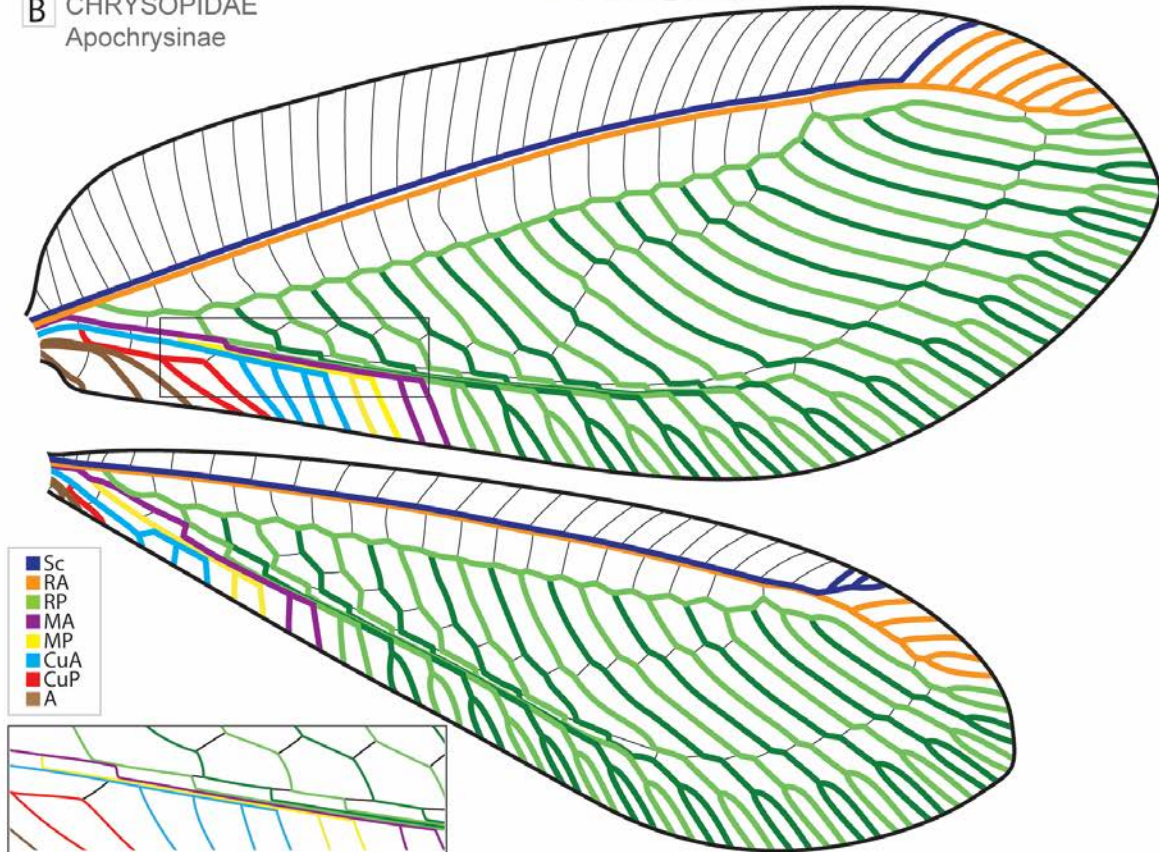
Species examined: *Hypochrysa elegans* (Burmeister) (figs. 15A, 17B), *Nothochrysa californica* Banks (fig. 18); in addition, we examined representatives of all genera of Nothochrysoidea except *Triplochrysa* Kimmins.



**A** CHRYSOPIDAE  
Nothochrysinæ



**B** CHRYSOPIDAE  
Apochrysinæ



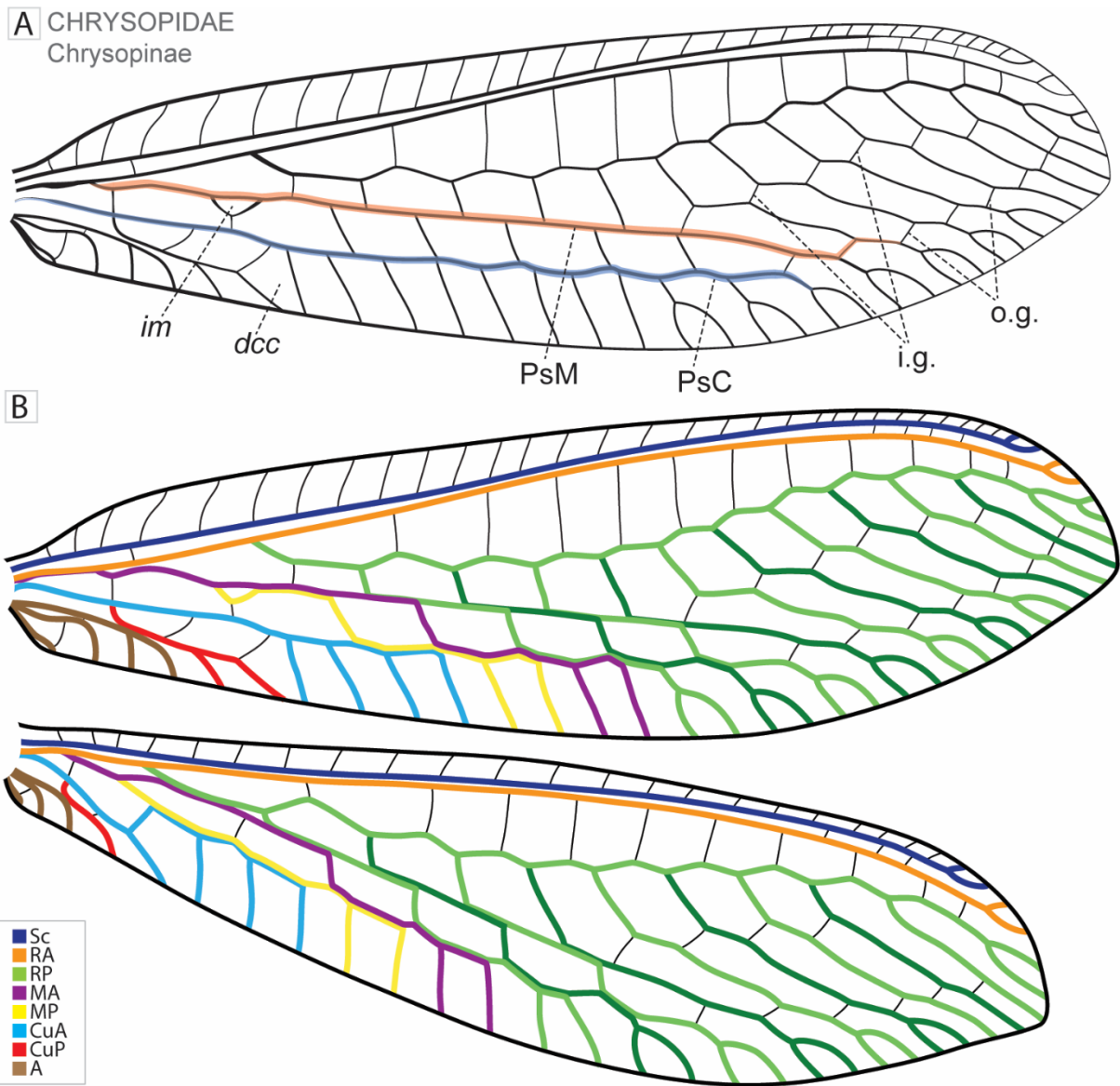
**Figure 119.** Line drawings of forewings and hind wings of green lacewings (Chrysopidae). A. *Hypochrysa elegans* (Burmeister) (Nothochrysinæ). B. *Apochrysa lutea* (Walker) (Apochrysinæ), with a detail of fusion in PSM (pseudomedial) and PsC (pseudocubital) (inset). See figure 2 for explanation of other abbreviations.

