

# XIII International Symposium of Neuropterology

17–22 June 2018, Laufen, Germany



# Proceedings



Edited by  
**Florian Weihrauch, Odile Frank, Axel Gruppe,  
James E. Jepson, Lukas Kirschey & Michael Ohl**





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**Osmylus Scientific Publishers  
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# Proceedings of the XIII International Symposium of Neuropterology 17–22 June 2018, Laufen, Germany

**Editors:** Florian Weihrauch, Odile Frank, Axel Gruppe, James E. Jepson, Lukas Kirschey & Michael Ohl

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Midsummer dusk during the Mid-Symposium tour; ‘Schönramer Filz’ near Laufen, Germany (19.vi.2018); Photo by Florian Weihrauch

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## Preface

The current volume is the printed result of the XIII International Symposium of Neuropterology, which took place in June 2018 and was hosted by the Academy for Nature Conservation and Landscape Management in Laufen in Bavaria, southern Germany. The symposium was attended by scientists from 16 countries from all over the world. The scientific program consisted of 31 lectures, four of which were keynote lectures, and 13 posters. Although the total number of participants was small, the symposium covered the spectrum of recent neuropterology in its entirety. The symposium reflected the current state of knowledge in the fields of paleoentomology, developmental biology, taxonomy, phylogeny, conservation, behavior, ecology and biogeography on Neuropterida. In addition, the symposium, like all others before, was also a place for discussion and scientific exchange on all topics within neuropterology. The organizers of the symposium are pleased that they have succeeded in finally presenting comprehensive conference proceedings after a successful conference.

Michael Ohl,  
on behalf of the organizing team: Axel Gruppe, Lukas Kirschey, and Florian Weihrauch

## Acknowledgements

The organizing team of the XIII International Symposium of Neuropterology would like to thank the Deutsche Forschungsgemeinschaft (DFG), the Leibniz Association, the Technische Universität München (TUM) and the Academy for Nature Conservation and Landscape Management (ANL) in Laufen for generous financial support that made the conference and the conference proceedings possible. We owe special thanks to Marianne Krause and Christian Stettmer (ANL) for their great work as local organizers that ensured a smooth and perfect course of the conference and the excursions.



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Technische Universität München

## Participant list

Al Rashdi Zamzam	UAE	zamzam.alrashdi@ead.ae
Aspöck Horst	Austria	horst.aspoeck@meduniwien.ac.at
Aspöck Ulrike	Austria	ulrike.aspoeck@nhm-wien.ac.at
Badano Davide	Italy	davide.badano@gmail.com
Bozdoğan Hakan	Turkey	hakan.bozdogan@ahievran.edu.tr
Breitkreuz Laura	USA	l.breitkreuz@gmail.com
Califre Martins Caleb	Brazil	calebcalifre@gmail.com
D'Auria Felicia Diodata	Italy	agostino.letardi@enea.it
Devetak Dušan	Slovenia	dusan.devetak@guest.arnes.si
Dobosz Roland	Poland	dobosz@muzeum.bytom.pl
Duelli Peter	Switzerland	peter.duelli@wsl.ch
Frank Odile	France	andre.prost@free.fr
Fenzl Felix	Germany	fenzlf@gmx.de
Gepp Johannes	Austria	j.gepp@naturschutzinstitut.at
Gruppe Axel	Germany	gruppe@wzw.tum.de
Han Xu	China	hanny_90@163.com
Jepson James E.	Ireland	james.jepson@ucc.ie
Jones Joshua R.	USA	doc.jonesresearch@gmail.com
Khramov Alexander	Russia	a-hramov@yandex.ru
Kim Seulki	South Korea	neurosk84@gmail.com
Kirschey Lukas	Germany	lukas.kirschey@mfn-berlin.de
Klokočovnik Vesna	Slovenia	vesna.klokocovnik@um.si
Koczor Sándor	Hungary	koczor.sandor@agrar.mta.hu
Krause Marianne	Germany	Marianne.Krause@anl.bayern.de
Kunjupillai Saji	UAE	sajienglish@gmail.com
Letardi Agostino	Italy	agostino.letardi@enea.it
Liu Zhiqi	China	liuzhiqi@cau.edu.cn
Liu Xingyue	China	xingyue_liu@yahoo.com
Lu Xiumei	China	xiumeilu@cau.edu.cn
Lyu Yanan	China	lyyanan214@cau.edu.cn
Michel Bruno	France	bruno.michel@cirad.fr
Nicoli Aldini Rinaldo	Italy	rinaldo.nicoli@unicatt.it
Oswald John	USA	j-oswald@tamu.edu
Podlesnik Jan	Slovenia	jan.podlesnik@um.si
Prost André	France	prostloisia@gmail.com
Ren Dong	China	rendong@mail.cnu.edu.cn
Saji Anitha	UAE	asaji@ead.ae
Shi Chaofan	China	paleobioscf@gmail.com
Stettmer Christian	Germany	Christian.Stettmer@anl.bayern.de
Szentkirályi Ferenc	Hungary	h2404sze@ella.hu
Thierry Catherine	France	dominique.thierry@wanadoo.fr
Thierry Dominique	France	dominique.thierry@wanadoo.fr
Tóth Judith	Hungary	h2404sze@ella.hu
Villenave-Chasset Johanna	France	johanna_villenave@hotmail.com
Wang Yongjie	China	wangyjosmy@gmail.com
Weihrauch Florian	Germany	mail@osmylus.com
Weissmair Werner	Austria	w.weissmair@aon.at

## **XIII International Symposium of Neuropterology: General information**

### **Host:**

Bayerische Akademie für Naturschutz und Landschaftspflege (ANL)  
Seethalerstraße 6  
83410 Laufen/Salzach, Germany

### **Symposium venue:**

Seminar- und Kongresshotel Kapuzinerhof  
Schlossplatz 4  
83410 Laufen/Salzach, Germany

## **XIII International Symposium of Neuropterology: Agenda**

**Monday, 18 June 2018**

### **Session 1. Phylogeny**

Chair: Ulrike Aspöck

#### **Keynote lecture:**

New insights into the phylogeny and evolution of Megaloptera

**Xingyue Liu**

Phylogeny of Chrysopidae with an emphasis on morphological evolution

**Laura C.V. Breitkreuz**, Michael S. Engel, Shaun L. Winterton & Ivonne J. Garzón-Orduña

Note on the immature stage and female morphology of *Osmylus bipapillatus*, with reference to the systematic significance (Neuroptera, Osmylidae)

**Han Xu**, Yongjie Wang & Zhiqi Liu

On the study of Korean Coniopteryginae (Neuroptera: Coniopterygidae): Molecular trees conflict between 16S and COI

**Kim Seulki** & Cho Soowon

### **Session 2. Fossils**

Chair: James E. Jepson

Geometric morphometrics and the evolution of wing patterns in fossil Neuroptera

**James E. Jepson**, Maria E. McNamara, Dong Ren, Chaofan Shi & Norman MacLeod

The Neuropterida from the mid-Cretaceous of Myanmar

**Xiumei Lu** & Xingyue Liu

New fossil Raphidioptera (Insecta: Neuropterida) in the Mesozoic of northeastern China  
**Yanan Lyu**

Mesozoic Chrysopidae: a review of current knowledge  
**Alexander Khramov**

### **Session 3. Neuropterology and beyond**

Chair: Xingyue Liu

»Catálogo Taxômico da Fauna do Brasil«: the technology contributing against taxonomic impediment – Neuroptera example

**Caleb Califre Martins** & Renato Jose Pires Machado

Setting up a Neuropterology research lab: Synergistic experiences in undergraduate mentorship

**Joshua R. Jones**

Lacewings and Citizen science in Italy: a young but very promising relationship

**Agostino Letardi**

**Tuesday, 19 June 2018**

### **Session 4. Morphology**

Chair: John Oswald

#### **Keynote lecture:**

Towards a homologization of the male genital sclerites of Coniopterygidae (Neuroptera) – a tightrope dance

**Ulrike Aspöck**

### **Session 5. Development, chemical ecology and microstructures**

Chair: John Oswald

Metathetely and its implications for the distribution of Raphidioptera

**Horst Aspöck**, Viktoria Abbt, Ulrike Aspöck & Axel Gruppe

Chemical ecology of Chrysopidae: perspectives of synthetic attractants

**Sandor Koczor**, Ferenc Szentkirályi & Miklós Tóth

The dimensions of the dust of dustywings (Neuroptera. Coniopterygidae)

**Axel Gruppe**, Sarah Bastyans, Felix Fenzl & Michael Gebhard

### **Mid-Symposium tour**

Coach journey, incl. brown-bagged dinner, collecting and light-trapping.

First stop: Weitsee-Lödensee (afternoon, collecting), second stop: Schönrammer Filz (evening, incl. barbecue and light-trapping)

Wednesday, 20 June 2018

**Session 6. A focus on Myrmeleontidae**

Chairs: Dušan Devetak, Bruno Michel

**Keynote lecture:**

Into the pit: evolution, diversity and biology of the larvae of Myrmeleontiformia

**Davide Badano**

In search of *Myrmeleon bore*: Bavaria's rarest Neuropteran?

**Florian Weihrauch**

Predatory behavior of two antlion species under different conditions

**Vesna Klokočovnik & Dušan Devetak**

The genus *Nosa* Navás, 1911 (Neuroptera, Myrmeleontidae, Palparinae)

**André Prost**

Owlflyes are derived antlions: anchored phylogenomics and a revised phylogenetic classification of the family Myrmeleontidae (Insecta: Neuroptera)

Renato J.P. Machado, Jessica Gillung, Shaun L. Winterton, Ivonne J. Garzon-Orduña, Alan Lemmon, Emily Lemmon & **John Oswald**

**Poster session**

including a brief oral presentation to each poster of max. 3 minutes

Chair: Florian Weihrauch

**Distribution of the Green Lacewing in France by Regions – In the frame of the LDL Lacewing Digital Library / World Neuropterida Faunas Module**

Michel Canard, Dominique Thierry & Matthieu Giacomino

**The current state of knowledge of Polish Chrysopidae: research history, distribution and present-day problems**

Roland Dobosz

**A review of the current state of knowledge of Mesozoic Mantispidae**

James E. Jepson & Michael Ohl

**Preliminary results of NEUIT (Barcoding of Italian Neuropterida) project**

Agostino Letardi

**Seven new species, one neotype, one new male and new distribution records for *Isostenosmylus* Krüger, 1913 (Neuroptera: Osmylidae)**

Adrian Ardila-Camacho, Oliver S. Flint, Jr., Renato J.P. Machado, Caleb Califre Martins & Lionel A. Stange

**Mantispidae of the Área de Conservación Privada (ACP) Panguana, Peru**

Axel Gruppe, Michael Gebhardt & Ernst-Gerhard Burmeister

**What is the presumed owlfly illustrated in Aldrovandi's *De animalibus insectis* (1602)?**

Rinaldo Nicoli Aldini

**On some morphological abnormalities found in Neuroptera**

Rinaldo Nicoli Aldini

**Contribution to the study of the fine structure of the egg in the genus *Pseudomallada* Tsukaguchi, 1995 (Neuroptera, Chrysopidae)**

Rinaldo Nicoli Aldini

**Geographic and seasonal range of the antlions recorded in the United Arab Emirates**

Anitha Saji

**Imaginal Diet of *Chrysoperla renoni* (Lacroix, 1933) (Neuropterida, Chrysopidae)**

Michel Canard, Dominique Thierry & Johanna Villenave-Chasset

**Diverse beaded lacewings from the Cretaceous Burmese amber**

Shuo Huang, Dong Ren & Yongjie Wang

**Current status and species diversity of the Neuroptera (lacewings, antlions & owlflies) in the United Arab Emirates**

Zamzam Al Rashdi, Anitha Saji, Pritpal Soorae & Shaikha Al Dhaheri

**Thursday, 21 June 2018**

**Session 7. Faunistics and biogeography**

Chairs: Horst Aspöck, André Prost, Agostino Letardi

**Keynote lecture:**

Neuropterida from South America: large diversity, largely unknown

**Caleb Califre Martins**

Fantastic lacewings and where to find them

**Agostino Letardi** & Roberto A. Pantaleoni

The impact of forest fire and wind-throw on Neuroptera, Raphidioptera and Mecoptera  
**Peter Duelli**, Beat Wermelinger, Marco Moretti & Martin K. Obrist

Lacewings (Neuropterida: Neuroptera, Raphidioptera) in three National Parks in the Balkan Peninsula: Results of short collection trips

**Dušan Devetak**, Predrag Jakšić, Vesna Klokočovnik, Tina Klenovšek, Jan Podlesnik, Franc Janžekovič & Hubert Rausch

Neuroptera of the region of Missouri (Morocco)

**Michel Bruno** & Alexandre François

Neuroptera in two protected sand dune areas in the southern rim of the Pannonian Plain

**Dušan Devetak**, Predrag Jakšić, Tina Klenovšek, Jan Podlesnik, Franc Janžekovič & Daniel Ivajnsič

Ascalaphidae larvae from Costa Rica

**Johannes Gepp**

Golden-eyed diversity (Neuroptera: Chrysopidae) in the agro-forest area of Amanous Mountains, Turkey

**Hakan Bozdoğan**

To the limit: Altitude records of Neuroptera in the Bavarian Alps

**Florian Weihrauch**, Axel Gruppe & Alfred Karle-Fendt

## **Session 8. Taxonomy**

Chair: Caleb Califre Martins

What is really the sub-species *nanceiensis* Séméria, 1980 of the Common green lacewings *Chrysoperla carnea* (Stephens, 1836) sensu lato? (Neuroptera, Chrysopidae)

**Dominique Thierry** & Michel Canard

Crucial first steps for a revision of the *Pseudomallada prasinus* group in Europe (Neuroptera: Chrysopidae)

**Peter Duelli**

**Friday, 22 June 2018**

Departure to **Post-Symposium excursion** to eastern Bavaria (4 days)

## **Pictorial memories of the 13<sup>th</sup> International Symposium of Neuropterology in Laufen, Germany, Bavaria, 17–24 June 2018**

Horst Aspöck

Institute of Specific Prophylaxis and Tropical Medicine, Medical Parasitology, Medical University of Vienna, Kinderspitalgasse 15, 1090 Vienna, Austria, horst.aspoeck@meduniwien.ac.at

*Received and accepted 20<sup>th</sup> August 2019*

Since the 1<sup>st</sup> International Symposium on Neuropterology in Graz, Austria, in September 1980, these events have become a unique possibility to contact colleagues personally, to establish scientific co-operations and – in many cases – long-lasting friendships.

Prior to 1980, very few photographs of neuropterologists were taken, but with the 1<sup>st</sup> Symposium a new period of the documentation of the scientific community in neuropterology began (H. ASPÖCK 2010).

This article intends to present a representative documentation of the Symposium in Laufen – as a pleasure for us who took part in this event to remember the days of intensive activity in the old monastery, which is now a congress center, in the lecture hall, at the posters, and during the excursions, and last but not least as a long-lasting source of information for future generations of neuropterologists.

The following 68 photographs, strictly in chronological order, are a guide through this unforgettable week.

### **Reference**

Aspöck H. 2010. Neuropterida research at the threshold of the 21<sup>st</sup> century reflected through the International Symposia on Neuropterology 1980–2008. In: Devetak D., Lipovšek S. & Arnett A.E. (Eds), Proceedings of the Tenth International Symposium on Neuropterology, Piran, Slovenia, 22–25 June 2008: 25-42. Faculty of Natural Sciences and Mathematics, University of Maribor



**Figure 1.** Axel Gruppe (left) and John Oswald. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 2.** From left: Xiumei Lu, Ulrike Aspöck and Lukas Kirschej. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 3.** From left: Axel Gruppe, John Oswald and Horst Aspöck. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 4.** From left: Christian Stettmer, Horst Aspöck and Florian Weihrrauch. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 5.** From left: Caleb Califre Martins, Xingyue Liu, Ulrike Aspöck and Roland Dobosz. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 6.** From left: Rinaldo Nicoli Aldini, Davide Badano, Seulki Kim and Xingyue Liu. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 7.** From left: Davide Badano, Ulrike Aspöck and Yongjie Wang. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 8.** In front, from left: Horst Aspöck, Bruno Michel, Xingyue Liu, Chaofan Shi, Yongjie Wang and John Oswald. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 9.** From left: Ulrike Aspöck, Caleb Califre Martins, Xingyue Liu, Odile Frank and Davide Badano. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 10.** From left: Caleb Califre Martins, Davide Badano and Alexander Khramov. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 11.** From left: Odile Frank, Bruno Michel and André Prost. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 12.** Joshua Jones (left) and André Prost. Laufen, Germany, 17.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 13.** Participants of the 13<sup>th</sup> IAN Symposium of Neuropterology in the lecture hall. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 14.** Xingyue Liu (left) and Ulrike Aspöck. Discussion after his keynote. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 15.** Horst Aspöck (left) and Johannes Gepp. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 16.** From left: Ulrike Aspöck, Hakan Bozdoğan and Vesna Klokočovnik. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 17.** First row, from left: Horst Aspöck, Ren Dong and Ulrike Aspöck. Second row, from left: Lukas Kirschej, Rinaldo Nicoli Aldini and John Oswald. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 18.** Laura Breitkreuz giving her presentation on the phylogeny of Chrysopidae. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 19.** Seulki Kim giving his presentation on Korean Coniopteryginae. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 20.** Alexander Khramov giving his presentation on Mesozoic Coniopterygidae. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 21.** From left: Horst Aspöck, Xingyue Liu, Xiumei Lu, James Jepson and Alexander Khramov. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 22.** From left: Horst Aspöck, Yanan Lyu, Ulrike Aspöck and Xingyue Liu. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 23.** Joshua Jones giving his presentation on setting up a Neuropterology research lab. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 24.** Agostino Letardi giving his presentation on lacewings and citizen science in Italy. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 25.** Participants of the 13<sup>th</sup> IAN Symposium of Neuropterology in the lecture hall. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).

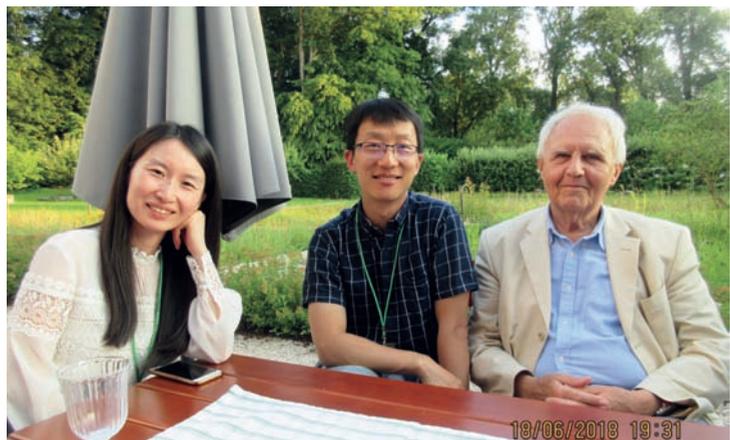
**Figure 26.** Ulrike Aspöck (left) and Davide Badano. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).

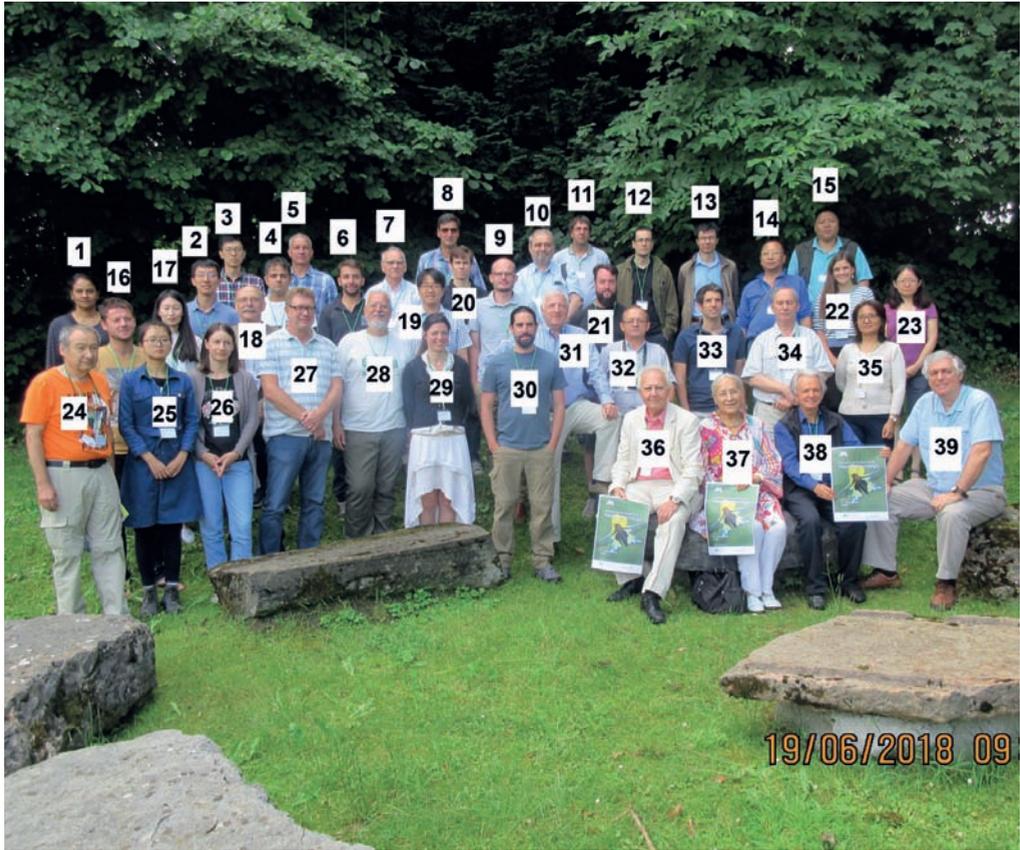


**Figure 27.** Horst Aspöck (left) and John Oswald. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 28.** From left: Xiumei Lu, Xingyue Liu and Horst Aspöck. Laufen, Germany, 18.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 29.** Group photograph of the participants of the 13<sup>th</sup> IAN Symposium of Neuropterology. 1 – Anitha Saji (UAE), 2 – Xingyue Liu (China), 3 – Xu Han (China), 4 – Hakan Bozdoğan (Turkey), 5 – Christian Stettmer (Germany), 6 – Felix Fenzl (Germany), 7 – Bruno Michel (France), 8 – Axel Gruppe (Germany), 9 – Alexander Khramov (Russia), 10 – Rinaldo Nicoli Aldini (Italy), 11 – Werner Weißmair (Austria), 12 – Caleb Califre Martins (Brazil), 13 – Sándor Koczor (Hungary), 14 – Dong Ren (China), 15 – Yongjie Wang (China), 16 – Jan Podlesnik (Slovenia), 17 – Xiumei Lu (China), 18 – Dominique Thierry (France), 19 – Seulki Kim (South Korea), 20 – James E. Jepson (Ireland), 21 – Lukas Kirschey (Germany), 22 – Laura Breitzkreuz (Germany), 23 – Chaofan Shi (China), 24 – Dušan Devetak (Slovenia), 25 – Yanan Lyu (China), 26 – Vesna Klokočovnik (Slovenia), 27 – Florian Weihrauch (Germany), 28 – Agostino Letardi (Italy), 29 – Johanna Villenave-Chasset (France), 30 – Joshua R. Jones (USA), 31 – Peter Duelli (Switzerland), 32 – Roland Dobosz (Poland), 33 – Davide Badano (Italy), 34 – Ferenc Szentkirályi (Hungary), 35 – Zhiqi Liu (China), 36 – Horst Aspöck (Austria), 37 – Ulrike Aspöck (Austria), 38 – Johannes Gepp (Austria), 39 – John Oswald (USA). Laufen, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 30.** The participants of the 13<sup>th</sup> Symposium who also attended the very first symposium in Graz 38 years ago, in September 1980. From left: Johannes Gepp, Peter Duelli, Ulrike Aspöck, Horst Aspöck and Dušan Devetak. Laufen, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 31.** Mid-congress tour. From left: Ulrike Aspöck, Axel Gruppe and Florian Weihrauch. Weitsee-Lödensee, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 32.** Mid-congress tour. Horst Aspöck (left) and Agostino Letardi. Weitsee-Lödensee, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 33.** Mid-congress tour. Ulrike Aspöck (left) and Laura Breitzkreuz. Weitsee-Lödensee, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 34.** Mid-congress tour. Ulrike Aspöck (left) and Caleb Califre Martins. Weitsee-Lödensee, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 35.** Participants of the 13<sup>th</sup> IAN Symposium of Neuropterology during the mid-congress tour. Schönramer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 36.** Mid-congress tour. From left: Xingyue Liu, Horst Aspöck, Ren Dong and Davide Badano. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).

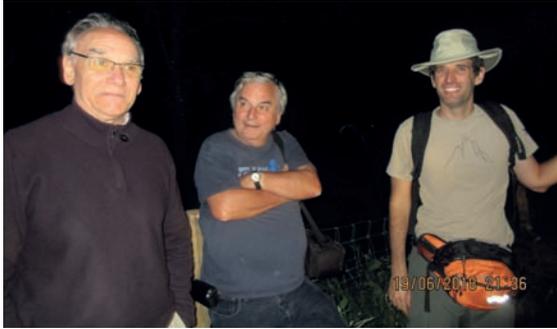


**Figure 37.** Mid-congress tour. From left: Lukas Kirschey, Alexander Khramov, Laura Breitzkreuz and Rinaldo Nicoli Aldini. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 38.** Mid-congress tour. From left: Rinaldo Nicoli Aldini, Davide Badano, Horst Aspöck and Zhiqi Liu. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 39.** Mid-congress tour, light trapping. From left: Bruno Michel, André Prost and Davide Badano. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 40.** Mid-congress tour, light trapping. From left: Bruno Michel, Dominique Thierry, Rinaldo Nicoli Aldini, Horst Aspöck and André Prost. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 41.** Mid-congress tour, light trapping. Yanan Lyu. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 42.** Mid-congress tour, light trapping. Vesna Klokočovnik (left) and Dušan Devetak. Schönrammer Filz, Germany, 19.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 43.** Davide Badano giving his keynote on Myrmeleontiformia. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 44.** From left: Hakan Bozdoğan, Horst Aspöck and Caleb Califre Martins. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 45.** IAN board meeting. From left: Agostino Letardi, Xingyue Liu, John Oswald, Dominique Thierry (back row); Dušan Devetak, André Prost and Horst Aspöck (front row). Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 46.** IAN board meeting. John Oswald (left) and Dominique Thierry. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 47.** The newly elected IAN board for the period 2018–2021. From left: Davide Badano, Chaofan Shi, André Prost (secretary), John Oswald (past president), Horst Aspöck, Xingyue Liu (president), Vesna Klokočovnik (vice-president), Caleb Califre Martins, Agostino Letardi (editor of the newsletter), Dušan Devetak and Dominique Thierry (treasurer). Not present in Laufen: Michael Ohl (past president), ex officio: Césare Freire de Carvalho (who had agreed to organize the next symposium in Lavras, Minas Gerais, Brazil in 2021). On 9<sup>th</sup> October 2018 we received the shocking message of the tragic death of Prof. Carvalho. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



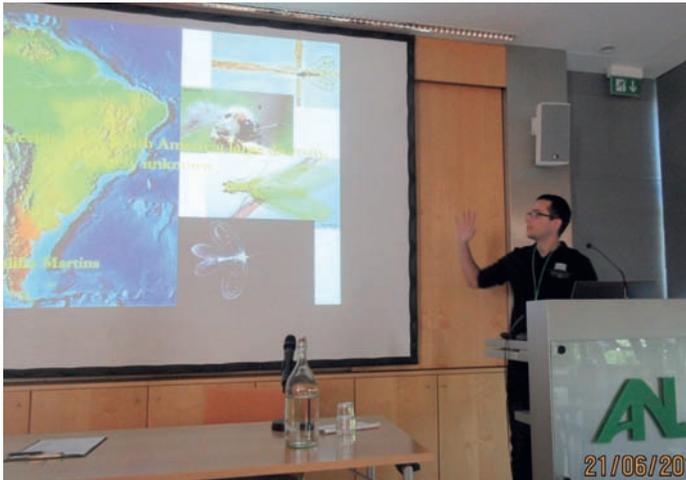
**Figure 48.** Horst Aspöck (left) and Dušan Devetak. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 49.** From left: Roland Dobosz, Peter Duelli and Davide Badano. Laufen, Germany, 20.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 50.** Caleb Califre Martins (left) and Horst Aspöck during the session on faunistics and biogeography. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 51.** Caleb Califre Martins giving his keynote on the Neuropterida of South America. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 52.** Agostino Letardi (left) and Horst Aspöck. Discussion after A. Letardi's presentation on 'Fantastic lacewings'. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).

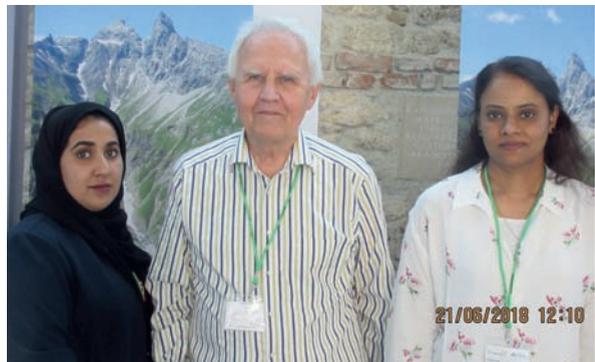
**Figure 53.** Dušan Devetak (left) and André Prost. Discussion after D. Devetak's presentation on Neuropterida in National Parks in the Balkan Peninsula. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 54.** Bruno Michel giving his presentation on Moroccan Neuroptera. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck)



**Figure 55.** From left: Zamzam Al Rashdi, Horst Aspöck and Anitha Saji. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 56.** From left: Peter Duelli, Davide Badano and Ulrike Aspöck. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 57.** Group photo of the participants of the 13<sup>th</sup> IAN Symposium of Neuropterology. 1 – Dušan Devetak, 2 – Dominique Thierry, 3 – Xu Han, 4 – Xingyue Liu, 5 – Alexander Khramov, 6 – Bruno Michel, 7 – Anitha Saji, 8 – Christian Stettmer, 9 – Felix Fenzl, 10 – Axel Gruppe, 11 – Seulki Kim, 12 – James E. Jepson, 13 – Lukas Kirschey, 14 – Caleb Califre Martins, 15 – Yongjie Wang, 16 – Agostino Letardi, 17 – Werner Weißmair, 18 – Sándor Koczor, 19 – Ferenc Szentkirályi, 20 – Vesna Klokočovnik, 21 – Jan Podlesnik, 22 – Xiumei Lu, 23 – Yanan Lyu, 24 – Zamzam Al Rashdi, 25 – Florian Weihrauch, 26 – Laura Breitreuz, 27 – André Prost, 28 – Davide Badano, 29 – Roland Dobosz, 30 – Zhiqi Liu, 31 – Joshua R. Jones, 32 – Rinaldo Nicoli Aldini, 33 – Odile Frank, 34 – John Oswald, 35 – Horst Aspöck, 36 – Ulrike Aspöck, 37 – Peter Duelli, 38 – Johannes Gepp. Laufen, Germany, 21.vi.2018; Photo: Marianne Krause (Photo archive H. & U. Aspöck).



**Figure 58.** The on-site organizing team during the closing ceremony appreciating the great work of Marianne Krause as guardian angel of the entire symposium. From left: Christian Stettmer, Marianne Krause, Axel Gruppe, Lukas Kirschey and Florian Weihrauch. Laufen, Germany, 21.vi.2018 (Photo: Rinaldo Nicoli Aldini).

**Figure 59.** John Oswald (left) and Ren Dong. Laufen, Germany, 21.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 60.** From left: Joshua Jones, James Jepson and Chaofan Shi. Laufen, Germany, 22.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 61.** Post-congress excursion. Seulki Kim (left) and Horst Aspöck. Haidmühle-Frauenberg Hostel, Germany, 22.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 62.** Post-congress excursion. From left: Xiumei Lu, Yanan Lyu, Lukas Kirschey, Xingyue Liu and James Jepson. Nature Reserve Bayerischer Wald, Germany, 23.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 63.** Group photo of the participants of the post-congress excursion. 1 – Xiumei Lu, 2 – Axel Gruppe, 3 – André Prost, 4 – Lukas Kirschey, 5 – Xu Han, 6 – Seulki Kim, 7 – Caleb Califre Martins, 8 – Peter Duelli, 9 – Horst Aspöck, 10 – Davide Badano, 11 – John Oswald, 12 – Ren Dong, 13 – Yongjie Wang, 14 – Odile Frank, 15 – James Jepson, 16 – Chaofan Shi, 17 – Zhiqi Liu, 18 – Ulrike Aspöck, 19 – Yanan Lyu, 20 – Xingyue Liu. Nature Reserve Bayerischer Wald, Germany, 23.vi.2018 (Photo archive H. & U. Aspöck).

**Figure 64.** Post-congress excursion. From left: Seulki Kim, Ulrike Aspöck, Caleb Califre Martins, Horst Aspöck and Xu Han. Nature Reserve Jochensteiner Hänge, Germany, 24.vi.2018 (Photo archive H. & U. Aspöck).

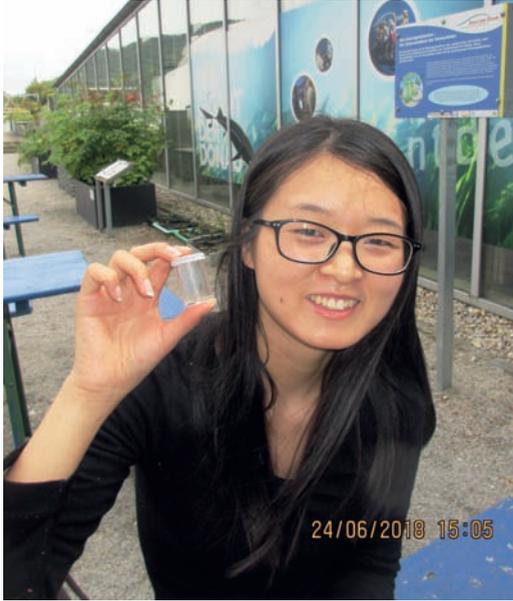


**Figure 65.** Post-congress excursion, searching for larvae of *Osmylus fulvicephalus*. From left: Chaofan Shi, Caleb Califre Martins, Ulrike Aspöck, Joshua Jones, Xu Han and Seulki Kim. Nature Reserve Jochensteiner Hänge, Germany, 24.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 66.** Post-congress excursion. From left: Ulrike Aspöck, Xiumei Lu and Xingyue Liu, collecting Hemerobiidae. Nature Reserve Jochensteiner Hänge, Germany, 24.vi.2018 (Photo archive H. & U. Aspöck).





**Figure 67.** Yanan Lyu having collected a female of *Dichrostigma flavipes*. Nature Reserve Bayerischer Wald, Germany, 24.vi.2018 (Photo archive H. & U. Aspöck).



**Figure 68.** Post-congress excursion. Ulrike Aspöck (left) and Caleb Califre Martins discussing future joint research projects. Haidmühle-Frauenberg Hostel, Germany, 24.vi.2018 (Photo archive H. & U. Aspöck).

# Phylogeny of Megaloptera: A review of present knowledge

Xingyue Liu

Department of Entomology, China Agricultural University, Beijing 100193, P.R. China;  
liuxingyue@cau.edu.cn

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**Abstract.** Megaloptera is the second smallest order in the Holometabola. The phylogeny and evolution of Megaloptera is of high interest concerning the origin of aquatic life-style of their larvae, the evolution of remarkable sexually selected traits, and the formation of their modern disjunctive distribution pattern. The present review summarizes the research progress on the phylogeny of Megaloptera. The higher-level phylogeny of Megaloptera appears to be resolved owing to the recent phylogenomic studies based on genome-scale data. The intergeneric and interspecific phylogenies of Megaloptera were analyzed in a number of works mainly based on morphological data. Thus, phylogenetic analysis based on molecular data is essential for testing the previous morphology-based hypotheses in future studies.

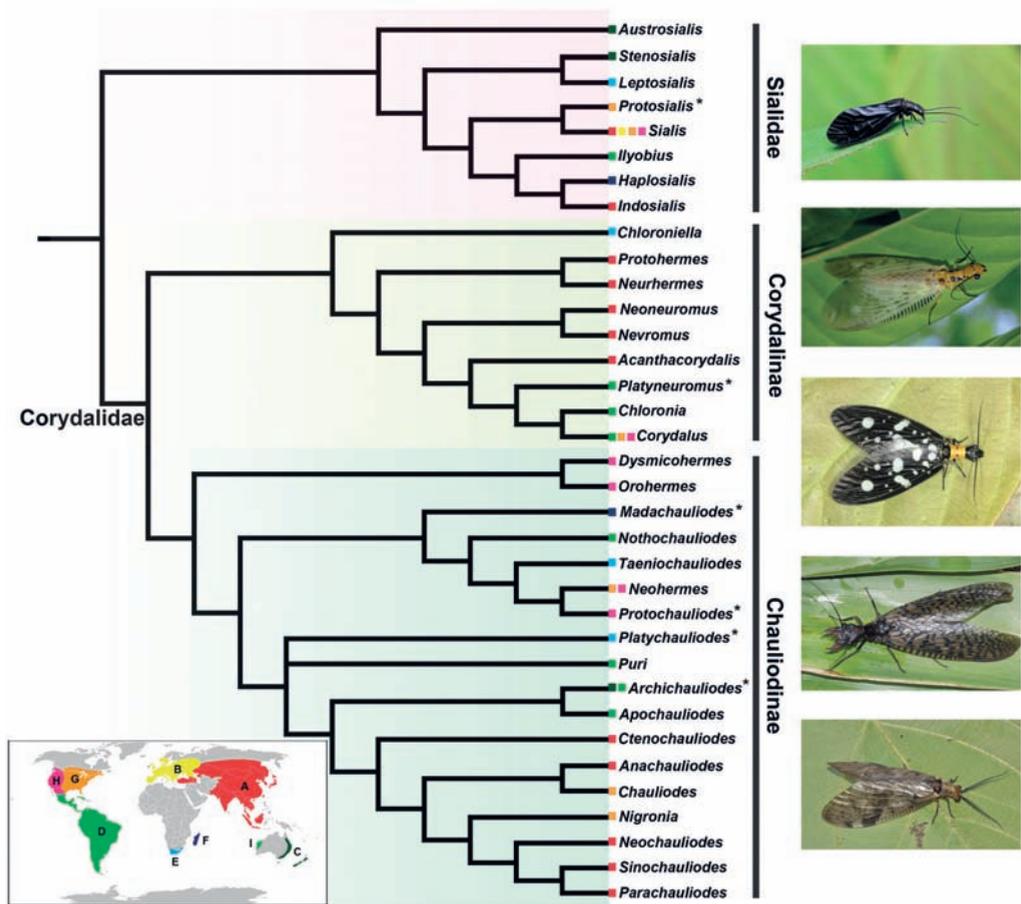
## Introduction

The order Megaloptera (dobsonflies, fishflies, and alderflies) belongs to the holometabolan superorder Neuropterida. Adults of Megaloptera are characterized by the prognathous head with well-developed gula and the broad hind wing anal area, while their larvae are exclusively aquatic, living in various freshwater habitats, and characterized by the presence of 7-8 pairs of lateral tracheal gills (NEW & THEISCHINGER 1993). Currently, 373 valid species of Megaloptera are described worldwide (OSWALD & MACHADO 2018). There are only two families in Megaloptera, *i.e.*, Sialidae (alderflies) and Corydalidae, which is divided into the subfamilies Corydalinae (dobsonflies) and Chaulioidinae (fishflies). In light of their “archaic” appearance Megaloptera were often mentioned as a primitive group of Holometabola (YANG & YANG 1999; GRIMALDI & ENGEL 2005). Therefore, the phylogeny and evolution of Megaloptera is of high interest, but the relevant studies have a long history of competing hypotheses.