## Subfamily Apochrysinæ (Figures 15B, 17D, 19)

Apochrysinæ comprise 26 species in six genera that have a pantropical distribution. Apochrysinæ have up to four overlapping longitudinal sectors in PsC (multiple RP branches, MA, MP, and CuA), with up to six tracheae in one vein, thus making this subfamily appear to have the most-derived venational scheme among Chrysopidae. Although PsC is the product of many fused veins, PsM can be largely composed of augmented crossveins between longitudinal branches of RP (a condition never present in Chrysopinae), in which PcM is mainly composed of overlapping RP branches. The traditional *im* cell is always lacking in Apochrysinæ (fig. 17D), with *mamp1* occupying the entire cell between PsM and PsC. Contrary to statements of earlier authors (Brooks and Barnard, 1990, Winterton and Brooks, 2002), we have not found a tympanal organ (see Chrysopinae, below) in Apochrysinæ (fig. 19). R is only slightly thickened, as is Sc, and this condition is similar to that of the wing base of Nothochrysinæ (fig. 18), in which the tympanal organ is lacking. During this study we were not able to find any of the characteristic features of the chrysopine tympanum (fig. 20), but a further examination with histology would be valuable, and could more appropriately address this issue.

Species examined: *Apochrysa lutea* (Walker) (figs. 15B, 19), *A. leptalea* (Rambur) (fig. 17D); in addition, representatives of all genera of Apochrysinæ were examined.





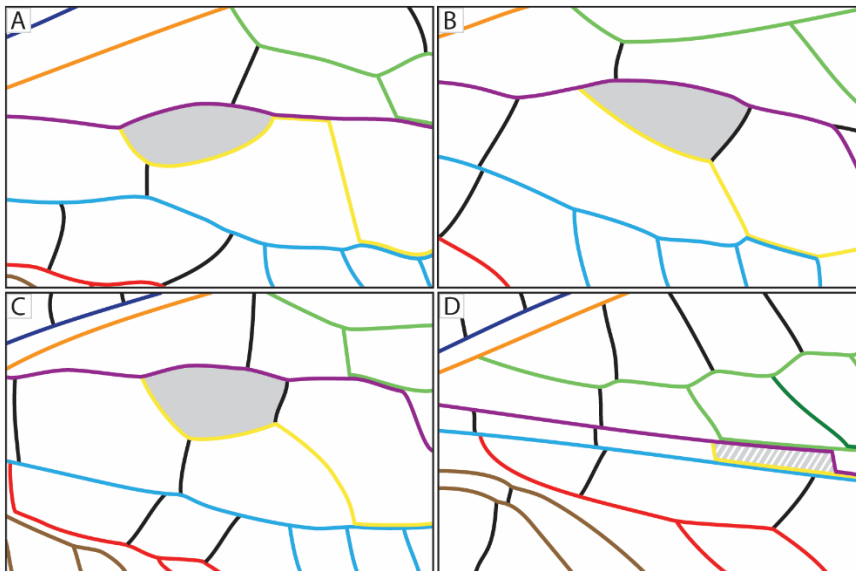
**Figure 120.** Line drawing *Cryptochrysa chloros* Freitas and Penny (Chrysopidae: Chrysopinae) A. Apparent wing venation of forewing, including traditional terminology. B. Forewing and hind wing, using revised, current vein terminology. Abbreviations: im, (intramedian cell); dcc, (distal cubital cell); PsM, (pseudomedial); PsC, (pseudocubital); i.g., (inner gradates); o.g., (outer gradates). See figure 2 for explanation of other abbreviations.

### Subfamily Chrysopinae (Figures 1, 16, 17A, 20)

All other green lacewings fall within the largest subfamily, Chrysopinae. Although they are a diverse taxon, the wing venation among the group is fairly uniform. As in Raphidioptera, Sisyridae, Berothidae, and Mantispidae, the bases of R and M are fused in the forewing. Both PsM

and PsC are consistently composed of fused longitudinal sectors. The *im* cell is most commonly eutriangular (figs. 1, 17A), sometimes quadrangular (fig. 17C), and in rare instances lacking. Chrysopinae are the only subfamily with a tympanal organ (fig. 20). This organ is composed of R and M and is positioned at the base of the forewing. Both tracheae of the veins are visible within the organ, with R anterior and M (very thin) posterior. The four tribes of Chrysopinae (Ankylopterygini, Belonopterygini, Chrysopini, and Leucochrysini) show a uniform general pattern of tracheation.

Species examined: *Cryptochrysa chloros* Freitas and Penny (fig. 16), *Chrysopa nigricornis* Burmeister (figs. 1, 20), *Chrysopa perla* Linnaeus (fig. 17a), *Nacarina balboana* (Banks); in addition, we examined representatives of all chrysopine genera except *Himalochrysa* Hölzel, *Neula* Navás, *Nuvol* Navás, *Sinochrysa* Yang, *Tibetochrysa* Yang, and *Turnerochrysa* Kimmins.

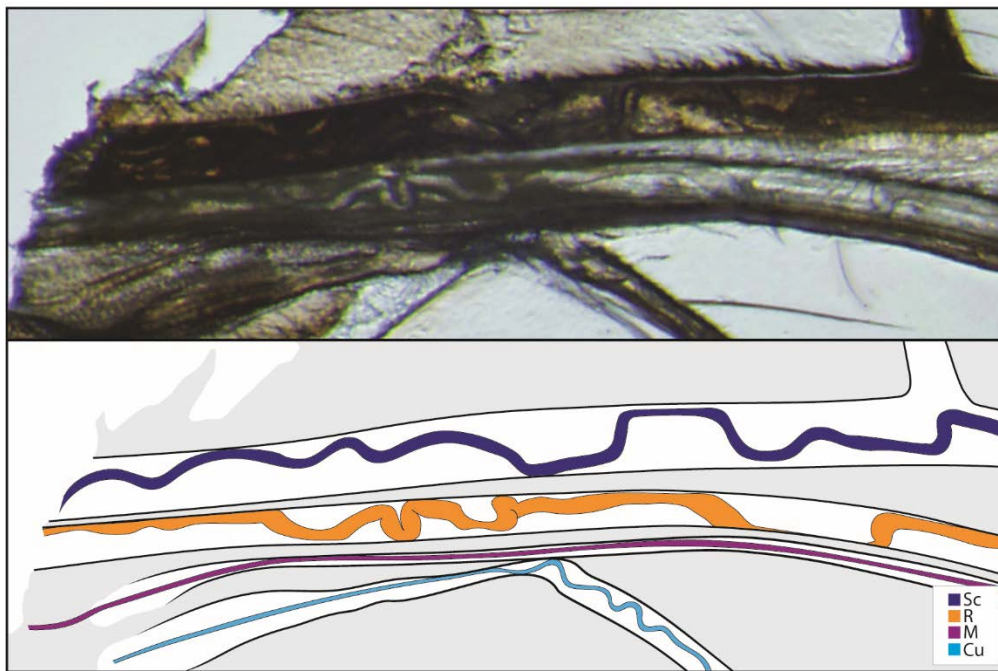


**Figure 121.** Line drawings of the variation of mamp1 (first intermedial cell) in Chrysopidae; mamp1 shaded in grey; refer to figure 16B for color legend. A. Eutriangular, *Chrysopa perla* Linnaeus. B. Pseudotriangular, *Hypochochrysa elegans* (Burmeister). C. Quadrangular, *Nacarina balboana* (Banks). D. Absent, *Apochrysa leptala* (Rambur).

## Discussion

Identifying actual vein homologies has an enormous impact on the interpretation of the evolution of lacewings. Because only true homologies should be the base for phylogenetic

hypotheses, comparing structures that appear similar but are not truly homologous inevitably leads to erroneous results. Hypotheses of insect wing venation have repeatedly been revised over the past century (see Introduction, above), including debates over the utility of tracheation (Kukalová-Peck, 1983; Rehn, 2003; Béthoux, 2005, 2008). In Neuroptera, the tracheation of wing veins appears to be a useful tool for determining the actual paths of the longitudinal sectors. The results presented here give insight into the evolution of lacewings and on that basis, we propose a revised system to identify and name these veins in Neuropterida. Each wing examined showed a similar overall pattern and we could not find differences in tracheation between conspecific specimens.

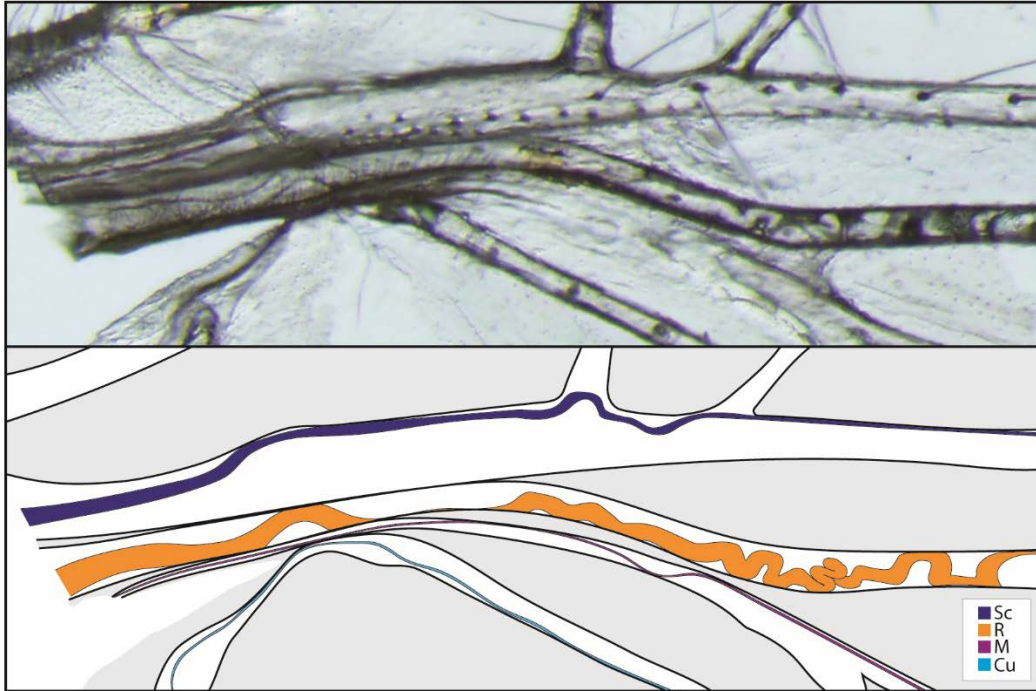


**Figure 122.** Photomicrograph and line drawing of the wing base of *Nothochrysa californica* Banks (Chrysopidae: Nothochrysinae), showing that R and M are not fused, ventral view.

Based on our observation of representatives of almost all neuropterid families we propose a revised nomenclature for veins and cells. Only veins with tracheation are longitudinal sectors (i.e., C: costa, Sc: subcosta, R: radius, M: media, Cu: cubitus, A: anal). These veins can be simple or branched and in the latter case these branches will be named, according to their position, anterior or posterior. Thus, the single media, called M basally, splits into the media anterior (MA) and

media posterior (MP). At the point of the first split in M the anterior portion becomes convex and the posterior portion concave, but this is not easily detectable in most modern taxa. For the sake of consistency, we advocate the use of RP over Rs for Neuropterida, rather than singling this sector out and using a different notation relative to other longitudinal veins. Rs was singled out largely given its more dramatically enlarged field, but this seems insufficient for an isolated change in vein nomenclature. In accordance to the revised system the two main branches of the radius are now named RA and RP. As is standard, further branching within the anterior and posterior sectors are denoted by a subscript number (in order from anterior to posterior) and following the abbreviation, such as MA<sub>4</sub> for the fourth branch of the media anterior.