Hitherto, the higher-level phylogeny of Megaloptera has been studied in a number of works for a long period, resulting in a monophyletic or paraphyletic Megaloptera, and controversial sister-group relationship of Megaloptera with either Raphidioptera or Neuroptera (reviewed in ASPÖCK *et al.* 2012). The phylogenetic relationships among genera and species within Megaloptera previously drew less attention than the higher-level phylogeny, although it is crucial for understanding the historical biogeography and character evolution of this group.

In this paper I provide an overview of the existing phylogenetic analyses on various groups of Megaloptera (Fig. 1). The following issues will be addressed: i) the higher-

level phylogeny of Megaloptera; ii) the intergeneric phylogeny within Corydalidae and Sialidae; and iii) the phylogenetic relationships among megalopteran species.



**Figure 1.** Phylogenetic relationships within Megaloptera: summarizing tree combining previous studies. Topology of Sialidae follows LIU et al. (2015a), topology of Corydalidae follows LIU et al. (2015c), and topology of Chaulioidinae follows LIU et al. (2012) except for *Puri* with unresolved position. Geographical distribution of each genus is indicated by color square, which is linked to the global distribution map of Megaloptera: red (A), Asia; yellow (B), Europe; dark green (C), eastern Australia and New Zealand; pale green (D), Central and South America; blue (E), South Africa; dark blue (F), Madagascar; orange (G), eastern North America; pink (H), western North America; green (I), western Australia. Genus lacking any phylogenetic analysis on interspecific relationships is marked by an asterisk. Photos of living megalopterans: a – *Sialis jiyuni* Liu, Hayashi & Yang, 2015. Photo by Yun Ji; b – *Protohermes arunachalensis* Ghosh, 1991. Photo by Zhiliang Wang; c – *Neurhermes selysi* (van der Weele, 1909). Photo by Ross Piper; d – *Acanthacorydalus fruhstorferi* van der Weele, 1907. Photo by Feiyang Liang; e – *Neochauliodes fraternus* (McLachlan, 1869). Photo by Xingyue Liu

### Higher-level phylogeny of Megaloptera

Due to morphological conservatism and consequent difficulties in identifying specific morphological apomorphies for the order in a phylogenetic context, the monophyly and higher phylogeny of Megaloptera have remained controversial. The monophyly of Megaloptera is supported in some morphology-based phylogenetic studies (ACHTELIG & KRISTENSEN 1973; ASPÖCK et al. 2001; ASPÖCK & ASPÖCK 2008; BEUTEL & FRIEDRICH 2008) by the larval head characters (*i.e.*, the presence of a special sensillum on the antepenultimate antennomere, a vestigial salivary duct, and a vertico-pharyngeal muscle with several subcomponents), by the presence of lateral tracheal gills in larval abdomen, and by the male genital characters (*i.e.*, the position of the male gonocoxite 9 close to the base of tergum 9, and the presence of eversible sacks of the male gonocoxites 11). However, a paraphyletic Megaloptera (*i.e.*, Sialidae as sister to Raphidioptera) had been proposed repeatedly based on the proximal fusion of fore wing MP and CuA veins and shared specialization of telotrophic ovarioles (HENNIG 1953; BÜNING 1979; AFZELIUS & DALLAI 1988; ŠTYS & BILIŃSKI 1990). Besides, a molecular phylogenetic analysis based on four gene fragments (nuclear genes: CAD, 18S rRNA; mitochondrial genes: COI, 16S rRNA) did not recover a monophyletic Megaloptera (WINTERTON et al. 2010).

Traditional classifications place Megaloptera and Raphidioptera as sister groups (HENNIG 1969), and in earlier studies Raphidioptera was even considered to be a family within Megaloptera (VAN DER WEELE 1910). The sister-group relationship between Megaloptera and Raphidioptera was also recovered in a recent comprehensive morphology-based study (BEUTEL et al. 2010) as well as in a molecular study (WIEGMANN et al. 2009). In contrast, with a broader sampling of Neuropterida, ASPÖCK et al. (2001) first proposed a sister-group relationship between Megaloptera and Neuroptera, which was also subsequently supported by both morphological and molecular evidence (KJER et al. 2006; ASPÖCK & ASPÖCK 2008; CAMERON et al. 2009).

Owing to the recent progress of phylogenomics, with considerable increase of the genome-scale data of insects, we are getting close to resolving the above questions on the higher-level phylogeny of Megaloptera. In two phylogenomic studies of Neuropterida, respectively based on mitochondrial genome data and anchored hybrid enrichment data and both with comprehensive sampling, corroborated the monophyly of Megaloptera and recovered the sister-group relationship between Megaloptera and Neuroptera (WANG et al. 2017; WINTERTON et al. 2018). Moreover, in the milestone study on insect phylogeny based on transcriptome data, Megaloptera was also recovered to be the sister-group of Neuroptera (MISOFF et al. 2014). These recent studies (WANG et al. 2017; WINTERTON et al. 2018) suggested that the aquatic larval life-style of Megaloptera might either be a plesiomorphic condition in Neuropterida or have been independently evolved with respect to the aquatic Neuroptera (*i.e.*, Nevrothidae and Sisyridae), but did not support the aquatic larval life-style as a synapomorphy of Megaloptera + Neuroptera, as proposed by ASPÖCK et al. (2001). The phylogenetic relationships among Corydalinae, Chauliodinae and Sialidae are also consistent in the above phylogenomic studies (WANG et al. 2017; WINTERTON et al. 2018), with Corydalinae + Chauliodinae as the sister-group of Sialidae.

It is encouraging that recent phylogenetic studies based on wing-base character data and genital character data also corroborate the above higher-level phylogeny of Megaloptera (ZHAO et al. 2014; LIU et al. 2016). In particular, LIU et al. (2016) proposed a series of autapomorphies of Megaloptera as well as the three major groups of the order based on genital character data. The autapomorphies of Megaloptera are the absence of male gonapophyses 9, the absence of the male hypandrium internum, and the paired female ectoprocts (LIU et al. 2016). Three autapomorphies of Corydalidae were proposed in LIU et al. (2016), including the reduced male gonocoxites 9, the female tergum 8 not enclosing spiracles, and the absence of female gonapophyses 8. Autapomorphies supporting the monophyly of Corydalinae are the presence of the male callus cerci between tergum 9 and ectoprocts and the arcuate male gonocoxites 10. Autapomorphies supporting the monophyly of Chauliodinae are the male tergum 9 with truncate anterior margin and the external position of male gonocoxites 10 with specialized lateral arms. The monophyly of Sialidae is supported by the reduced or obsolete male gonocoxites 10, the sub-oval female gonocoxites 9, and the reduced female ectoprocts.

### Phylogenetic relationships among genera of Megaloptera

The extant Megaloptera include 35 genera worldwide (8 genera of Sialidae and 27 genera of Corydalidae; OSWALD & MACHADO 2018). In addition, there are five fossil genera of Sialidae and five fossil genera of Corydalidae (LIU et al. 2012a, 2015a; JEPSON & HEADS 2016). The extant genera of Megaloptera are largely different between major zoogeographical regions and show a disjunct distribution pattern.

Herman Willem van der Weele may have been the first researcher dealing with the relationships among the megalopteran genera, and in his monograph of world Megaloptera (VAN DER WEELE 1910) some genera are considered to be »primitive« in Corydalinae as well as in Chauliodinae, while some of them are considered »derived« based on a few morphological characters. These hypotheses were proposed before the development of application of strict cladistic methods, but can be regarded as a starting point for later phylogenetic studies.

### Corydalinae

The subfamily Corydalinae is the first group of which the intergeneric phylogeny was studied by modern cladistic analysis: in GLORIOSO (1981), 70 characters were used to infer the intergeneric phylogeny after a comprehensive comparative morphological study. This analysis that was performed manually recovered three assemblages of genera, i.e., the *Protohermes* assemblage (*Protohermes* + *Neurhermes*), the *Nevromus* assemblage (*Nevromus* + *Neoneuromus*), and the *Corydalus* assemblage [*Acanthacorydalis* + [*Platyneuromus* + (*Chloronia* + *Corydalus*)]], with the latter two assemblages as each other's sister-group. PENNY (1993) added the South African endemic genus *Chloroniella* Esben-Petersen that was not included by GLORIOSO (1981) and re-analyzed the matrix with a computer program. This analysis resulted in a mostly consistent phylogeny with that recovered in GLORIOSO (1981) but assigned *Chloroniella* as

the sister-group of the lineage comprising the *Nevromus* and *Corydalus* assemblages. CONTRERAS-RAMOS (1998) performed a phylogenetic analysis including all dobsonfly genera by adding and revising characters, although he deemed this analysis to be a test for the monophyly of *Corydalus* Latreille. In this work *Chloroniella* was recovered to be the sister-group of the lineage including all the other dobsonfly genera and *Acanthacorydalus* van der Weele was assigned to be the sister-group of *Nevromus* + *Neoneuromus*, which is incongruent with the results of GLORIOSO (1981) and PENNY (1993). CONTRERAS-RAMOS (2011) presented a phylogenetic review of Corydalinae with re-analyses of all previous matrices in GLORIOSO (1981), PENNY (1993) and CONTRERAS-RAMOS (1998). The resulting phylogeny of the dobsonfly genera was largely consistent with that in CONTRERAS-RAMOS (1998) except *Platyneuromus* van der Weele, which was assigned to be the sister-group of *Corydalus*. LIU et al. (2015c) reconstructed the phylogeny of Corydalinae based on a combined dataset of 71 morphological characters and multi-loci (16S rRNA+COI+ND2) sequences to investigate the evolutionary pattern of the sexually selected traits of male dobsonflies. This phylogeny is generally congruent with the morphology-based phylogeny in CONTRERAS-RAMOS (1998). However, *Acanthacorydalus* was assigned as sister group to the *Corydalus* assemblage. Moreover, *Protohermes* van der Weele was recovered to be paraphyletic with *Neurhermes* Navás included.

### Chauliodinae

Using the fore wing anal veins as the basis for a phylogenetic scheme, MUNROE (1951) considered *Protochauliodes* van der Weele and *Neohermes* Banks being primitive or ancestral fishflies, while *Archichauliodes* van der Weele, *Chauliodes* Latreille, *Parachauliodes* van der Weele, *Neochauliodes* van der Weele and *Nigronia* Banks are derived genera. EVANS (1972) in his doctoral thesis proposed a scheme of intergeneric relationships of the world Chauliodinae based mainly on wing venation supplemented by distributions, but lacking rigorous phylogenetic analysis. Notably, the phylogenetic position of *Dysmicohermes* + *Orohermes* as the sister-group of the other fishfly genera as well as the monophylum comprising all Asian genera plus *Archichauliodes*, *Platychauliodes* Esben-Petersen, *Chauliodes* and *Nigronia*, hypothesized in EVANS (1972), were also recovered in recent phylogenetic analyses (see LIU et al. 2012a, 2016). LIU & YANG (2006a) first performed a phylogenetic analysis based on morphological characters to infer the relationships among the fishfly genera. A monophyletic group comprising all Asian fishfly genera and two eastern North American genera (*i.e.*, *Chauliodes* and *Nigronia*) was recovered in this study. However, the phylogenetic positions of the other fishfly genera were poorly resolved due to incomplete sampling. By adding more genera, LIU et al. (2012a) again reconstructed a morphology-based intergeneric phylogeny of Chauliodinae including all extant and fossil genera worldwide. The phylogeny shows that the extant fishfly genera respectively belong to three main clades, *i.e.*, the *Dysmicohermes* clade, the *Protochauliodes* clade, and the *Archichauliodes* clade. A group of genera, referred to as the *Protochauliodes* lineage, formed a monophylum based on the unique

fusion between stem of 1A and anterior branch of 2A in the fore wing. All Asian genera plus *Chauliodes* and *Nigronia* were also recovered to be monophyletic, supported by the pectinate or subserrate antennae.

By using ancestral area reconstruction, LIU et al. (2012a) fully discussed the historical biogeography of Chauliodinae. The result indicated a Pangaeian distribution of fishflies before the Middle Jurassic and suggested the Gondwanan origin of most fishfly genera whose diversification might be affected by the subsequent breakup of Pangaea. It also demonstrated that the modern fauna of Asian fishflies is probably derived from Gondwanan ancestors, rather than directly descended from Mesozoic fossil genera from Asia.

### Sialidae

The phylogeny of Sialidae was completely untreated for a long period. NEL et al. (2002) first attempted to reconstruct a phylogeny of the alderfly genera based on wing characters in order to reveal the systematic position of the Baltic amber genus *Eosialis* Nel et al. that was described in that study. Unfortunately, the wing character data is too limited to resolve the intergeneric phylogeny of Sialidae. LIU et al. (2015a) reconstructed the first phylogeny for Sialidae worldwide based on the most comprehensive sampling and broadest morphological data ever presented. Within extant Sialidae, *Austrosialis* Tillyard was recovered to be the sister-group of the monophylum including the remaining genera. The latter monophyletic group consists of three lineages, namely the *Stenosialis* lineage (*Leptosialis* + *Stenosialis*), the *Ilyobius* lineage [(*Haplosialis* + *Indosialis*) + *Ilyobius*], and the *Sialis* lineage (*Protosialis* + *Sialis*). According to the phylogenetic scheme of Sialidae, LIU et al. (2015a) clarified that *Ilyobius* Enderlein and *Protosialis* van der Weele are valid genera, while *Nipponosialis* Kuwayama was treated as a junior synonym of *Sialis* Latreille. The ancestral area reconstruction performed in LIU et al. (2015a) suggested a Pangaeian distribution of ancestral alderflies and suggested that the deep divergence of several lineages might have also occurred before the breakup of the supercontinent Pangaea during the Jurassic and Cretaceous.

All of the aforementioned phylogenetic studies concern one of the three major groups of Megaloptera. Based on a comprehensive study of the homology of the genital sclerites, LIU et al. (2016) first reconstructed the intergeneric phylogenetic relationships including all extant genera of Megaloptera. The recovered relationships among dobsonfly genera are congruent with the result in LIU et al. (2015c). In Chauliodinae the monophyly of the *Dysmicohermes* clade, the *Protochauliodes* clade, and the *Archichauliodes* clade was respectively corroborated in LIU et al. (2016), and the sister-group relationship of the *Dysmicohermes* clade to the *Protochauliodes* clade + the *Archichauliodes* clade, as recovered in LIU et al. (2012a), was supported again. However, the Oriental endemic genus *Ctenochauliodes* van der Weele was grouped with *Archichauliodes* and *Platychnauliodes* in the analysis using genital characters, and the phylogenetic position of the enigmatic genus *Puri* Cardoso-Costa, Azevedo & Ferreira-Jr, recently discovered from Brazil, remains unresolved. With respect to Sialidae, the sister-group relationship

of *Protosialis* + *Sialis*, as well as that of *Haplosialis* + *Indosialis*, are consistent with the morphology-based phylogeny of Sialidae (LIU et al. 2015a). Moreover, the monophyletic group including *Ilyobius*, *Protosialis*, *Sialis*, *Haplosialis* Navás and *Indosialis* Banks was also recovered in LIU et al. (2016), while the phylogenetic positions of the remaining genera, especially *Leptosialis* Esben-Petersen and *Stenosialis* Tillyard, were not resolved.

So far, the molecular phylogenetic studies focusing on the intergeneric phylogeny of Megaloptera are limited. Besides the phylogenetic analysis of Corydalinae based on multi-loci data (LIU et al. 2015c), there are a few works on mitochondrial phylogenomics of Corydalidae (WANG et al. 2014; JIANG et al. 2015, 2016; YANG et al. 2017). Considering Corydalinae, *Acanthacorydalis* was repeatedly recovered to be the sister group of the clade including the American dobsonfly genera but not the sister-group of *Neoneuromus* + *Nevromus*, and *Protohermes* was assigned to be the sister-group of the clade including *Neoneuromus* + *Nevromus*, *Acanthacorydalis*, and the American dobsonfly genera (WANG et al. 2014; JIANG et al. 2015, 2016). In YANG et al. (2017) the relationship among the three major clades of Chauliodynae was recovered as the *Dysmicohermes* clade + (the *Protochauliodes* clade + the *Archichauliodes* clade). These results corroborate the previous results from the morphological evidence (e.g., LIU et al. 2012a, 2016). However, broader sampling is needed for further testing of the intergeneric phylogeny including all world genera of Megaloptera.

Although fossils of Megaloptera are scarce, revealing their phylogenetic positions is important for better understanding the evolutionary history of the order. However, it is usually difficult to clearly resolve this question because the morphological characters preserved in fossils are incomplete and thus provide limited information for phylogenetic reconstruction. LIU et al. (2012a) attempted a morphology-based phylogenetic analysis including fossil and extant genera of Chauliodynae and found that the hitherto oldest fishflies (*Jurochauliodes* Wang and *Eochauliodes* Liu et al.) have distant positions with *Eochauliodes* assigned to be in the crown group of the subfamily. LIU et al. (2015a) also investigated the phylogenetic positions of fossil genera of Sialidae following the method used in LIU et al. (2012a). Unfortunately, the resulted phylogeny including all fossil and extant alderfly genera is poorly resolved largely due to data deficiency. Nevertheless, LIU et al. (2015a) recovered a sister group relationship between the fossil genus *Sharasialis* Ponomarenko from the Upper Jurassic of Mongolia (PONOMARENKO 2012) and the clade including all Cenozoic alderfly genera. The larva of *Sharasialis* has a pair of short lateral tracheal gills on the abdominal segment 8 (similar to Corydalidae), while all Cenozoic Sialidae lack the 8th pair of larval lateral tracheal gills. Accordingly, LIU et al. (2015a) established a new alderfly subfamily, namely Sharasialinae Liu, Hayashi & Yang. Besides Sharasialinae, there are other fossil megalopterans which are neither typical Sialidae nor Corydalidae. For example, the genus *Chauliosialis* Ponomarenko from the Upper Cretaceous of Russia lacks the lateral filaments of larval abdominal segments 7 and 8, while there is a pair of ventral prolegs that are similar to Corydalidae as well as a short and thick terminal appendage that is similar to Sialidae (PONOMARENKO 1976). JEPSON & HEADS (2016) described two corydalid genera, i.e., *Cratocorydalopsis* Jepson

& Heads and *Lithocorydalus* Jepson & Heads from the Lower Cretaceous of Brazil, both of which have fishfly-like wing venation but possess a very short and relatively wide pronotum that is similar to Sialidae. Therefore, the early divergence of Megaloptera appears to be much more complicated than could be expected in the light of findings of putative transitional lineages of Corydalidae and Sialidae.

### Phylogeny of Megaloptera at species-level

#### Corydalinae

Of the nine dobsonfly genera, seven were subject to phylogenetic analyses, but mostly based solely on morphological data. The Neotropical genus *Chloronia* Banks was the first genus with the interspecific phylogeny studied (PENNY & FLINT 1982). PENNY & FLINT (1982) proposed the phylogenetic relationships among the ten species recorded at that time primarily based on male genital characters, *e.g.*, the shape of sternum 9, ectoprocts and gonostyli 10. However, no rigorous phylogenetic analysis was applied in this study, and no updated work has been presented with the subsequent discoveries of species in this genus (CONTRERAS-RAMOS 1995, 2000, 2002).

CONTRERAS-RAMOS (1998) performed a comprehensive phylogenetic analysis to infer the relationships among the 30 species of the American endemic genus *Corydalus* based on 120 morphological characters. By adding four species described in CONTRERAS-RAMOS (2002), CONTRERAS-RAMOS (2011) again reconstructed the interspecific phylogeny of *Corydalus* based on updated morphological data. Accordingly, 19 species are placed into five species-groups of *Corydalus*, namely, the *Corydalus arpi* group, the *Corydalus nubilus* group, the *Corydalus armatus* group, the *Corydalus cornutus* group, and the *Corydalus batesii* group. However, the topology received only moderate or low nodal supports, so the phylogenetic positions of some species were not resolved. The historical biogeography of *Corydalus* was also constructed in CONTRERAS-RAMOS (1998), in which *Corydalus* was considered to have originated during the Late Jurassic and subsequent speciation generally lasted from the Early Cretaceous to the early Miocene due to some geographical isolation (*e.g.*, the uplifting of the Andes) as well as land connection (*e.g.*, the connection between North and South America).

The remaining published studies on the interspecific phylogeny of Corydalinae are a series of works done by Xingyue Liu and colleagues on the Asian endemic dobsonflies. LIU *et al.* (2005) presented a phylogenetic review of the genus *Acanthacorydalis* (giant dobsonflies) from China, in which, however, the interspecific relationships were poorly resolved due to the limited number of morphological characters used. YANG & LIU (2010) revised the character matrix and added *Acanthacorydalis asiatica* in an updated analysis, which yielded a better resolved topology. Biogeography of *Acanthacorydalis* was also discussed based on the resulting phylogeny, but no clear pattern of speciation was found to correlate with their distributions.

LIU *et al.* (2012b) reconstructed an interspecific phylogeny of the genus *Nevromus* Rambur based on morphological data, resulting in two main clades within the genus,

*i.e.*, the mainland clade (*Nevromus austroindicus*, *Nevromus aspoeck*, *Nevromus exterior*, and *Nevromus intimus*) and the insular clade (*Nevromus gloriosoi* and *Nevromus testaceus*). An Indian origin and a historically widespread distribution in southern Eurasia were proposed for *Nevromus*, while the deep divergence between the mainland and insular clades was postulated to have taken place during the separation of Sundaland from Eurasia (LIU et al. 2012b).

Concerning the genus *Neoneuromus* van der Weele, which is the sister-group of *Nevromus*, the interspecific phylogeny is difficult to infer based on morphological data, because the genitalia of *Neoneuromus* are conserved in morphology with very limited number of phylogenetically informative characters, and because the other diagnostic characters, *e.g.*, body coloration and wing patterns, are highly variable not only among species but also among conspecific individuals (YANG et al. 2018). Therefore, YANG et al. (2018) reconstructed the interspecific phylogeny of *Neoneuromus* based on multi-loci sequence data. The molecular data appears to be efficient to resolve the species delimitation and interspecific relationships of *Neoneuromus*, and five new species were found by using this method (YANG et al. 2018). The dated phylogeny with reconstructed ancestral areas indicates an initial divergence of *Neoneuromus* during the mid-Eocene and that a broad area including northeastern India and northern Indochina could be the center for early divergence of the genus (YANG et al. 2018).

The genus *Protohermes* is the most speciose group of Megaloptera. Currently, there are 76 species and the genus is divided into 13 species-groups that comprise most of these species (YANG & LIU 2010; LIU et al. 2013b). So far there is no study to infer the phylogenetic relationships among all species of *Protohermes*. Nevertheless, there are some works with phylogenetic analyses on the interspecific relationships within certain species-groups. Based on morphological data, these works inferred the interspecific phylogeny of the *Protohermes changninganus* group (LIU & YANG 2005), the *Protohermes costalis* group (LIU et al. 2007), the *Protohermes davidi* group (LIU & YANG 2006c; LIU et al. 2010a), the *Protohermes parvus* group (LIU et al. 2009), and the *Protohermes xanthodes* group (LIU et al. 2006). The aim of future works should be to reconstruct the relationships among these species-groups or even among all *Protohermes* species, which will be helpful for understanding the evolutionary pattern of their diverse wing patterns and genital sclerites as well as the historical biogeography.

The genus *Neurhermes* is one of the most impressive dobsonflies on account of striking coloration and patterns that probably imitate some diurnal toxic moths (HAYASHI 1995). The systematic position of *Neurhermes* is probably within *Protohermes* (see LIU et al. 2015b), while no taxonomic treatment/change has been made. The phylogenetic relationship among the seven species of *Neurhermes* was reconstructed based on the morphological data in LIU et al. (2015b) and the historical biogeography of *Neurhermes* was also discussed. Origin and a historically widespread distribution in southern Eurasia at least during Eocene were proposed, and the speciation within the genus was suggested to be correlated with the Tertiary orogenic events after the collision between the Indian subcontinent and Eurasia (LIU et al. 2015b).

## Chauliodinae

Without performing phylogenetic analyses, EVANS (1972) proposed relationships among the fishfly species of *Dysmicohermes* Munroe, *Orohermes* Evans, *Neohermes* and *Protochauliodes* from the Pacific Coastal Region of the USA based on wing venation, male genital characters, larval habitats and distribution. Subsequently, most works on the interspecific phylogeny of fishflies were done by Xingyue Liu and colleagues. Most of these works refer to the Asian fishflies.

In the first morphology-based phylogenetic analysis of fishfly genera (LIU & YANG 2006a), the interspecific relationships of *Sinochauliodes* Liu & Yang, that was simultaneously described, were recovered. However, the result is very preliminary with limited characters to support the relationships. Furthermore, the generic status of *Sinochauliodes* with respect to *Parachauliodes* van der Weele is questioned based on our unpublished molecular data, and there are also some undescribed species of *Sinochauliodes*. Thus, the phylogeny of *Sinochauliodes* requires further analysis.

By using morphological data, LIU & YANG (2006b) also reconstructed the phylogenetic relationships among the species of *Ctenochauliodes*. Under a revised classification of *Ctenochauliodes*, LIU et al. (2011) re-analyzed the interspecific phylogeny of *Ctenochauliodes* based on morphological characters. The results between these two studies were mostly consistent. *Ctenochauliodes* splits into two main clades, each of which contains nearly a half of the species of the genus, supported by the shape of ectoproct and male gonocoxites 10.

The interspecific phylogeny of *Parachauliodes*, which mainly ranges along Taiwan, Japan, and Korea, was reconstructed based on morphological data by LIU et al. (2008). Two main clades within the genus were recovered, with one including *Parachauliodes asahinai* and *Parachauliodes continentalis* and another one including the remaining four species. By combining the phylogenetic scheme and distribution pattern, the dispersal track of *Parachauliodes* was considered leading from Taiwan via the Ryukyu Arc to the Japanese archipelago, and the speciation was thought to be correlated with the isolations of several islands in its distribution range (LIU et al. 2008).

Regarding *Neochauliodes*, the largest genus of Chauliodinae, the interspecific phylogeny is poorly known. The only published work (LIU et al. 2010b) refers to a species-group of *Neochauliodes*, viz. the *N. sundaicus* species-group with six species endemic to Indo-Malaysia. The morphology-based phylogeny of the *N. sundaicus* species-group suggested that the speciation of this group might be correlated to the formation of Borneo, Java, Sumatra and some other islands in the Cenozoic.

YUE et al. (2015) presented a phylogeny of *Anachauliodes* Kimmins based on the DNA sequence data from three mitochondrial genes. This work confirmed that the two known species of *Anachauliodes* are the same. Accordingly, a taxonomic revision of *Anachauliodes* was provided.

LIU et al. (2013) inferred the interspecific phylogeny of *Taeniochauliodes* Esben-Petersen, a genus endemic to South Africa, based on adult morphological data. This represents the only published phylogenetic analysis on the African Megaloptera. *Taenio-*

*chauliodes natalensis* was recovered to be the sister of the clade including the remaining species, which suggested an early vicariance event occurring between KwaZulu-Natal and western South Africa. Speciation of the remaining *Taeniochauliodes* species was hypothesized to be correlated with fragmentation of their forest habitats during the Plio-Pleistocene (LIU et al. 2013a).

With the surprising discovery of new species of the endemic North American genus *Neohermes*, LIU & WINTERTON (2016) performed a phylogenetic analysis using adult morphological data to recover the interspecific relationships of this genus. *Neohermes inexpectatus* was recovered as the sister to the remaining *Neohermes*, which splits into two clades, one including two species from western North America and the other including three species from eastern North America. The ancestral areas reconstruction suggested that the initial divergence within *Neohermes* might have taken place in western North America with a subsequent eastward dispersal, and the uplift of the Cordilleran System probably accounted for the divergence between the eastern and western *Neohermes* species (LIU & WINTERTON 2016).

The phylogeny of the Australian species of Chauliodinae is the most poorly known. The latest classification of Australian Chauliodinae was proposed by THEISCHINGER (1999) based on adult and larval morphological characters. Following this classification, *Archichauliodes* and *Apochauliodes* Theischinger are closely related; *Archichauliodes* includes two subgenera; the subgenus *Riekochauliodes* splits into three species-groups, the *Archichauliodes* (*R.*) *guttiferus* group, the *Archichauliodes* (*R.*) *deceptor* group and the *Archichauliodes* (*R.*) *polypastus* group. However, no phylogenetic analysis has been made to test this classification. BAKER & THEISCHINGER (2004) attempted to use DNA sequence data for a test of the classification based on morphology, and they deemed that the morphological classification is concordant with the result from molecular data. Nevertheless, the sampling of this study was insufficient, with only three species of *Archichauliodes* and *Protochauliodes* included. It is notable that *Archichauliodes* and *Protochauliodes* are not endemic to the Australian region. Both genera comprise some species in South America, while there are some species of *Protochauliodes* distributed in western North America. The phylogenetic relationships among congeneric species from disjunct areas of different zoogeographical regions are of high interest and in need of resolution.

### Sialidae

Among the eight extant genera of Sialidae, only four genera comprise three or more species, namely *Indosialis*, *Ilyobius*, *Protosialis*, and *Sialis*. Most studies have focused on the interspecific phylogeny of *Sialis*. In a taxonomic revision of the North American *Sialis*, ROSS (1937) divided the genus into four species-groups, *i.e.*, the *S. californica* group, the *S. americana* group (currently regarded as genus *Protosialis*; see LIU et al. 2015a), the *S. infumata* group, and the *S. aequalis* group. This hypothesis is based on a few male genital characters but lacks a test of phylogenetic analysis. EVANS (1972) followed the above classification and proposed an evolutionary scheme for the *Sialis*

species from the Pacific Coastal Region of USA based on geographical distribution. The first phylogenetic analysis on *Sialis* was made by WHITING (1994). This study provided a fine comparison of the male genital sclerites of *Sialis* and presented an interspecific phylogeny including all North American species based on a matrix with 35 morphological characters. The species-group division of ROSS (1937) was largely corroborated by WHITING (1994), while the relationships among these species-groups were not recovered. In a comprehensive phylogenetic study on Sialidae based on morphological data (LIU et al. 2015a), the interspecific phylogeny of world *Sialis* was recovered. The Nearctic species, *Sialis americana* and *S. glabella*, were revised to be placed in *Protosialis*. The species previously placed in *Nipponosialis*, i.e., *Sialis kumejimai*, *S. jezoensis*, and *S. kuwayamai*, were found to have diverged relatively earlier. All North American and European species as well as a few Asian species form the crown-group of *Sialis*, which is supported by the male mandible without additional distal tooth. This group splits into three main lineages, namely the *S. lutaria* lineage (monophyly supported by the lingulate male sternum 9), the *S. infumata* lineage (monophyly supported by the male ectoproct entirely sclerotized ventrally and the male gonocoxite 11 with rather elongate and arcuately curved median processes), and the *S. sinensis* lineage (monophyly supported by the transversely band-like male sternum 9), and the latter two lineages were recovered to be sister-groups. The three species-groups of the North American *Sialis* were also supported in LIU et al. (2015a), while four other species-groups were also proposed, i.e., the *S. lutaria* group, the *S. longidens* group, the *S. sinensis* group, and the *S. melania* group. It is notable that the *Sialis* species respectively endemic to Asia, Europe, and North America do not form three monophyletic groups as hypothesized by EVANS (1972). The sister-group relationship, e.g., between the European *S. nigripes* and the North American *S. infumata* group, suggests faunal exchange of ancestral *Sialis* via intercontinental dispersal.

Considering the Neotropical genus *Ilyobius*, two species-groups were proposed based on the phylogenetic scheme of LIU et al. (2015a), namely the *Ilyobius chilensis* group and the *Ilyobius mexicana* group. However, the phylogenetic analysis of LIU et al. (2015a) did not include all known species of *Ilyobius*, particularly the fossil species recorded from Eocene Baltic amber. It would be of value to figure out the phylogenetic relationships between the extant *Ilyobius* and their fossil counterparts from the Northern Hemisphere.

The interspecific phylogeny within the Oriental endemic genus *Indosialis* was recovered in LIU et al. (2015a). *Indosialis bannaensis* and *I. indicus* are sisters, while *I. minora* is the sister of the former two species. However, the systematic position of the fossil *Indosialis* species is still unclear.

### Conclusion

The aforementioned recent works considerably increased our knowledge on the phylogeny of Megaloptera at different taxonomic levels. Future works may focus on the following issues. First and most importantly, phylogenetic analyses based on molecular

data needs to be done for many groups of Megaloptera, which will provide an opportunity to critically test the previous results from the morphological data as well as the hypotheses concerning the historical biogeography. Second, exploration of more morphological characters for phylogenetic analysis is desirable using modern techniques of morphology, such as the micro-CT and 3D tomography. Last, as a group of aquatic insects that are sensitive to the quality of the freshwater environment, the population genetics of some widespread species of Megaloptera need more attention and will be valuable for our understanding on the global change and conservation of insect biodiversity.

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## Lacewings and Citizen science in Italy: a young but very promising relationship

Agostino Letardi

ENEA, Lungotevere Thaon di Revel, 76, 00196 Roma, Italy; agostino.letardi@enea.it

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**Abstract.** Citizen science is growing as a field of research with contributions from diverse disciplines, promoting innovation in science, society, and policy. Citizen science platforms (*i.e.*, iNat, <https://www.inaturalist.org/>) and capacity-building programmes foster the visibility of projects and establish networks for knowledge exchange within and among members of the citizen science community. Several recent events of citizen science in Italy (mainly by means of bioblitzes) have given a new perspective to the knowledge of Neuropterida in Italy.

### Introduction

As a scientist, I have continuously been involved in training activities and in engaging the public in scientific subjects. Entomology, but more generally the dissemination of scientific knowledge, and social commitment have always been two sectors I have walked together. For this reason, one of the first objectives that I gave myself in the study of Neuropterida was to create a web site to disseminate information to an Italian audience: this web site (URL: <http://neuroterri.casaccia.enea.it/>), online since 2000, has been updated to 03.viii.2018. From the beginning, it has been perfectly clear to me that researchers benefit from using the Internet on a one-to-one basis (e-mail, File Transfer Protocol), a one-to-many basis (discussion groups, Internet conferences), and from accessing large databases of knowledge (YOUNG et al. 2014).

Although only a few researchers have devoted themselves intensely to the study of Neuropterida in Italy, collaboration with many colleagues has led to a widespread and more in-depth knowledge. Meanwhile, several of us have also dedicated ourselves to the dissemination of scientific knowledge by creating basic texts, contributing to the knowledge of the value of biodiversity, in addition to establishing and taking care of a vast audience of people who have contributed over time to help document the presence of Neuropterida in nature (NICOLI ALDINI 2007; PANTALEONI et al. 2011; LETARDI 2016). This convergence of interests between a wide audience of naturalists, who through various web media (Forums, Social Media, Mailing Lists), send daily comments, often accompanied by photographs, has enabled us, the Italian specialists of Neuropterida, to greatly accelerate the advance of knowledge of these insects for Italy and beyond. But this collaboration between entomologists and passionate nature photographers has not exhausted our intention for wider engagement, and the citizen science sector has always opened up new and promising developments (MCKINLEY et al. 2017; TREDICK et al. 2017).

## Materials and methods

In order to quantify the recent contribution that active citizenship has provided to the development of knowledge in the neuropterological field, data collected between 2014 and 2017 has been analysed. Every semester, I am collecting, from the main Italian entomological and naturalist forums, social media and other sources, reports relating to species of Neuropterida photographed in Italy. Each report is evaluated by expert entomologists and only those deemed plausible are recorded.

## Results and discussion

Within the four years, a total of 570 valid reports were collected, relating to 82 taxa – almost half of the Italian species of Neuropterida. Of these, almost 500 were attributed to species level, whereas the remaining 70 were only able to be determined to genus level (Table 1). As was expected, the owly sulphur *Libelloides coccajus* (Denis & Schiffermüller, 1775) and the spotted antlion *Distoleon tetragrammicus* (Fabricius, 1798) are the most frequently photographed species; some other common antlions, owlflies, green and brown lacewings, the inocellid snakefly *Parainocellia bicolor* (A. Costa, 1855) and the charismatic mantidfly *Mantispa styriaca* (Poda, 1761) are also frequently photographed. Huge numbers of photographs of the common green lacewing, *i.e.*, the *Chrysoperla* species-complex were received, a group very rarely determinable to species level on the basis of a photograph: nevertheless some species of that complex are listed in Table 1.

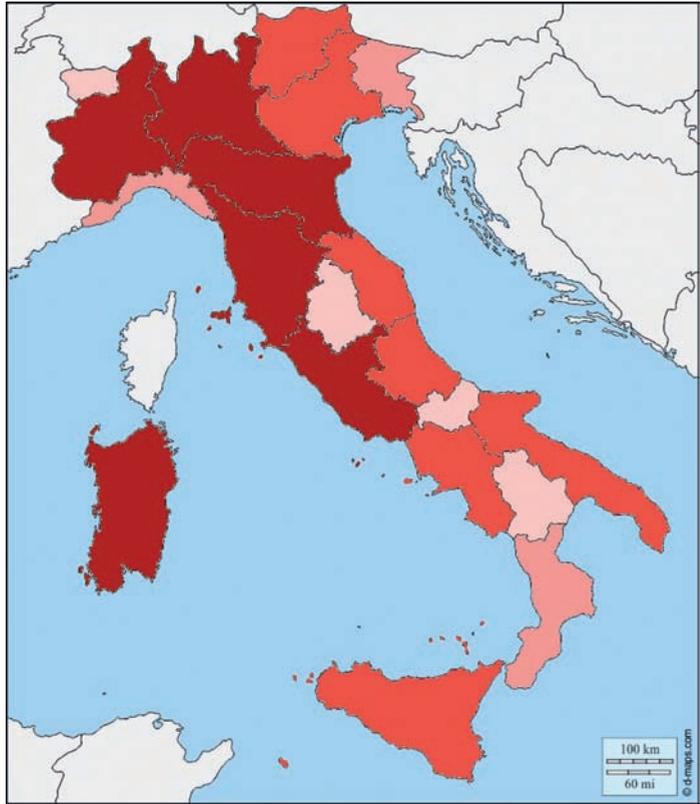
An elaboration of the regional distributions of the photographic records is illustrated in Figure 1. Considering the high biodiversity of Neuropterida in that region (LETARDI & SCALERCIO 2018), we must regard Calabria as an underestimated area by our naturalist photographers.

Between 2014 and 2017, almost all the families of Neuropterida present in Italy have been reported by the Italian naturalist photographers, except for Dilaridae and Berthidae; however, more than three-quarters of the total number of reports are antlions, owlflies or green lacewings (Fig. 2).

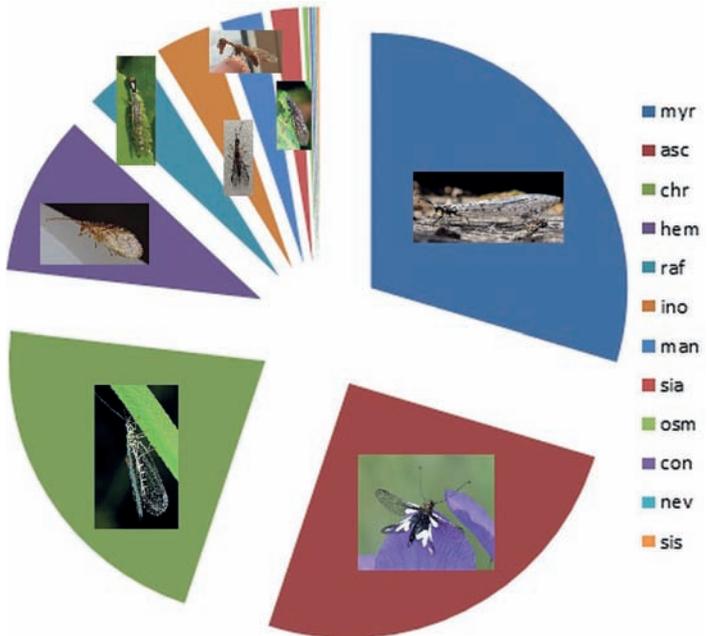
From analysing the data of the four-year period, it can be observed that the reports often refer to the same year that the photo was taken, or to the years just before (Fig. 3). Therefore unlike the study of museum material this source of information provides updated data on the current state of the habitats from which these reports come from.

Results of this survey give a useful contribution to updated knowledge about the regional distribution of Neuropterida in Italy.

Nevertheless, if the ‘parterre’ of naturalist photographers has greatly expanded in Italy in recent decades resulting in hundreds of reports every year for a group of insects considered ‘minor’ like the Neuropterida, the primary task of every scientist of this country should not be forgotten, *i.e.*, to contribute to the growth of a basic collective knowledge of the value of biodiversity in Italy.



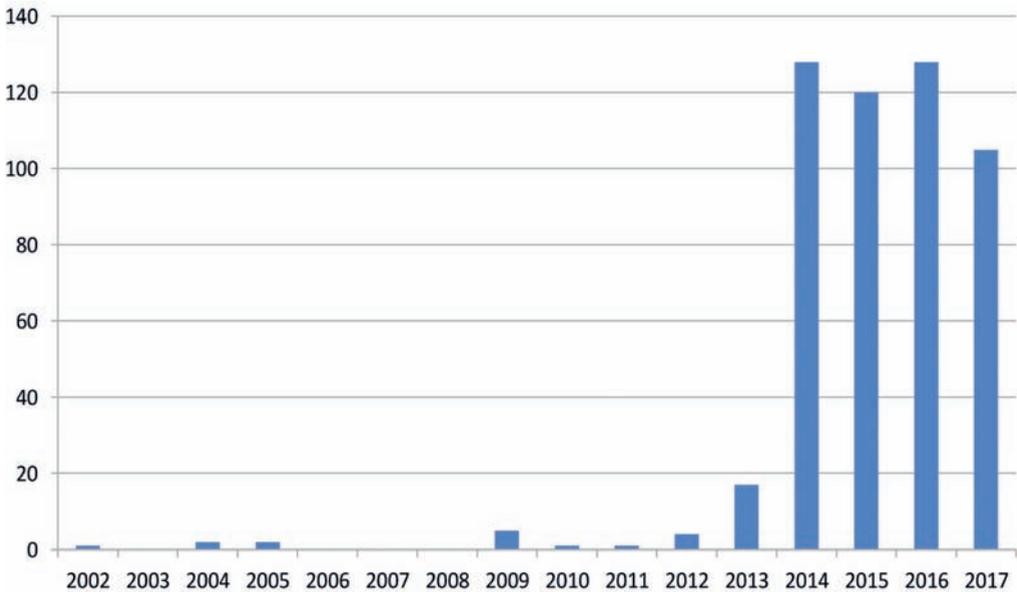
**Figure 1.** Regional distribution of photographic records in the four years 2014–2017 of the Italian species of Neuropterida. The different shades of red indicate: Pale pink – < 10 records; pink – 10–19 records; light red – 20–39 records; dark red – >40 records.



**Figure 2.** Frequency of photographic records 2014–2017 of the different families of Neuropterida in Italy.

**Table 1.** Frequency of specific photographic reports of the Italian species of Neuropterida in the four-year period 2014–2017. +++ – more than 40 times; ++ – between 10 and 20 times; + – less than ten times but on average more than one time per year; +/- – more than one time per year on average but more than one record; r – only one record in the four-year period 2014–2017.

Species	frequency	Species	frequency
<i>Libelloides coccajus</i>	+++	<i>Neuroleon microstenus</i>	+/-
<i>Distoleon tetragrammicus</i>	+++	<i>Pseudomallada flavifrons</i>	+/-
<i>Palpares libelluloides</i>	++	<i>Chrysopa pallens</i>	+/-
<i>Libelloides longicornis</i>	++	<i>Chrysoperla agilis</i>	+/-
<i>Libelloides latinus</i>	++	<i>Dichrostigma flavipes</i>	+/-
<i>Macronemurus appendiculatus</i>	++	<i>Hemerobius lutescens</i>	+/-
<i>Parainocellia bicolor</i>	++	<i>Hemerobius micans</i>	+/-
<i>Chrysopa perla</i>	++	<i>Hemerobius stigma</i>	+/-
<i>Micromus angulatus</i>	++	<i>Mantispa aphavexelthe</i>	+/-
<i>Libelloides lacteus</i>	++	<i>Nineta principiae</i>	+/-
<i>Italochrysa italica</i>	++	<i>Osmylus fulvicephalus</i>	+/-
<i>Mantispa styriaca</i>	++	<i>Peyerimhoffina gracilis</i>	+/-
<i>Synclisis baetica</i>	++	<i>Pseudomallada inornatus</i>	+/-
<i>Euroleon nostras</i>	+	<i>Symphorobius fallax</i>	+/-
<i>Xanthostigma corsicum</i>	+	<i>Symphorobius pygmaeus</i>	+/-
<i>Chrysoperla pallida</i>	+	<i>Venustoraphidia nigricollis</i>	+/-
<i>Gymnocnemia variegata</i>	+	<i>Wesmaelius quadrifasciatus</i>	+/-
<i>Acanthaclisis occitanica</i>	+	<i>Bubopsis agrionoides</i>	r
<i>Creoleon lugdunensis</i>	+	<i>Chrysopa viridana</i>	r
<i>Deleproctophylla australis</i>	+	<i>Chrysopidia ciliata</i>	r
<i>Libelloides corsicus</i>	+	<i>Conwentzia</i> sp.	r
<i>Nothochrysa capitata</i>	+	<i>Distoleon annulatus</i>	r
<i>Raphidia mediterranea</i>	+	<i>Drepanepteryx algida</i>	r
<i>Chrysoperla lucasina</i>	+	<i>Hemerobius atrifrons</i>	r
<i>Drepanepteryx phalaenoides</i>	+	<i>Hemerobius gilvus</i>	r
<i>Hemerobius humulinus</i>	+	<i>Libelloides macaronius</i>	r
<i>Megistopus flaviconis</i>	+	<i>Megalomus</i> cf. <i>hirtus</i>	r
<i>Myrmecaelurus trigrammus</i>	+	<i>Megalomus tortricoides</i>	r
<i>Pseudomallada prasinus</i>	+	<i>Myrmeleon gerlindae</i>	r
<i>Dendroleon pantherinus</i>	+/-	<i>Neuroleon nemausiensis</i>	r
<i>Fibla maclachlani</i>	+/-	<i>Nevrorthus fallax</i>	r
<i>Myrmeleon formicarius</i>	+/-	<i>Nineta flava</i>	r
<i>Chrysopa formosa</i>	+/-	<i>Nothochrysa fulviceps</i>	r
<i>Chrysopa walkeri</i>	+/-	<i>Phaeostigma notatum</i>	r
<i>Creoleon plumbeus</i>	+/-	<i>Psectra diptera</i>	r
<i>Hypochrysa elegans</i>	+/-	<i>Puncha ratzeburgi</i>	r
<i>Libelloides siculus</i>	+/-	<i>Sialis lutaria</i>	r
<i>Micromus variegatus</i>	+/-	<i>Sisyra terminalis</i>	r
<i>Myrmeleon hyalinus</i>	+/-	<i>Symphorobius luqueti</i>	r
<i>Myrmeleon inconspicuus</i>	+/-	<i>Wesmaelius malladai</i>	r
<i>Neuroleon arenarius</i>	+/-	<i>Wesmaelius subnebulosus</i>	r



**Figure 3.** Number of records of Neuropterida species per year in Italy.

Everything started from the classic question: how often does the public get to see scientists having fun doing science? And what if everyone who comes to watch, young or old, went away with a much better understanding of biodiversity? This happens every year in many North American, Australian, and European locations. It's called a BioBlitz. From 2012, I have dedicated myself to all the bioblitzes that I have been able to attend. Since then, every year, I have attended 3–5 events of this kind, these have had an extremely varied participation (from hundreds of people to a few couples with children), with school groups, organized groups and occasionally single people (Fig. 4). Throughout these years, and thanks to this type of engagement between science and citizenship, I have established a wide network of relationships that have often continued even after the event itself. Over time, this commitment of mine has always convinced me that, overall, the innovative potential of citizen science should embrace the manifold expertise of participants with different backgrounds across different disciplines, and should incorporate opportunities to work at the science-policy interface and thereby gaining new perspectives. Citizen science needs to be considered as a suitable approach to face general issues like global challenges as well as basic knowledge about insects (HECKER et al. 2018).

A crucial aspect is certainly the role that this approach can bring to the diffusion of knowledge on Neuroptera in Italy. In this sense the choices for optimal communication are crucial. The widespread use of technical tools such as smartphones has been a great help in this regard. There are many actions, projects and research that have started up in Italy in this sense (Fig. 5).



Figure 4. Young bioblitzers and an old citizen scientist. Photo: Marco Bastianini (15.vi.2015)

**ANMS**  
ASSOCIAZIONE NAZIONALE MUSEI SCIENTIFICI

**CSMON-Life**

**LTER Italia**  
LIFE Long-Term Ecological Research Network

**EUROPEAN CITIZEN SCIENCE ASSOCIATION**

**LIFE+ NATURA 2000**

**MIPP**

**FIRST ITALIAN CITIZEN SCIENCE CONFERENCE**  
ROMA 2017

**Consiglio Nazionale delle Ricerche**

**ACCADEMIA NAZIONALE DELLE SCIENZE E LETTERE ITALIANE**  
1782

**CITIZEN SCIENCE ITALIA CSI**

**MINISTERO DELL'AMBIENTE E DELLA TUTELA DEL TERRITORIO E DEL MARE**

**LifeWatch ITALIA**

**ETTORE MAJORANA FOUNDATION AND CENTRE FOR SCIENTIFIC CULTURE**  
TO PAY A PERMANENT TRIBUTE TO GALILEO GALILEI, FOUNDER OF MODERN SCIENCE AND TO ENRICO FERMI, "THE ITALIAN NAVIGATOR", FATHER OF THE WEAK FORCES

**LifeMIPP**

The LIFE+ Nature project "Monitoring of insects with public participation" (MIPP) has the main aim to develop and test standardized monitoring methods for the assessment of the conservation status of insect species listed in the annexes of the Habitats Directive. The species considered are: *Osmoderma eremita* s.l., *Lucanus cervus*, *Cerambyx cerdo*, *Rosalia alpina*, *Morimus funereus*.

The main purpose of this web portal is to collect and display faunistic data collected from citizens concerning the presence of the above species and of the species *Lopinga achine*, *Parnassius apollo*, *Saga pedo*, *Zerynthia polyxena*, which are also included in the annexes of the Habitats Directive

Figure 5. Actions, projects, and research recently started up in Italy about the diffusion of scientific knowledge.

Citizen science is primarily a means of extended knowledge-gathering. It is important and timely to consider the larger implications of citizen science: as a way of developing new knowledge practices, shifting the institutional boundaries around science, and raising new questions and gaining new perspectives.

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In the last five years I have been able to participate in dozens of bioblitzes as an entomologist, but without the commitment, dedication and expertise of dozens of organizers, such research would not have taken place or would have been much more thinned out over time. Many thanks in particular to Dr. Fabio Coccia Collepardo (Comitato Nazionale Bioblitz Italia), Dr. Andrea Sforzi (Museo di Storia Naturale della Maremma, Grosseto), and Lieutenant Colonel Bruno Petriccione (Comando Unità Tutela Forestale, Ambientale e Agroalimentare dell'Arma dei Carabinieri).

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## Toward a homologization of male genital sclerites in Coniopterygidae (Neuroptera) – A tightrope dance

Ulrike Aspöck

Natural History Museum, 2<sup>nd</sup> Zoological Department, Burgring 7, A-1010 Vienna, Austria; ulrike.aspoeck@nhm-wien.ac.at; ulrike.aspoeck@univie.ac.at

Department of Integrative Zoology, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria

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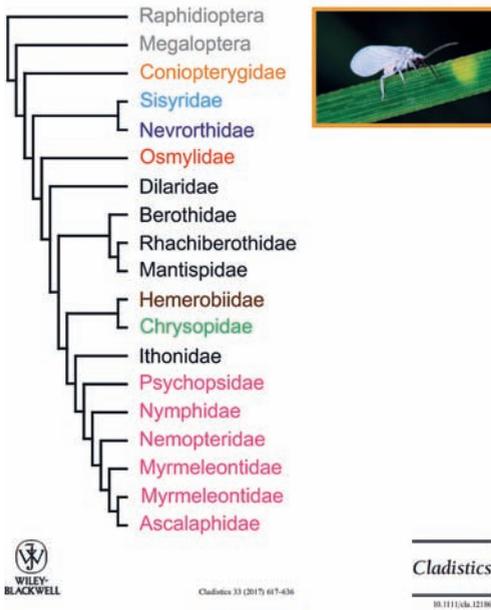
**Abstract.** Archaeognathan Machilidae serve as a model for the serially homologous sclerites of the terminal abdominal segments 9, 10, and 11: the gonocoxites, gonostyli and gonapophyses, which have copulative function in male Neuropterida. The identity of these genital sclerites may be camouflaged by excessive modelling of form, reduction, loss or fusion of single sclerites to complexes. If the identity of a sclerite is problematic, then a hypothesis based on a gonocoxite-concept has greater heuristic value than to interpret it as an accessorial *de novo* structure and to assign a new name. Coniopterygidae, with a fore wing length less than 6 mm, are truly the dwarfs among Neuroptera and comprise almost 580 known species representing three subfamilies. i) Bruchaiserinae – apart from their unusual eidonomic appearance – surprise us with a complete set of genital sclerites; the fact that they possess a callus cerci indicates a rather plesiomorphic pattern within the family. ii) Coniopteryginae – in spite of their heterogeneity – allow us to distinguish the gonocoxite-complexes 9, 10, and 11. iii) Aleuropteryginae are also extremely heterogeneous and confront us with completely invaginated tergite and sternite 9, as in the genus *Aleuropteryx*, nevertheless the gonocoxite-complexes 9, 10 and 11 are otherwise recognizable. The male gonocoxite-complex 10 generally serves as a morphological landmark in Coniopterygidae. The present hypothesis of a sister-group relationship between Aleuropteryginae and the clade Bruchaiserinae + Coniopteryginae remains valid. The phylogenetic position of Coniopterygidae within the order Neuroptera – either as sister-group of all other families or of the dilarid-clade or nested somewhere else – might be resolved by the current campaign of homologization.



**Figure 1.** *Coniopteryx pygmaea* Enderlein, 1906, on a pine needle, habitus. Photo H. Bruckner. Length of fore wing: 2.4 mm

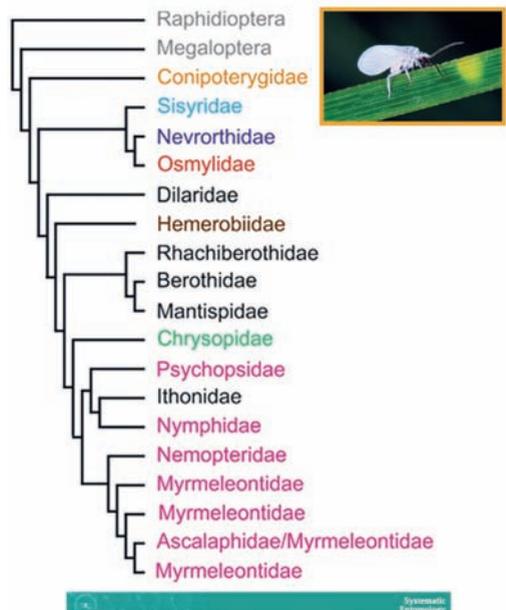
### Background

History of the early research on the neuropteran family Coniopterygidae Burmeister, 1839, was thoroughly documented almost ten years ago by ASPÖCK & ASPÖCK (2009), who emphasized that Coniopterygidae were once primarily associated with Psocidae. With a fore wing length between 1.2 to 6 mm, Coniopterygidae (Fig. 1) are the dwarfs among Neuropterida. Nonetheless, they have been a matter of permanent excitement concerning their systematics and phylogeny as they light-footedly switch seats in the evolutionary carousel of the Neuropterida. In phylogenetic analyses of the order Neuroptera, Coniopterygidae emerge either as the sister-group to all other families, or they are nested within a tree, predominately as the sister-group to the dilarid-clade. Analyses based on molecular data, *e.g.*, mitochondrial phylogenomics (WANG et al. 2017; Fig. 2) or anchored phylogenomics (WINTERTON et al. 2018; Fig. 3), corroborate each other in



Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida

Yuyu Wang<sup>a,b</sup>, Xingyue Liu<sup>a,c</sup>, Ivonne J. Garzón-Ordúña<sup>d</sup>, Shaun L. Winterton<sup>e</sup>, Yan Yan<sup>a</sup>, Ulrike Aspöck<sup>d</sup>, Horst Aspöck<sup>d</sup> and Ding Yang<sup>a,d</sup>



Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera)

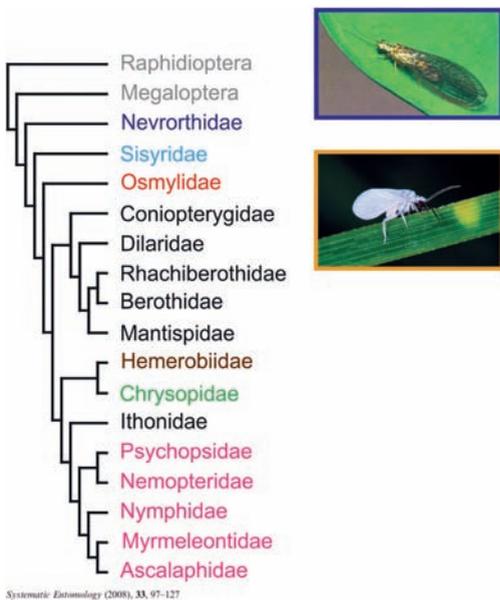
SHAUN L. WINTERTON<sup>1,2,3</sup>, ALAN R. LEMMON<sup>1,4</sup>, JESSICA P. GILLUNG<sup>1</sup>, IVONNE J. GARZÓN-ORDUÑA<sup>5</sup>, DAVIDE BADANO<sup>1</sup>, DEON K. BAKKER<sup>6,7</sup>, LAURA C.V. BREITKREUZ<sup>2</sup>, MICHAEL S. ENGEL<sup>8,9</sup>, EMILY MORIARTY LEMMON<sup>1</sup>, XINGYUE LIU<sup>3</sup>, RENATO J.F. MACHADO<sup>10</sup>, JEFFREY H. SKEVINGTON<sup>11</sup> and JOHN D. OSWALD<sup>12</sup>

**Figure 2.** Mitochondrial phylogenomics presenting Coniopterygidae as sister-group to all other families of the order Neuroptera. Within the monophyletic Myrmeleontiformia (pink) the family Myrmeleontidae is paraphyletic. After WANG et al. (2017).

**Figure 3.** Anchored phylogenomics showing Coniopterygidae as sister-group to all other families of the order Neuroptera. Myrmeleontiformia (pink) are disrupted, and the family Myrmeleontidae is paraphyletic. After WINTERTON et al. (2018).

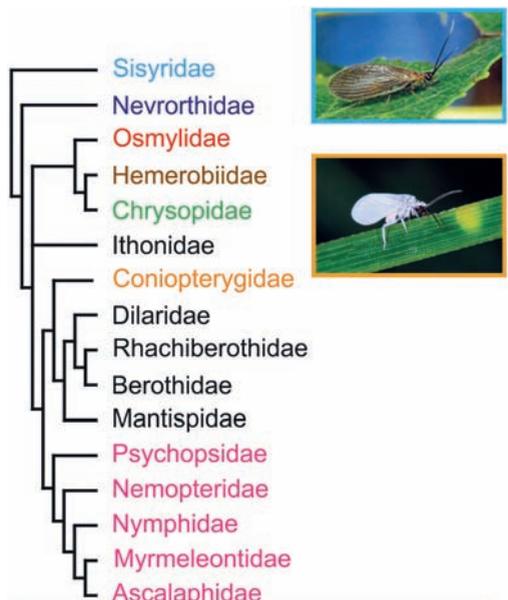
presenting Coniopterygidae as the sister-group to all other families. Nonetheless, there are severe conflicts between these trees concerning the positions of other families, e.g., the separation of the Hemeroibiidae and Chrysopidae, and the disruption of the Myrmeleontiformia in the tree gained by anchored phylogenomics.

Alternatively in several morphology-based trees, but also in a previous molecular tree (HARING & ASPÖCK 2004), Coniopterygidae emerge as sister-group to the dilarid-clade: either with Nevrothidae as the sister-group to all other families, a result which is mainly based on the morphology of genital sclerites (ASPÖCK & ASPÖCK 2008; Fig. 4), or with Sisyridae as sister-group to all other Neuropteran families, which is mainly based on head morphology (RANDOLF et al. 2014; Fig. 5).



**Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola)**

ULRIKE ASPÖCK<sup>1</sup> and HORST ASPÖCK<sup>2</sup>  
<sup>1</sup>Department of Entomology, Museum of Natural History Vienna, Austria and <sup>2</sup>Department of Medical Parasitology, Medical University of Vienna, Austria



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Head anatomy of adult *Nevrothus apatelios* and basal splitting events in Neuroptera (Neuroptera: Nevrothidae)

SUSANNE RANDOLF<sup>\*1,2</sup>, DOMINIQUE ZIMMERMANN<sup>1,2</sup> & ULRIKE ASPÖCK<sup>1,2</sup>

**Figure 4.** Phylogeny based on morphology of the genital sclerites inferring that the Nevrothidae are the sister-group to all other families, and Coniopterygidae as sister-group to the dilarid-clade. After ASPÖCK & ASPÖCK (2008). Top insert: *Nevrothus apatelios* H.A., U.A. & Hölzel, 1977. Photo: P. Duelli.

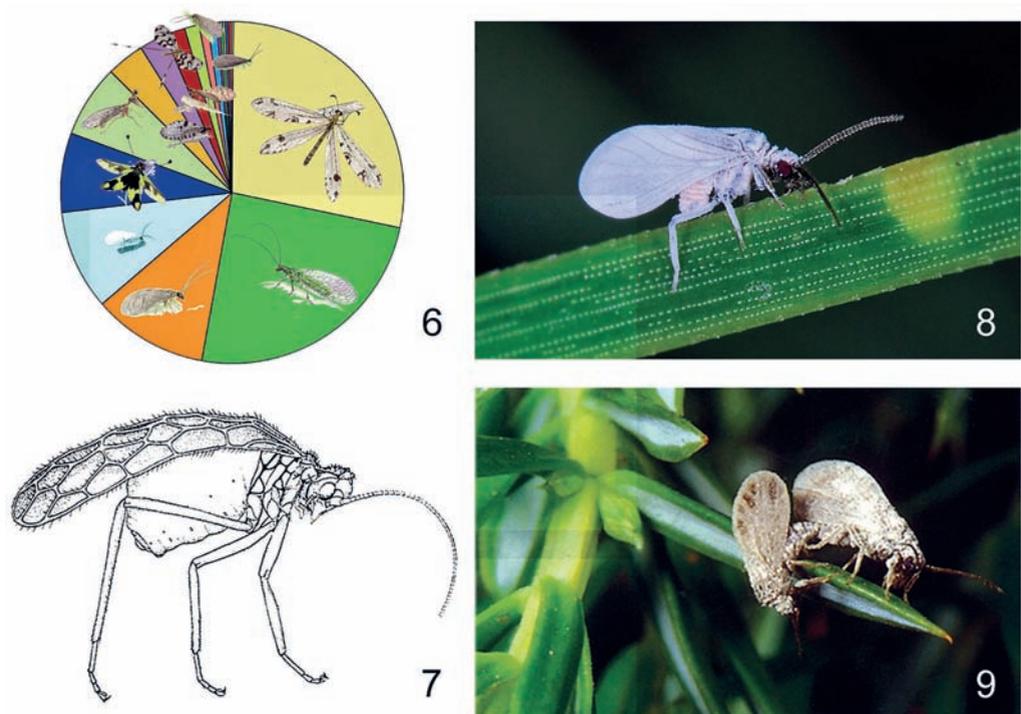
**Figure 5.** Phylogeny based on adult head morphology presenting Sisyridae as sister-group to all other families, Nevrothidae as sister-group to the rest and Coniopterygidae as sister-group to the dilarid-clade. After RANDOLF et al. (2014). Top insert: *Sisyra terminalis* Curtis, 1854. Photo: H. Rausch.

In the fancy cake chart of Neuroptera (ASPÖCK & ASPÖCK 2007) the slice representing Coniopterygidae is medium-sized (Fig. 6). The approximately 580 species (OSWALD & MACHADO 2018) are assigned to three extremely heterogeneous subfamilies: i) the enigmatic Bruceiserinae Navás, 1927 (Fig. 7), with only a few known species restricted to certain arid and semiarid areas of South America, and ii) the species-rich subfamilies Coniopteryginae Burmeister, 1839 (Fig. 8) and iii) Aleuropteryginae Enderlein, 1905 (Fig. 9), both of which have a worldwide distribution.

The enigmatic Bruceiserinae, with hitherto only a few known species, are restricted to some arid and semiarid territories of South America, while the species-rich subfamilies Coniopteryginae and Aleuropteryginae are distributed worldwide.

The first modern monograph on Coniopterygidae and an additional check-list of the species of the world (MEINANDER 1972, 1990) were recently updated (SZIRÁKI 2011).

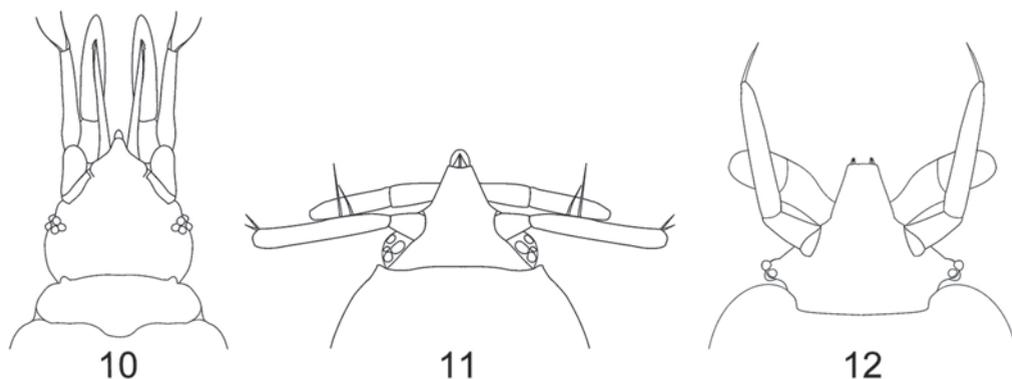
The sustaining current phylogenetic hypothesis places Aleuropteryginae (Fig. 10) as the sister-group to the clade Bruceiserinae + Coniopteryginae (Figs 11, 12; ZIMMER-



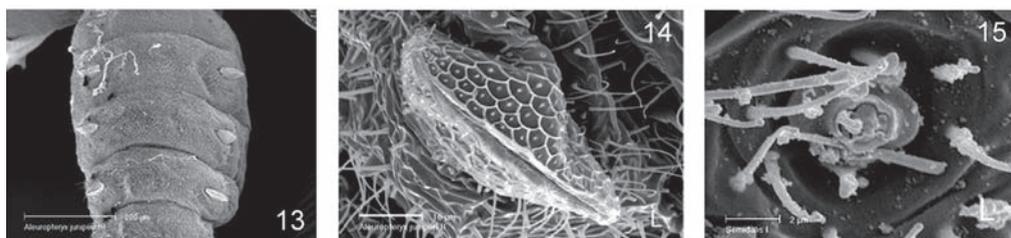
**Figure 6.** In the fancy cake chart of Neuroptera (from ASPÖCK & ASPÖCK 2007) the section of Coniopterygidae (light blue slice), comprising almost 580 species, is of medium size.

**Figures 7–9.** Representatives of the three subfamilies of the Coniopterygidae. 7 – Bruceiserinae, *Bruceiser penai* Riek, 1975 (after RIEK 1975); 8 – Coniopteryginae, *Coniopteryx pygmaea* Enderlein, 1906. Photo: H. Bruckner; 9 – Aleuropteryginae, *Aleuropteryx juniperi* Ohm, 1968. Photo: H. Rausch.

MANN et al. 2009). The larvae of Brucheiserinae and Coniopteryginae have laterally extended heads – a result of the prominence of the ocular regions. Both subfamilies have short sucking tubes which barely project beyond the tip of the labral margin (Figs 11, 12). These characters have been interpreted as synapomorphies. Consequently, the plicatures (Figs 13, 14) of the abdomen, which are expressed in Brucheiserinae and Aleuropteryginae but absent in Coniopteryginae, must belong to the ground pattern of Coniopterygidae and were presumably secondarily lost in Coniopteryginae. The possession of wax glands (Fig. 15) and the wax covering of body and wings – a phenomenon which characterizes adult Coniopteryginae and Aleuropteryginae but which is absent in Brucheiserinae – is apparently an apomorphy of the family Coniopterygidae that has been secondarily lost in Brucheiserinae.



**Figures 10–12.** The larvae of Brucheiserinae (Fig. 11) and Coniopteryginae (Fig. 12) are characterized by laterally extended heads and short sucking tubes – synapomorphies of both families. The current hypothesis posits a sister-group relationship of Aleuropteryginae (Fig. 10) to the clade Brucheiserinae + Coniopteryginae (Figs 11, 12; from ZIMMERMANN et al. 2009).



**Figures 13, 14.** *Aleuropteryx juniperi*, 13: abdomen with plicatures, 14: closed plicature (from ZIMMERMANN et al. 2009). The plicatures of the abdomen are expressed in Aleuropteryginae and Brucheiserinae, but are lost in Coniopteryginae.

**Figure 15.** *Semidalis aleyrodiformis* (Stephens, 1836), wax gland. From ZIMMERMANN et al. (2009). The possession of wax glands is a joint character of Aleuropteryginae and Coniopteryginae, and they are apparently lost in Brucheiserinae.

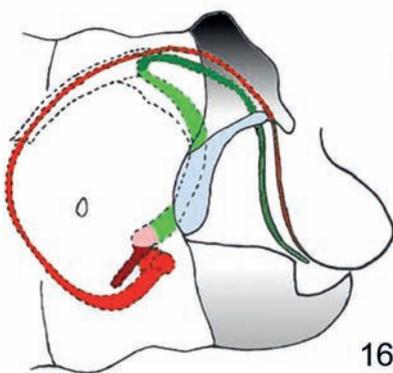
### Genital sclerites – The favorite toys of evolution

Neuropterida (Fig. 17) and especially Coniopterygidae (Fig. 16) are equipped with excessively heterogeneous male genital sclerites, which are of high phylogenetic relevance. Interestingly and worth mentioning – as a paradox – is fact that the head morphology and anatomy of Coniopterygidae are characterized by a considerable degree of miniaturization (RANDOLF et al. 2017), while the genital sclerites – on the contrary – show no corresponding signs of these phenomena.

OWEN'S (1843) famous definition of homology is given in his glossary: »HOMOLOGUE The same organ in different animals under every variety of form and function«. The statement expresses exactly the situation we are dealing with when attempting to homologize the male genital sclerites of Coniopterygidae.

The first “portraits” of genital sclerites of Coniopterygidae were published by ENDERLEIN (1906; Fig. 18). Günther Enderlein (Fig. 19) was a pioneer and his 1906 paper was a milestone not only with respect to genitalia of Coniopterygidae but for Neuropterida, in general. Addressing the individual sclerites, he started with descriptive terms. Although not explicitly declared, these descriptive labels imply homologization.

Bo Tjeder (1901–1992), a friend and mentor of many of us, created new set of terminology for genital sclerites of Neuropterida in 1954, which still serves as a reference for many neuropterologists. However, several of his “neutral” terms, e.g., gonarcus, mediuncus, arcessus, tignum and gonapsis, represent sclerites that he regarded as “inventions” of Neuropterida and not necessarily as homologons. This problematic situation was discussed in a glossary of the genital sclerites of Neuropterida in ASPÖCK et al. (1980). TJEDER (1954) clearly labelled tergite and sternite 9 in *Coniopteryx borealis* Tjeder, 1930, and identified the terminal ventral sclerite as the hypandrium externum



16



17

**Figures 16, 17.** Genital sclerites are the favorite toys of evolution. 16: *Coniopteryx tjederi* Kimmins, 1934, terminal segments and genital sclerites, lateral view. 17: a potpourri of male genital sclerites of Neuropterida. See Fig. 25 for the color-coding scheme, which is based on a gonocoxite hypothesis, as explained in the text.

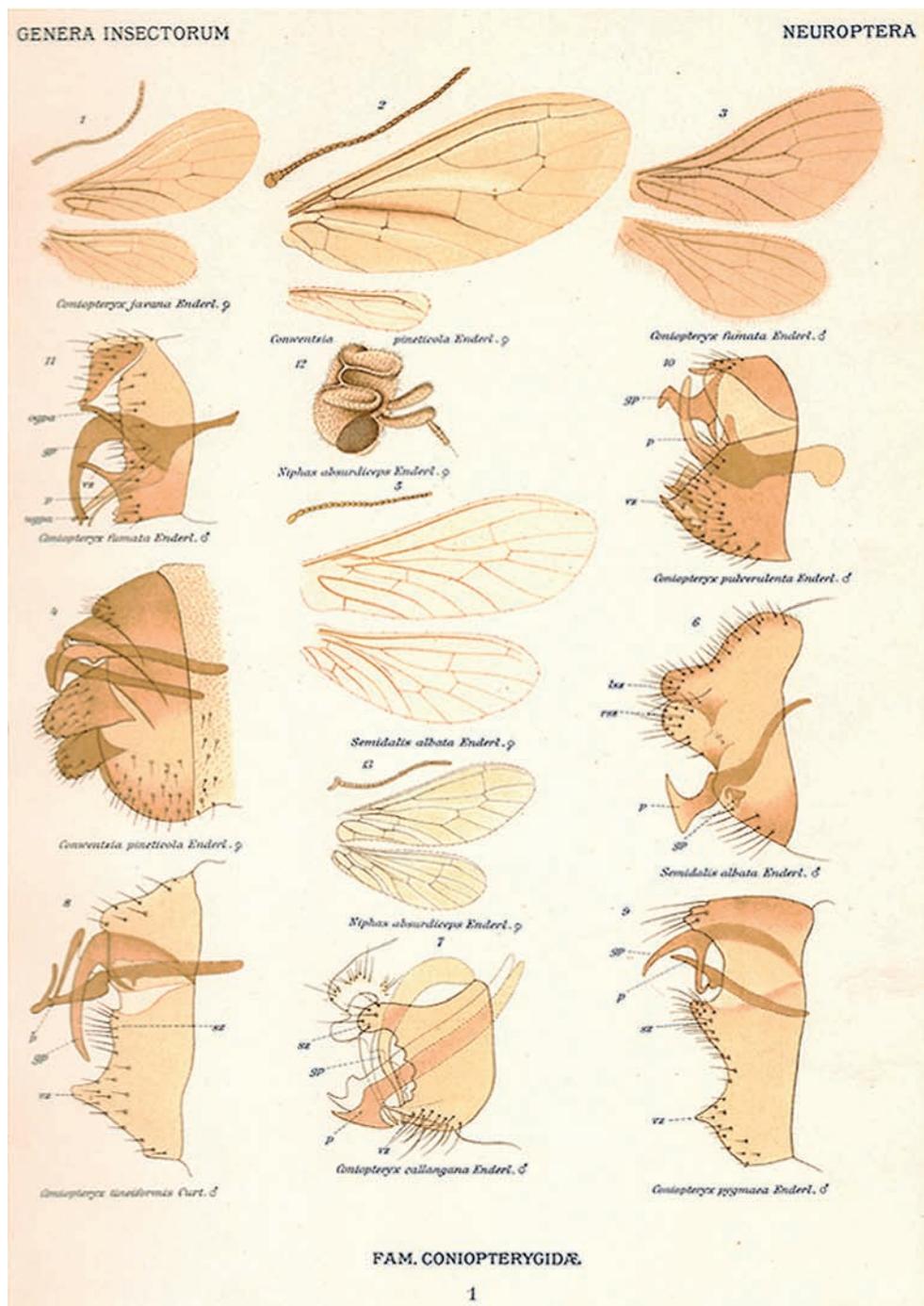


Figure 18. The first “portraits” of genital sclerites of Coniopterygidae were published by ENDERLEIN (1906).

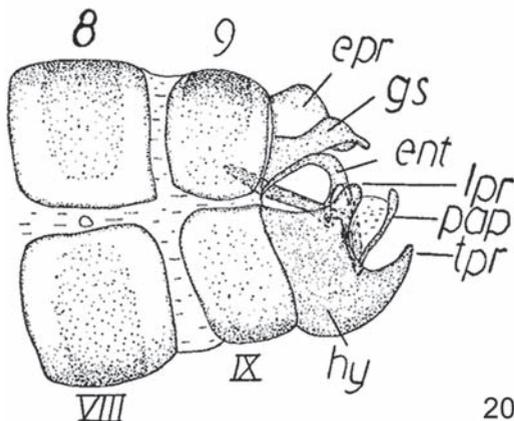
(hy) (Fig. 20) – which he considered to be the fused gonocoxites of Coniopterygidae. Yet, the hypandrium internum, a keel-shaped sclerite, which appears in almost all neuropteran families is absent in Coniopterygidae – a condition which Tjeder actually confirmed.

In September 1985, my husband and I visited Bo Tjeder (Fig. 21) at his home in Lund, Sweden together with Peter Ohm – an occasion which endures in our memory as a holy reminiscence and for which we are grateful.