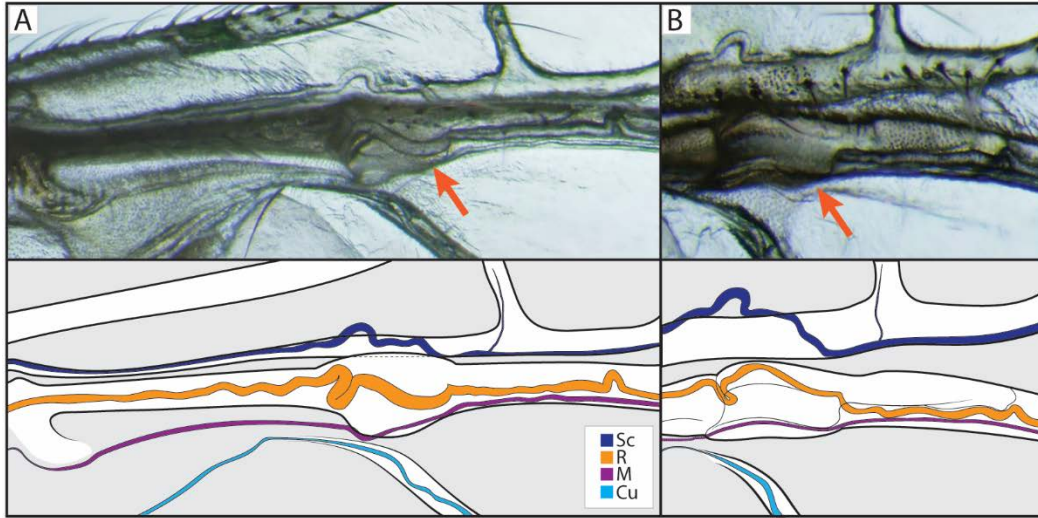
The crossveins are named for the longitudinal sectors they connect and are numbered from proximal to apical. As is customary, they are denoted with lowercase letters and a hyphen between the two longitudinal vein abbreviations. In this manner, the first crossvein between R and M would be 1r-m, or the third crossvein between Sc and R is 3sc-r. For clarity, crossveins within a single field include the full name of that branch, e.g., 2ma-mp for the second crossvein between MA and MP, or 1ma<sub>2</sub>-ma<sub>3</sub> for the first crossvein between the second and third branch of MA. These very specific names will rarely be used, because the crossveins of descriptive and phylogenetic importance are most often the basal ones, but it is nonetheless an aid to workers if there is consistency in application. In the case of fused veins, the combined veins are employed, such as first crossvein between Sc and R+M being 1sc-r+m, while the first crossvein between R+M and Cu would be 1r+m-cu.



**Figure 123.** Photomicrograph and line drawing of the wing base of *Apochrysa* sp. (Chrysopidae: Apochrysinæ), showing that R and M are not fused, ventral view.

An analogous system for the naming of cells can be employed. The field of a longitudinal vein is thus defined as the area posterior to the longitudinal vein up to the next longitudinal vein of a different field. The denotation of cells depends on the two bordering longitudinal veins and the number of the cell within this field, from proximal to apical. The name is formed by the italic lowercase abbreviation of these two longitudinal veins, without a hyphen, followed by the number of the cell. In this manner the second cell between R and M would be named *rm2*, and the first cell between MA and MP *mamp1*. Just as the naming system for crossveins, this can be extrapolated for all other longitudinal veins and all their branches. With names that are easier to grasp, these abbreviations can be applied more intuitively. The respective field is used for cells that are bordered by two longitudinal veins of two fields and “inter-“ is added to the name when the cell is between branches of the same field, such as “second radial cell” for *rm2* or “first intermedial cell” for *mamp1*.





**Figure 124.** Photomicrograph and line drawing of the wing base of *Chrysopa nigricornis* Burmeister (Chrysopidae: Chrysopinae), showing the tympanal organ and the associated basal fusion of R and M. A. Ventral view, tympanal organ indicated by arrows. B. Dorsal view.

The great degree of fusion in the chrysopid wing adds difficulty to the consistent naming of veins in this taxon. The use of pseudomedia (PsM) and pseudocubital (PsC) should be maintained to correctly describe the path of the fused longitudinal veins. Most apparent crossveins between PsM and PsC are actually longitudinal veins and only the first two crossveins lack tracheation. The third apparent crossvein between PsM and PsC (or 3psm-psc) is actually MP, while the fourth is MA and the fifth is a branch of RP. The concept of PsM and PsC should not be extended to the naming of cells as to do so would complicate phylogenetic comparisons. Thus, in a typical wing of *Chrysopa* Leach the cell formerly known as *im* (intramedian) will be denoted as the first intermedial (*mamp1*), and the second intermedial cell is located between PsM and PsC (fourth cell between these two pseudoveins), but will simply be called *mamp2* so as to correctly denote the homologous veins it resides between. Accordingly, Apochrysinae, which lack the traditional *im* cell, do have a *mamp1*, which merely appears as a cell between PsC and PsM (fig. 17D).

## The Controversy of ‘MA’

One of the challenges in the venation of Neuropterida, and other insect lineages, is the basal path of the media anterior. The two competing hypotheses are that MA is either basally fused with R and therefore its path is encompassed within the first branching point within RP (i.e., RP’s posteriormost branch), versus the notion that MA is not fused with R at the base but instead splits off from M at the same point as MP. Most entomologists have adopted the notion of basal fusion of R and MA (e.g., Orthoptera: Béthoux and Nel, 2001; Odonata: Rehn, 2003, Mantodea: Béthoux and Wieland, 2009, Holometabola: Haas and Kukalová-Peck, 2001) including Neuroptera (Riek, 1970; Aspöck et al., 1980; Adams, 1996; Nel et al., 2005). However, the evidence supporting these two alternative hypotheses leaves much to be desired.

Resolution of the actual path of MA has a significant influence not only over the nomenclature of particular veinal elements in the wing, but also the interpretation of homologies and recognition of shared character states and therein relationships among major lineages within Neuropterida. Fusion of MA with R has been advocated based on the paired nature of longitudinal veins, the pattern of corrugation (fluting), and the course of longitudinally oriented “crossveins” such as the sigmoid vein or arculus (interpreted thereby as abscissae of longitudinal sectors rather than as an augmented crossvein) (e.g., Kukalová-Peck, 1983). In the hypothetical primitive insect wing presented by Kukalová-Peck and Lawrence (2004) (itself based on the earlier works of Kukalová-Peck as cited in the Introduction, above), each sector has paired veins originating from their associated axillary sclerite. The lack of MA as an individual branch at the wing base in most modern insects was therefore interpreted as the result of a fusion with R, with MA reappearing at the first branching of RP.

The sigmoid vein (fig. 8) in the hind wing of Neuropterida has traditionally served as one of the most compelling pieces of evidence for the fusion of MA into R (e.g., Megaloptera,

Ithonidae, Hemerobiidae, Rhachiberothidae, Mantispidae, etc.: refer to individual family accounts, above). The sigmoid vein is an elongate, arched vein between R or RP and M (figs. 2A, 7A, 8, 10, 12B and 14A), i.e., 1r-m, 1rp-m, or 1rp-ma. It has been argued that its curved form and longitudinal orientation indicate it to be an abscissa of a longitudinal sector, specifically a portion of MA (Adams, 1996; Kukalová-Peck and Lawrence, 2004). However, in several families the same vein appears as a typical, transverse crossvein (e.g., Nymphidae, Ascalaphidae, Berothidae, Chrysopidae: refer to individual family accounts, above). The absence of tracheation favors the conclusion that the sigmoid vein is nothing more than a distorted and elongate crossvein in certain lineages. Moreover, the sigmoid crossvein would have little bearing on reconstructing a hypothesis for the groundplan venation of the insect wing as Neuropterida are highly derived pterygote insects, well removed from the base of Paraneoptera, let alone Neoptera or Pterygota as a whole.