Less than 10 years after publication of Tjeder's »Genital structures and terminology in the order Neuroptera«, Thomas Stephen Acker favored terminology based on a coxo-



**Figure 19.** Günther Enderlein (1872–1968) was a pioneer in the taxonomy of the Coniopterygidae – he introduced morphological characters of the genital sclerites into the taxonomy. From the Portrait Collection of Deutsches Entomologisches Institut, Müncheberg, Germany.



**Figure 20.** Genital sclerites of *Coniopteryx borealis* Tjeder, 1930, from TJEDER (1954), showing spiraculum 8 and the clearly defined tergite and sternite of segment 9. His abbreviations: ent – entoprocessus, epr – ectoproct, gs – gonarcus, hy – hypandrium, lpr – processus lateralis, pap – processus apicalis, tpr – processus terminales. For present interpretation, cf. Figure 35.

podite concept that was of enormous heuristic value for us (ACKER 1960). It was predominantly constructive with regard to segment 9. However, ACKER (1960) introduced the term spinasternum (originally a sclerite known from the thorax) for elements of segment 10, which is contradictory. In addition, he proposed the hypothesis that the hypandrium internum, which had so far not been found in Coniopterygidae, was identical with the “penis” in the sense of TJEDER (1957), and thus part of the gonocoxite 10 complex in our terminology (see below).

Three years before ACKER’s (1960) publication, an important paper by MATSUDA (1957) appeared with the title »Comparative morphology of the abdomen of a Machilid and a Raphidiid«. The machilid is representative of the Archaeognathan Machilidae, which are equipped with serially homologous gonocoxites, gonostyli and gonapophyses in the abdominal segments (Fig. 22) and stand as a model for Neuropterida. The raphidiid in MATSUDA (1957) is *Agulla adnixa* (Hagen, 1861) – here *Italoraphidia solariana* (Navás, 1928) is preferred (Figs 23–24), which serves as an ideal example to illustrate the colour-coded scheme for the sclerites forming the gonocoxites, gonapophyses and gonostyli of segments 9, 10 and 11, respectively (Fig. 25).

The box with colored fields (Fig. 25) is a tool for homologization (ASPÖCK & ASPÖCK 2008). Each segment is characterized by a different color, and different shades of these colors are used for the gonocoxites, gonostyli and gonapophyses of the respective segments.

Segments 7, 8 and 9 involve genital segments of the females (which are not treated in the present paper), while segments 9, 10 and 11 are relevant to the males. In a first step,

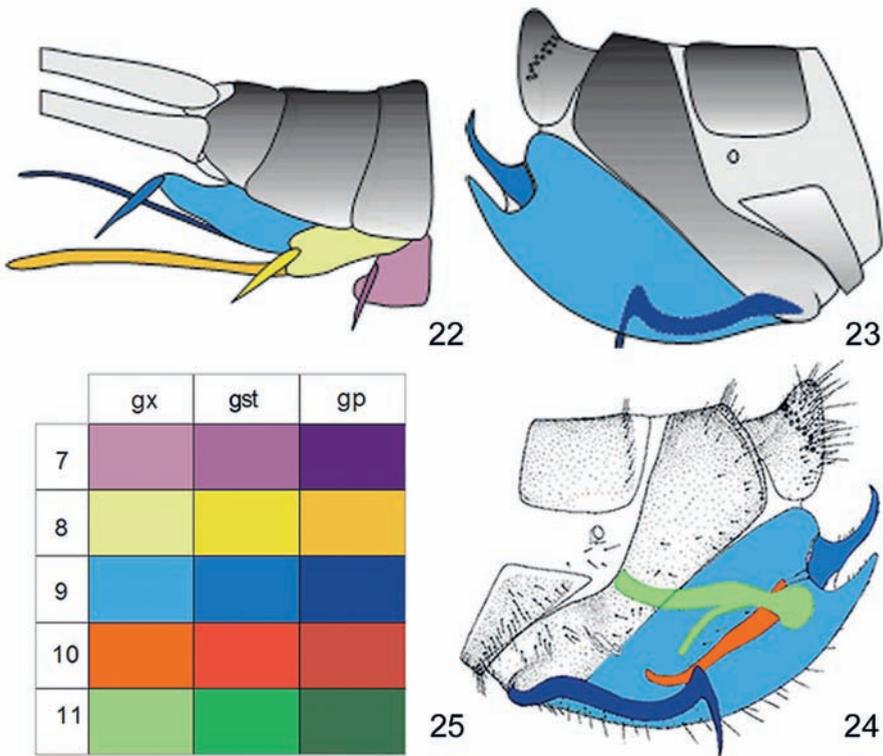


**Figure 21.** Bo Tjeder at his home in Lund, Sweden, with Horst Aspöck and Ulrike Aspöck in September 1985 (Photo archive H. & U. Aspöck).

it must be considered which specific sclerite belongs to what segment. For example, with regard to *Italoraphidia solariana*, the blue color symbolizes gonocoxites 9, gonostyli 9 and gonapophyses 9 (Fig. 23), while the corresponding sclerites of segment 10 (orange-red) and 11 (green) are hidden within the abdomen (Fig. 24).

In a second step, sclerites are addressed as gonocoxites, gonostyli or gonapophyses 9, 10 or 11, respectively. If these parts are not discernible in the compound of a sclerite, the sclerite is addressed as gonocoxite-complex 9, 10, or 11.

In case the identity of a sclerite is doubtful, a hypothesis formulated on a gonocoxite concept is at any rate of more heuristic value than to hypothesize accessorial *de novo* structures and create new names for them. Therefore, the essential statement and message is that gonocoxite-patterns trump accessory-patterns.



**Figure 22.** Terminal segments of a female machilid showing the serially homologous gonocoxites, gonapophyses and gonostyli. See Fig. 25 for system for color-coding the sclerites. After ASPÖCK & ASPÖCK (2008).

**Figures 23, 24.** *Italoraphidia solariana* (Navás, 1928) with gonocoxites, gonostyli and gonapophyses of segments 9, 10 and 11, respectively. See Fig. 25 for color-coding scheme.

**Figure 25.** Color-coded scheme for the homologization of gonocoxites, gonostyli and gonapophyses of the genital segments 7 to 9 (females), and 9 to 11 (males). After ASPÖCK & ASPÖCK (2008).

### Species sampled

In the following, the homology of coniopterygid male genital sclerites is discussed based on examples from all three subfamilies.

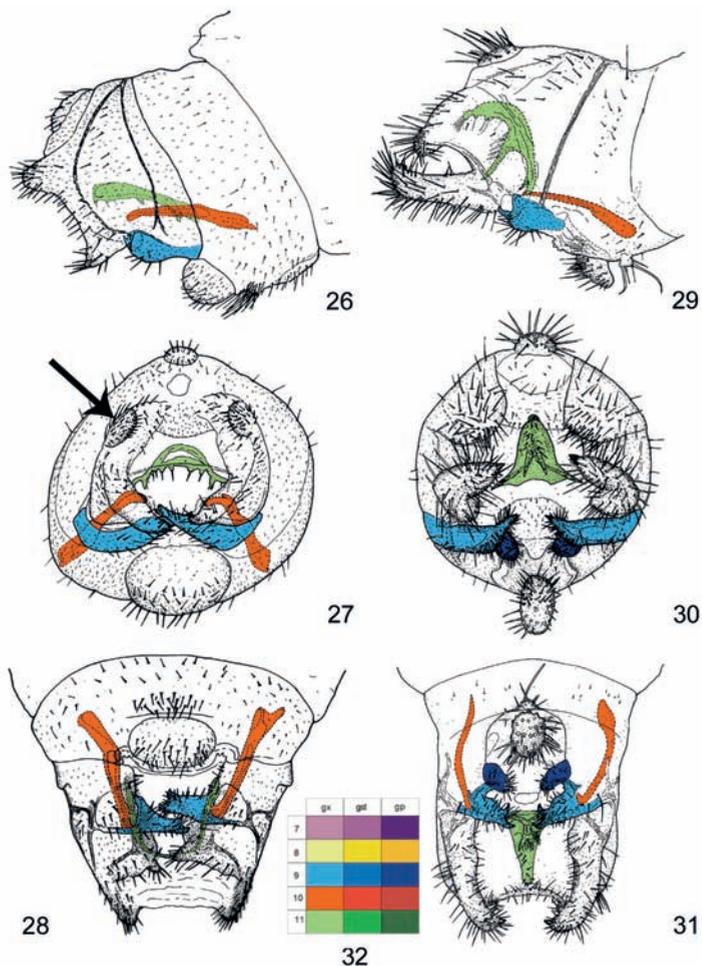
#### Brucheiserinae Figs 26–32

Apart from their unusual eidonomic appearance, Brucheiserinae surprise us with a rather simple set of gonocoxite-complexes 9, 10, and 11. The evidence of a callus cerci, e.g., in *Brucheiser penai* Riek, 1975, Fig. 27 (labelled as “cpe” in SZIRÁKI 2007) seemingly exhibits a plesiomorphic pattern within the family. The spiraculum of segment 8, another morphological landmark, can be seen in *Flintoconis gozmanyi* Sziráki, 2007 (SZIRÁKI 2007: Fig. 17); the gonocoxites 9 are even equipped with gonapophyses (Figs 30, 31, dark blue) in *Flintoconis* Sziráki, 2007. Gonocoxites 10 are simple rods (Figs 26–31, orange-red) in all Brucheiserinae. Gonocoxites 11 are fused to an arch (Figs 26, 27, 29–31, green), which is either simple or may be structured.

**Figures 26–28.** *Brucheiser penai* Riek, 1975, Brucheiserinae. Genital sclerites, lateral (26), caudal (27), ventral (28) views. Coloration according to Figure 32. The possession of a callus cerci (black arrow in Figure 27) indicates a rather ancestral pattern of these genital sclerites. After SZIRÁKI (2007).

**Figures 29–31.** *Flintoconis petorcana* Sziráki, 2007, Brucheiserinae. Genital sclerites, lateral (29), caudal (30), ventral (31) views. This species has retained the gonapophyses 9 (dark blue in Figs. 30, 31). After SZIRÁKI (2007). Coloration according to Figure 32.

**Figure 32.** See explanation in Figure 25.



### **Coniopteryginae** Figs 33–38

The genital sclerites of this subfamily are extremely heterogeneous, and the selected species, *Conwentzia pineticola* Enderlein, 1905, *Coniopteryx pygmaea* Enderlein, 1906, and *Coniopteryx loipetsederi* H. Aspöck, 1963, serve as an introduction and as *pars pro toto* for a forthcoming comprehensive analysis of the genital sclerites of the Coniopterygidae.

*Conwentzia pineticola* (Figs 33, 34) is equipped with unspectacular gonocoxites 9 (light blue), and plesiomorphically paired gonapophyses 9 (dark blue), which are homologous with the unpaired hypandrium externum in *C. pygmaea* (see below). Gonocoxites 10 appear as simple rods (orange-red), and their apices are addressed as styli. A tiny sclerite between the gonocoxites 10 might be the reduced gonapophyses 10, but this is speculative. The unpaired caudal sclerite represents the gonocoxites 11 (green).

The large unpaired terminal sclerite in *C. pygmaea* was interpreted as the hypandrium externum by TJEDER (1954). Subsequently, the hypandrium externum was re-interpreted as sternite 9, as in *Coniopteryx loipetsederi* by ASPÖCK & ASPÖCK (2008). The present interpretation of the hypandrium externum as gonapophyses 9 (Figs 35–37) is a thought-provoking alternative – waiting for falsification.

Thus, *C. loipetsederi* H. Aspöck, 1963, (Figs 36, 37) and *C. pygmaea* (Fig. 35) are equipped with simple gonocoxites 9 (light blue) with fused gonapophyses 9 (formerly the hypandrium externum) (dark blue) and ventrally bent gonostyli (medium blue). Rod-like gonocoxites 10 (orange-red) are equipped with apices (medium red) possibly representing modified styli. The unpaired tiny sclerite might be the fused and reduced gonapophyses 10 (dark red). There is no trace of gonocoxites 11 (therefore no green color).

### **Aleuropteryginae** Figs 39–44

As emphasized above for the Coniopteryginae, the genital sclerites of the Aleuropteryginae are likewise extremely heterogeneous, and the selected species *Helicoconis lutea* (Wallengren, 1871) and *Aleuropteryx juniperi* Ohm, 1968, serve as a basic introduction for the planned more comprehensive analysis.

In *Helicoconis lutea* (Figs 39, 40) tergite 9 forms a well-sclerotized ring to which sternite 9 (formerly the hypandrium externum) is connected. Gonocoxites 9 (light blue) are finger-like in *H. lutea* but are diversely shaped in other species.

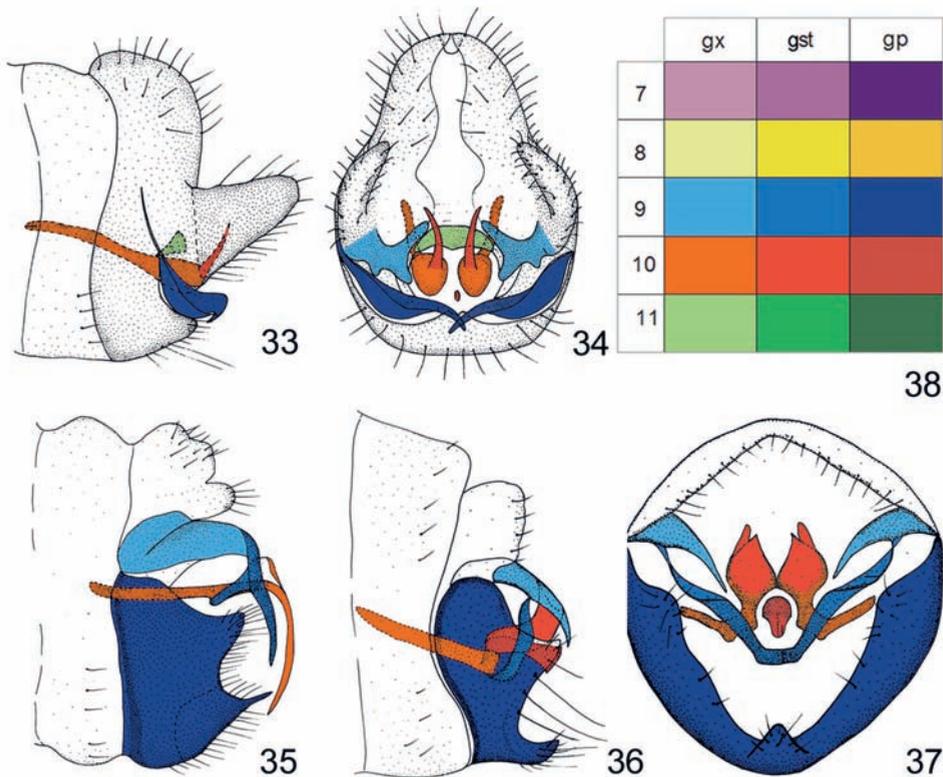
As mentioned above, the former hypandrium externum of sternite 9 has been newly re-deciphered to be the fused gonapophyses 9 in *Coniopteryx*; extending this hypothesis to *Helicoconis* means that its former hypandrium externum would likewise be suggestive of a fused gonapophyses 9 (Handschuh & U. Aspöck unpubl.).

The landmark of the genital sclerites is the gonocoxites 10 complex with dominant paired rods, one of which represents the gonocoxites 10 (orange-red) with apical styli, and the other pair represents the gonapophyses with fused apices. There is no trace of gonocoxites 11. Generally, the gonocoxite 10 complexes are the predominant component of the genital armature in most Coniopterygidae.

The genus *Aleuropteryx* Löw, 1885 – represented by the species *A. juniperi* Ohm, 1968, (Figs 41–43) – is characterized by having tergite 9 and sternite 9 fused to a huge

sclerite, which does not form a simple ring, and which is completely withdrawn into the abdomen. Gonocoxites 9 (light blue) are equipped with a terminal appendix which may be interpreted as the styli.

As discussed above for *Helicoconis*, the present interpretation of sternite 9 (formerly the hypandrium externum) may likewise be hypothesized as the fused gonapophyses 9 in *Aleuropteryx* (Handsuh & U. Aspöck unpubl.). Our landmark is again the complex of the gonocoxites 10 and gonapophyses 10 (both indiscernibly fused, thus both in orange-red). A fused pair of sclerites with caudally directed teeth is regarded as the gonocoxites 11 (green).



**Figures 33, 34.** *Conwentzia pineticola* Enderlein, 1905, Coniopteryginae. Genital sclerites lateral (33) and caudal (34) views. Coloration according to Figure 38, for color-coding scheme see Fig. 25. *Conwentzia* is still equipped with gonocoxites 11! After ASPÖCK & ASPÖCK (2008).

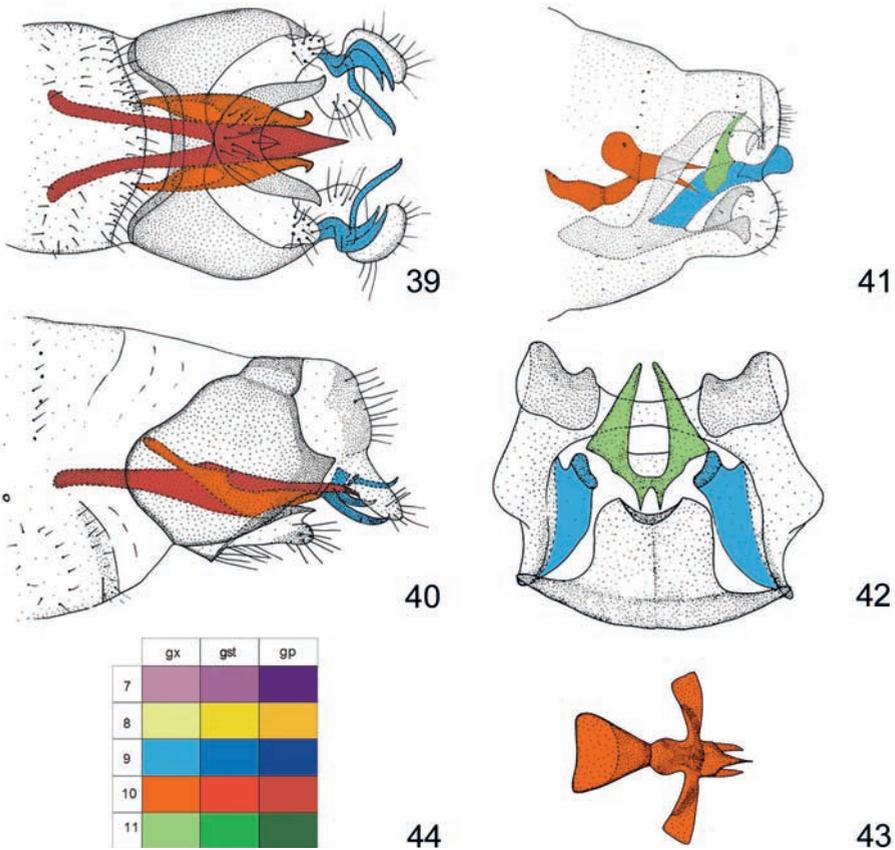
**Figure 35.** *Coniopteryx pygmaea* Enderlein, 1906, Coniopteryginae. Genital sclerites, lateral view. Coloration according to Figure 38. See Fig. 25 for color-coding scheme. Sternite 9 is interpreted as the fused gonapophyses 9 – an alternative hypothesis waiting for falsification.

**Figures 36, 37.** *Coniopteryx loipetsederi* H. Aspöck, 1963, Coniopteryginae. Genital sclerites, lateral (36) and caudal (37) views. Coloration according to Figure 38. See Fig. 25 for color-coding scheme. Sternite 9 is interpreted as the fused gonapophyses 9, see above.

**Figure 38.** See explanation in Figure 25.

In conclusion, it must be stated that the interpretations presented here on the coniopterygid genital sclerites are, in a way, the kick off or catalyzer for a future larger study on the homology of these sclerites as mentioned previously. In the course of further performances, corrections and modifications of the present visions and versions should not be a surprise.

Finally, I want to emphasize that the current campaign of homologization of male genital sclerites of Coniopterygidae has enormous potential to invigorate the classification of the family.



**Figures 39, 40.** *Helicoconis lutea* (Wallengren, 1871), Aleuropteryginae, ventral (39) and lateral (40) views. Coloration according to Figure 44. See Fig. 25 for color-coding scheme.

**Figures 41–44.** *Aleuropteryx juniperi* Ohm, 1968, Aleuropteryginae, genital sclerites, lateral (41), caudal (42) views. The gonocoxites 10 complex (43) comprises the fused gonocoxites and gonapophyses. Coloration according to Figure 44. See Figure 25 for color-coding scheme and explanation.

## Acknowledgements

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# Metathetely and its implications for the distribution of Raphidioptera (Insecta, Holometabola: Neuropterida)

Horst Aspöck<sup>1</sup>, Ulrike Aspöck<sup>2,3</sup> & Axel Gruppe<sup>4,5</sup>

<sup>1</sup> Institute of Specific Prophylaxis and Tropical Medicine, Medical Parasitology, Medical University of Vienna, Kinderspitalgasse 15, 1090 Vienna, Austria; horst.aspoeck@meduniwien.ac.at

<sup>2</sup> Natural History Museum Vienna, Department of Entomology, Burgring 7, 1010 Vienna, Austria; ulrike.aspoeck@nhm-wien.ac.at

<sup>3</sup> Department of Integrative Zoology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria; ulrike.aspoeck@univie.ac.at

<sup>4</sup> Chair of Zoology – Entomology group, Department of Animal Sciences, Technical University of Munich (TUM), Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>5</sup> Corresponding author: gruppe@wzw.tum.de

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**Abstract.** The complete life cycle of snakeflies (order Raphidioptera) usually lasts for two years and always includes one hibernation at least. Three types of life cycles can be differentiated. In >95 % of all snakefly species the mature larva hibernates in quiescence, pupates in spring and molts two to three weeks later to the imago (Type I). If, however, decrease of temperature in winter is withheld, larvae cannot pupate successfully, but develop various pathomorphological disorders, which represent a form of metathetely in which they are pupae but retain many larval characters. Metathetelous pupae usually die sooner or later and can never molt to adults capable of reproduction. In experimental studies on three biogeographically different species – *Raphidia (R.) mediterranea*, *Phaeostigma (Ph.) notata* (nomenclature *sensu* H. ASPÖCK & U. ASPÖCK 2013a), and *Mongoloraphidia (M.) sororcula* – a distinct correlation between the distribution and the degree and length of chilling necessary to prevent metathetely was detected. Metathetely is apparently a determining factor for the distribution of snakeflies and a possible explanation for their lack in the south of the Northern Hemisphere as well as in the Southern Hemisphere.

## Raphidioptera in brief

Raphidioptera (snakeflies) contain fewer than 250 described valid species and is thus the smallest order of holometabolous insects. It comprises two families: Raphidiidae (<210 species; Figs 1–5) and Inocelliidae (slightly >40 species; Fig. 6).

Nowadays the distribution of snakeflies (Fig. 7) is restricted to arboreal parts of the Northern Hemisphere in latitudes and altitudes that have a distinct decrease of temperature during winter (H. ASPÖCK & U. ASPÖCK 2009, 2012, 2013b, 2014; U. ASPÖCK & H. ASPÖCK 2009).

Both adults and larvae have an entomophagous mode of feeding on a variety of soft-bodied arthropods (H. ASPÖCK et al. 1991; RAUSCH & H. ASPÖCK 1992; H. ASPÖCK 2002). Larvae live under bark (about 50 % of Raphidiidae species and probably all In-



**Figure 1.** Male of *Mongoloraphidia sororcula* (H. Aspöck & U. Aspöck, 1966) reared *ab ovo* in the lab; Mongolia, Province Baian-Olgii, Olgi Khovd Gol, 07.vi.2012, leg. A. Gruppe.



**Figure 2.** Female of *Mongoloraphidia sororcula* reared *ab ovo* in the lab; data as Figure 1.



**Figure 3.** Mature larva of *Mongoloraphidia sororcula*.



**Figure 4.** Prepupa of *Mongoloraphidia sororcula* reared *ab ovo* in the lab.



**Figure 5.** Pupa of *Mongoloraphidia sororcula* reared *ab ovo* in the lab.



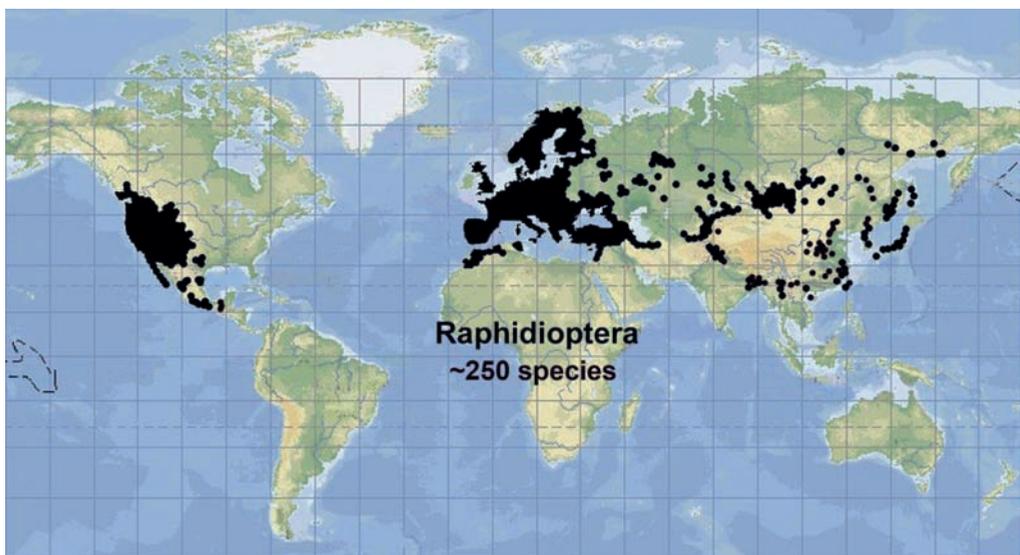
**Figure 6.** Female of *Inocellia crassicornis* (Schummel, 1832); Mongolia, Province Selenge, Khan Khentii National Park, 20.vi.2012, leg. A. Gruppe.

ocelliidae), in the leaf litter of soil, the detritus around roots of bushes, or crevices of rocky ground with sparse vegetation (H. ASPÖCK & U. ASPÖCK 2009, 2012).

The Raphidioptera – living fossils par excellence – had their Golden Age in the Mesozoic, when these insects reigned with probably thousands of species including the Southern Hemisphere and tropical regions (U. ASPÖCK & H. ASPÖCK 2007; JEPSON & JARZEMBOWSKI 2008; LIU et al. 2016; LYU et al. 2017a, b, 2018). It was hypothesized (H. ASPÖCK 1998) that the dramatic events after the K/T impact, when an asteroid of 10 km diameter crashed into our planet causing worldwide fires, darkness, and decrease of temperature for several years, nearly led to an extinction of the Raphidioptera. However, at least two lines survived representing the two extant families, Raphidiidae and Inocelliidae (H. ASPÖCK 1998, 2000; HARING et al. 2010; H. ASPÖCK et al. 2012; U. ASPÖCK et al. 2012).

### Development of Raphidioptera

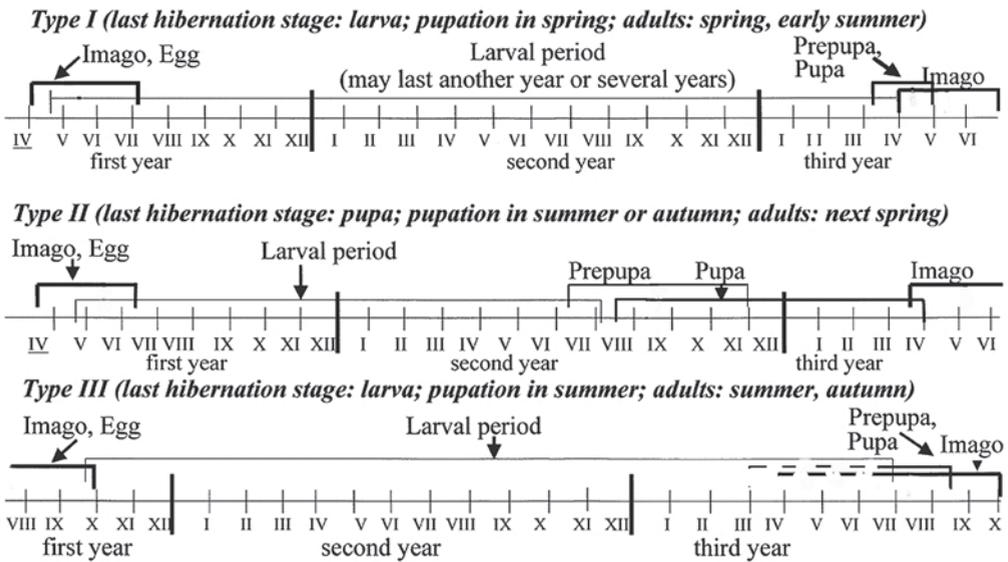
Most species of Raphidioptera require two years for the development from the egg to the imago, while few species in the Old World and at least several (perhaps all?) species of the Nearctic genus *Agulla* Navás complete their development within one year (WOGLUM & MCGREGOR 1958, 1959; KOVARIK et al. 1991; H. ASPÖCK 2002). However, many species of Raphidiidae and Inocelliidae develop to the adult stage after a larval period of three or more (up to six!) years (H. ASPÖCK et al. 1991). Yet the length of development may vary not only within individual species, but also within the descendants of a single female (GRUPPE & ABBT 2018). The number of larval instars varies between nine and 15, even within one species, but exact comparative studies have not yet been carried out. Three types of development are distinguished in Raphidioptera (H. ASPÖCK 2002: see Fig. 8) and are described below.



**Figure 7.** World distribution of the order Raphidioptera. Modified after H. ASPÖCK et al. (2018).

Type I adults appear in spring, the egg stage lasts for one to two weeks and the larval period comprises at least one hibernation, but usually at least two. In early spring after the last hibernation, pupation is induced: The mature larva (Fig. 3) becomes a prepupa, i.e. a larva with head and thorax bent to the ventral side (Fig. 4). The prepupa is entirely inactive, it lies quietly, and after a few days it molts into a pupa (Fig. 5). The pupal stage lasts about two to three weeks. Type I is represented by the majority of the Raphidiidae of Europe and Asia (which include the large genera *Phaeostigma* Navás, 1909, and *Mongoloraphidia* H.A. & U.A., 1968, moreover *Italoraphidia* H.A. & U.A., 1968, *Venustoraphidia* H.A. & U.A., 1968, *Xanthostigma* Navás, 1909, *Puncha* Navás, 1915, *Turcoraphidia* H.A. & U.A., 1968, *Subilla* Navás, 1916, *Tauroraphidia* H.A., U.A. & Rausch, 1982, *Ulrike* H.A., 1968, *Raphidia* L., 1758, *Dichrostigma* Navás, 1909), most Nearctic species of the genus *Agulla* Navás, 1914, some species of *Alena* Navás, 1916, and almost all Inocelliidae, with few exceptions among Nearctic species.

Type II adults also appear in spring, eggs are laid, and after a few days larvae hatch and molt several times in the following months. After two or more years, usually in late summer or even later, the larvae pupate, but the pupae hibernate and molt to adults in the spring of the following year. Type II comprises several genera of Raphidiidae mainly



**Figure 8.** Life cycles of Raphidioptera. Three types (I, II, III) are distinguished. Type I is represented by probably >95 % of all snakeflies of both families. In Type II there is a long period in which the mature larva pupate: (IV-)VII-X(-XII); at any rate the overwintering stage is always the pupa, except for *Ornatoraphidia flavilabris*, which may hibernate either as pupa or as prepupa. In *Tjederiraphidia santuzza* the mature larva may (rarely) hibernate and pupate in spring, thus representing Type I. In Type III there is an unusually long period after the last hibernation of a larva (III-XI) in which pupation and subsequent hatching of the imago may occur. Modified after H. ASPÖCK (2002).

occurring in the Iberian Peninsula and/or in the North of Africa: *Atlantoraphidia* H.A. & U.A., 1968, *Harraphidia* Steinmann, 1963, *Hispanoraphidia* H.A. & U.A., 1968, *Africoraphidia* U.A. & H.A., 1969, and *Ohmella* H.A. & U.A., 1968. In addition, Type II is represented by the species of the genera *Tjederiraphidia* H.A., U.A. & Rausch, 1985, which is endemic to mountains in the south of Italy, and *Ornatoraphidia* H.A. & U.A., 1968, which is occurring in the Balkans, the Apennine Peninsula and the south of Central Europe. The crucial criterion of Type II is hibernation in the pupal stage, *i.e.*, pupation before the last winter of the life cycle. However, regarding Type II species, a hibernation of the mature larva and pupation in spring have been observed in some individuals of some species. This means that the life cycle resembles very much that of species of Type I. Several species – or, more correctly, some individuals of some species – of Type II pupate in June, but some extremely late in October, November or even December – however, they all hibernate as pupae. In one species of *Ornatoraphidia*, *O. flavilabris* (Costa, 1855), there is a very unusual and strange condition – the larvae become inactive very late in the year, enter the prepupal stage and hibernate as prepupae. However, in some cases, the larvae pupate in August and hibernate as pupae. *Ornatoraphidia flavilabris* is the only known species of snakeflies that can overwinter in the prepupal stage. The second species of *Ornatoraphidia* – *O. christianodagmara* (H.A. & U.A., 1970) – shows similar variability of development, but exceptionally hibernation of the last larval stage and pupation in spring have been found (RAUSCH & ASPÖCK 1992).

As far as we know, Type III species are represented by only (some) species of the Nearctic genus *Alena* Navás of the family Raphidiidae, and probably as well by species of the genus *Indianoinocellia* U. Aspöck & H. Aspöck, 1970, whose adults appear in (late) summer or even in (late) autumn. The egg stage lasts most probably – as in Type I and Type II species – a few days to about two weeks. The larvae pass at least two hibernations and pupation takes place in the third year usually in summer. However, at least under laboratory conditions pupation and shortly later the appearance of adults may (exceptionally?) occur in early spring, sometimes, however, very late autumn or even winter (U. ASPÖCK et al. 1992, 1994).

### Periods of dormancy in development of Raphidioptera

Dormancy in insects occurs in two markedly different forms: as quiescence or as a diapause (MÜLLER 1970, 1992). In quiescence the triggering factor immediately induces dormancy, and abolition of the factor leads to an immediate end of dormancy. Diapause is induced slowly by endogenic or exogenic factors and does not end abruptly, but necessitates a second trigger for termination.

Dormancy in Raphidioptera, as far as known, is always quiescence and always induced by low temperature. Other exogenic factors, such as light or darkness (photo-period), bear no significance on dormancy. Thus, quiescence in Raphidioptera in nature pertains only to hibernating stages, *i.e.*, larvae (in all three types) and the pupa (in Type II). In *Ornatoraphidia flavilabris*, a Type II species, sometimes the prepupa is the last hibernating stage.

Under laboratory conditions quiescence can be induced in all larval stages at any time by exposure to low temperatures (e.g., +4°C, but most probably considerably different in different species), which leads immediately to inactivity of a larva, and the transfer of the quiescent larva to higher temperatures results, within seconds, in activity. Further, when a hibernating larva, e.g., at -10°C, is subjected to warm temperature it immediately begins to run and take up food.

### Metathetely in Raphidioptera

Eighty years ago, EGLIN (1939) observed in his rearings of *Raphidia major* Burmeister, 1839 (today: *Phaeostigma (Magnoraphidia) major*; nomenclature *sensu* H. ASPÖCK & U. ASPÖCK 2013a) – a larva with various morphological disorders reminiscent of pupal characters such as altered eyes and wing pads. Eglin referred to this individual as a »Larvenpuppe« (larval pupa) and pointed out that it was the result of an incomplete molt to a pupa. Eglin kept his larvae at room temperature even during the winter, but he did not associate the pathomorphologies with the withholding of decrease of temperature. More than twenty years passed before another publication appeared (VANNIER & CONDÉ 1962) dealing with this phenomenon. The authors reared larvae of *Raphidia notata* (Fabricius, 1781) (today: *Phaeostigma (Ph.) notata*; nomenclature *sensu* H. ASPÖCK & U. ASPÖCK 2013a), kept them at room temperature until December and then transferred them to an outdoor location with +5°C. Some larvae died, some developed to adults, but one individual developed pathomorphological disorders (disordered eyes, wing pads) like the »Larvenpuppe« of EGLIN (1939). The authors designated this phenomenon as »prothetely«. Around 1970, two of us (H.A. & U.A.) together with Hubert and Renate Rausch began rearing larvae of many snakefly species on a large scale (H. ASPÖCK et al. 1974, 1991), and it turned out that the pathomorphological characters described by EGLIN (1939) and VANNIER & CONDÉ (1962) could easily be induced when the larvae were kept continuously at room temperature also in winter. In other words, withholding low temperature during hibernation of the mature larva led to these pathomorphologies. In agreement with VANNIER & CONDÉ (1962) we termed the phenomenon »prothetely« (H. ASPÖCK et al. 1974, 1991).

Today we know that this phenomenon in Raphidioptera should be identified as 'metathetely' instead of 'prothetely' (H. ASPÖCK et al. 2018). Prothetely means the appearance of characters of a later stage, while metathetely is a developmental retardation, when characters of a former stage remain in the following stage. This is the case in Raphidioptera: The last larval instar failed to achieve a complete pupation, but retains larval characters. It behaves and looks like a larva, but has pupal or pathomorphological eyes, sometimes also antennae, wing pads and alterations of the last abdominal segments (Figs 9–21). However, it is the result of an unsuccessful pupation, and therefore it is a metathetelous pupa. Perhaps the term 'larval pupa' would be more appropriate. These peculiar creatures may live for several more weeks or months, but by far in most cases they die. However, in very few cases we have observed that they molt again (even two subsequent molts have been observed) and very exceptionally – after another hi-

bernation in decreased temperature – an imago with pathomorphological alterations hatched. This means that a metathetelous pupa behaves like a larva in the successive year: It molts and pupates after the next hibernation. Indeed, very strange!

What has been described here applies to Raphidiidae of Type I and probably to almost all Inocelliidae. Raphidiidae of Type II overwinter as pupae and require chilling, otherwise they would decrease. As regards Raphidiidae (and some Inocelliidae) of Type III, we lack experimental data to confirm that chilling of the last hibernating larva is a precondition for the completion of the development to the imago. We assume that this is the case; otherwise the restriction of the distribution of these species to areas with low temperatures in winter could hardly be explained.



**Figure 9.** Head of a mature larva of *Mongoloraphidia sororcula*.



**Figure 10.** Head of a metathetelous pupa of *Mongoloraphidia sororcula* with pathomorphologically developed eyes (exposure to chill of 4°C: 8 weeks).



**Figure 11.** Head of a metathetelous pupa of *Mongoloraphidia sororcula* with pathomorphologically developed eyes (exposure to chill of 4°C: 4 weeks).



**Figure 12.** Head of a metathetelous pupa of *Mongoloraphidia sororcula* with pathomorphologically developed eyes and antennae (exposure to chill of 4°C: 4 weeks).

### Experimental data on specific differences in different species

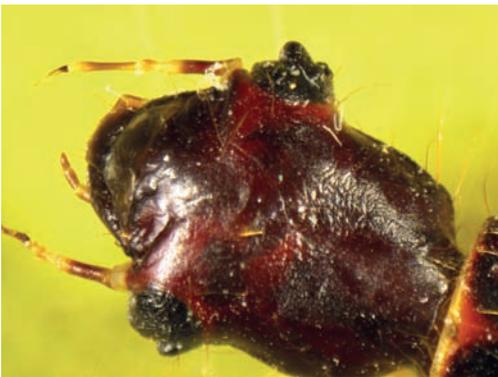
Two of us (H.A. & U.A. together with H. & R. Rausch) have been rearing Raphidioptera for about fifty years (for methods see H. ASPÖCK & U. ASPÖCK 2009) and have amassed considerable experience and concrete data. However, although we assumed that the degree and the duration of chilling of hibernating mature larvae necessary for successful pupation in spring varies for different species, we had no opportunity to check this by controlled experiments. Even Inocelliidae from tropical regions emerged after hibernation under natural climatic conditions in Austria. It should, however, be emphasized that these species occur in Thailand in high altitudes.



**Figure 13.** Thorax of a metathelous pupa of *Mongoloraphidia sororcula* with wing pads (exposure to chill of 4°C: 4 weeks).



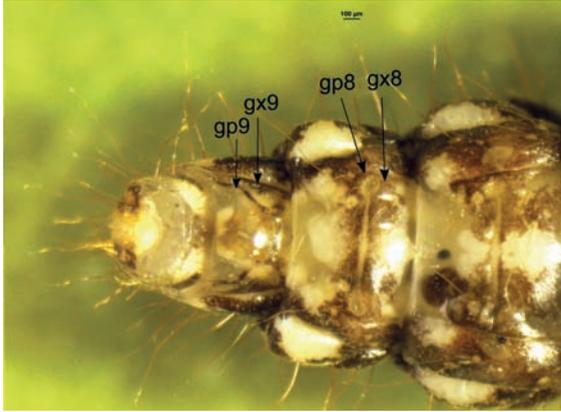
**Figure 14.** Head of a metathelous pupa of *Phaeostigma notata* with pathomorphologically developed eyes and head sculpture (exposure to chill of 4°C: 4 weeks).



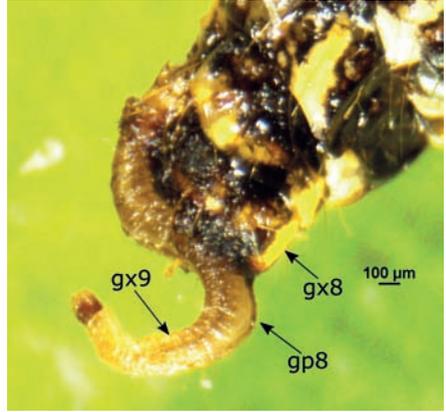
**Figure 15.** Head of a metathelous pupa of *Phaeostigma notata* with pathomorphologically developed eyes (exposure to chill of 4°C: 4 weeks).



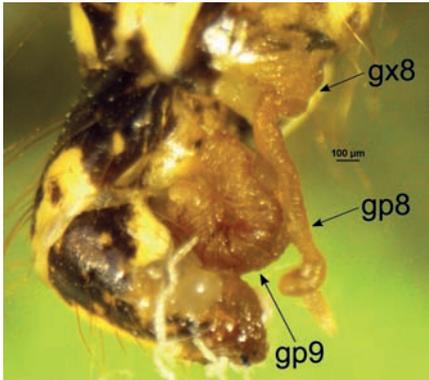
**Figure 16.** Thorax of a metathelous pupa of *Phaeostigma notata* with wing pads (exposure to chill of 4°C: 4 weeks).



**Figure 17.** Ventral view of terminalia in a metathetelous male pupa of *Phaeostigma notata* (exposure to chill of 4°C: 8 weeks). gx – gonocoxite; gp – gonapophysis.



**Figure 18.** Lateral view of terminalia in a metathetelous female pupa of *Phaeostigma notata* (exposure to chill of 4°C: 12 weeks).



**Figure 19.** Ventral view of terminalia in a metathetelous female pupa of *Phaeostigma notata* (exposure to chill of 4°C: 4 weeks).



**Figure 20.** Head of a metathetelous pupa of *Raphidia mediterranea* with pathomorphologically developed eyes (exposure to chill of 4°C: 12 weeks).

**Figure 21.** Thorax of a metathetelous pupa of *Raphidia mediterranea* with wing pads (exposure to chill of 4°C: 12 weeks).



In a recent thesis for a master degree (ABBT 2016), three Type I species from three genera of Raphidiidae were investigated with respect to length of chilling at +4°C necessary for preventing development of metathetely (Fig. 25): *Phaeostigma (Ph.) notata*, *Raphidia (R.) mediterranea* and *Mongoloraphidia (M.) sororcula*. The three species have biogeographically markedly different distribution patterns, which are summarized below.

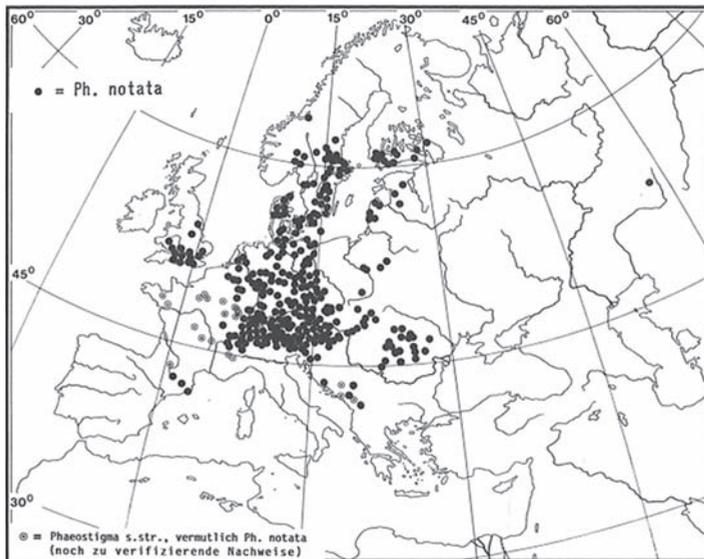
*Phaeostigma (Ph.) notata* (Fig. 22) is a polycentric and expansive extra-Mediterranean-European faunal element occurring in large parts of extra-Mediterranean Europe (Central Europe, southern parts of Fennoscandia, Eastern Europe, northern Italy, France, and northern Spain).

*Raphidia (R.) mediterranea* (Fig. 23) is a Mediterranean (probably a Balkano-Pontomediterranean) faunal element, which occurs in the Balkan Peninsula, several Aegean islands, Italy, and Eastern Europe, with an isolated location in Upper Austria (RAUSCH et al. 2016). The species is likely to have been introduced by human activities into many parts of its present distribution area from Greece, possibly since antiquity (H. ASPÖCK et al. 2017).

*Mongoloraphidia (M.) sororcula* (Fig. 24) is a monocentric, stationary Mongolian faunal element only known from high altitudes in the northwest of Mongolia (H. ASPÖCK et al. 1991; GRUPPE & ABBT 2018).

Figure 25 demonstrates impressively that a chilling temperature of +4°C for four or eight weeks results in a high percentage of specimens developing metathetely in *M. sororcula* as well as in *Ph. notata* (although with distinct differences), whereas in *R. mediterranea* altogether only two of 158 larvae became metathetelous, one after exposure to +4°C for four weeks and one after chilling for twelve weeks.

Chilling for twenty weeks at +4°C was enough to completely prevent metathetely in all three species (ASPÖCK et al. 2018).

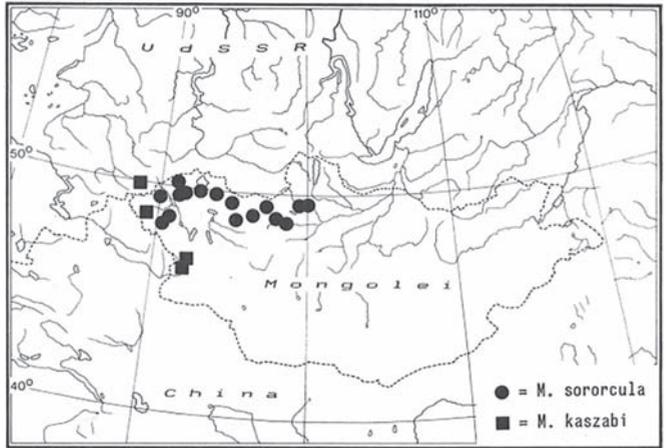


**Figure 22.** Distribution of *Phaeostigma (Ph.) notata* (Fabricius, 1781). From H. ASPÖCK et al. (1991).

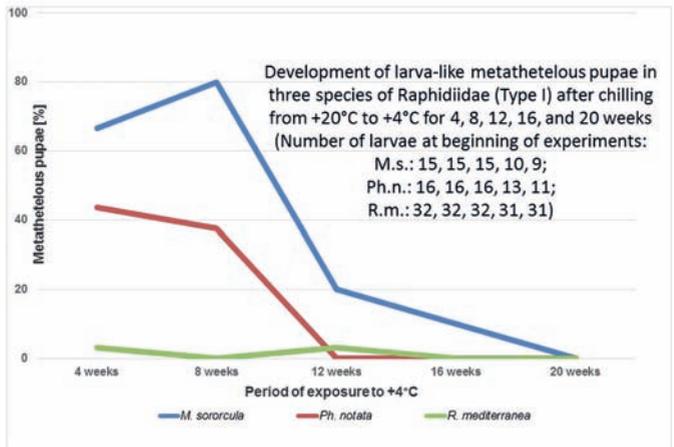
**Figure 23.** Distribution of *Raphidia (R.) mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977. From H. ASPÖCK et al. (2017).



**Figure 24.** Distribution of *Mongoloraphidia (M.) sororcula* (H. Aspöck & U. Aspöck, 1966). From H. ASPÖCK et al. (1991).



**Figure 25.** Metathetelous pupae after various periods of exposure of final stage larvae to a temperature of +4°C. Modified after ABBT (2016).



## Discussion

It is obvious that the distribution areas of the extant species of both families of the order Raphidioptera are restricted to regions having a distinct decrease of temperature in winter. In extensive rearings it was shown that last instar larvae of snakeflies of Type I (hibernation of mature larva, pupation in spring) cannot pupate successfully in spring, when chilling during hibernation is withheld (H. ASPÖCK 1991; H. ASPÖCK et al. 2018).

As assumed long ago, striking differences in different species were found with respect to correlation between duration of chilling and appearance of metathetely (ABBT 2016; H. ASPÖCK et al. 2018).

In *R. mediterranea*, a species that occurs also in coastal areas of Aegean islands where there is only a moderate decrease of temperature in winter for few weeks, chilling to +4°C even for four weeks is sufficient for a normal pupation in most individuals.

In *Ph. notata*, which occurs in large parts of extra-Mediterranean Europe, with much lower temperatures and for longer periods in winter, about 40 % of larvae became metathetelous, when kept for four or eight weeks at +4°C.

In *M. sororcula*, chilling for four, eight or even 12 weeks is too short to guarantee pupation of a sufficiently high percentage of mature larvae; however, 20 weeks is sufficient (GRUPPE & ABBT 2018). *Mongoloraphidia sororcula* inhabits an extreme continental climate in high altitudes where temperatures in winter may fall to -40°C or even lower.

We assume that significant differences and specific patterns of length and degree of chilling will be detected in future investigations that would fully demonstrate the correlation between distribution and temperatures in winter for all three types of development, which we discuss below.

Type I comprises probably more than 95 % of all *ca* 250 species of Raphidioptera. In these species the hibernating mature larva must undergo a chilling; otherwise it will not be able to pupate successfully in spring. This results in a geographical restriction of these species to regions with a marked decrease of temperature in winter.

Less than 5 % represent Type II. In this case the last overwintering stage is the pupa, which requires chilling, otherwise it will de cease. Thus, the restriction of Type II species of Raphidioptera to regions with low temperature in winter can easily be understood. We do not know whether metathetely may occur in these species, if the last hibernating instar does not receive chilling before pupation in summer or autumn. These experiments have not yet been carried out, simply because the larvae had been reared to yield imagines. These simple trials should be conducted as soon as possible.

Type III comprises a few species of the genus *Alena* and the genus *Indianoinocellia*, altogether certainly less than 5 % of all snakefly species. The Type III species are restricted to high altitudes in the southern Nearctic. The biology of all the species is either poorly known or entirely unknown. The last overwintering stage of probably all these species is a late but not necessarily the last larval instar. Adults appear mainly in summer, but

under laboratory conditions adults hatched also in (early) spring, after hibernation of the mature larva or mostly in late summer to late autumn. The biology of the species of *Alena* as well as of *Indianoinocellia* should be urgently studied.

As regards Type III species we can only conclude from the known distribution that low winter temperatures are a precondition for successful completion of the life cycle. However, this must be confirmed, since we do not know at what particular period of the life cycle chilling is necessary and whether metathetely would occur.

A considerable number of questions remain unanswered.

- We assume that most Inocelliidae species are assigned to Type I. However, so far no experimental studies have been carried out to confirm this.
- We do not know the physiological/endocrinological background that leads to metathetely. We only know that withholding chilling of the hibernating mature larva leads to metathetely. Likewise, we do not know which hormones must be expressed or suppressed at which time of the life cycle for inducing or preventing metathetely.
- Do factors other than withholding a decrease of temperature also lead to metathetely?
- What happens in the rare cases, when metathetelous pupae revert to larval behavior and pupate after another hibernation?
- So far controlled experiments to determine the necessary length of chilling have been carried out at +4°C. Can the length be shortened by exposure to lower temperatures? Which temperatures are tolerated by certain species?
- Do larvae of species with two (or more) years of development require chilling also during the first hibernation?
- Do larvae of Type II species develop metathetely and under what circumstances?
- At which period of development is chilling a precondition for completion of development in Type III species?

We now understand that in the Northern Hemisphere snakeflies only occur in those parts and at those altitudes where there is a sufficient decrease of temperature during winter. However, such conditions would be fulfilled in large parts of the Southern Hemisphere; thus the question arises why snakeflies are entirely lacking in the Southern Hemisphere. According to the fossil record, families within the Raphidioptera other than Raphidiidae or Inocelliidae occurred during the Mesozoic south of the equator. Presumably, these went extinct following the K/T-impact. Was it the lack of sufficiently low temperature in winter in the south of the Northern Hemisphere, which prevented the survivors in the Northern Hemisphere, *i.e.*, Raphidiidae and Inocelliidae, from migrating to and re-colonizing the Southern Hemisphere? Some of these questions may be answered, at least partly, when the hormonal dynamics in the course of the post-embryonic development of snakeflies will be determined. These studies have been recently initiated and results should be expected in the near future.

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# Chemical ecology of Chrysopidae: prospects for synthetic attractants

Sándor Koczor<sup>1</sup>, Ferenc Szentkirályi & Miklós Tóth

Plant Protection Institute, CAR, HAS, Budapest, Hungary

<sup>1</sup> Corresponding author: koczor.sandor@agrar.mta.hu

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**Abstract.** Acquisition or exchange of information by means of chemical substances is a very ancestral form of interaction between an individual and its environment. Several organisms use chemical stimuli for orientation to food sources, partners or to avoid potential hazards. Chemical ecology deals with the chemical mechanisms included in these intra- and interspecific interactions, and the compounds involved are called semiochemicals. As predatory organisms, green lacewings (Chrysopidae) are important agents of biological control, some species being available commercially as well. However, commercial species are generally from international sources and may contain non-native species, therefore it seems more desirable to apply native species in biological control of pests. A promising way to attract native lacewings present in the environment to a given site could be achieved by the use of semiochemicals. Several reports are available on the response of green lacewing adults to olfactory stimuli, such as plant-, aphid- or lacewing-derived semiochemicals. In some cases, the behavioural effects of these stimuli are very remarkable, including influence on oviposition site choice of females. Our aim is to provide a brief overview of the chemical ecology of Chrysopidae, including prospects for both research and practical applications.

**Further key words.** Green lacewings, semiochemicals, aphid sex pheromones, (*Z*)-4-tridecene, ternary floral bait

## Introduction

Chemical ecology is an interdisciplinary field of science at the interface of chemistry and biology and it deals with the chemical mechanisms involved in intra- and interspecific interactions between living organisms (BERGSTRÖM 2007). The chemicals involved in these interactions are termed semiochemicals. The semiochemicals involved in intraspecific interactions are termed pheromones, and those involved in interspecific interactions are termed allelochemicals (NORDLUND & LEWIS 1976). Recently ALDRICH & ZHANG (2016) published a comprehensive review on the chemical ecology of Neuroptera.

Green lacewings (Neuroptera: Chrysopidae) comprise a species-rich family with more than 1 200 taxa described worldwide (BROOKS & BARNARD 1990). Green lacewing larvae are predators of many soft-bodied insect pests, with a preference for Sternorrhyncha, especially aphids (CANARD 2001) and scale insects (MILLER et al. 2004). For this reason, some species have importance in agroecosystems (STELZL & DEVETAK

1999; PAPPAS et al. 2011). *Chrysoperla* spp. are of special importance in respect of biological control (PAPPAS et al. 2011). According to our current understanding, the taxon previously referred to as '*Chrysoperla carnea*' includes a multitude of species present in different geographic regions (e.g., HENRY et al. 2001). Due to their importance as biological control agents, *Chrysoperla* spp. are also available commercially; however the taxon referred to as '*Chrysoperla carnea*' by the industry may include several species from different geographic regions, thus, use of these insects for biological control purposes may pose the risk of introducing non-native species (HENRY & WELLS 2007). As a result, the attraction of native species with semiochemicals may offer a safer perspective for biological control.

In the present paper, our aim is to provide a brief overview of the chemical ecology of Chrysopidae with special reference to stimuli eliciting behavioural responses from adult green lacewings. Furthermore, we also intend to give emphasis to potential applications in respect of both research and agricultural practice.

### Semiochemicals for Chrysopidae

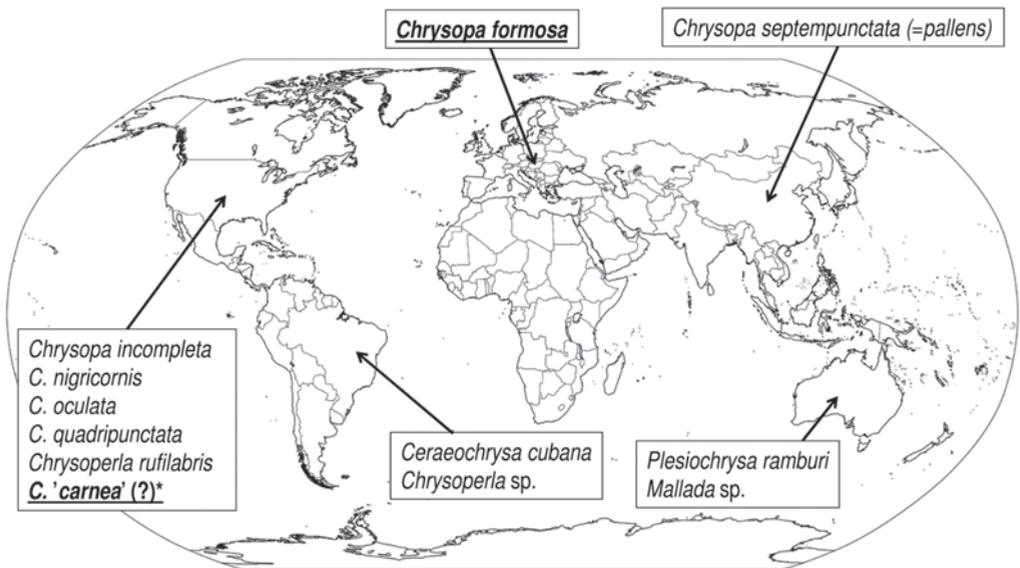
#### Compounds produced by green lacewings

Sex pheromones have not been identified from Chrysopidae (ALDRICH & ZHANG 2016) to date. However, (1*R*,2*S*,5*R*,8*R*)-iridodial was identified from abdominal extracts of males of a Nearctic green lacewing species, *Chrysopa oculata* Say, 1839, as a conspecific male attractant (ZHANG et al. 2004). This compound has also been reported from thoracic extracts of male *Chrysopa nigricornis* Burmeister, 1839 (ZHANG et al. 2006a), and it was found to be attractive to other green lacewing species as well (ALDRICH & ZHANG 2016). Interestingly, ALDRICH et al. (2016) reported that this compound was not produced by laboratory-reared *C. oculata*, only by field-collected individuals. To date the behavioural relevance of attraction of males to this male-produced compound is not, however, known. CHAUHAN et al. (2007) hypothesized the phenomenon to be related to lekking behavior. In their field experiment, they found very few females in the vicinity of the odour source, however, more female *C. oculata* were found at a few metres' distance from the baits in a field experiment, and the authors suggested that males aggregate and form leks, and find females in the vicinity by vibratory signals (CHAUHAN et al. 2007).

Based on laboratory experiments, reduced oviposition of females of *Chrysopa comata* Kis & Újhelyi, 1965, *C. oculata*, *Chrysopa perla* (Linnaeus, 1758), and '*C. carnea* (Stephens)' was recorded on surfaces where hatched first instar larvae had been present (RŮŽIČKA 1994, 1996, 1998, 2010). Unfortunately, however, potential semiochemicals were not identified. Also, later studies conducted with *Chrysoperla* species did not confirm the effect of previously laid eggs on oviposition of females (FRÉCHETTE et al. 2006; KOCZOR et al. 2017).

*Chrysopa* species are characteristic for the bad odour they emit when disturbed. In laboratory experiments, BLUM et al. (1973) found that the odorous secretion from the prothoracic glands had a defensive function against potential vertebrate and inverte-

brate predators. BLUM et al. (1973) suggested skatole, the strong-smelling component of the secretion, to be responsible for the defensive function. The compounds of the prothoracic gland of some selected green lacewing species from different geographic regions have been reported (ALDRICH et al. 2009; ALDRICH & ZHANG 2016). ZHU et al. (2000) identified (Z)-4-tridecene from a Nearctic *Chrysoperla* species and found that the compound decreased attraction to the floral volatile compound 2-phenylethanol in a field experiment. Nevertheless, it is important to note that according to the current understanding of the taxonomy of *Chrysoperla* spp., the taxon previously referred to as '*Chrysoperla carnea*' includes a multitude of species present in different geographic regions and, thus, the taxon mentioned in North American studies as '*C. carnea*' probably refers to another species, possibly the Nearctic *Chrysoperla plorabunda* (Fitch, 1855) (DUELLI 2001; HENRY et al. 2001; HENRY & WELLS 2007). (Z)-4-tridecene has also been identified from adults of *Chrysopa formosa* Brauer, 1850, and in field experiments it significantly decreased attraction of *C. formosa* and *C. carnea* complex to otherwise highly attractive stimuli (KOCZOR et al. 2018), which, considering its potential importance in defence, might suggest an alarm function for both taxa. Since this compound has been identified from several green lacewing species (Fig. 1), it may have a similar role in other species as well, serving as a common alarm signal in different green lacewing taxa.



**Figure 1.** Green lacewing species from which (Z)-4-tridecene has been identified so far. Species for which behavioural responses to the compound have been tested are bold and underlined. Based on: ALDRICH & ZHANG (2016) and KOCZOR et al. (2018). \*In North American studies, the taxon mentioned as '*C. carnea*' probably refers to another species, possibly the Nearctic *C. plorabunda* (Fitch, 1855) (DUELLI 2001; HENRY et al. 2001; HENRY & WELLS 2007).

### Aphid sex pheromones

Sex pheromones of many aphid species consist of enantiomers of nepetalactol and nepetalactone (PICKETT et al. 2013). Attraction of some green lacewing species to aphid sex pheromones have been reported including *Chrysopa cognata* McLachlan, 1867 (= *Chrysopa pallens* Rambur, 1838, according to ASPÖCK et al. 2001) (BOO et al. 1998, 1999, 2003; HOOPER et al. 2002), *Chrysopa formosa* Brauer, 1850 (HOOPER et al. 2002; KOCZOR et al. 2010, 2015a), *C. nigricornis* (ZHANG et al. 2006a), *C. oculata* (ZHANG et al. 2004; ZHU et al. 2005), *C. pallens* (KOCZOR et al. 2010), *Chrysopa septempunctata* Wesmael, 1841 (= *C. pallens* according to ASPÖCK et al. 2001) (ZHANG et al. 2006b), *Nineta vittata* (Wesmael, 1841) (HOOPER et al. 2002) and *Peyerimhoffina gracilis* (Schneider, 1851) (HOOPER et al. 2002; WEIHRAUCH 2005). Interestingly, these compounds are not produced by asexual morphs of aphids (FERNÁNDEZ-GRANDON et al. 2013) that are present in the season when green lacewings are active. Thus, the ecological relevance of this attraction is unclear; it is interesting, however, that the compounds attracted males almost exclusively (e.g., HOOPER et al. 2002). This male-biased attraction is similar to that found for iridodial and it was suggested that isomers of iridodial are unavoidable impurities in synthetic nepetalactol (CHAUHAN et al. 2004; ZHANG et al. 2004), which could explain the phenomenon. However, no trace of iridodial was found in synthetic nepetalactol samples used for later field experiments, thus the attraction is most probably due to the aphid sex pheromone compounds themselves (KOCZOR et al. 2010).

Interestingly the aphid sex pheromone compounds were not attractive to *Chrysoperla carnea* species complex; moreover, both nepetalactol and nepetalactone decreased attraction of these lacewings to an otherwise highly attractive ternary floral bait (KOCZOR et al. 2010, 2015a).

### Plant-derived compounds

Adults of most green lacewing species are not predatory, feeding instead on pollen, nectar or honeydew (CANARD 2001), and, although predatory, *Chrysopa* adults may probably also use these food sources occasionally (BOZSIK 1992). In respect of biological control, *Chrysoperla* spp. are of special importance (PAPPAS et al. 2011) and several studies have focused on attraction in these lacewings for that reason. Nevertheless, adults of *Chrysoperla* spp. are not predatory, but feed on nectar, pollen and honeydew (CANARD 2001). In accordance with these feeding habits, some floral volatiles have been suggested as attractants, including caryophyllene (FLINT et al. 1979), 2-phenylethanol (ZHU et al. 1999) and phenylacetaldehyde (TÓTH et al. 2006).

More recently, a ternary floral bait was developed with the combination of phenylacetaldehyde, methyl-salicylate and acetic acid (TÓTH et al. 2009). The bait was found to be a powerful attractant to adults of *Chrysoperla carnea* species complex, including *Chrysoperla carnea* s.str. (Stephens, 1836), *C. lucasina* (Lacroix, 1912) and *C. pallida* Henry, Brooks, Duelli & Johnson, 2002 (TÓTH et al. 2009). Furthermore, the ternary combination was also found to be attractive to *Chrysoperla sinica* Tjeder, 1968 (DENG et al. 2013).

The bait attracted both sexes in field experiments; furthermore, females oviposited in the vicinity of the baits (TÓTH et al. 2009; JAASTAD et al. 2010; KOCZOR et al. 2015b). In another field experiment, more green lacewings chose overwintering chambers baited with the ternary floral bait over unbaited ones (KOCZOR et al. 2015b). The ratio of the species within the *C. carnea* complex (*C. carnea* s.str., *C. lucasina*, *C. pallida*) was not substantially different between baited and unbaited overwintering chambers, suggesting a similar attraction to the ternary floral bait of these species (KOCZOR et al. 2015b).

Green lacewings have been reported to lay their eggs preferably on protruding parts of plants, including hairy and spiny surfaces (SZENTKIRÁLYI 2001). When different artificial surfaces were compared in combination with the ternary floral bait, lacewings preferred spiny surfaces over smooth ones. In this way, based on the combination of appropriate surface characteristics and chemical stimuli, oviposition of *C. carnea* complex lacewings can be concentrated in a relatively small area (KOCZOR et al. 2017).

### Perspectives of semiochemicals

Insect semiochemicals are widely used in agricultural practice for many different purposes, including attraction of beneficial insects (PICKETT et al. 2012). Green lacewings and especially *Chrysoperla* spp. are important agents of biological control in agroecosystems (PAPPAS et al. 2011). Since only larvae of *Chrysoperla* spp. are predatory (CANARD 2001), oviposition is of crucial importance. The ternary floral bait (TÓTH et al. 2009) may provide prospects for biological control by offering means to manipulate oviposition site choice of females, concentrating oviposition in a relatively small area (KOCZOR et al. 2015b, 2017), leaving hatching larvae to thereby also hunt for prey in the vicinity. The oviposition activity can be more pronounced with the combination of olfactory stimuli and appropriate surface characteristics (KOCZOR et al. 2017). Furthermore, if females oviposit on a portable substrate, eggs can be moved to greenhouses as well.

Nevertheless, since adults of *Chrysoperla* spp. are not predatory (CANARD 2001), attraction of green lacewings whose adults are predatory (e.g., *Chrysopa* spp.) could be a promising approach as well. However, although there are powerful attractants for male *Chrysopa* (e.g., HOOPER et al. 2002; ALDRICH & ZHANG 2016), no such attractants for females are available to date.

Beside their potential application for biological control purposes, attractive semiochemicals can also be used for detection, or to study seasonal dynamics of the given species. For instance, attractant-baited traps may be used to evaluate the impact of an agricultural management practice on the population of a given beneficial insect species. With the effect of the ternary floral bait (TÓTH et al. 2009) on oviposition site choice, monitoring of the seasonal dynamics of oviposition can also be done; furthermore, it may provide more precise estimates on future abundance and activity of predatory larvae than monitoring of adults. Moreover, applying this method in the case of beneficial insects means their monitoring can be performed in a non-destructive way, compared to catching adults in traps.

Beside pheromones, plant volatiles gain more and more importance in agricultural practice; for some pests pheromones are unknown, however, plant volatile-based baits provide means for monitoring (e.g., VUTS et al. 2010). Moreover, in some other species, even if sex pheromone baits are available, they do not offer the means for monitoring in a crop managed by mating disruption technique (e.g., HÁRI et al. 2011). It should be noted that plant volatiles may, however, be attractive to beneficial insects as well; thus monitoring of pests with these semiochemicals may lead to increased mortality of non-target species, including beneficial insects. In these cases, therefore, semiochemicals with repellent, or repellent-like effect for the beneficial insects may provide the prospect to decrease mortality of these, in case the compounds do not affect attraction of the target species considerably. For green lacewings, (*Z*)-4-tridecene may offer similar prospects, as addition of this compound to phenylacetaldehyde decreased lacewing catches to zero while, at the same time, the combination still attracted considerable numbers of noctuid moths (KOCZOR et al. 2018).

In summary, green lacewings appear to be a special taxonomic group in respect of chemical ecology with unusual mechanisms which are not completely understood currently. Furthermore, compared to the total number of species in the family, data on only a few species are available, so potentially there may be a large number of novel, interesting phenomena to discover. At the same time, the studies on *Chrysoperla* spp. have shown that semiochemicals may have remarkable effects on behaviour, which may also provide prospects for agricultural practice as well.

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# The dimensions of the dust of dustywings (Neuroptera: Coniopterygidae)

Axel Gruppe<sup>1</sup>, Sarah Bastyans, Felix Fenzl, Anja Domes & Michael Gebhardt

Chair for Zoology – Entomology group, Technical University Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>1</sup> Corresponding author: [gruppe@wzw.tum.de](mailto:gruppe@wzw.tum.de)

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**Abstract.** The dusty cover of adult Coniopterygidae was hitherto only rarely studied. According to three published studies, the ‘dust’ consists of wheel-like micro-particles secreted by wax-glands on the bodies of the insects. Chemically, it is composed mainly of lipids with a 24-carbon fatty acid as its main component. To elucidate the actual dimensions of the micro-particles of Coniopterygidae, we have defined six parameters to quantitatively describe shape and size of the particles, which were measured on SEM micrographs. We present data on the micro-particles found on the external surfaces of *Coniopteryx pygmaea* Enderlein, 1906. The shape of the particles conforms to current knowledge; however we have discovered two different particle types in *Aleuropteryx juniperi*. Most dimensional parameters differ significantly between taxa. We conclude that there might be a phylogenetic signal in these micro-particles, in addition to a so far unknown function.

## Introduction

Apart from the waxy epicuticle, several insect taxa such as Aleurodidae, Aphididae, Psyllidae (Homoptera), Coccidae (Coccoidea) Coccinellidae (Coleoptera), Hymenoptera and Lepidoptera produce hydrocarbons covering their body or parts of it; for a review, see HOWARD & BLOMQUIST (2005). These waxes are produced in cuticular wax glands. Wax glands may be organized in plates on different parts of the body. Waxy structures of most insects are filamentary or band-shaped. Apart from waxy particles, brochosomes, spherical particles in the nm-range, may cover the surface of certain insects, e.g., Cicadellidae (TULLOCH & SHAPIRO 1954). However, these structures do not consist of hydrocarbons but of proteins (SMITH & LITTAU 1960).

Among the wax producing insects is also the family Coniopterygidae (Neuropterida: Neuroptera) (MEINANDER 1972). All known species of the subfamilies Aleuropteryginae and Coniopteryginae are covered by waxy particles. Brucheiserinae, however, which is represented by very few species, lacks these particles. In contrast to most other taxa, the wax of Coniopterygidae is organized in particles with a shape resembling a car wheel-rim with fluted edges (NAVONE 1987; NELSON et al. 2003; ZIMMERMANN et al. 2009). The first documentation of dustywing particles was published by ENDERLEIN (1906), including a drawing showing ring-like particles. NAVONE (1987) shows SEM images of *Coniopteryx haemastica* MacLachlan, 1868, and *Conwentzia psociformis* (Curtis, 1834),

also discussing their functional aspects. NELSON et al. (2003) describe the chemical composition of the waxes produced by *Semidalis flinti* Meinander, 1972, the process of production of the particles, and give information on their dimensions. ZIMMERMANN et al. (2009) describe the distribution and shape of wax glands in *Aleuropteryx juniperi* Ohm, 1968, and *Semidalis aleyrodiformis* (Stephens, 1836). They also discuss the function of the particles produced by these glands. MEINANDER (1972) suspects that the particles were secreted throughout the greater part of the life span of the adult; from observation of individuals with very sparse particle cover in the field, however, the production seems to be limited to the first part of adult life.

To our knowledge, only NAVONE (1987), NELSON et al. (2003) and ZIMMERMANN et al. (2009) have published detailed studies of the particles forming the 'dust' of dusty-wings (Coniopterygidae). These papers also include images of the secreting glands and indicate that from one gland two particles are secreted simultaneously, due to the presence of a dividing structure in the centre of the gland openings. The hypodermal wax glands are mostly located in distinct patches on the abdomen, as well as on the head and wing bases (ENDERLEIN 1906; MEINANDER 1972; NAVONE 1987; NELSON et al. 2003). From these locations the particles are spread over the entire surface of the insect using their hind legs. The eyes, however, are not covered by waxy particles. MEINANDER (1972) mentions that the number and distribution of glands on the bodies of the insects seems to be of systematic value.

The present study quantitatively describes the dimensions of the wax particles in detail. In particular, our focus was on the variability of the particles within individuals and between individuals of a single species. Concluding with MEINANDER (1972) that variation within a species should be low, thus, the waxy particles could be of systematic value.

### Material and methods

Our target species were *Coniopteryx pygmaea* (Enderlein, 1906), which is the most common coniopterygid species in Central European coniferous forests, and the Mediterranean *Aleuropteryx juniperi* Ohm, 1968. Specimens of *C. pygmaea* were collected between 2016 and 2018 by sweep netting Norway spruce *Picea abies* in the surroundings of Freising, Upper Bavaria, Germany (48.41°N, 11.71°E, 490 m a.s.l.) and pine *Pinus sylvestris* near Vieste, Apulia, Italy (41.89°N, 16.45°E, 50 m a.s.l.). *Aleuropteryx juniperi* was collected near Le Lavandou in the departement Var, France, from a cypress (*Cupressus* sp.) hedge (43.11°N, 6.35°E, 40 m a.s.l.). Specimens were killed with KCN and stored air dried in small vials. In the lab, the tip of the abdomen of each dried individual was dissected for species determination. Abdomina were cleared in KOH-solution at ambient temperature, rinsed with distilled water and transferred to glycerin for determination, following the recommendation of ASPÖCK (1971). Measurements of particles were taken exclusively from male specimens.

After species determination, dried specimens or dissected parts of them, *i.e.*, legs or wings, were mounted on double-sided sticky carbon tape attached to standard aluminium stubs for scanning electron microscope (SEM) inspection (Jeol JSM-IT 100LV). The

uncoated specimens were examined at acceleration voltages of 3–8 kV. The total wing (30× magnification), in addition to 5 to 20 spots per specimen from the wing, leg or abdomen were imaged (5000×).

From the images, we selected particles to take measurements of different parameters of the same particle (ImageJ, Rasband 1997–2018). The particles were quantitatively characterized by six parameters of their dimensions: length (L), inner length (iL), curl length (cL), width (W), base width (bW) and inner width (iW) (Fig. 1). Variation of parameters within *C. pygmaea* was compared at two different levels:

i) variation within one individual: from five individuals, we measured six parameters of five particles each from the abdomen, leg and wing. Data were tested for significant differences using the Kruskal-Wallis rank sum test (R version 3.2.2, The R Core Team 2015).

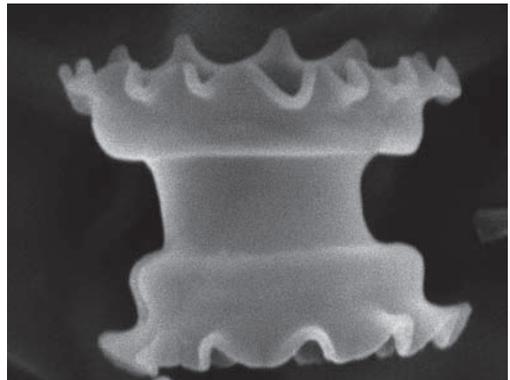
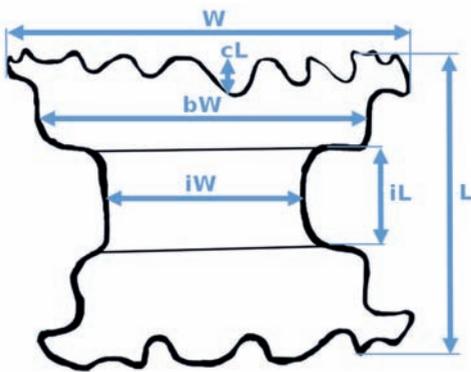
ii) variation between individuals: from ten individuals we measured the wing length and six parameters of ten particles on the right wing and tested them for significance using the same test. Additionally, we calculated the Spearman rank correlation between fore wing length and the different parameters to check the influence of body size on the parameters. Finally, we compared the dimension of length and width of the particles found on *C. pygmaea* and *A. juniperi* measuring five particles on the right wing of each of the five individuals.

## Results

The wax particles produced by *Coniopteryx pygmaea* exhibited a shape resembling an automobile wheel-rim with fluted edges (Fig. 2).