In opposition to the R+MA hypothesis are our observations here, which found dual tracheation in those places where M (not just MA) is basally fused with R, and the absence of such dual tracheation in taxa where MA is supposedly fused with R and RP. Most importantly, there is no trachea running through the sigmoid vein, revealing it to be nothing more than a modified crossvein. We also could not find a trachea running from the medial plate to the base of R as would be supposed under the R+MA hypothesis.

Inferring modern wing-venation homologies from the notion of a basally fused R+MA raises two difficulties. The first is a minor point but of some significance: M is not the only vein that is formed of a singular stem at the base in the modern wing, at least the more derived wings of Neoptera. Like the media, all of the major veins are single stems at their base rather than paired anterior (convex) and posterior (concave) stems.



The second point and, in our opinion, the most difficult for the R+MA hypothesis is the original evidence itself for the notion of paired stems at the wing base. This scheme was based on purported characters in the prothoracic “wing” of the Carboniferous *Stenodictya lobata* (Brongniart). This species belongs to the Palaeodictyoptera, one of a series of orders in the extinct superorder Palaeodictyoptera (Grimaldi and Engel, 2005). Palaeodictyoptera, while certainly more basal among Pterygota than any Neoptera are still rather phylogenetically divorced from the pterygotan ancestor, a hypothetical taxon that would have existed in the earliest Devonian or even latest Silurian (Engel and Grimaldi, 2004; Engel et al., 2013). There is no reason to surmise that *S. lobata* embodies venation identical to the groundplan for Palaeodictyoptera, let alone Pterygota. Most importantly, there is no reason to believe the venation of prothoracic winglets is more reflective of the groundplan wing, particularly as the presence of prothoracic winglets is not clearly plesiomorphic, although such immoveable winglets are present in putatively primitive forms of Odonatoptera, Palaeodictyoptera, and even some Neoptera. Any pattern of venation in these winglets may be autapomorphically augmented relative to their particular function. Moreover, the actual meso- and metathoracic wings of such extinct taxa do not demonstrate clear evidence for paired stems at the wing base. Indeed, in *S. lobata* the meso- and metathoracic wing venation is congruent with other insects, with singular stems at the base. In fact, no extinct or extant taxa are documented in which there are paired stems at each axillary point (i.e., paired stems at the base for each longitudinal vein system). Moreover, recent evidence from the nymphal pads of Palaeodictyoptera (Prokop et al., 2017) tends to support Hamilton’s (1972a) hypothesis regarding the groundplan venation for insect wings, one that does not include paired, basal stems.

The combination of the above tends to refute the hypothesis that MA is fused into the stem of R at its origin from the axillary sclerite. Instead, tracheation and the lack of convincing evidence for the “paired stems hypothesis” concurs with a more likely origin of MA from the stem of M.

An enigma remains in that there is a change in fluting within the posteriormost branch of RP, and the corrugation (convexity versus concavity) of the longitudinal sectors has served as convincing evidence for vein identities (e.g., Redtenbacher, 1886; Kukalová-Peck, 1983; Béthoux and Nel, 2001; Rasnitsyn, 2007). Such evidence has been used to identify and trace the course, loss, or fusion of particular longitudinal sectors. In several modern insects the corrugation has become modified or lost. Given the derived position of Neuropterida as well as the numerous other observations we have outlined above, it seems most likely that this is merely a derived feature within RP rather than definitive evidence for MA’s presence within this sector. While we cannot absolutely demonstrate such a hypothesis at the moment, it remains more convincing than the alternative R+MA hypothesis owing to the lack of any observational support for the latter. Accordingly, we conclude that there is presently no compelling evidence in favor of the R+MA hypothesis, and that instead MA appears to have a simpler course than previously surmised. It is hoped that advances in developmental biology and an understanding of vein formations during ontogeny may provide further insights, and, it is hoped, corroborate the patterns we have documented here.

## References

- Adams, P. A. 1996. Venational homologies and nomenclature in Chrysopidae, with comments on the Myrmeleontoidea (Insecta: Neuroptera). *In* M. Canard, H. Aspöck, and M.W. Mansell (editors), *Pure and applied research in Neuropterology* [Proceedings of the Fifth

- International Symposium on Neuropterology, Cairo, Egypt, 1994]: 19–30. Toulouse: SACCO [Société d'aide à la Création et à la Communication d'Opinion], 341 pp.
- Adolf, G. E. 1879. Ueber Insectenflügel. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* 41-2 (3): 213–291, +6 pls. [pls. xxvii–xxxii].
- Aspöck, H. 1986. The Raphidioptera of the world: a review of present knowledge. *In* J. Gepp, H. Aspöck, and H. Hölzel (editors), *Recent research in Neuropterology* [Proceedings of the Second International Symposium on Neuropterology in Hamburg, Federal Republic of Germany]: 15–29. Graz: Druckhaus Thalerhof, 176 pp.
- Aspöck, H., Aspöck, U., and H. Hölzel. 1980. *Die Neuropteren Europas: eine zusammenfassende Darstellung der Systematik, Ökologie und Chorologie der Neuropteroidea (Megaloptera, Raphidioptera, Planipennia) Europas* [2 vols.]. Krefeld: Goecke and Evers, 495 pp. [vol. 1], 355 pp. [vol. 2].
- Bakkes, D. K., Mansell, M. W., and C. L. Sole. 2017. Phylogeny and historical biogeography of silky lacewings (Neuroptera: Psychopsidae). *Systematic Entomology* 43 (1): 43–55.
- Béthoux, O. 2005. Wing venation pattern of Plecoptera (Neoptera). *Illiesia* 1 (9): 52–81.
- Béthoux, O. 2008. Groundplan, nomenclature, homology, phylogeny, and the question of the insect wing venation pattern. *Alavesia* 2: 219–232.
- Béthoux, O., and D. E. G. Briggs. 2008. How *Gerarus* lost its head: stem-group Orthoptera and Paraneoptera revisited. *Systematic Entomology* 33 (3): 529–547.
- Béthoux, O., and A. Nel. 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research* 10 (2): 195–198.
- Béthoux, O., and A. Nel. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa* 96: 1–88.