Within one species, we did not find significant differences between the dimension of the particles on different parts of the insect, *i.e.*, abdomen, leg or fore wing. The dimensions of the particles and their variation are given in Figure 3.

In contrast to the lack of a significant differences between different parts of the individuals, the dimensions of parameters between individuals were shown not to be identi-



**Figure 1.** Definition of six parameters used for the characterization of wax particles produced by Coniopterygidae.

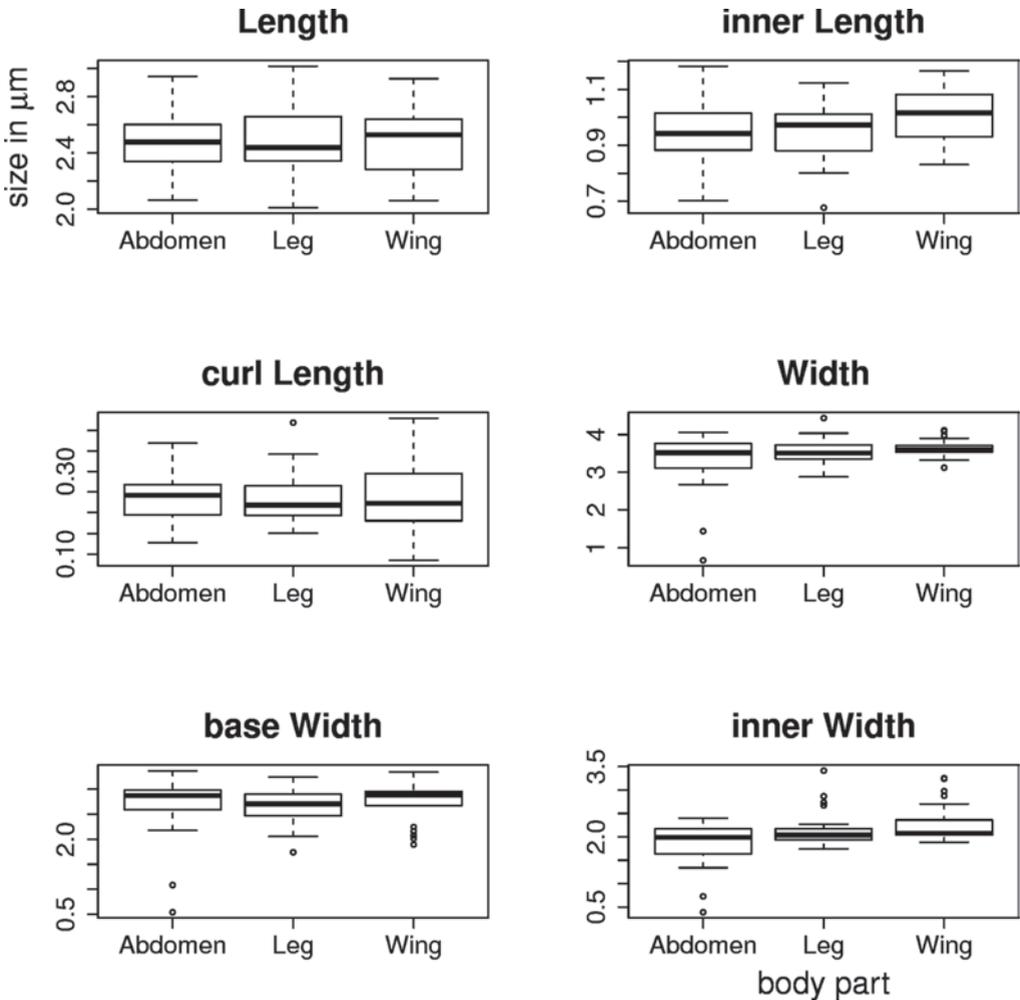
**Figure 2.** Wax particle produced by *Coniopteryx pygmaea*. Magnification *ca* 8000×.

cal ( $n = 10$ ; Table 1). Significant differences appeared between individuals for all parameters except width. However, none of our parameters correlated significantly with wing length as a parameter for the size of individuals (Spearman's rank correlation; Table 1).

Surprisingly, we found two types of particles differing in 'length' and 'width' in *Aleuropteryx juniperi*, a smaller one as compared to *C. pygmaea* and a larger one. The latter was roughly twice the size of the smaller particle with no overlap (Fig. 4).

### Discussion

The dust of dustywings is a well-known phenomenon in Neuropterology. This is because of the change in appearance of the same insect from a whitish colour in life to

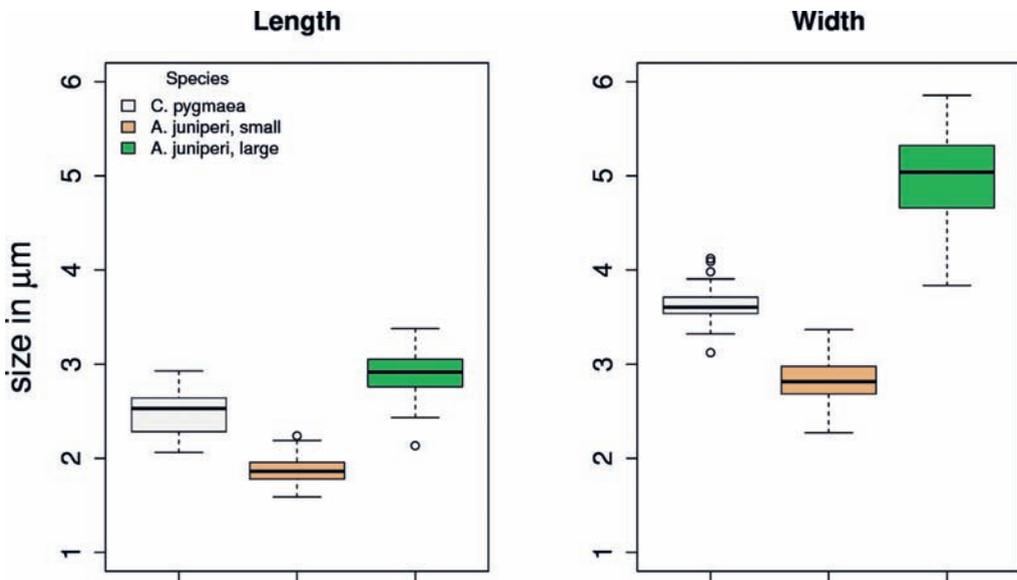


**Figure 3.** Dimensions of six parameters used for the characterization of wax particles produced by Coniopterygidae, measured on particles of *Coniopteryx pygmaea* ( $n = 25$ ).

**Table 1.** Comparison of the six parameters of particles on the fore wing produced by ten individuals of *Coniopteryx pygmaea* (n = 10).

Parameter	length	inner length	curl length	width	base width	inner width
Kruskal-Wallis-Test, significance	< 0.001	0.006	< 0.001	0.088	0.006	0.002
Spearman's rank correlation, particle ~ wing length	0.250	0.235	-0.167	0.021	0.074	0.096

hyaline when preserved in alcohol. Even in the early literature the dust is mentioned. The wings were described as »whiten« by Müller in 1764 and as »floury dusted« by von Block in 1799 (cf. ASPÖCK & ASPÖCK 2009). ENDERLEIN (1906) illustrated and described the particles for the first time in detail as small rings with a dimension of  $3 \times 4 \mu\text{m}$ . In his drawings (700 $\times$  magnification) the shape of a car wheel-rim is shown. He also indicated their waxy composition when describing the loss of particles in alcohol. In his monograph, MEINANDER (1972) focused on the glands that secrete the wax and their distribution on the bodies of the insects. SEM micrographs of the particles, showing all details, were already published by NAVONE (1987). The chemical composition of the particles is described by NELSON et al. (2003), who also present SEM micrographs in higher magnification. More recently, ZIMMERMANN et al. (2009) document the distribution of wax glands by SEM. NAVONE (1987), NELSON et al. (2003) as well as ZIMMERMANN et al. (2009) mention species names in their studies, viz. *Coniopteryx haemastica*

**Figure 4.** Size of the parameters 'length' and 'width' in particles of *Coniopteryx pygmaea* and of *Aleyropteryx juniperi*. The latter species produces two types of particles of different dimensions.

MacLachlan, 1868, *Conwentzia psociformis* (Curtis, 1834), and *Semidalis flinti* Meinander, 1972, *Aleuropteryx juniperi* Ohm, 1968, and *Semidalis aleyrodiformis* (Stephens, 1836), respectively. To our knowledge, no other publication does exist dealing with the particles or their dimensions.

The particles covering the surface of members of the family Coniopterygidae have therefore been described, but their dimensions have not been well studied. We confirm the general shape of the particles produced by *Coniopteryx pygmaea* and *Aleuropteryx juniperi* as described by NAVONE (1987), NELSON et al. (2003) and ZIMMERMANN et al. (2009). ENDERLEIN (1906), in order to get a better view, removed the particles by passing the wing between a microscope slide and coverslip, therefore the convoluted form of the particles reported by him might represent an artefact due to handling.

Based on the uniform form of the particles, we have defined six parameters to describe them quantitatively. The parameters 'length', 'inner length' and probably 'curl length' are determined by the geometry of the gland opening, whereas 'width', 'base width' and 'inner width' might depend on environmental conditions, such as humidity or temperature. According to NELSON et al. (2003), a ribbon of wax is secreted from the opening of the glands, which self-organizes immediately to a ring. After completing the ring, the particle breaks off. The six parameters of particles from different body parts of *C. pygmaea* did not show significant differences, although they exhibited high variability. The particles produced by the glands on the different parts of the insect body are formed under the same environmental conditions and seem to be spread uniformly over the whole body using the hind legs. In contrast, we found significant differences between individuals in all parameters except width. There was very low correlation ( $R$  between 0.02 and 0.25) of the dimensions of the particle with the size of the specimen as measured by wing length. Thus, the individual itself, not its size, seems to be an important source for this variability.

In a second species, *Aleuropteryx juniperi*, we obtained different results in two aspects. This species produces two types of particles differing significantly in length and width with no overlap. This supports the hypothesis of MEINANDER (1972), who expected a phylogenetic signal associated with the waxy particles. Species belonging to Coniopteryginae, *C. pygmaea* in this study as well as *Semidalis flinti* in NELSON et al. (2003) and *Coniopteryx haematica* and *Conwentzia psociformis* in NAVONE (1987), seem to produce only one type of particle, although they might exhibit an individual, significant variation within the species. In contrast, Aleuropteryginae, *Aleuropteryx juniperi* in this study, produce two types of particle differing in both, length and width. The origin of these different particles, *i.e.*, the distribution of the large or the small particle-producing glands is hitherto unknown. ZIMMERMANN et al. (2009) indicate differences in the shape of the wax gland openings between *A. juniperi* and *S. aleyrodiformis*; however, these differences are not described in detail. However, any phylogenetic significance would need to be confirmed through studying the dimensions of the particles of more species of Aleuropteryginae or Coniopteryginae, respectively, and by comparing the particles and distribution of the glands between the taxa.

The production and secretion of hydrocarbons seems to be an evolutionary innovation of Coniopterygidae and is likely to be a costly physiological process. Thus, hydrocarbon production should be under selective control. However, the function of the waxy particles in Coniopterygidae is so far unknown. For other wax secreting insects, it is known or assumed that particles composed of hydrophobic substances act as a water-repellent or as evaporation regulation (e.g., WIGGLESWORTH 1945). Similarly, waxy particles might protect against contamination by honeydew, produced, for example, by aphids (SMITH 1999). Other hypotheses suggest a function in camouflaging against predators or parasitoids (e.g., MOSS et al. 2006; review in HOWARD & BLOMQUIST 2005).

In conclusion, the ecological significance of the waxy dust of Coniopterygidae still remains unknown. Thus, the particles on the body surface of Coniopterygidae opens up a broad field for future research.

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## In search of *Myrmeleon bore*: Bavaria's rarest neuropteran?

Florian Weihrauch

Osmylus Scientific Publishers, Postfach 1212, 85280 Wolnzach, Germany; mail@osmylus.com

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**Abstract.** The district of Kelheim in Lower Bavaria harbours an extremely isolated population of *Myrmeleon bore*, representing the only known Bavarian population of this species and, in addition, the only one north of the Alpine arc up to the Upper Rhine Valley in Rhineland-Palatinate. In order to elucidate the actual status of this occurrence of *M. bore*, which is of nationwide significance, in 2012 the regional situation of funnel-building Myrmeleontidae was monitored. In the course of the study, a method was developed to discriminate the three Myrmeleontidae species occurring in the area, *Euroleon nostras*, *Myrmeleon bore* and *M. formicarius*, as second and third instars in the field. In total, more than 5 000 antlion funnels were recorded and assigned to one of the three species by determining 5–10 % of unearthed larvae per funnel field. Using only the maximum number of funnels found during each monitoring, a total of 776 individuals of *E. nostras*, 323 of *M. bore*, and 2 886 of *M. formicarius* were identified. In a conservative extrapolation, annual larval populations of at least 2 000 *E. nostras*, 1 000 *M. bore* and 10 000 *M. formicarius* are to be expected in the area. The occurrence of *M. bore* was confirmed with certainty only for a partial area near Offenstetten, where it was found on a small scale in five subareas. This underscores the urgent need to protect *M. bore* in the region, because the only Bavarian population could become extinct in a single catastrophe. Targeted searches for the species in other dune regions of Bavaria, especially in Franconia, have so far not yielded any records of *M. bore*.

### Introduction

In the German federal state of Bavaria records of four species of Myrmeleontidae are known. Of the more widespread and more common species, *Myrmeleon formicarius* Linnaeus, 1767, is classified in the Red List (PRÖSE & GRUPPE 2003) as 'Near threatened' and *Euroleon nostras* (Geoffroy in Fourcroy, 1785) as 'Endangered'. *Distoleon tetragrammicus* (Fabricius, 1798), a rare species that is not easy to detect, has been found twice in Bavaria, once in a sandy area ('Alzenauer Sande') in the 'Kahlgrund' region of Lower Franconia and once in the valley of River Danube near Kelheimwinzer (OCHSE & GRUPPE 2014). Finally, *Myrmeleon bore* (Tjeder, 1941), is classified as 'Critically endangered', with only one known local occurrence in the district of Kelheim in Lower Bavaria. In order to elucidate the actual status of this occurrence of *M. bore*, which is of nationwide significance, monitoring of the regional situation of funnel-building Myrmeleontidae was undertaken in 2012.

### Situation of *Myrmeleon bore* in Bavaria and adjacent regions

Prior to this study, there existed only five published records (two of them in 'grey' literature) concerning this isolated population of *M. bore* in Bavaria. The very first was based

on larval records dating from early May 1960 »in Lower Bavaria, between Siegenburg and Abensberg« (OHM 1965). The second was based on the capture of two imagines at light on 24.vii.1992, »3 km east of Abensberg« (PRÖSE 1995). A further reference, referring however to the same record of 1992, can be found as record No. 210 in RÖHRICHT (1998). A targeted search for the species as part of the ecological development plan for the Nature Reserve 'Inland dunes near Offenstetten' yielded the discovery of larvae in 1996 (VORTH 1997). The most recent record by WEIHRAUCH & GRUPPE (2009) relates to a larva that had been collected on 21.vii.2006 in a gravel pit between Abensberg and Offenstetten on an open sandy area; after rearing the larva for a year it turned out to actually be *M. bore*. Thus, in the two decades between 1990 and 2010, only three records of the species were made, all coming from a restricted area of ca 2 km<sup>2</sup>, viz. the forest between Abensberg and Offenstetten from gravel pits and a small inland dune area (cf. Fig. 9).

In conclusion, the district of Kelheim without doubt harbours an extremely isolated population of the »very local and rare« (GEPPE 2010) *M. bore*, which represents the only known occurrence north of the Alpine arc up to the Upper Rhine valley around Heidelberg and Mannheim. From this region there exist records from the 'Mainzer Sand' (SCHENCK 1877; OHM 1965), from near Speyer (PREUSS 1982) and from Sandhausen near Heidelberg (Scherer, Tröger in RÖHRICHT 1998). At a distance of about 250 km as the crow flies, the latter records constitute the nearest known occurrences of the species to the Bavarian population (Fig. 1). South of the main chain of the Alps, the few published localities are even more distant (Fig. 1): They refer in Switzerland to the Pfynwald in Valais (Kurth in DUELLI 2010) and to Ticino (TRÖGER & REZBANYAI-RESER 1998), in Italy to Bolzano in the South Tyrol (ASPÖCK & ASPÖCK 1969) and in Austria to River Drava in Carinthia (HÖLZEL 1964, 1973; HÖLZEL & WIESER 1999). To the East, the River Drava valley yields two more records of *M. bore* in Croatia, both taken only recently (ÁBRAHÁM 2008; DEVETAK et al. 2019; not shown in Fig. 1). Further to the South, there is only one record from the River Po Valley (NICOLI ALDINI 2007, not shown in Fig. 1), which is the southernmost known occurrence of the species in Europe. To the North-east, the closed range of *M. bore* begins in northern Thuringia (JESSAT 2000; KÖHLER & CREUTZBURG 2016) and in Saxonia, north of Dresden (Güsten in RÖHRICHT 1998, not shown in Fig. 1).

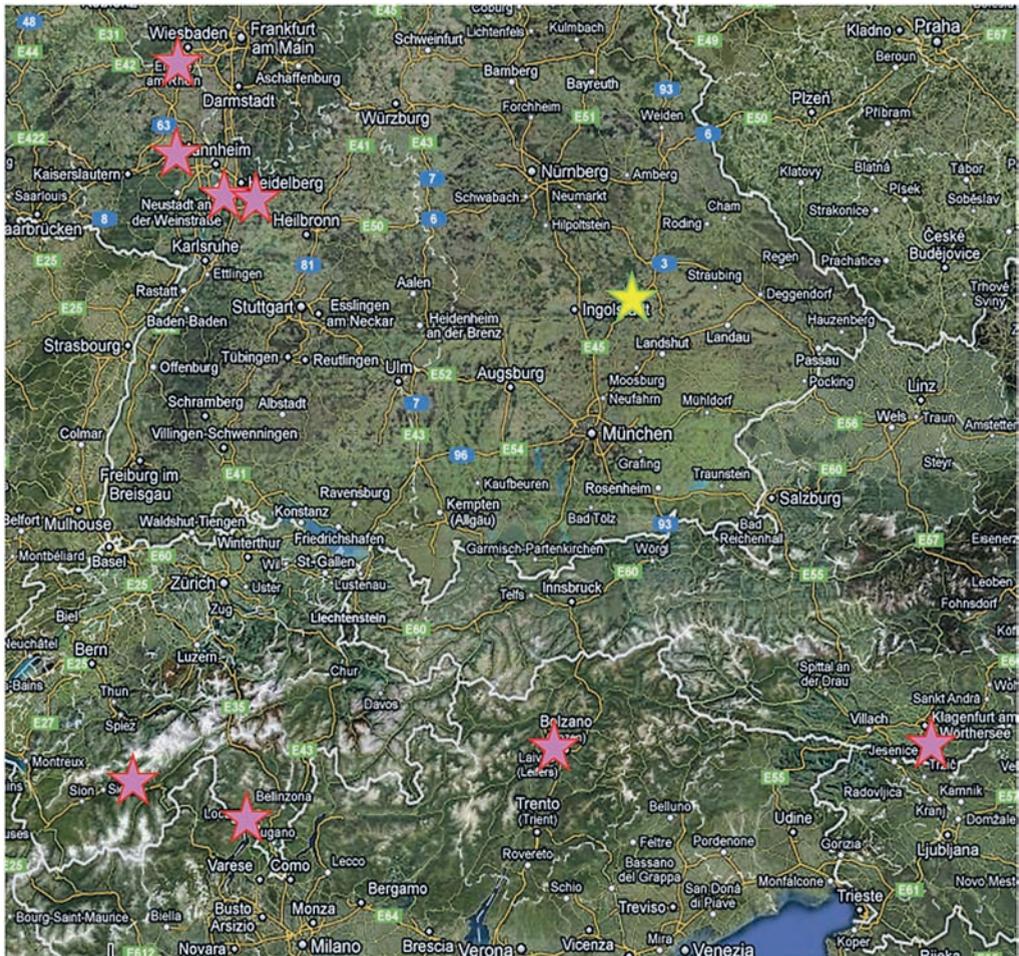
### Material and methods

Ten partial areas were targeted for monitoring in the region around Siegenburg and Abensberg in Lower Bavaria, Germany (ca 48°45'N, 11°50'E). These had been chosen based on previous monitoring of inland dunes in the region in the 1960s.

These ten partial areas were inspected during fieldwork over 18 days between 11.v.2012 and 25.x.2012, and the presence of antlion funnels was monitored. Altogether 137.5 hours were spent in the field for this study. The most intensely studied partial area (TF 3) was a core area situated between the small towns of Abensberg and Offenstetten, where 49 working hours were spent (cf. Fig. 9).

### Discrimination of larval Myrmeleontidae in the field

The crucial point of the entire monitoring was the fact that only antlions, *i.e.*, larval Myrmeleontidae, were recorded via the presence of 'active' funnels. In order to enable an accurate identification and quantitative monitoring of species, a method was developed to discriminate the three antlion species occurring in the area, *Euroleon nostras*, *Myrmeleon bore* and *M. formicarius*, as second and third instars in the field (*cf.* FRIHEDEN 1973; GEPP 2010; BADANO & PANTALEONI 2014). During the first days of monitoring, in each funnel field many antlions were unearthed, examined in detail and photographed. Typical individuals (third instars) from several fields were then taken to the laboratory and



**Figure 1.** Sites of published records of *Myrmeleon bore* in southern Germany and the adjacent Alpine region. The yellow asterisk depicts the locality of the only known population of the species in Bavaria, in the district of Kelheim. See text for the references to the depicted records. Basic picture © Google Earth™ map service.

reared to the easily identifiable adults, enabling the characteristics from the larval phenotypes to be linked to one of the three species. One actual problem was that one species-specific characteristic – the coloration of femora and coxae in *M. formicarius* – can only be seen in ventral view; however, antlions that are turned over on their back usually tend to revert back to a normal position at lightning speed, making it almost impossible to investigate the coloration of legs in live individuals. This problem was solved by placing the unearthed antlions into a plastic petri dish to enable investigation from below. Later, this method was improved by simply taking a photograph with autofocus from beneath, which additionally enabled documentation of the species identification.

### ***Myrmeleon bore***

Over the course of the monitoring, it soon turned out that *M. bore* funnels were found almost exclusively in open conditions without any shelter, especially in open Pleistocenic blow sands (Fig. 2). Such funnel fields, often accompanied by vermiform burrows of larvae in open sand, were examined with particular diligence. Unearthed larvae of *M. bore* were then identified in all three stadia without problems according to their vivid greyish-brownish markings on a yellow background, making them distinctive to *M. formicarius* that often colonised neighbouring structures (Fig. 3). This colour pattern is in accordance with images from specimens from other regions (e.g., NICOLI ALDINI 2007; BADANO & PANTALEONI 2014). In addition, *M. bore* larvae exhibit much less developed bristles than the other two species (Figs 3, 4), facilitating a quantitative monitoring.



**Figure 2.** Funnels of *Myrmeleon bore* with vermiform burrows of larvae in open early Pleistocenic blow sand. The size of the funnels suggest first instar larvae hatched in the same year. Sand pit ‘Stanglmeier’ near Abensberg, Germany. Photo: FW (20.viii.2012)

### ***Myrmeleon formicarius* and *Euroleon nostras***

The discrimination of larval *Euroleon nostras* from *Myrmeleon formicarius*, which are distinctive as imagines, was more difficult. Larvae of both species have a gloomy coloration dorsally without distinctive markings, in addition to having similar bristling (Figs 5, 6). The faint yellow marking in *E. nostras*, which can be discerned in Figure 5, is usually hidden by a dust cover. An accurate discrimination is only possible by a characteristic trait on the ventral side of the antlion: According to FRIHEDEN (1973) and BADANO & PANTALEONI (2014), larvae of *M. formicarius* have a species-specific round spot on the underside of the coxa and an elongate spot on the underside of the femur of the hind leg. (Fig. 7). These traits are lacking in *E. nostras* (Fig. 8) as well as *M. bore*, making larvae of *M. formicarius* directly identifiable via the mottling of their hind legs. In the field this was usually accomplished by the aforementioned method of placing the antlion in a petri dish and taking a photo with auto focus from beneath. All similar larvae without spotted legs were then attributed to *E. nostras*.

The attribution of monitored funnels to one of the three species was then done according to the identification of *ca* 5–10% of unearthed larvae per funnel field; this was followed by a tentative projection of the actual counts.



**Figure 3.** Larvae of *Myrmeleon bore* (right) and *M. formicarius* (left) in dorsal view, unearthed from two neighbouring funnels. Note the much stronger bristles in *M. formicarius* and the characteristic, vivid yellow-dark grey colour pattern in *M. bore*. Nature Reserve 'Binnendünen bei Offenstetten' near Abensberg, Germany. Photo: FW (25.v.2012)



**Figure 4.** Larva of *Myrmeleon bore*, dorsolateral view. Nature Reserve 'Binnendünen bei Offenstetten' near Abensberg, Germany. Photo: FW (16.vi.2012)



**Figure 5.** Larva of *Myrmeleon formicarius*, dorsal view. Forest NE of Abensberg, Germany. Photo: FW (16.vi.2012)



**Figure 6.** Larva of *Euroleon nostras*, dorsal view. Forest near Mühlhausen, NW of Siegenburg, Germany. Photo: FW (23.vi.2012)



**Figure 7.** Larva of *Myrmeleon formicarius*, ventral view. The red circles highlight two species-specific spots on the hind legs, a round spot on the underside of the coxa (left) and an elongate spot on the underside of the femur (right). Forest NE of Abensberg, Germany. Photo: FW (16.vi.2012)

## Results

Altogether, during the 2012 field monitoring, more than 5 000 funnels of antlions were recorded. Based on the maximum numbers of funnels recorded during one day on a separate partial area, 776 individuals of *E. nostras*, 323 of *M. bore* and 2 886 of *M. formicarius* were recorded (Table 1). Using these numbers for a tentative projection, taking into account that at least two thirds of larvae of a population do not occupy open funnels, the larval population sizes in the monitored area roughly reach a magnitude of at least 2 000 *E. nostras*, 1 000 *M. bore* and 10 000 *M. formicarius*.

A vital population of the target species, *Myrmeleon bore*, was recorded with certainty only in partial area PA3 (inland dunes near Offenstetten; Fig. 9), where it was found on a small-scale level in five sectors of the partial area (Fig. 10). Besides this core population, only the Nature Reserve ‘Binnendünen bei Siegenburg’ provided an indication of a second occurrence of the species. On 31.vii.2012 I found several larvae (*ca* 15) of *M. bore* in the first instar stadium, which is not 100 % identifiable. This extremely small funnel field could not be relocated during other searches later that year. The presence of a small population of *M. bore* in the vicinity of Siegenburg is therefore uncertain. In all other partial areas *M. bore* was definitely absent.



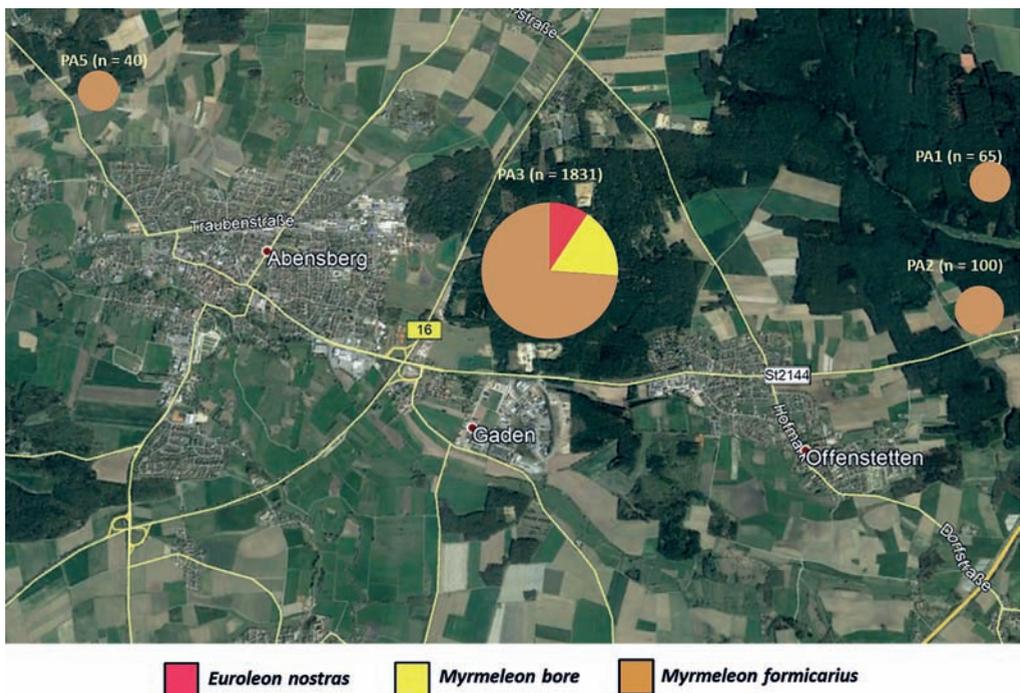
**Figure 8.** Larva of *Euroleon nostras*, ventral view. Note the absence of dark spots on the underside of coxa and femur of the hind leg. Forest near Mühlhausen, NW of Siegenburg, Germany. Photo: FW (23.vi.2012)

Among the ten partial areas that were laid out at the beginning of the project, PA3 (Nature Reserve and its surroundings between Abensberg and Offenstetten) and PA10 (Nature Reserve and its surroundings W of Siegenburg) were identified as the most important areas for antlions in the region by far (Table 1). This concerns not only the target species *M. bore* but also the two other species. Therefore, only the results from the by far most important partial area PA3 are given in detail below.

### Brief characteristics of the most important *M. bore* habitats (cf. Fig. 10)

PA3b, Nature Reserve on inland dune ('Dünen im Seeholz'), western sector (Fig. 11). This partly open slope of a near-natural inland dune is a typical habitat of *M. bore* and yielded several active funnels during each visit, with a maximum of 20 on 15.viii.2012. This very small dune was imminently threatened by succession, especially by pine seedlings.

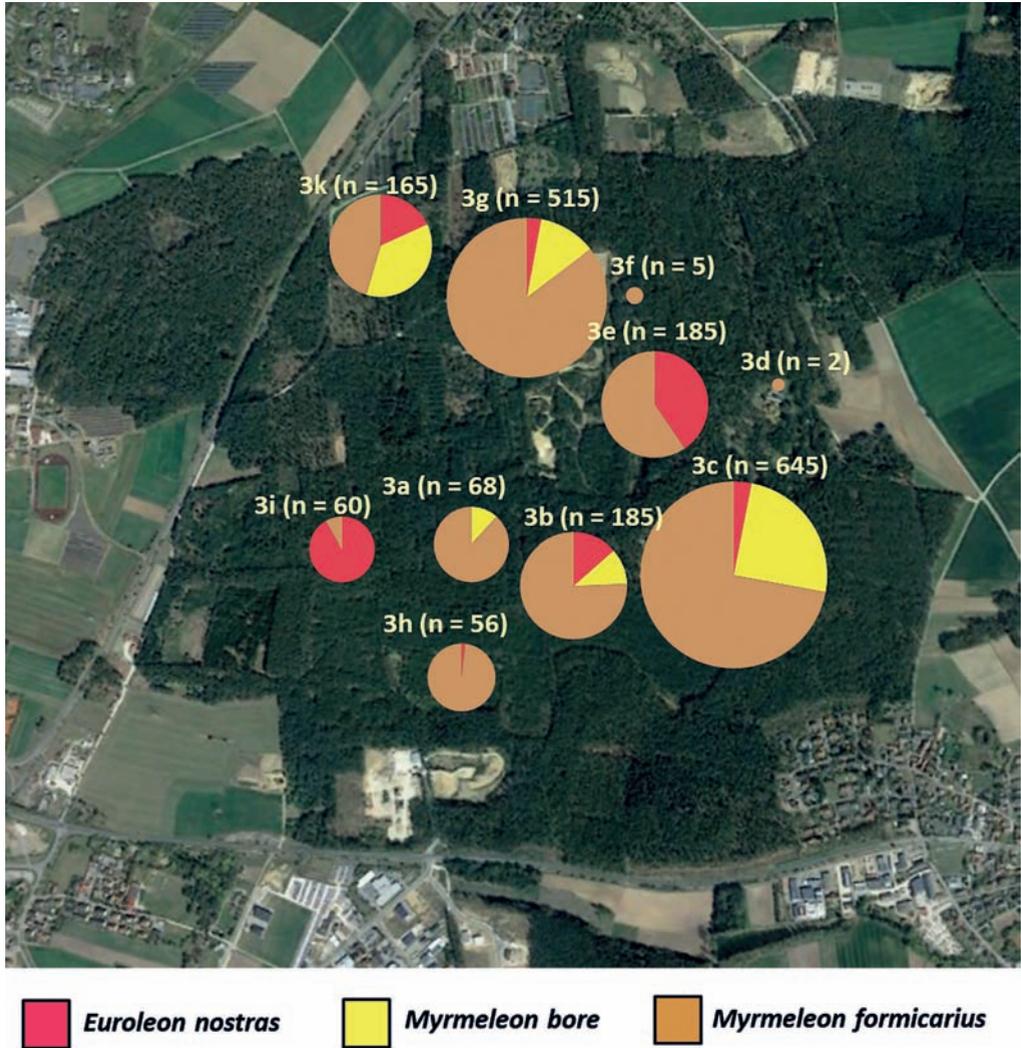
PA3c, Nature Reserve on inland dune ('Dünen im Seeholz'), eastern sector. Here the slope of an inland dune is continuously kept open because it is used as a bridleway, thus being one of the core sectors with occurrences of *M. bore*. In addition, in the course of tending strategies formerly overgrown parts of the sector had been cleared mechani-



**Figure 9.** Monitored sites in the Abensberg-Offenstetten region and environs in Lower Bavaria, Germany, with the relative occurrences of three species of Myrmeleontidae. The forested triangle in the centre (PA3) was identified as the focus of the occurrence of *Myrmeleon bore*. Basic picture © Google Earth™ map service.

cally by caterpillars and were largely re-colonised by *M. bore*, with a maximum of 150 active funnels on 15.viii.2012.

PA3g, sand pit ‚Stanglmeier‘: This former limestone and sand mining area has manifold structures and turned out to be another focus for the occurrence of *M. bore* as well as the two other antlion species. Especially a scarcement that had been left during



**Figure 10.** The Abensberg-Offenstetten region and environs in Lower Bavaria, Germany. Forested triangle between Abensberg and Offenstetten in Lower Bavaria, Germany. Detailed view of partial area PA3 with ten separately monitored sectors and the relative occurrences of the three species, *Myrmeleon bore*, *M. formicarius* and *Euroleon nostras*. Basic picture © Google Earth™ map service.

**Table 1.** Absolute records of the active funnels of three species of Myrmeleontidae in the single sectors of partial areas (PA) in the region Siegenburg-Abensberg, Lower Bavaria, Germany, during 2012. Monitored partial areas without antlion records have been omitted. *E.n.* – *Euroleon nostras*; *M.b.* – *Myrmeleon bore*; *M.f.* – *Myrmeleon formicarius*; NR – Nature Reserve.

Partial area	Sector	Date 2012	<i>E.n.</i>	<i>M.b.</i>	<i>M.f.</i>	Partial area	Sector	Date 2012	<i>E.n.</i>	<i>M.b.</i>	<i>M.f.</i>
PA1	Clearing SE	16.vi.			10	PA3	Stone quarry	15.viii.			2
PA1	Clearing SE	08.ix.			45	PA3	Central slope	15.viii.	75		110
PA1	Clearing SW	30.vi.			1	PA5	Forest edge S	15.vi.			1
PA1	Dirt track	16.vi.			6	PA5	Forest edge S	08.ix.			40
PA1	Dirt track	08.ix.			19	PA7	Forest edge SE	23.vi.	50		10
PA2	Old dune hill	30.vi.			1	PA7	Forest edge SE	25.ix.	80		20
PA3b	NR, dunes W	24.v.		15	30	PA7	Forest edge S	23.vi.	20		5
PA3b	NR, dunes W	15.vi.		7	15	PA7	Forest edge S	25.ix.	8		2
PA3b	NR, dunes W	15.viii.	25	20	140	PA7	Forest edge SW	23.vi.	30		20
PA3b	NR, dunes W	17.ix.		15	10	PA7	Forest edge SW	25.ix.	40		65
PA3c	NR, dunes E	31.v.		20	100	PA7	Sandy clearing	23.vi.	10		
PA3c	NR, dunes E	15.vi.		30	50	PA7	Sandy clearing	28.vii.	20		30
PA3c	NR, dunes E	15.viii.	20	160	465	PA7	Sandy clearing	25.ix.	10		5
PA3c	NR, dunes E	17.ix.		15	20	PA7	Barn	23.vi.	10		
PA3a	NR, W driveway	11.v.		2	5	PA9	Dirt track river Abens	31.v.			2
PA3a	NR, W driveway	15.vi.			7	PA9	Dirt track river Abens	29.viii.			3
PA3a	NR, W driveway	15.viii.			60	PA10	Sand pit N small	20.vii.	110		160
PA3a	NR, W driveway	17.ix.		8	10	PA10	Sand pit N large	20.vii.	35		
PA3g	Stanglmeier pit	16.vi.	5	60	145	PA10	Siegenburg Range	23.vii.			150
PA3g	Stanglmeier pit	23.vii.	15	30	425	PA10	NR	31.vii.	200	15	900
PA3g	Stanglmeier pit	17.ix.		60	40	PA10	NR	29.viii.	60		95
PA3f	E Stanglmeier pit	16.vi.			5	PA10	NR	08.ix.	2		35
PA3k	Gravel pit N	31.vii.	15	10	75	PA10	NR	25.ix.	20		20
PA3k	Gravel pit N	17.ix.	30	60	10	PA10	Dune small	29.viii.			30
PA3h	Gravel pit S	31.vii.	1		55	PA10	Dune large	29.viii.			80
PA3i	Gravel pit W	31.vii.	55		5	PA10	Dune large	25.ix.	40		20

sand excavation, with an area of only 300 m<sup>2</sup>, this was obviously a relic of the preferred structures once colonised by *M. bore* (Fig. 12). On this plateau the most likely primary substrate of *M. bore* was still in existence, viz. a thin (5–10 cm) layer of early Pleistocene blow sand on firm, coarse-grained sand that had been excavated here. On the plateau numerous active *M. bore* funnels were recorded on each monitoring day, with a maximum of 60 funnels on 16.vi. and 17.ix.2012.

PA3k, former mining area: This locality had already been overgrown by succession on a large scale, but in the course of tending strategies a southerly exposed, open slope of the sector had undergone scrub clearance (Fig. 13). This site was largely re-colonised by *M. bore*, with a maximum of 60 active funnels on 17.ix.2012 and was also inhabited by both *M. formicarius* and *E. nostras*.