- Béthoux, O., and F. Wieland. 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. *Zoological Journal of the Linnean Society* 156 (1): 79–113.
- Béthoux, O., Kristensen, N. P., and M. S. Engel. 2008. Hennigian phylogenetic systematics and the ‘groundplan’ vs. ‘post-groundplan’ approaches: a reply to Kukalová-Peck. *Evolutionary Biology* 35 (4): 317–323.
- Brauer, F. 1885. Systematische-zoologische Studien. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe [Erste Abtheilung: Enthält die Abhandlungen aus dem Gebiete der Mineralogie, Botanik, Zoologie, Geologie und Paläontologie] 91 (5): 237–413, +1 pl.
- Brauer, F., and J. Redtenbacher. 1888. Ein Beitrag zur Entwicklung des Flügelgäders der Insecten. *Zoologischer Anzeiger* 11 (286): 443–447.
- Brodsky, A. K. 1994. *The evolution of insect flight*. Oxford: Oxford University Press, xiv + 229 pp.
- Brooks, S. J., and P. C. Barnard. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History, Entomology* 59 (2): 117–286.
- Carpenter, F. M. 1940. A revision of the Nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). *Proceedings of the American Academy of Arts and Sciences* 74 (7): 193–280, +3 pls.
- Carpenter, F. M. 1966. The Lower Permian insects of Kansas, part 11, the orders Protorthoptera and Orthoptera. *Psyche* 73 (1): 46–88.

- Comstock, J.H. 1918. *The wings of insects*. Ithaca: Comstock Publishing Company, xviii+[i]+430 pp., +10 pls.
- Comstock, J. H., and J. G. Needham. 1898a. The wings of insects [Chapter 1: an introduction to the study of the homologies of the wing veins]. *American Naturalist* 32 (373): 43–48.
- Comstock, J. H., and J. G. Needham. 1898b. The wings of insects [Chapter 2: the venation of a typical insect wing]. *American Naturalist* 32 (374): 81–89.
- Comstock, J. H., and J. G. Needham. 1898c. The wings of insects [Chapter 3: the specialization of wings by reduction]. *American Naturalist* 32 (376): 231–257. [covers parts 1 (introduction), 2 (Plecoptera), 3 (Psocoptera), 4 (Hemiptera: Auchenorrhyncha), 5 (Hemiptera: Heteroptera), 6 (Lepidoptera), and 7 (Trichoptera)]
- Comstock, J. H., and J. G. Needham. 1898d. The wings of insects [Chapter 3 (continued)]. *American Naturalist* 32 (377): 335–340. [covers part 8 (Diptera)]
- Comstock, J. H., and J. G. Needham. 1898e. The wings of insects [Chapter 3 (continued)]. *American Naturalist* 32 (378): 413–424. [covers parts 9 and 10 (Hymenoptera), and part 11 (Embiodea)]
- Comstock, J. H., and J. G. Needham. 1898f. The wings of insects [Chapter 3 (concluded)]. *American Naturalist* 32 (380): 561–565. [covers part 12 (Coleoptera)]
- Comstock, J. H., and J. G. Needham. 1898g. The wings of insects [Chapter 4: The specialization of wings by addition]. *American Naturalist* 32 (382): 769–777. [covers parts 1 (accessory veins) and 2 (suppression of branching)]
- Comstock, J. H., and J. G. Needham. 1898h. The wings of insects [Chapter 4 (continued)]. *American Naturalist* 32 (384): 903–911. [covers part 3 (Odonata)].

- Comstock, J. H., and J. G. Needham. 1899a. The wings of insects [Chapter 4 (continued)].  
American Naturalist 33 (386): 117–126. [covers part 4 (Ephemeroptera)]
- Comstock, J. H., and J. G. Needham. 1899b. The wings of insects [Chapter 4 (concluded)].  
American Naturalist 33 (391): 573–582. [covers parts 5 (Orthoptera) and 6 (conclusion)]
- Comstock, J. H., and J. G. Needham. 1899c. The wings of insects [Chapter 5: the development of wings]. American Naturalist 33 (395): 845–860. [covers parts 1 (position and growth), 2 (origin of tracheae), 3 (hypodermis), and 4 (tracheae and hypodermis)]
- Cousin, G., and O. Béthoux. 2016. The steps towards an inconspicuous vein fusion documented in Stenosmylinae forewings (Neuroptera: Osmylidae). *Organisms, Diversity and Evolution* 16 (1): 225–232.
- Crampton, G. 1916. The phylogenetic origin and the nature of wings of insects according to the paranotal theory. *Journal of the New York Entomological Society* 24 (1): 267–301.
- Engel, M. S. 2002. A new dustywing (Neuroptera: Coniopterygidae) in Turonian amber from New Jersey, with a reassessment of *Glaesoconis* in Neocomian amber from Lebanon. *Journal of the Kansas Entomological Society* 75 (1): 38–42.
- Engel, M. S. 2015. Insect evolution. *Current Biology* 25 (19): R868–R872.
- Engel, M. S. 2016. Two new genera of Cretaceous dustywings in amber from northern Myanmar (Neuroptera: Coniopterygidae). *Novitates Paleoentomologicae* 17: 1–16.
- Engel, M. S., and D. A. Grimaldi. 2004. New light shed on the oldest insect. *Nature* 427 (6975): 627–630.
- Engel, M. S., Davis, S. R., and J. Prokop. 2013. Insect wings: the evolutionary developmental origins of Nature's first flyers. In A. Minelli, G. Boxshall, and G. Fusco (editors),

- Arthropod biology and evolution: molecules, development, morphology: 269–298.  
Berling: Springer Verlag, ix + 532 pp.
- Engel, M. S., Winterton, S. L., and L. Breitkreuz. 2018. Phylogeny and evolution of Neuropterida: where have wings of lace taken us? *Annual Review of Entomology* 63: 531–551.
- Fennah, R. G. 1944. The morphology of the tegmina and wings in Fulgoroidea. *Proceedings of the Entomological Society of Washington* 46 (7): 185–199.
- Fraser, J. C. 1938. A note on the fallaciousness of the theory of pretracheation in the venation of Odonata. *Proceedings of the Royal Entomological Society of London, Series A, General Entomology* 13 (4–6): 60–70.
- Fraser, J. C. 1943. The origin of wings and venational types in insects. *American Midland Naturalist* 29 (2): 381–405.
- Grimaldi, D. 2000. A diverse fauna of Neuropterodea in amber from the Cretaceous of New Jersey. *In* D. Grimaldi (editor), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*: 259–303. Leiden: Backhuys Publishers, viii + 498 pp.
- Grimaldi, D., and M. S. Engel. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press, xv + 755 pp.
- Haas, F., and J. Kukalová-Peck. 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *European Journal of Entomology* 98 (4): 445–509.
- Hagen, H. A. 1870. Ueber rationelle Benennung des Geäders in den Flügeln der Insekten. *Stett. Entomologische Zeitung* 31 (7–9): 316–320, +1 pl. [pl. iii].
- Hamilton, K. G. A. 1971. The insect wing, part I. Origin and development of wings from notal lobes. *Journal of the Kansas Entomological Society* 44 (4): 421–433.

- Hamilton, K. G. A. 1972a. The insect wing, part II. Vein homology and the archetypal insect wing. *Journal of the Kansas Entomological Society* 45 (1): 54–58.
- Hamilton, K. G. A. 1972b. The insect wing, part III. Venation of the orders. *Journal of the Kansas Entomological Society* 45 (2): 145–162.
- Hamilton, K. G. A. 1972c. The insect wing, part IV. Venational trends and the phylogeny of the winged orders. *Journal of the Kansas Entomological Society* 45 (3): 295–308.
- Handlirsch, A. 1906. Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen. Leipzig: Engelmann, ix + pp. 1–640, + pls. 1–36.
- Handlirsch, A. 1907. Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen. Leipzig: Engelmann, pp. 641–1120, + pls. 37–51.
- Handlirsch, A. 1908. Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen. Leipzig: Engelmann, pp. 1121–1430.
- Holdsworth, R. P. Jr. 1942. The wing development of *Pteronarcys proteus* Newman (Pteronarcidae: Plecoptera). *Journal of Morphology* 70 (3): 431–461.
- Kukalová-Peck, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *Journal of Morphology* 156 (1): 53–126.
- Kukalová-Peck, J. 1983. Origin of the insect wing and wing articulation from the arthropod leg. *Canadian Journal of Zoology* 61 (7): 1618–1669.
- Kukalová-Peck, J. 1991. Fossil history and the evolution of hexapod structures. In I. D. Naumann (editor), *The insects of Australia: a textbook for students and research workers* [2nd ed., vol. 1]: 141–179. Ithaca: Cornell University Press, xvi + [i] + 542 pp., +8 pls.



- Kukalová-Peck, J. 1997. Arthropod phylogeny and 'basal' morphological structures. *In* R. A. Fortey and R. H. Thomas (editors), *Arthropod relationships*: 249–268. London: Chapman and Hall, xii + 383 pp.
- Kukalová-Peck, J. 2008. Phylogeny of higher taxa in Insecta: finding synapomorphies in the extant fauna and separating them from homoplasies. *Evolutionary Biology* 35 (1): 4–51.
- Kukalová-Peck, J. 2009. Carboniferous protodonatoid dragonfly nymphs and the synapomorphies of Odonoptera and Ephemeroptera (Insecta: Palaeoptera). *Palaeodiversity* 2: 169–198.
- Kukalová-Peck, J., and C. Brauckmann. 1992. Most Paleozoic Protorthoptera are ancestral hemipteroids: major wing braces as clues to a new phylogeny of Neoptera (Insecta). *Canadian Journal of Zoology* 70 (12): 2452–2473.
- Kukalová-Peck, J., and J. F. Lawrence. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wings characters. *European Journal of Entomology* 101 (1): 95–144.
- Kukalová-Peck, J., and E. S. Richardson, Jr. 1983. New Homiopteridae (Insecta: Paleodictyoptera) with wing articulation from Upper Carboniferous strata of Mazon Creek, Illinois. *Canadian Journal of Zoology* 61 (7): 1670–1687.
- Kukalová-Peck, J., Peters, J. G., and T. Söldan. 2009. Homologisation of the anterior articular plate in the wing base of Ephemeroptera and Odonoptera. *Aquatic Insects* 31 (Supplement 1): 459–470.
- Lameere, A. 1922. Sur la nervation alaire des insectes. *Bulletin de la Classe des Sciences, Académie Royal de Belgique* 1922 (4): 38–149.
- Lameere, A. 1923. On the wing-venation of insects. *Psyche* 30 (3–4): 123–132.

- Landois, H. 1871. Beiträge zur Entwicklungsgeschichte des Schmetterlingsflügel in der Raupe und Puppe. *Zeitschrift für Wissenschaftliche Zoologie* 21: 306–316, +1 pl. [pl. xxiii]
- Latreille, P. A. 1807. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata* [vol. 3]. Parisiis et Argentorati [Paris and Strasbourg]: A. Koenig, 258 pp.
- Latreille, P. A. 1817 [1816]. Les crustacés, les arachnides et les insectes. *In* G. Cuvier, *Le règne animal distribué d'après son organisation: pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. Avec figures, dessinées d'après nature* [vol. 3]: 1–653. Paris: Déterville, xxix + 653 pp.
- Liu, X.-Y., Aspöck, H., Winterton, S. L., Zhang, W.-W., and U. Aspöck. 2017. Phylogeny of pleasing lacewings (Neuroptera: Dilaridae) with a revised generic classification and description of a new subfamily. *Systematic Entomology* 42 (2): 448–471.
- Martynov, A. V. 1924. Sur l'interprétation de la nervuration et de la tracheation des ailes des Odonates et des Agnathes. *Russkoe Entomologicheskoe Obozrenie* [Revue Russe d'Entomologie] 18: 145–174. [in Russian, with French summary]
- Martynov, A. V. 1925. Über zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. *Zeitschrift für Morphologie und Ökologie der Tiere* 4 (3): 465–501.
- Martynov, A. V. 1928. Permian fossil insects of north-east Europe. *Travaux du Musée Géologique près l'Académie des Sciences de l'URSS* [Trudy Geologicheskogo Muzeya Akademii Nauk SSSR] 4: 1–118, +19 pls.
- Martynov, A. V. 1930. The interpretation of the wing venation and tracheation of the Odonata and Agnatha. *Psyche* 37 (3): 245–280.

- Martynov, A. V. 1938. Étude sur l'histoire géologique et de phylogénie des ordres des insectes (Pterygota). Première partie. Palaeoptera et Neoptera – Polyneoptera. Trudy Paleontologicheskogo Instituta, Akademia Nauk SSSR 7 (4): 1–149, +1 pl. [pl. i]. [in Russian, with French summary]
- Matsuda, R. 1970. Morphology and evolution of the insect thorax. Memoirs of the Entomological Society of Canada 76: 1–431.
- Meinander, M. 1972. A revision of the family Coniopterygidae (Planipennia). Acta Zoologica Fennica 136: 1–357.
- Meinander, M. 1975. Fossil Coniopterygidae (Neuroptera). Notulae Entomologicae 55 (2): 53–57.
- Montserrat, V. J., and O. Gavira. 2014. A new European species of *Nevrorthus* in the Iberian Peninsula (Insecta, Neuropterida). Zootaxa 3796 (2): 349–360.
- Müller, F. 1873a. Beiträge zur Kenntnis der Termiten. Jenaische Zeitschrift für Medizin und Naturwissenschaft 7 (3): 333–358, + pls. xix–xx.
- Müller, F. 1873b. Beiträge zur Kenntnis der Termiten. Jenaische Zeitschrift für Medizin und Naturwissenschaft 7: 451–463.
- Müller, F. 1875. Beiträge zur Kenntnis der Termiten. Jenaische Zeitschrift für Naturwissenschaft 9: 241–264, + pls. x–xiii.
- Myskowiak, J., Escuillié, F., and A. Nel. 2015. A new Osmylidae (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation in Brazil. Cretaceous Research 54: 27–33.
- Needham, J. G. 1903. A genealogic study of dragon-fly wing venation. Proceedings of the U.S. National Museum 26 (1331): 703–764, + pls. xxxi–liv.
- Needham, J. G. 1935. Some basic principles of insect wing venation. Journal of the New York Entomological Society 43 (2): 113–129.