### Discussion

Conservation and advancement of this unique population of *Myrmeleon bore* in the Kelheim district in Lower Bavaria is definitely of countrywide importance. According to the knowledge gained during this study, we must consider a – for an insect – extremely small population of the species, with not much more than approximately 1 000 larvae and an unknown number of adults in 2012.

The target species *M. bore* was definitely found only in a forested triangle between the towns of Abensberg and Offenstetten (Fig. 9). Here, a small but vivid population inhabits the few small-scale areas with open sandy soils, ideally with a layer of early Pleistocenic blow sand, and thus was able to survive here for *ca* 10 000 years. Protection and conservation of these core areas for the existence of this population is therefore of top priority. The measures that have to be taken to achieve this objective are rather simple: It is all about preserving or recreating as much as possible of the original habitat of *M. bore*, *i.e.*, open, barren, sandy areas that undergo constant dynamics and to simulate the former dynamics of sand re-deposition. The grainsize of the sand obviously plays



**Figure 11.** Open, near-natural sector of an inland dune (PA3b) as typical habitat of *Myrmeleon bore*, with a maximum of 20 registered open funnels. Nature Reserve ‘Binnendünen bei Offenstetten’ near Abensberg, Germany. Photo: FW (16.vi.2012)



**Figure 12.** Scarcement left during sand excavation. The soil cover of early Pleistocenic blow sand was preferred substrate for *Myrmeleon bore*; here a maximum of 60 active funnels were recorded. Sand pit 'Stanglmeier' (PA3g) near Abensberg, Germany. Photo: FW (23.vii.2012)



**Figure 13.** Southerly exposed, open slope, after scrub clearance. This sector was re-colonised by *Myrmeleon bore*, with a maximum of 60 recorded active funnels, and was also inhabited by *Euroleon nostras* and *M. formicarius*. W of sand pit 'Stanglmeier' (PA3k) near Abensberg, Germany. Photo: FW (31.vii.2012)

an important role, and fine loess sands, deposited in the early Pleistocene, seem to be the preferred substrate for the species' funnels. In contrast, sand areas with very coarse grains and higher clay content are no longer accepted by *M. bore* for oviposition or funnel building. Without appropriate tending strategies, all remaining inland dune relics will probably become completely overgrown in a few years due to succession caused by atmospheric deposition of nitrogen (e.g., SRU 2015), as it was already observed during the study partially in all monitored areas.

Finally, to answer the question posed in the title of this paper: There are two species of antlion competing for the title 'Bavaria's rarest neuropteran', viz. *M. bore* and *Distoleon tetragrammicus*. The latter is generally a rare species that is not easy to detect and was hitherto recorded in Bavaria in two quite distant regions, twice in Lower Franconia and once in the valley of River Danube (OCHSE & GRUPPE 2014), making other inter-jacent small populations likely. On the other hand, *M. bore* was recorded several times since May 1960 (OHM 1965) in exactly the same area, which was also subject to this study. Although several targeted searches for the species had already been performed in seemingly fitting regions, especially in the Sand Belt of Franconia (J. Schmidl pers. comm.), there have been no other recorded occurrences so far in Bavaria. Thus, the small and highly endangered population of *M. bore* in the Kelheim district must be regarded as a pre-glacial relic largely isolated from any other conspecific population. As such, I suggest that the title 'Bavaria's rarest neuropteran' is well-deserved for *Myrmeleon bore*.

### Acknowledgement

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## The genus *Nosa* Navás, 1911 (Neuroptera, Myrmeleontidae, Palparinae)

André Prost

1 rue de l'Eglise, F-39320 Loisia, France; prostloisia@gmail.com

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**Abstract.** The genus *Nosa* introduced by NAVÁS (1911) was redefined by INSOM & CARFI (1989). Fifteen taxa were eventually assigned to the genus, although as a result of synonymies, the catalogue by STANGE (2004) recognizes only two species: *Nosa tigris* (Dalman) and *Nosa tristis* (Hagen). A review of the type material, and a review of male genitalia, indicates that the taxon *tristis* Hagen and its two subspecies, *tristis niansanus* Kolbe and *tristis brevifasciatus* Stitz, do not belong to *Nosa* and should return to the group of species within African *Palpares* that have not yet been assigned to new genera. On the other hand, it is proposed to consider that the genus *Nosa* Navás consists of four valid species: *Nosa leonina* Navás, *Nosa tigris* (Dalman), *Nosa hamata* (Kolbe), and *Nosa adspersa* Navás. Synonymies are discussed. The geographical distribution of each species is given.

**Further key words.** Afrotropical region, taxonomy, revision of genus, distribution

### Introduction

NAVÁS (1911a) introduced the genus *Nosa*, to differentiate those species within the genus *Palpares* Rambur which possess two radial sectors in the fore wings. He did not propose any other discriminant character. He included at that time a single species, *Nosa leonina* from the Belgian Congo, which is consequently the type species for the genus, as he formally confirmed it in a subsequent publication (NAVÁS 1912a).

ESBEN-PETERSEN (1916) considered radial sectors to be »an inconstant artefact« and wrote, »In this species the second branch from *Rs* arises often in such a manner that there seems to be two radial sectors«, and »In the very same specimen of this species one or two wings have normal nervation, and the other wings divergent nervature«. He therefore reintegrated all specimens into the genus *Palpares*. As a result of the controversy, a number of authors, following Navás, used the name *Nosa*, whereas others considered it to be an integral part of *Palpares* of which *Nosa* was a junior synonym.

MARKL (1954) discussed in detail the question of a second radial sector in the Neuroptera. He concluded that it is a character of good taxonomic value, which permits a differentiation of species depending on the number and arrangement of bifurcations. He recognized *Nosa* as a valid genus, monospecific for *Nosa tigris* (Dalman).

INSOM & CARFI (1989) had no doubts about the generic value of *Nosa*. According to them, differences from other Palparinae include very long ectoprocts that are clearly differentiated into two sections, the proximal one rather short and bent towards the

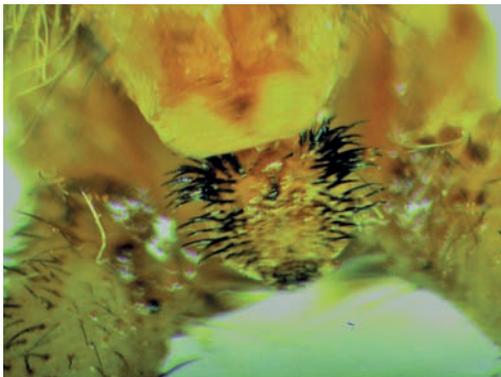
midline, and the distal one very long and of varied thickness. A dorsal process is inserted where the two sections join (Figs 4, 6). The subgenital plate is unique among the Palparinae, medially membranous to its tip, and with lamina bent downwards as seen in lateral view. Labial palps are fusiform, with a spindle-shaped terminal article, and with two very small sensory cones and a sensory pore dorsally placed at about the middle of the spindle-shaped portion; the whole palp is as short as the maxillary palp (Fig. 5). In male genitalia, the gonarcus-parameres complex is totally sclerotized, and the hypandrium internum is the largest in the subfamily, except for *Stenares* Hagen (Figs 1–3). These features justify the separation of *Nosa* from all other Palparinae. INSOM & CARFI (1989) concluded that »the taxa with a fusiform labial palp are *Nosa* from Africa, which genitalia are so peculiar as to leave no doubt as to its generic validity« and therefore reinstated the genus *Nosa* with a new definition based on discriminating characters that had not even been envisaged when the genus was originally established.



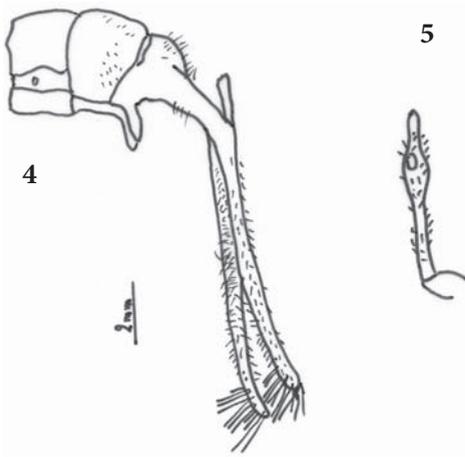
**Figure 1.** *Nosa hamata*, holotype, ZMHB Berlin, male genitalia (parameres). Photo: AP



**Figure 2.** *Nosa tigris*, from Nigeria, male genitalia (parameres in ventral view). Photo: AP



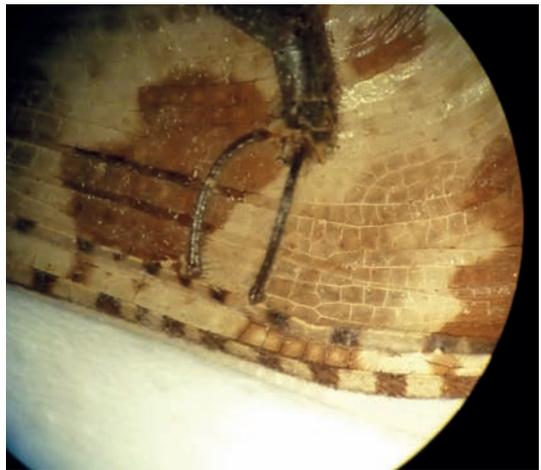
**Figure 3.** *Nosa leonina*, 'cotype' in MRAC Tervuren, from Democratic Republic of Congo, male genitalia (parameres). Photo: AP



**Figure 4.** *Nosa tigris*, ectoprocts.  
**Figure 5.** *Nosa tigris*, labial palp.



**Figure 6.** *Nosa tigris*, from Nigeria, ectoprocts in lateral view. Photo: AP



**Figure 7.** *Palpares tristis*, cotype, ZMHB Berlin, ectoprocts. Photo: AP

### Taxonomy and historical changes

Fifteen taxa, all from the Afrotropical region, were assigned to the genus *Nosa* in successive publications. They are listed chronologically:

- *Nosa leonina* Navás, 1911a
- *Nosa pardina* Navás, 1912a
- *Nosa tigris* (Dalman) new combination for *Myrmeleon tigris* Dalman, 1823 (NAVÁS 1912b)
- *Nosa hamata* (Kolbe) new combination for *Palpares hamatus* Kolbe, 1898 (NAVÁS 1912b)

- *Nosa calceata* Navás, 1912c
- *Nosa lupina* Navás, 1912c
- *Palpares manicatus* Rambur, 1842 as a synonym of *Nosa tigris* (Dalman, 1823) (BANKS 1913)
- *Palpares sylphis* Kolbe, 1898 as a synonym of *Nosa tigris* (Dalman, 1823) (BANKS 1913)
- *Nosa adspersa* Navás, 1914
- *Palpares tigris guineense* Fraser, 1954 as a subspecies of *Nosa tigris* (Dalman, 1823)
- *Palpares manicatus connexus* Banks, 1930 as a synonym of *Nosa tigris* (Dalman, 1823) (PROST 1995)
- *Nosa tristis* (Hagen, 1853) new combination for *Palpares tristis* Hagen, 1853 (WHITTINGTON 2002) confirmed by STANGE (2004) who included the subspecies *Palpares tristis niansanus* Kolbe, 1897 and *Palpares tristis brevifasciatus* Stitz, 1912 within *Nosa*.
- *Palpares sylphis signatus* Stitz, 1912 as a synonym of *Nosa tigris* (Dalman, 1823) (STANGE 2004)

The most important nomenclatural acts were the following:

- NAVÁS (1911a) created the genus *Nosa* for the new species *Nosa leonina*.
- BANKS (1913) expressed doubts about the validity of a distinct genus *Nosa* and the specific validity of many related taxa; he placed all species in synonymy, with *Palpares tigris* (Dalman, 1823) = *N. leonina* Navás, 1911 = *N. pardina* Navás, 1912 = *N. calceata* Navás, 1912 = *N. lupina* Navás, 1912 = *P. manicatus* Rambur, 1842 = *P. hamatus* Kolbe, 1898 = *P. sylphis* Kolbe, 1898. A majority of authors endorsed his opinion.
- INSOM & CARFI (1989) validated genus *Nosa* (Navás, 1911) and gave it a new definition.
- WHITTINGTON (2002) transferred into *Nosa* the species *Palpares tristis* Hagen, 1853, without argument.
- STANGE (2004) excluded *N. adspersa* Navás, 1914, which he transferred to the genus *Palpares* without explanation; he included the subspecies *Palpares tristis niansanus* Kolbe, 1897, and *Palpares tristis brevifasciatus* Stitz, 1912, within *Nosa*; he also synonymized the subspecies *Palpares sylphis signatus* Stitz, 1912, with *Nosa tigris* (Dalman, 1823).

At the time of the revision of West African Palparinae (PROST 1995), *Nosa* was a monotypic genus that included only *Nosa tigris* (Dalman, 1823). I suggested then that specimens from Central Africa were not conspecific, and that the species *Nosa leonina* Navás, 1911 was probably valid.

In his recent systematic catalogue of world antlions, STANGE (2004) recognizes two valid species: *Nosa tigris* (Dalman, 1823) and *Nosa tristis* (Hagen, 1853).

### Methods

For the purpose of this paper, I examined the following type specimens in according collections:

- *Myrmeleon tigris* Dalman [Naturhistoriska Riksmuseet (NHRM), Stockholm, Sweden],
- *Nosa leonina* Navás [Musée royal de l'Afrique centrale (MRAC), Tervuren, Belgium],
- *Palpares hamatus* Kolbe, *Palpares sylphis* Kolbe, *Palpares sylphis signatus* Stitz, *Palpares tristis* Hagen, *Palpares tristis brevifasciatus* Stitz, *Palpares tristis niansanus* Kolbe, and *Palpares tristis ugandanus* Stitz [Museum für Naturkunde der Humboldt Universität zu Berlin (ZMHB), Germany],
- *Nosa lupina* Navás, *Nosa adspersa* Navás, and *Palpares tigris guineense* Fraser [Museum national d'Histoire naturelle (MNHN), Paris, France].

### Discussion

First, *Palpares tristis* Hagen, 1853, and its subspecies lack all the characters that INSOM & CARFI (1989) recognized as taxonomic discriminants of the genus *Nosa*, to which the species certainly does not belong. These include: parameres are separated and only distally sclerotized, ectoprocts comprise a single cylindrical and slightly arched segment (Fig. 7), labial palps are long, slender; their club-shaped apex occupies one third of the length of the segment with a slit-shaped sensory organ that cuts along the whole dorsal surface of the club-shaped portion. Based on these features, it is not possible to include *P. tristis* Hagen in one of the new genera proposed by INSOM & CARFI (1989), and certainly not in the genus *Nosa*. The species should return to the group of species within African *Palpares* that have not yet been assigned to new genera. The two subspecies, *P. tristis brevifasciatus* Stitz, and *P. tristis niansanus* Kolbe are also not part of *Nosa*. The third subspecies, *Palpares tristis ugandanus* Stitz, 1912, was synonymized with *Palpares papilionoides* (Klug, 1834) by ESBEN-PETERSEN (1928); it was never included in *Nosa*.

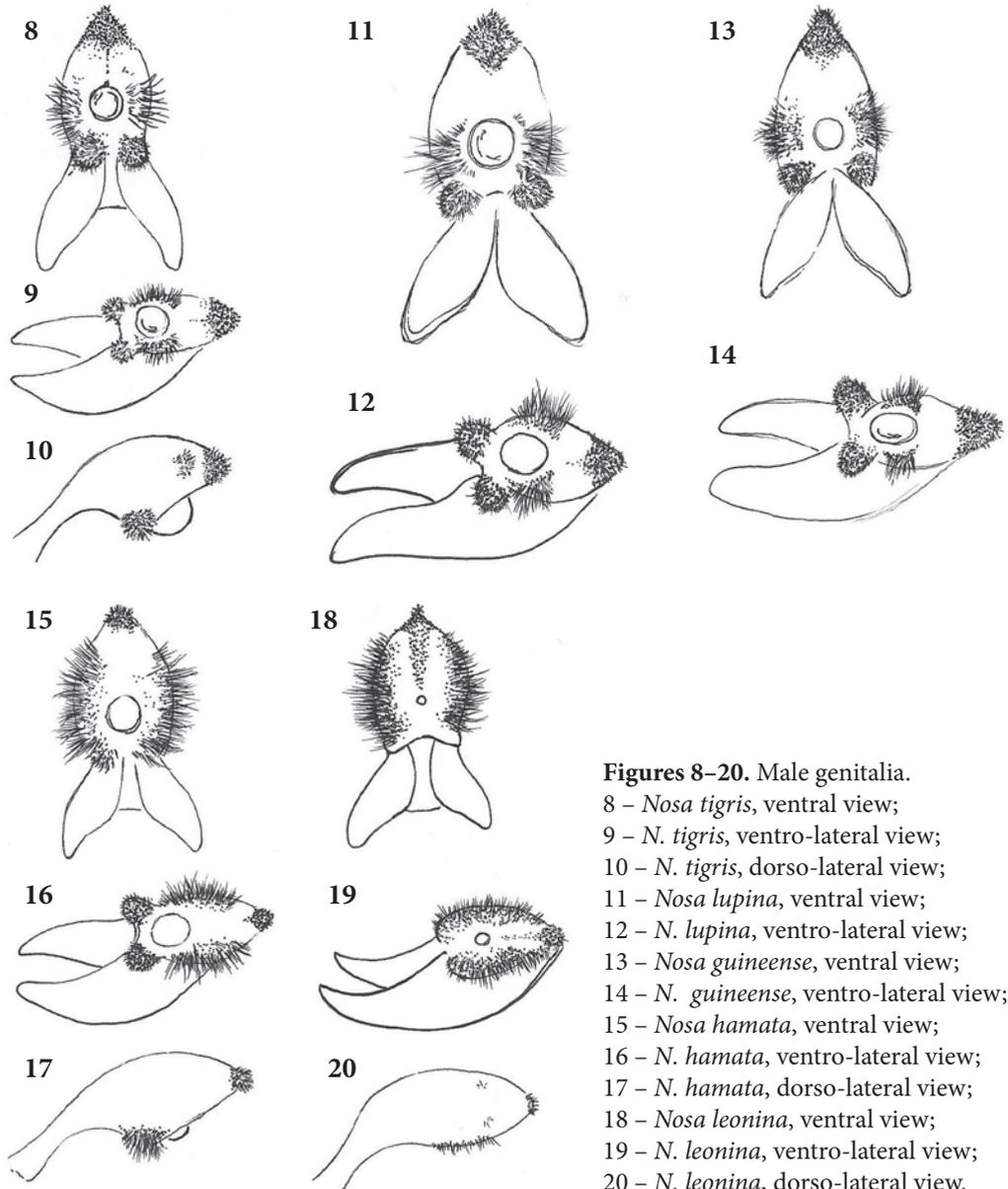
All *Nosa* species have a similar size and consistent wing patterns; individual variations do not support *per se* taxonomic separations, except for *Nosa adspersa* which has the fore wings tessellated with small brown dots and no large brown marks. The male genitalia, which distinguish *Nosa* from other genera, provide further criteria for differentiation.

In *Nosa leonina* (Figs 3, 18–20), the ventral face of the gonarcus complex has the aspect of an ace of spades, gently concave with a small proximal tubercle which is not visible in lateral view. The distal extremity and the middle of the concavity are covered with short black spines. Both sides are covered with three to four irregular rows of long and thick black spines. The dorsal face is perfectly smooth and polished.

In *Nosa tigris* (Figs 2, 8–10) the concavity of the ventral face is more pronounced, with an elevated proximal tubercle, in front of which two lateral processes replace the gentle curves of an ace of spades. Small black spines densely cover only the distal extremity, they do not reach the central concavity. Long black spines are localized in two tufts on each side of the proximal tubercle. The anterior processes are also covered with

black spines of medium size. The aspect of the two lateral tufts of black spines shows no variability among the specimens.

In *Palpares hamatus* (Figs 1, 15–17) the general aspect is of the *N. tigris* type, with a proximal tubercle of medium size, flattened on the top, no anterior processes, with long and dense black spines covering the first half of both sides, continuing with spines of decreasing size down to the distal extremity.



**Figures 8–20.** Male genitalia.

- 8 – *Nosa tigris*, ventral view;
- 9 – *N. tigris*, ventro-lateral view;
- 10 – *N. tigris*, dorso-lateral view;
- 11 – *Nosa lupina*, ventral view;
- 12 – *N. lupina*, ventro-lateral view;
- 13 – *Nosa guineense*, ventral view;
- 14 – *N. guineense*, ventro-lateral view;
- 15 – *Nosa hamata*, ventral view;
- 16 – *N. hamata*, ventro-lateral view;
- 17 – *N. hamata*, dorso-lateral view;
- 18 – *Nosa leonina*, ventral view;
- 19 – *N. leonina*, ventro-lateral view;
- 20 – *N. leonina*, dorso-lateral view.

The male genitalia of *Palpares sylphis*, *Palpares tigris guineense* (Figs 13, 14), and *Nosa lupina* (Figs 11, 12) show only minor variations compared with *Nosa tigris*, which can be attributed to individual variability.

As a result of this study, it is proposed (i) to exclude *Palpares tristis* Hagen and its sub-species from the genus *Nosa*, and (ii) to recognize that *Nosa* Navás consists of four valid species: *Nosa leonina* Navás, *N. tigris* (Dalman), *N. hamata* (Kolbe), and *N. adspersa* Navás, the synonymy of which is detailed below.

#### List of valid species in the genus *Nosa* Navás, 1911

*Nosa* Navás, Rev. Zool. afr., 1911, 1: 239

*Nosa* Navás, Insom & Carfi, Neuroptera international, 1989 (redefinition)

Type species *Nosa leonina* Navás by monotypy

***Nosa adspersa* Navás, 1914**; Mem. r. Acad. Ci. Arts. Barcelona, 1914, 10: 630-631

*Palpares adspersus* (Navás): Stange, Catalogue, 2004: 48

**Holotype** ♂ (labeled holotype J. Legrand dét. 1992, unpublished designation): MNHN, Paris, France, from »Assabot, Abyssinia, J. Surcouf 1912« (Fig. 21).

The holotype of *Nosa adspersa*, a male from Ethiopia, is the only known specimen of the species. It has lost the ectoprocts that characterize the genus *Nosa*, but one of them was still present when I reviewed the African Palparinae of the MNHN in 1994. The handwritten notes taken at that time read: »a single ectoproct preserved, the left one, the



**Figure 21.** *Nosa adspersa* Navás, 1914, holotype, MNHN Paris.

other one missing; dorsal process inserted at the level of the downwards curve shorter than the dorsal process of the ectoprocts of *N. tigris*. Parameres fused and sclerotized with an acute tip«. I did not examine the full genitalia because of the fragile state of the specimen and of its unique status. Nevertheless I can confidently certify that *N. adspersa* belongs to *Nosa* and not to *Palpares*. Stange's recombination is not justified.

Differences in wing patterns and geographical isolation from both *N. tigris* and *N. leonina* support the recognition of *Nosa adspersa* Navás, 1914, as a valid species. We cannot exclude the possibility, however, that it is a pale form of *Nosa hamata* (Kolbe), which comes from the same geographic area and of which it could be a junior synonym.

***Nosa hamata* (Kolbe, 1898)**; Ent. Z. Stettin, 1898, 59: 232

*Palpares hamatus* Kolbe, Ent. Z. Stettin, 1898, 59: 232

*Nosa hamata* (Kolbe), Navás, Brotéria, 1912b, 10: 85

**Holotype** ♂: ZMHB, Berlin, Germany, original description based on a single male from »Abyssinien« (Fig. 22)

The study of male genitalia shows original features that are not individual variations from the related taxa *N. leonina* or *N. tigris* (Figs 1–3). *Nosa hamata* is a valid species known with certainty from Ethiopia and Eritrea.

Records from Sierra Leone (NAVÁS 1911b), Togo (STITZ 1912), and Democratic Republic of Congo (BANKS 1920) were misidentifications of specimens that did not differ significantly from *N. tigris* and *N. leonina*.



**Figure 22.** *Nosa hamata* (Kolbe, 1898), holotype (sub *Palpares hamatus* Kolbe, 1898), ZMHB Berlin.

*Nosa leonina* Navás, 1911; Rev. Zool. afr., 1911, 1: 239-240

*Nosa tigris leonina* Navás, Ent. Mitt. Berlin, 1926, 15: 60

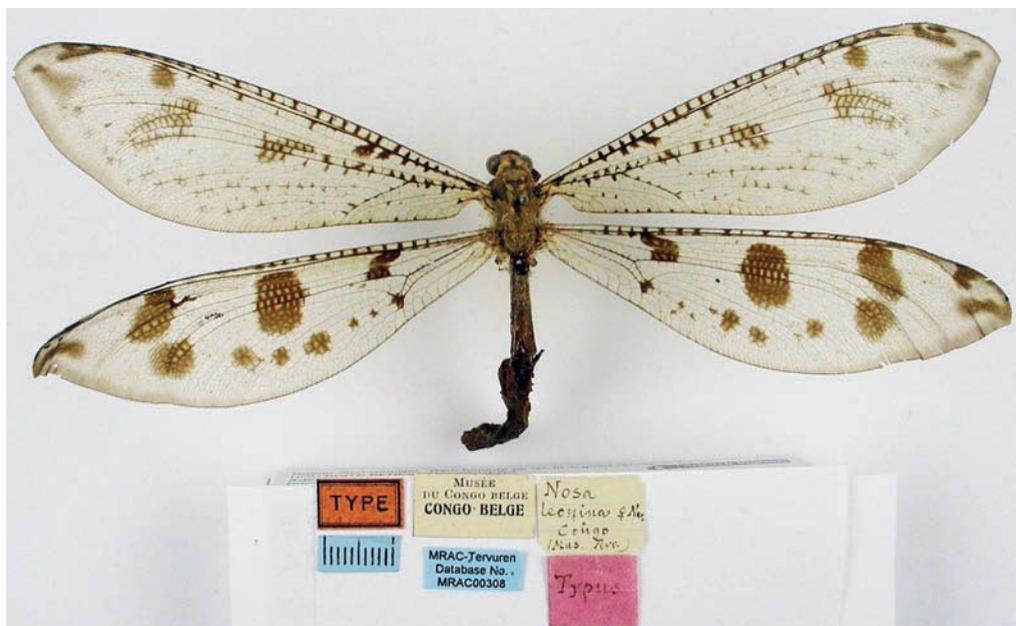
**Type specimen:** 1♀, MRAC, Tervuren, Belgium, from Democratic Republic of Congo (no locality, no date), should be regarded as the holotype since Navás mentions a single female as the basis of his description (Fig. 23).

The male specimen labelled »cotype« in the collection of the MRAC, collected in Kalassa, Democratic Republic of Congo on 17.ii.1912, one year after the original publication, does not belong to the original series. It is not part of the type material.

As the original description was based on a female specimen, the study of male genitalia can only be carried out on males from the same region from which specimens have come that have been attributed to the species. I examined males from the Democratic Republic of Congo and from Uganda. In male genitalia, the absence of an elevated proximal tubercle on the ventral side of the gonarcus-paramere complex, and the presence of long spines on both sides of its ventral face are distinguishing features (Figs 1–3).

The synonymy with *Palpares tigris* proposed by BANKS (1913) and subsequently adopted by a majority of authors is not substantiated by the study of male genitalia. *Nosa leonina* Navás is a valid species.

Distribution – The locality of the type is the former Belgian Congo. The known distribution of the species covers the Democratic Republic of Congo, Central African Republic,



**Figure 23.** *Nosa leonina* Navás, 1911, female type specimen, MRAC Tervuren. © Musée royal de l'Afrique centrale (MRAC), Tervuren, Belgium. Printed with permission.

South Sudan, Uganda and Zimbabwe. To the best of our knowledge, *Nosa tigris* and *Nosa leonina* have separate distribution areas, as they have not been found in the same localities.

***Nosa tigris* (Dalman, 1823)**; *Analecta ent.*, 1823: 88

*Palpares tigris* (Dalman): Rambur, *Hist. nat. Ins. Nev.*, 1842: 374

*Myrmeleon tigris* Dalman: Walker, *List Spec. Neuropt. Ins. Coll. Brit. Mus.*, 1853: 307

Syn. *Palpares tigris guineense* Fraser, *Mem. IFAN*, 1954, 40: 13.

Syn. *Palpares manicatus* Rambur, *Hist. nat. Ins. Nev.*, 1842: 372

Syn. *Myrmeleon manicatus* (Rambur): Walker, *List Spec. Neur. Ins. Coll. Brit. Mus.*, 1853: 312

Syn. *Palpares manicatus connexus* Strong, *The African Rep. Liberia*, 1930, 2: 1045.

Syn. *Palpares sylphis* Kolbe, *Ent. Z. Stettin*, 1898, 59: 234-235

Syn. *Palpares sylphis signatus*: Stitz, *Mitt. Zool. Mus. Berlin*, 1912, 6: 106

Syn. *Nosa calceata* Navás, *Bull. Soc. Scient. Bruxelles*, 1912, 36: 208-209

Syn. *Nosa lupina* Navás, *Ann. Soc. Scient. Bruxelles*, 1912, 36: 206-207

Syn. *Nosa pardina* Navás, *Mitt. Münch. ent. Ges.*, 1912, 3: 23-24

Syn. *Palpares pardina* (Navás): Fraser, *Bull. IFAN*, 1953, 15: 1525

**Type material:** Several specimens, ♂♀, NHRM, Stockholm, Sweden, from Sierra Leone (Figs 24, 25). A lectotype has not yet been designated.

MONSERRAT (1985) recorded the presence in the Museo de Zoología de Barcelona (MZBS) of a specimen labelled »*Nosa tigris* (Dalman, 1823), COTIPO, Reg. de Zinder, Niger« which belonged to Navás' personal collection. The original series in Stockholm comes from Sierra Leone, contains both sexes, and is the only basis for the name *tigris* according to ICZN rules. Labelling of the Barcelona specimen as a cotype by Navás must be disregarded.

In *Nosa tigris* specimens, the wings tend to be narrower with markings that are usually paler and smaller than those of *N. leonina*. There is no general pattern, however, that could support a differentiation based on the external aspect.



**Figure 24.** *Nosa tigris* (Dalman, 1823), type specimen (sub *Myrmeleon tigris* Dalman, 1823), NHRM Stockholm.

**Figure 25.** *Nosa tigris* (Dalman, 1823), type specimen (sub *Myrmeleon tigris* Dalman, 1823), NHRM Stockholm.



**Figure 26.** *Nosa lupina* Navás, 1912, type specimen, MNHM Paris, synonym to *Nosa tigris* (Dalman, 1823).



**Figure 27.** *Palpares tigris guineense* Fraser, 1954, type specimen, MNHM Paris, synonym to *Nosa tigris* (Dalman, 1823).



*Nosa lupina* Navás (Fig. 26) and *Palpares tigris guineense* Fraser (Fig. 27) are similar to *N. tigris* (Dalman). There is no difference in male genitalia (Figs 11–14). The synonymy is thus confirmed.



**Figure 28.** *Palpares sylphis* Kolbe, 1898, female type specimen, ZMHB Berlin, synonym to *Nosa tigris* (Dalman, 1823).



**Figure 29.** *Palpares sylphis signatus* Stitz, 1912, female type specimen, ZMHB Berlin, synonym to *Nosa tigris* (Dalman, 1823).

Both types of *P. sylphis* Kolbe (Fig. 28) and *P. sylphis signatus* Stitz (Fig. 29) are females from Togo. I examined a male specimen from Cameroon, identified as *P. sylphis* Kolbe, in the ZMHB, Berlin, collected during the pre-1900 period. The male genitalia do not differ from those of *N. tigris* (Dalman). There are therefore no arguments to challenge the synonymy established by BANKS (1913).

The original description of *P. manicatus* by RAMBUR (1842) was based on a female which the author says is »of unknown origin«. HAGEN (1860) considered it a synonym of *P. tigris* (Dalman). MAC LACHLAN (1873) confirmed the synonymy based on the examination of a specimen labelled »Senegal« which he considered questionably as Rambur's type. The detailed description by Rambur conforms exactly to *N. tigris*. Since *N. tigris* is the only *Nosa* species known from Senegal, there is no argument to question the synonymy. Banks' proposal to reinstate *P. manicatus* because of slight differences in male parameres from *P. tigris* (BANKS 1930) is irrelevant considering that the only name-bearing specimen of *P. manicatus* was a female. Moreover Banks' description of *P. manicatus* parameres conforms to what this paper defines as the *tigris* type model.

*Nosa pardina* was described by NAVÁS (1912a) on the basis of a female of unknown origin, labelled »Afrika«, preserved in alcohol and with deteriorated colours. I did not examine it. The illustration which supports the description agrees with the identification as a female *N. tigris*, as already established by BANKS (1913).

I did not examine the type specimen of *Nosa calceata* Navás, 1912, a name applied by NAVÁS (1912c) to a male specimen from Nigeria that had been sent to him by the Natural History Museum, London (NHM), with a previous identification as *Palpares submaculatus* Kolbe (a species from Uganda and East Africa). NAVÁS (1912c) indicates himself that it is similar to *N. tigris* with minor variations in the colour and shape of the dark markings on the wings. BANKS (1913) considered it a junior synonym of *P. tigris* (Dalman), an opinion which is supported by the illustration of the description and which we can accept.

Whereas substantial variations occur in the size and colour of the markings of the wings, the specimens show a striking consistency with regard to male genitalia, especially with the limitation of the long and thick black spines to two lateral tufts on both sides of a prominent anterior tubercle.

Distribution – *Nosa tigris* is distributed all over African savannas north of the Equator, from Senegal to Sudan. To date it is the only species present in West Africa and was recorded from Benin, Burkina Faso, Cameroon, Chad, Congo, Côte d'Ivoire, The Gambia, Ghana, Guinea, Liberia, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan and Togo. It is likely to be present in Southern Mauritania and in Guinea-Bissau, although no material exists. Records from the Central African Republic, the Congo and Gabon should be checked for possible confusion with *N. leonina*.

## Conclusion

*Nosa* is characterized by unique features within the Palparinae: ectoprocts bent downwards with a dorsal process, spindle shaped terminal article of the labial palps, parameres sclerotized and fused

It includes four species: *Nosa leonina* Navás, type species, from the Congo river basin; *Nosa tigris* (Dalman) from the Sudan savannas of Africa; *Nosa hamata* (Kolbe) and *Nosa adspersa* Navás from the horn of East Africa.

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## Neuropterida from South America: large diversity, largely unknown

Caleb Califre Martins

Laboratório de Morfologia e Evolução de Díptera – FFCLRP, Universidade de São Paulo, São Paulo, Brazil; calebcalfre@gmail.com

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**Abstract.** Neuropterida comprises about 6 430 extant and 930 fossil species distributed all over the world, except in Antarctica. In South America, 919 extant species of 135 genera in 13 families of Neuroptera and Megaloptera – 15 % of the world’s diversity – have been recorded so far. With regard to fossils in the region, 91 species of 53 genera in 19 families of Glosselytrodea, Raphidioptera, Neuroptera and Megaloptera – 10 % of the world’s diversity – are known to date.

### Introduction

In the last 250 Ma, the evolutionary history of South America was affected by several events: opening of the Atlantic Ocean during the Gondwana fragmentation; high volcanic activity on the eastern margin of the continent during the Cretaceous resulting in the rock formation named as ‘Serra Geral’; uplift of the Andes mountain range from southern Chile to northern Colombia; mass extinctions, especially those that occurred in the passage from the Permian to the Triassic (*ca* 245 Ma), in the Triassic-Jurassic (*ca* 208 Ma) and in the Cretaceous-Paleogene (~65 Ma); glaciation increasing the ice volume on the continent and a reduction in the level of the oceans (LAVINA & FAUTH 2010). All these events resulted in a complex geological history and heterogeneous relief and climate, as well as several biogeographical domains and great biological diversity (including for the species of Neuropterida) (LAVINA & FAUTH 2010; MORRONE 2014).

Neuroptera (lacewings) and allied orders Megaloptera (dobsonflies, alderflies) and Raphidioptera (snakeflies) make up the clade Neuropterida, which is well established as the sister group of the Coleoptera (beetles) plus Strepsiptera (twisted-wings parasites) forming the Neuropteroidea clade (MISOFF *et al.* 2014; WINTERTON *et al.* 2017). Raphidioptera, Neuroptera and Megaloptera are considered minor orders based on the low number of extant species (*ca* 6 430 species). Their fossil record – composed of approximately 930 species – is, however, considered rich and highly diverse (WINTERTON *et al.* 2017; OSWALD & MACHADO 2018).

Neuropterida is considered a relict superorder that has all families originating in the Mesozoic period, larval stages with disparate morphology and extant lineages with disjunct distribution (ASPÖCK *et al.* 2001; WINTERTON *et al.* 2017; ENGEL *et al.* 2018). Representatives of the three orders belonging to Neuropterida are present all over the world, except in Antarctica (OSWALD 2019). Among a total of about 6 430 Neuropterida extant species, 919 occur in South America representing 15 % of the world’s known

diversity, fauna that has a relatively high degree of endemism even at higher taxonomic levels – 46 % (63 of 135) of their genera are known to occur only in South America (OSWALD 2019). From a total of approximately 930 fossil species of Neuropterida, 91 are present in South America (88 from the lower Cretaceous Crato Formation of Ceará State, Brazil), representing almost 10 % of the world's known diversity of Neuropterida fossils (OSWALD 2019).

Despite the great diversity of Neuropterida already known for South America (HECKMAN 2017), there is still an unknown diversity of the group in this continent deemed to be of substantial magnitude, which demonstrates the necessity for further studies to understand this diversity. This paper reviews and organizes the main information on the diversity of South American Neuropterida with the aim of facilitating future studies.

### Material and methods

The data used for counting South American Neuropterida species and checked their distribution have been accessed via the web portal 'Lacewing Digital Library' (OSWALD 2019), and in specialized articles for each family or order. Microsoft Excel software was used to tabulate and organize the data, as well as to create graphics.

### Results

#### Extant species of South American Neuropterida (Table 1)

Megaloptera: Sialidae. Sialidae (alderflies) comprise seven recorded species of *Ilyobius* Enderlein, 1910, across the South American continent (LIU et al 2015; OSWALD 2019), representing 10% of the world's fauna. Brazil and Colombia have the greatest alderfly diversity for the region; there are, however, no records of species of alderflies for Ecuador, French Guiana, Guyana, Paraguay, Suriname and Uruguay (LIU et al 2015; OSWALD 2019). The immature stages of five South American species are unknown; larvae of only *Ilyobius flammatus* (Penny, 1982) and *Ilyobius chilensis* (McLachlan, 1871) are known to this region.

Megaloptera: Corydalidae. About 17 % of Corydalidae (dobsonflies, fishflies) diversity is present in South America and 52 species of six genera have records from this continent (OSWALD 2019). Venezuela and Brazil have the greatest diversity of the family for the region, whereas Suriname, Uruguay and Paraguay have no record of Corydalidae species. *Corydalus* Latreille, 1802, is the largest South American genus and *Chloronia* Banks, 1908, is the second largest; *Nothochauliodes* Flint, 1983, and *Puri* Cardoso-Costa et al., 2013, occur only in South America; and *Protochauliodes* van der Weele, 1909, and *Archichauliodes* van der Weele, 1909, have records only in Chile. Despite some knowledge of the immature stages of the South American Corydalidae, the immature stages of *Puri* and *Nothochauliodes* are still unknown to date.