- Nel, A., Bechly, G., Garrouste, R., Pohl, B., and F. Escuillié. 2005. A new extraordinary neuropterid family from the Lower Cretaceous Crato Formation of Brazil: a new insect order? (Insecta, Neuropterida). *Cretaceous Research* 26 (6): 845–852.
- Niwa, N., Akimoto-Kato, A., Niimi, T., Tojo, K., Machida, R., and S. Hayashi. 2010. Evolutionary origin of the insect wing via integration of two developmental modules. *Evolution and Development* 12 (2): 168–176.
- Oswald, J. D. 1993. Phylogeny, taxonomy, and biogeography of extant silky lacewings (Insecta: Neuroptera: Psychopsidae). *Memoirs of the American Entomological Society* 40: 1–65.
- Oswald, J. D. 1998. *Osmylops* Banks (Neuroptera: Nymphidae): generic review and revision of the *armatus* species group. *Journal of Neuropterology* 1: 79–108.
- Oswald, J. D. 2017. Neuropterida species of the world. Version 5.0. Online resource (<http://lacewing.tamu.edu/SpeciesCatalog/Main>), accessed on 27 November 2017.
- Prokop, J., Pecharová, M., Nel, A., Hörnschemeyer, T., Krzemińska, E., Krzemiński, W., and M. S. Engel. 2017. Paleozoic nymphal wing pads support dual model of insect wing origins. *Current Biology* 27 (2): 263–269.
- Rambur, J. P. 1842. *Histoire naturelle des insectes. Néuroptères*. Paris: Roret, xvii +[i] + 534 pp., +12 pls.
- Rasnitsyn, A. P. 1981. A modified paranotal theory of insect wing origin. *Journal of Morphology* 168 (3): 331–338.
- Rasnitsyn, A. P. 2007. On the discussion of the wing venation of (Archae) Orthoptera (Insecta). *Paleontological Journal* 41 (3): 341–344.

- Redtenbacher, J. 1886. Vergleichende Studien über das Flügelgeäder der Insecten. *Annalen des K.K. [Kaiserlich-Königlichen] Naturhistorischen Hofmuseums* 1 (3): 153–232, + pls. ix–xx.
- Rehn, A. C. 2003. Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology* 28 (2): 181–239.
- Riek, E. F. 1970. Neuroptera (lacewings). *In* D.F. Waterhouse (editor), *The insects of Australia: a textbook for students and research workers*: 472–494. Melbourne: Melbourne University Press, xiii + 1029 pp., + pls. i, 1–8.
- Riek, E. F., and J. Kukalová-Peck. 1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology* 62 (6): 1150–1166.
- Ross, H. H. 1936. The ancestry and wing venation of the Hymenoptera. *Annals of the Entomological Society of America* 29 (1): 99–111.
- Shi, C., O. Bethoux, C. Shih, and D. Ren. 2012. *Guyiling jianboni* gen. et sp. n., an antlion-like lacewing, illuminating homologies and transformations in Neuroptera wing venation. *Systematic Entomology* 37 (3): 617–631.
- Shi, C. F., S. L. Winterton, and D. Ren. 2015. Phylogeny of split-footed lacewings (Neuroptera, Nymphidae), with descriptions of new Cretaceous fossil species from China. *Cladistics* 31 (5): 455–490.
- Snodgrass, R. E. 1909. The thorax of insects and the articulation of the wings. *Proceedings of the U.S. National Museum* 36 (1687): 511–595.
- Snodgrass, R. E. 1935. *Principles of insect morphology*. New York: McGraw-Hill, ix+ 667 pp.

- Stephens, J. F. 1835. Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable [Mandibulata, vol. 6]. London: Baldwin and Cradock, 240 pp., + pls. xxviii–xxxiv.
- Tillyard, R. J. 1914. On some problems concerning the development of the wing-venation of Odonata. *Proceedings of the Linnean Society of New South Wales* 39 (153): 163–216, + pls. xi–xiii.
- Tillyard, R. J. 1916. Studies in Australian Neuroptera. No. 3. The wing-venation of the Chrysopidae. *Proceedings of the Linnean Society of New South Wales* 41 (162): 221–248, + pls. x–xi.
- Tillyard, R. J. 1932. Kansas Permian insects. Part 14. The order Neuroptera. *American Journal of Science, Fifth Series* 23 (133): 1–30.
- Westwood, J. O. 1839. An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families [vol. 1]. London: Longman, Orme, Brown, Green, and Longmans, xii + 462 pp.
- Westwood, J. O. 1840. An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families [vol. 2]. London: Longman, Orme, Brown, Green, and Longmans, xi + 587 + [i] + 158 pp.
- Whitten, J. M. 1962. Homology and development of insect wing tracheae. *Annals of the Entomological Society of America* 55 (3): 288–295.
- Wigglesworth, V. B. 1976. The evolution of insect flight. *In* R.C. Rainey (editor), *Insect flight*: 255–269. Oxford: Blackwell, xi + 287 pp.

- Withycombe, C. L. 1922. The wing venation of the Coniopterygidae. *Entomologist* 55 (713): 224–225.
- Winterton, S. L. and S. J. Brooks. 2002. Phylogeny of the apochrysin green lacewings (Neuroptera: Chrysopidae: Apochrysinae). *Annals of the Entomological Society of America* 95 (1): 16–28.
- Winterton, S. L., and V. N. Makarkin. 2010. Phylogeny of moth lacewings and giant lacewings (Neuroptera: Ithonidae, Polystoechotidae) using DNA sequence data, morphology, and fossils. *Annals of the Entomological Society of America* 103 (4): 511–522.
- Winterton, S. L., N. B. Hardy, and B. M. Wiegmann. 2010. On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Systematic Entomology* 35 (3): 349–378.
- Winterton, S. L., J. Zhao, I. J. Garzón-Orduña, Y. Wang, and Z. Liu. 2017. The phylogeny of lance lacewings (Neuroptera: Osmylidae). *Systematic Entomology* 42 (3): 555–574.
- Winterton, S. L., et al. 2017. Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology* DOI: 10.1111/syen.12278.
- Wootton, R. J. 1965. Evidence for tracheal capture in early Heteroptera. *Proceedings of the 12th International Congress of Entomology, London 1964*: 65–67.
- Wootton, R. J. 1976. The fossil record and insect flight. *In* R.C. Rainey (editor), *Insect flight*: 235–254. Oxford: Blackwell, xi + 287 pp.
- Wootton, R. J. 1979. Function, homology and terminology in insect wings. *Systematic Entomology* 4 (1): 81–93.

Wootton, R. J. 1992. Functional morphology of insect wings. *Annual Review of Entomology* 37:  
113–140.