Neuroptera, Coniopterygoidea: Coniopterygidae. There are records for 88 species and eight genera of dustywings in the South American region, representing approximately

15 % of the world fauna (SZIRÁKI 2011; OSWALD 2019). Brazil and Argentina have the greatest Coniopterygidae diversity on the continent, and there are no records of Coniopterygidae species for French Guiana, Guyana, Suriname or Venezuela (Table 1) (MARTINS & AMORIM 2016; MACHADO & MARTINS 2019a; OSWALD 2019). *Coniopteryx* Curtis, 1834, and *Semidalis* Enderlein, 1905, are part of the subfamily Coniopteryginae and are the most diverse genera with a number of South American species (Table 1) (SZIRÁKI 2011; OSWALD 2019); Brucheiserinae occurs only in South America and comprises *Brucheiser* Navás, 1927, and *Flintoconis* Sziráki, 2007 (SZIRÁKI 2011; OSWALD 2019) (Table 1). The other four genera of South American dustywings are *Pampoconis* Meinander, 1972 and *Neoconis* Enderlein, 1929, from Aleuropteryginae, and *Incasemidalis* Meinander, 1972 and *Parasemidalis* Enderlein, 1905, from Coniopteryginae (SZIRÁKI 2011; OSWALD 2019). Immature stages of Coniopterygidae are practically unknown for the South American genera; immature of species of only *Brucheiser*, *Coniopteryx* and *Semidalis* are currently known, whereas immature stages of *Flintoconis*, *Pampoconis*, *Neoconis*, *Incasemidalis* and *Parasemidalis* are not known.

Neuroptera, Osmyloidea: Sisyridae. There is about 30 % of the world fauna of spongillaflyies in South America; to date, 22 species of *Sisyra* Burmeister, 1839, and *Climacia* McLachlan, 1869, have been recorded in the region (OSWALD 2019). Brazil, Guyana and Argentina have the greatest diversity in spongillaflyies on the continent, whereas there are no records of Sisyridae species in Ecuador or French Guiana (MACHADO & MARTINS 2019b; OSWALD 2019). With respect to the immatures stages of South American Sisyridae, only a small part is currently known (MARTINS & ARDILA-CAMACHO 2018; OSWALD 2019).

Neuroptera, Osmyloidea: Osmylidae. Currently, 12 % of the world diversity (25 species) of lance lacewings has been recorded in South America (MARTINS et al. 2016, 2019; MARTINS & ARDILA-CAMACHO 2018; WINTERTON et al. 2019). The greatest number of species is found in the Andes mountain range, especially in Peru, Colombia and Chile; there are no records of Osmylidae for French Guiana, Guyana, Suriname or Uruguay. *Gumilla* Navás, 1912, is the only genus of the subfamily Gumillinae and occurs in the South American region; *Phymatosmylus* Adams, 1969 (Stenosmylinae) and *Paryphosmylus* Krüger, 1913 (Protosmylinae) are monotypic genera; *Kempynus* Navás, 1912 (Kempyninae) has four species in South America; and *Isostenosmylus* Krüger, 1913 (Stenosmylinae) is the most diverse genus occurring in eight countries. Immature stages of Osmylidae are virtually unknown in South America; larvae of only *Isostenosmylus pulverulentus* (Gerstaecker, 1893) and *Kempynus* sp. have been described in this region (MARTINS et al. 2018).

Neuroptera, Dilaroidea: Dilaridae. All South American representatives of pleasing lacewings belong to the genus *Nallachus* Navás, 1909 (OSWALD 2019), and represent 22 % of the world diversity in this family. Brazil, Paraguay and Argentina are the coun-

tries with the greatest diversity of Dilaridae for the region, whereas there are no records of Dilaridae for Bolivia, French Guiana, Guyana, Peru, Suriname or Uruguay (MACHADO & MARTINS 2019c; OSWALD 2019). Among all the species of Dilaridae that occur in South America, there is information only for *Nallachus americanus* (McLachlan, 1881) and its immature stages (GEPF 1984).

Neuroptera, Hemerobioidea: Hemerobiidae. The South American fauna of brown lacewings consists of 81 species of 12 genera distributed in eight subfamilies (OSWALD 2019), which represent approximately 14 % of the world fauna. Brazil, Argentina, Peru and Chile have the greatest Hemerobiidae diversity for the South American region (MACHADO & MARTINS 2019d, OSWALD 2019). *Hemerobius* Linnaeus, 1758, is the most diverse genus of South America, *Symphorobius* Banks, 1904, and *Megalomus* Rambur, 1842, are second in number of species (OSWALD 2019). *Adelphohemerobius* Oswald, 1994, *Gayomyia* Banks, 1915, *Conchopterella* Handschin, 1955, and *Neosymphorobius* Kimmins, 1929, are endemic to South America (OSWALD 2019); *Hemerobiella* Kimmins, 1940, has three species that occur mainly in northern South America, although there is one occurrence in southern Mexico (SOSA et al. 2015; OSWALD 2019). *Notiobiella* Banks, 1909, *Nomerobius* Navás, 1915, and *Biramus* Oswald, 1993, have been recorded in South America and also occur in other world regions (OSWALD 2019). Despite their economic importance, immature stages of South American Hemerobiidae are poorly studied; only few species of *Gayomyia*, *Nusalala*, *Nomerobius*, *Symphorobius*, *Megalomus* and *Hemerobius* have known immature stages (MONSERRAT 2003; OSWALD 2019).

Neuroptera, Mantispoidae: Berothidae. Species of *Lomamyia* Banks, 1904, and *Spiroberotha* Adams, 1989, of Berothinae; *Berothimerobius* Monserrat & Deretzky, 1999, of Berothimerobiinae; *Cyrenoberotha* MacLeod & Adams, 1967, and *Ormiscocerus* Blanchard, 1851, of Cyrenoberothinae; and *Naizema* Navás, 1919, of Nosybininae (ASPÖCK & RANDOLF 2014; OSWALD 2019) have been recorded in South America, representing 7 % of the world diversity within Berothidae. Only Argentina, Brazil, Chile, Colombia and Venezuela have records of beaded lacewings. The monotypic genera *Berothimerobius*, *Cyrenoberotha* and *Ormiscocerus*, plus *Naizema*, occur only in South America, whereas *Spiroberotha* and *Lomamyia* also have species recorded in Central and North America (OSWALD 2019). With the exception of *Berothimerobius*, the immature stages of all five other genera of South American Berothidae are unknown (MONSERRAT 2006).

Neuroptera, Mantispoidae: Mantispidae. There are 87 South American species of mantidflies distributed in *Anchieta* Navás, 1909, *Plega* Navás, 1928, and *Trichoscelia* Westwood, 1852, of Symphrasinae; *Drepanicus* Blanchard in Gay, 1851, and *Gerstaeckerella* Enderlein, 1910, of Drepanicinae; *Nolima* Navás, 1914, of Calomantispinae; *Buyda* Navás, 1926, *Climaciella* Enderlein, 1910, *Dicromantispa* Hoffman in Penny, 2002, *Entanoneura* Enderlein, 1910, *Haematomantispa* Hoffman in Penny, 2002, *Leptomantispa*

Hoffman in Penny, 2002, *Mantispa* Illiger, 1758, *Paramantispa* Williner & Kormilev, 1958, and *Zeugomantispa* Hoffman in Penny, 2002, of Mantispiinae (OSWALD 2019), representing about of 21% of the world fauna. All South American countries have records of Mantispidae species, Brazil has the greatest South American diversity of mantidflies species, and Colombia follows in number of species, whereas Guyana and Paraguay have the lowest diversity of Mantispidae in the region (MACHADO & MARTINS 2019e; ARDILA-CAMACHO et al. 2018). *Anchieta* and *Paramantispa* are endemic to the region, and the genera *Mantispa* and *Trichoscelia* are the most diverse (OSWALD 2019). The immature stages of few species in South America are known, mainly species of *Plega* and *Zeugomantispa* (HOFFMAN & BRUSHWEIN 1992).

Neuroptera, Chrysopoidea: Chrysopidae. Representatives of 316 species of 27 genera of green lacewings have been recorded in South America, which is equivalent to about 23% of the world's fauna (OSWALD 2019). There are records of Chrysopidae for all South American countries; among them Brazil has the largest number of species on the continent and Venezuela is the second country in number of Chrysopidae species, whereas Chile, French Guiana and Uruguay have the lowest diversity (MARTINS & MACHADO 2019). *Leucochrysa* McLachlan, 1868, is the most diverse genus in South America, followed by *Ceraeochrysa* Adams, 1982, and *Chrysopodes* Navás, 1913. A total of 11 genera are endemic to South America: *Asthenochrysa* Adams & Penny, 1992, and *Leptochrysa* Adams & Penny, 1992, of Nothochrysiniae; *Belonopteryx* Gerstaecker, 1863, *Vieira* Navás, 1913, *Furcochrysa* Freitas & Penny, 2001, *Parachrysopiella* Brooks & Barnard, 1990, *Titanochrysa* Sosa & Freitas, 2012, *Cacarulla* Navás, 1913, *Neula* Navás, 1917, *Nuvol* Navás, 1916, and *Santocellus* Tauber & Albuquerque, 2008, of Chrysopinae (OSWALD 2019), although there is no genus of Apochrysiniae that is endemic to this region. Immature stages of South American green lacewings are relatively well known when compared to the other Neuropterida families.

Neuroptera, Myrmeleontoidea: Ithonidae. In South America, there are records of only *Fontecilla graphicus* Navás, 1932, and *Polystoechotes gazullai* Navás, 1924, representing 5% of world diversity, both species have been recorded in Chile (OSWALD 2019) and their immature stages are unknown.

Neuroptera, Myrmeleontoidea: Nemopteridae. Eight species of five genera of spoonwings have been recorded in South America, and all of them are endemic to this region: *Amerocroce* Mansell, 1983, *Moranida* Mansell, 1983, *Veurise* Navás, 1927, and *Pastranaia* Orfila, 1955, of Croninae; and *Stenorrhachus* McLachlan, 1886, of Nemopterinae (OSWALD 2019). Only Argentina, Bolivia, Chile, Peru and Venezuela have records of Nemopteridae species, and the former three countries are the most diverse on the continent. Immature stages of Nemopteridae are well known in the South American region, with larvae of all genera except *Pastranaia* being known (MILLER & STANGE 2012; OSWALD 2019).

**Table 1.** Number of extant genera and species of Neuropterida per country recorded in South America.

Order (Family: Subfamily)	Genus	Number of species per Country										Total spe- cies			
		Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	French Guiana	Guyana	Paraguay	Peru		Suriname	Uruguay	Venezuela
Megaloptera (Corydalidae)	1. <i>Archichauliodes</i> van der Weele, 1909				2									2	
	2. <i>Chloronia</i> Banks, 1908		2	5		2	2	1	1	4			4	11	
	3. <i>Corydalus</i> Latreille, 1802	6	5	11		8	8	4	3	2	7	1	1	13	33
	4. <i>Nothochauliodes</i> Flint, 1983				1										1
	5. <i>Protochauliodes</i> van der Weele, 1909				4										4
	6. <i>Puri</i> Cardoso-Costa et al., 2013			1											1
Megaloptera (Sialidae)	7. <i>Ilyobius</i> Enderlein, 1910	1	1	3	1	2				1			1	7	
Neuroptera (Coniopterygidae: Aleuropteryginae)	8. <i>Pampoconis</i> Meinander, 1972	4			5									7	
	9. <i>Neoconis</i> Enderlein, 1930		1	6		1			1	2			1	9	
Neuroptera (Coniopterygidae: Brucheiserinae)	10. <i>Brucheiser</i> Navás, 1927	1			1									2	
Neuroptera (Coniopterygidae: Coniopteryginae)	11. <i>Flintoconis</i> Sziráki, 2007				2									2	
	12. <i>Coniopteryx</i> Curtis, 1834	6	2	30	1	6			1	4		2	8	37	
	13. <i>Incasemidalis</i> Meinander, 1972	3	1	2	1					1				7	
	14. <i>Parasemidalis</i> Enderlein, 1905	3			1									3	
	15. <i>Semidalis</i> Enderlein, 1905	5	3	9	1	5	1			1	7			21	
Neuroptera (Sisyridae)	16. <i>Climacia</i> McLachlan, 1869	6	1	11	1				5	1	2	1	3	4	16
	17. <i>Sisyra</i> Burmeister, 1839		1	6		1			1	1	3	1	1	1	6
Neuroptera (Osmyli- dae: Gumillinae)	18. <i>Gumilla</i> Navás, 1912			1										2	
Neuroptera (Osmyli- dae: Kempyninae)	19. <i>Kempynus</i> Navás, 1912	3			4									4	
Neuroptera (Osmyli- dae: Protosmylinae)	20. <i>Paryphosmylus</i> Krüger, 1913						1							1	
Neuroptera (Osmyli- dae: Stenosmylinae)	21. <i>Isostenosmylus</i> Krüger, 1913	1	2	2		4	3			1	6		2	17	
	22. <i>Phymatosmylus</i> Adams, 1969	1	1											1	
Neuroptera (Dilaridae: Nallachiinae)	23. <i>Nallachus</i> Navás, 1909	2	10	1	1	1	1		2				1	17	
Neuroptera (Hemerobiidae: Adel- phohemerobiinae)	24. <i>Adelphohemerobius</i> Oswald, 1994	1			1									2	
Neuroptera (Hemero- biidae: Drepanacrinae)	25. <i>Conchopterella</i> Handschin, 1955	1			3									3	
Neuroptera (Hemerobiidae: Drepanopteryginae)	26. <i>Gayomyia</i> Banks, 1913	1	1		2					1				2	

Order (Family: Subfamily)	Genus	Number of species per Country										Total spe- cies		
		Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	French Guiana	Guyana	Paraguay	Peru		Suriname	Uruguay
Neuroptera (Hemerobiidae: Hemerobiinae)	27. <i>Biramus</i> Oswald, 1993												1	1
	28. <i>Hemerobiella</i> Kimmins, 1940						1						2	3
	29. <i>Hemerobius</i> Linnaeus, 1758	3	3	5	4	9	5			2	5	1	1	8
Neuroptera (Hemero- biidae: Megalominae)	30. <i>Megalomus</i> Rambur, 1842	5	2	6	5	3	2		1	5			2	13
Neuroptera (Hemero- biidae: Microminae)	31. <i>Nusalala</i> Navás, 1913	2	2	4		5	4		2	6		1	3	9
Neuroptera (Hemero- biidae: Notiobiellinae)	32. <i>Notiobiella</i> Banks, 1909		1	4		2			2	1			2	4
Neuroptera (Hemerobiidae: Sympherobiinae)	33. <i>Neosympherobius</i> Kimmins, 1929	1												1
	34. <i>Nomerobius</i> Navás, 1915	6	1	1	4					3		1		7
	35. <i>Sympherobius</i> Banks, 1905	5	1	4	4	2	2		2	3		2		13
Neuroptera (Berothidae: Berothimerobiinae)	36. <i>Berothimerobius</i> Monserrat & Deretsky, 1999				1									1
Neuroptera (Berothi- dae: Berothinae)	37. <i>Lomamyia</i> Banks, 1904			1										1
	38. <i>Spiroberotha</i> Adams, 1989			1		1							2	3
Neuroptera (Berothidae: Cyrenoberothinae)	39. <i>Cyrenoberotha</i> MacLeod & Adams, 1967				1									1
	40. <i>Ormiscocerus</i> Blanchard, 1851				1									1
Neuroptera (Berothi- dae: Nosybinae)	41. <i>Naizema</i> Navás, 1919	2												2
Neuroptera (Mantispida- dae: Calomantispinae)	42. <i>Nolima</i> Navás, 1914							1						1
	43. <i>Drepanicus</i> Blanchard, 1851	2			5									5
Neuroptera (Mantispida- dae: Drepanicinae)	44. <i>Gerstaeckerella</i> Enderlein, 1910	1	3	3	1				1			1		6
Neuroptera (Mantispidae: Mantispinae)	45. <i>Buyda</i> Navás, 1926	1	1	1	2		1			1	1	1		2
	46. <i>Climaciella</i> Enderlein, 1910	3	4	3	5	2	3		1	4	2	2		8
	47. <i>Dicromantispa</i> Hoffman, 2002	1	2	6	3	3	2	2		1	1	1	2	6
	48. <i>Entanoneura</i> Enderlein, 1910	1		5	1		1	1					1	4
	49. <i>Haematomantispa</i> Hoffman, 2002			1	1									2
	50. <i>Leptomantispa</i> Hoffman, 2002			5	2		2						1	6
	51. <i>Mantispa</i> Illiger, 1758		2	5	2				3		1			13
	52. <i>Paramantispa</i> Williner & Kormilev, 1958	3	1	3					1	1		1	2	3
	53. <i>Zeugomantispa</i> Hoffman, 2002	2	1	2	3	2	2	1	1	2	3	2	3	3
Neuroptera (Mantispidae: Symphrasinae)	54. <i>Anchieta</i> Navás, 1909			5	3		2							8
	55. <i>Plega</i> Navás, 1928		1	5	2								1	6
	56. <i>Trichoscelia</i> Westwood, 1852	1	1	8	1	4	1	1	1	1		1	1	14

Order (Family: Subfamily)	Genus	Number of species per Country										Total spe- cies			
		Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	French Guiana	Guyana	Paraguay	Peru		Suriname	Uruguay	Venezuela
Neuroptera (Chrysopidae: Apochrysinae)	57. <i>Domenechus</i> Navás, 1913			1										1	
	58. <i>Joguina</i> Navás, 1912	?	?	?	?	?	?	?	?	?	?	?	?	1	
	59. <i>Loyola</i> Navás, 1913			3										3	
	60. <i>Belonopteryx</i> Gerstaecker, 1863			1										1	
Neuroptera (Chrysopidae: Chrysopinae)	61. <i>Berchmansus</i> Navás, 1913		1	1						1				1	
	62. <i>Cacarulla</i> Navás, 1913		1			1				1				1	
	63. <i>Ceraeochrysa</i> Adams, 1982	3	3	33		8	3	2	5	7	2	5	1	13	41
	64. <i>Chrysopa</i> Leach, 1815	9		4	2	3	6			2	2	2	1	2	30
	65. <i>Chrysoperla</i> Steinmann, 1964	3	1	4	1	2	2			1	2		1	2	7
	66. <i>Chrysopodes</i> Navás, 1913	3	1	23	2	6	5	1	3	2	3	4	1	5	40
	67. <i>Furcochrysa</i> Freitas & Penny, 2001			1											1
	68. <i>Gonzaga</i> Navás, 1913			6			1		3		1	1		2	7
	69. <i>Italochrysa</i> Principi, 1946			1											1
	70. <i>Leucochrysa</i> McLachlan, 1868	5	4	78		20	13	5	5	5	5	13		13	114
	71. <i>Meleoma</i> Fitch, 1855					1								1	2
	72. <i>Nacarina</i> Navás, 1915	4	1	10		1			3					3	17
	73. <i>Neula</i> Navás, 1917					1									1
	74. <i>Nuvol</i> Navás, 1916			1											1
	75. <i>Parachrysopiella</i> Brooks & Barnard, 1990	2	1		3										3
	76. <i>Plesiochrysa</i> Adams, 1982	1		4		1	1		1		2			1	5
	77. <i>Santocellus</i> Tauber & Albuquerque, 2008			2											3
	78. <i>Titanochrysa</i> Sosa & Freitas, 2012	1	1	4		1	1					1		4	4
	79. <i>Ungla</i> Navás, 1914	6	5	1		5	2				5			6	23
	80. <i>Vieira</i> Navás, 1913			3	4	1		1	1		2	3		3	5
Neuroptera (Chrysopidae: Nothochrysinae)	81. <i>Asthenochrysa</i> Adams & Penny, 1992	1		1										1	
	82. <i>Leptochrysa</i> Adams & Penny, 1992									1				1	
	83. <i>Nothochrysa</i> McLachlan, 1868				1									1	
Neuroptera (Ithonidae)	84. <i>Fontecilla</i> Navás, 1932				1									1	
	85. <i>Polystoechotes</i> Burmeister, 1839				1									1	
Neuroptera (Nemopteridae: Crocinae)	86. <i>Amerocroce</i> Mansell, 1983		1											1	
	87. <i>Moranida</i> Mansell, 1983									1			1	2	
	88. <i>Pastranaia</i> Orfila, 1954	1												1	
	89. <i>Veurise</i> Navás, 1927	1	1											2	
Neuroptera (Nemopteridae: Nemopterinae)	90. <i>Stenorrhachus</i> McLachlan, 1885				2									2	

Order (Family: Subfamily)	Genus	Number of species per Country										Total spe- cies			
		Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	French Guiana	Guyana	Paraguay	Peru		Suriname	Uruguay	Venezuela
Neuroptera (Myrmeleontidae: Ascalaphinae)	91. <i>Albardia</i> van der Weele, 1903			1										1	
	92. <i>Ameropterus</i> Esben-Petersen, 1922	5	2	9			1	1		4			2	18	
	93. <i>Amoea</i> Lefebvre, 1842	2	1	4		1				3	1		1	8	
	94. <i>Ascalobyas</i> Penny, 1981			3		1	2	1						3	
	95. <i>Ascalorphne</i> Banks, 1915	1	1	2						2				4	
	96. <i>Cordulecerus</i> Rambur, 1842	2		6		2	4	1	1		1	3	1	9	
	97. <i>Dimares</i> Hagen, 1866	1	1	1						1			1	1	
	98. <i>Fillus</i> Navás, 1919	1		1						1				3	
	99. <i>Haploglenius</i> Burmeister, 1839	2	5	5		3	4	2	2		4		2	11	
	100. <i>Millerleon</i> Stange, 1989				1		3				3			3	
	101. <i>Nephasca</i> Navás, 1914					1								1	
	102. <i>Ululodes</i> Currie, 1899	6		6		3	4	2	1	3	1	1	1	3	13
	103. <i>Verticillecerus</i> van der Weele, 1909	1		1						1				1	
	104. <i>Sodirus</i> Navás, 1912						1							1	
Neuroptera (Myrmeleontidae: Myrmeleontinae)	105. <i>Abatoleon</i> Banks, 1943	2												2	
	106. <i>Ameromyia</i> Banks, 1913	6		10	1	1			3		1	3	3	12	
	107. <i>Argentoleon</i> Stange, 1994	2	1	1					2			1	1	2	
	108. <i>Austroleon</i> Banks, 1909	3	1	2		1			2			1	1	3	
	109. <i>Dejunaleon</i> Miller & Stange, 2017				2									2	
	110. <i>Ecualeon</i> Stange, 1994						1			1				1	
	111. <i>Elicura</i> Navás, 1911	3		1	1								1	3	
	112. <i>Ensorra</i> Navás, 1915	1	1											1	
	113. <i>Galapagoleon</i> Stange, 1994						1							1	
	114. <i>Jaffuelia</i> Navás, 1918					2								2	
	115. <i>Lemolemus</i> Navás, 1911					3								3	
	116. <i>Myrmeleon</i> Linnaeus, 1767	2	3	11	2	1	1		1	2	1	1	2	2	15
	117. <i>Neulatus</i> Navás, 1912				1									1	
	118. <i>Peruveleon</i> Miller & Stange, 2011	1					1			1	1		1	2	
119. <i>Porrerus</i> Navás, 1913			2						1			1	2		
120. <i>Scotoleon</i> Banks, 1913			1										1		
121. <i>Sical</i> Navás, 1928				2									3		
122. <i>Stangeleon</i> Miller, 2008												1	1		
123. <i>Vella</i> Navás, 1913	1		1		2	1		1		1		3	5		
124. <i>Venezueleon</i> Stange, 1994												1	1		

Order (Family: Subfamily)	Genus	Number of species per Country										Total spe- cies												
		Argentina	Bolivia	Brazil	Chile	Colombia	Ecuador	French Guiana	Guyana	Paraguay	Peru		Suriname	Uruguay	Venezuela									
Neuroptera (Myrmeleontidae: Nemoleontinae)	125. <i>Brasileon</i> Miller & Stange, 1989			2											2									
	126. <i>Dimarella</i> Banks, 1913	2	2	7	1	2	3	4	1	3	4	1	8	13										
	127. <i>Elachyleon</i> Esben-Petersen, 1927	1		1				1				1		2										
	128. <i>Eremoleon</i> Banks, 1901	2	2	1		4	2		1	4			8	16										
	129. <i>Euptilon</i> Westwood, 1837			1	1									1										
	130. <i>Glenurus</i> Hagen, 1866	3	2	1			1	1	1	1	1		1	5										
	131. <i>Navasoleon</i> Banks, 1943	3	1	2			1	1		2			2	10										
	132. <i>Purenleon</i> Stange, 2002			5	4								3	9										
	133. <i>Ripalda</i> Navás, 1915		1	1			1		1	1			1	4										
	134. <i>Rovira</i> Navás, 1914	2												2										
	135. <i>Sericoleon</i> Esben-Petersen, 1933				1									1										
<b>Total species</b>		<b>179</b>	<b>91</b>	<b>446</b>	<b>45</b>	<b>159</b>	<b>38</b>	<b>100</b>	<b>22</b>	<b>40</b>	<b>27</b>	<b>52</b>	<b>39</b>	<b>69</b>	<b>50</b>	<b>127</b>	<b>24</b>	<b>54</b>	<b>29</b>	<b>39</b>	<b>53</b>	<b>164</b>	<b>135</b>	
<b>Total genera</b>		<b>69</b>	<b>52</b>	<b>82</b>	<b>45</b>	<b>91</b>	<b>55</b>	<b>159</b>	<b>38</b>	<b>100</b>	<b>22</b>	<b>40</b>	<b>27</b>	<b>52</b>	<b>39</b>	<b>69</b>	<b>50</b>	<b>127</b>	<b>24</b>	<b>54</b>	<b>29</b>	<b>39</b>	<b>53</b>	<b>135</b>

Neuroptera, Myrmeleontoidea: Myrmeleontidae. Myrmeleontidae is second largest Neuroptera family in numbers of South American species, with 205 species of 45 genera being currently known (OSWALD 2019; MACHADO et al. 2019). Brazil has the greatest diversity of South American Myrmeleontidae, followed by Argentina, whereas French Guiana, Suriname and Uruguay have the lowest Myrmeleontidae diversity (MACHADO & MARTINS 2019f; OSWALD 2019). Some small South American genera of antlions occur only in this region, e.g., *Dimares* Hagen, 1866, *Millerleon* Stange, 1989, *Nephalesca* Navás, 1914, and *Verticillecerus* van der Weele, 1909, of Ascalaphinae; *Ensorra* Navás, 1915, *Stangeleon* Miller, 2008, of the Myrmeleontinae; and *Brasileon* Miller & Stange, 1989, of Nemoleontinae. *Ameropterus* Esben-Petersen, 1922, and *Eremoleon* Banks, 1901, have the largest number of species occurring in South America. Immature stages of the South American Myrmeleontidae species are relatively well known when compared to the other families of Neuropterida, although there are still many genera with unknown immature stages, e.g., *Ecuaeon* Stange, 1994, *Elicura* Navas, 1911, and *Galapogoleon* Stange, 1994.

### Fossil species of South American Neuropterida (Table 2)

Glosselytrodea. This is a small fossil insect order which has been considered “orthopterids”, Mecopterida, Neuropterida, or some problematic Holometabola (BÉTHOUX et al. 2007). Due to the possibility of this order being related to Neuropterida, the two South American species of Glosselytridae from the late Triassic Los Rastros Formation of La Rioja, Argentina were added in this review: *Argentinoglosselytrina pulchella* Martins-Neto & Gallego, 2001, and *Chanarelytrina nana* Martins-Neto & Gallego, 2006 (MARTINS-NETO et al. 2006).

Raphidioptera. Extant species of snakeflies are not known to South America, although there are seven South American fossil species from the lower Cretaceous Crato Formation of Ceará State, Brazil (OSWALD 2019). Of the seven, five species are members of Baissopteridae: *Austroraphidia brasiliensis* (Nel et al., 1990), *Baissoptera brasiliensis* Oswald, 1990, *Baissoptera lisae* Jepson et al., 2011, *Baissoptera pulchra* (Martins-Neto & Nel, 1993), and *Baissoptera rochai* (Martins-Neto & Vulcano, 1990); and two species are considered *incertae sedis*: *Caririraphidia reticulate* Martins-Neto, 2003, and *Caririraphidia sertaneja* Martins-Neto, 2003 (OSWALD 2019).

Megaloptera. There are two South American fossil species of Corydalidae from the lower Cretaceous Crato Formation of Ceará State, Brazil: *Cratocorydalopsis brasiliensis* Jepson & Heads, 2016 and *Lithocorydalus fuscatus* Jepson & Heads, 2016 (JEPSON & HEADS 2016; OSWALD 2019).

Neuroptera. Neuroptera show great diversity in South American fossil species. There are 76 neuropteran species of 45 genera distributed in 15 families from the lower Cretaceous Crato Formation of Ceará State, Brazil (OSWALD 2019; MAKARKIN et al. 2018). Also there is one species of Pemithonidae from the Late Permian Irati Formation of Rio Grande do Sul State, Brazil: *Permipsythone panfilovi* Pinto & Ornellas, 1980 (PINTO & PINTO DE ORNELLAS 1980).

### Discussion

South America has a complex geological history and heterogeneous relief and climate, which have resulted in more than 25 biogeographical domains and great biological diversity, including that of Neuropterida (MORRONE 2014). Currently, South America is the home of 15% of the Neuropterida extant species and 10% of the fossil species of this group. Among the 6 430 valid extant species of Neuropterida, 919 occur in South America (only Megaloptera and Neuroptera), and among the 930 fossil species of this group, a total of 91 species (Raphidioptera, Glosselytrodea, Neuroptera and Megaloptera) are present in this region (OSWALD 2019).

There are records of 13 extant families of Neuropterida for South America and 135 genera, of which 63 (approximately 46%) occur only in this region; also there are records of 19 families with fossil species of 53 genera, of which 45 (about 88%) have species only in

**Table 2.** Number of fossil genera and species of Neuropterida per country recorded in South America.

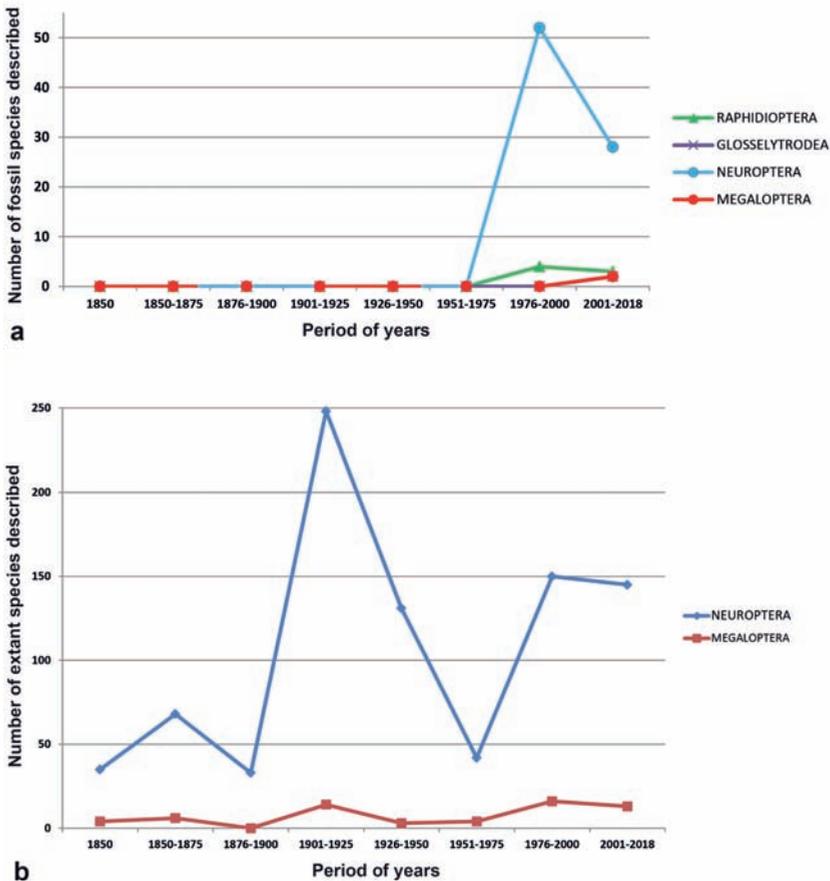
Order (Family: Subfamily)	Genus	Number of species per Country	
		Argentina	Brazil
Glosselytrodea (Glosselytridae)	1. <i>Argentinoglosselytrina</i> Martins-Neto & Gallego, 2001	1	
	2. <i>Chanarelytrina</i> Martins-Neto & Gallego, 2006	1	
Megaloptera (Corydalidae)	3. <i>Cratocorydalopsis</i> Jepson & Heads, 2016		1
	4. <i>Lithocorydalus</i> Jepson & Heads, 2016		1
Raphidioptera (Baissopteridae)	5. <i>Austroraphidia</i> Willmann, 1994		1
	6. <i>Baissoptera</i> Martynova, 1961		4
Raphidioptera ( <i>incertae sedis</i> )	7. <i>Caririraphidia</i> Martins-Neto, 2003		2
Neuroptera (Araripeneuridae)	8. <i>Araripeneura</i> Martins-Neto & Vulcano, 1989		5
	9. <i>Bleyeria</i> Martins-Neto, 1992		1
	10. <i>Caldasia</i> Martins-Neto & Vulcano, 1989		1
	11. <i>Caririneura</i> Martins-Neto & Vulcano, 1989		2
	12. <i>Cratoalloneura</i> Martins-Neto, 1992		2
	13. <i>Cratoneura</i> Martins-Neto, 1992		4
	14. <i>Cratopteryx</i> Martins-Neto & Vulcano, 1989		2
	15. <i>Diegopteryx</i> Martins-Neto & Rodrigues, 2010		1
	16. <i>Paracaririneura</i> Martins-Neto & Vulcano, 1997		1
Neuroptera (Ascalaphidae)	17. <i>Cratoscalapha</i> Martins-Neto & Vulcano, 1997		1
Neuroptera (Babinskaiidae)	18. <i>Babinskaia</i> Martins-Neto & Vulcano, 1989		2
	19. <i>Neliana</i> Martins-Neto, 1992		2
	20. <i>Parababinskaia</i> Makarkin et al., 2017		1
Neuroptera (Berothidae: Cyrenoberothisinae)	21. <i>Araripeberotha</i> Martins-Neto & Vulcano, 1990		1
	22. <i>Caririberotha</i> Martins-Neto & Vulcano, 1990		1
Neuroptera (Chrysopidae: Limaiinae)	23. <i>Araripechrysa</i> Martins-Neto & Vulcano, 1989		1
	24. <i>Caririchrysa</i> Martins-Neto & Vulcano, 1989		1
	25. <i>Limaia</i> Martins-Neto & Vulcano, 1988		2
	26. <i>Mesypochrysa</i> Martinov, 1927		2
Neuroptera (Corydasialidae)	27. <i>Cratochrysa</i> Martins-Neto, 1994		3
Neuroptera ( <i>incertae sedis</i> )	28. <i>Brasilopsychopsis</i> Rumbucher, 1995		1
	29. <i>Cratopsychopsis</i> Rumbucher, 1995		1
	30. <i>Cratosisyrops</i> Martins-Neto, 1997		1
Neuroptera (Ithonidae)	31. <i>Principiala</i> Makarkin & Menon, 2007		1
Neuroptera (Kalligrammatidae)	32. <i>Makarkinia</i> Martins-Neto, 1997		2

Order (Family: Subfamily)	Genus	Number of species per Country	
		Argentina	Brazil
Neuroptera (Mesochrysopidae: Allopterinae )	33. <i>Cratovoluptia</i> Martins-Neto & Rodrigues, 2009		1
	34. <i>Karenina</i> Martins-Neto, 1997		4
	35. <i>Triangulochrysopa</i> Nel et al., 2005		1
Neuroptera (Mesochrysopidae: <i>incertae sedis</i> )	36. <i>Dryellina</i> Martins-Neto & Rodrigues, 2009		1
Neuroptera (Nemopteridae: <i>incertae sedis</i> )	37. <i>Cratonemopteryx</i> Martins-Neto, 1992		3
	38. <i>Krika</i> Martins-Neto, 1992		1
Neuroptera (Nemopteridae: Roeslerianinae)	39. <i>Roesleriana</i> Martins-Neto, 1997		1
Neuroptera (Nymphidae)	40. <i>Araripenymphes</i> Menon et al., 2005		1
	41. <i>Olindanymphes</i> Martins-Neto, 2005		1
	42. <i>Santananymphe</i> Martins-Neto, 2005		1
	43. <i>Cratosmylus</i> Myskowiak et al., 2015		1
Neuroptera (Osmylidae: Gumillinae)	44. <i>Nuddsia</i> Menon & Makarkin, 2008.		2
Neuroptera (Palaeoleontidae)	45. <i>Araripeleon</i> Millet & Nel, 2010		1
	46. <i>Neurastenyx</i> Martins-Neto & Vulcano, 1997		5
	47. <i>Paraneurastenyx</i> Martins-Neto, 1998		1
	48. <i>Parapalaeoleon</i> Menon & Makarkin, 2008		1
Neuroptera (Permithonidae)	49. <i>Permipsythone</i> Pinto & de Ornellas, 1980		1
Neuroptera (Pseudonymphidae)	50. <i>Blittersdorffia</i> Martins-Neto & Vulcano, 1989		5
	51. <i>Pseudonymphes</i> Martins-Neto & Vulcano, 1989		4
Neuroptera (Psychopsidae)	52. <i>Pulchroptilonia</i> Martins-Neto, 1997		1
	53. <i>Putzneura</i> Martins-Neto, 2010		1
<b>Total species</b>		<b>2</b>	<b>89</b>
<b>Total genera</b>		<b>2</b>	<b>51</b>

the South American region (OSWALD 2019). The small order Glosselytroidea has only two fossil species of two genera that belong to Glosselytridae; Raphidioptera is also known in the South American continent only through fossil species; there are seven species of three genera considered *incertae sedis* or belonging to Baissopteridae; Megaloptera is the second order in number of species recorded in South America; there are 60 extant species from seven genera of Corydalidae and Sialidae, plus two fossil species of two genera in Corydalidae (OSWALD 2019). The order Neuroptera dominates the South American Neuropterida in species richness: there are 860 extant species of 128 genera from 11 families, plus 80 fossil species of 46 genera from 16 families, highlighting the great diversity present in the lower Cretaceous Crato Formation of Ceará State, Brazil (OSWALD 2019).

Chrysopidae is the Neuropterida family with the greatest diversity in South America; extant species of green lacewing represent 35 % of all Neuropterida diversity in this region. Chile, Venezuela and Argentina have the greatest number of extant Neuropterida families in South America, while Brazil, Argentina, Colombia and Peru have the greatest number of extant genera in the region (Table 1). South American fossil species have been recorded in only Brazil and Argentina (Table 2).

Brazil has the greatest number of Neuropterida species with 446 extant and 89 fossil species (MACHADO 2019; OSWALD 2019), and it is estimated that the number of recorded species will at least double over the next few years (FREITAS & PENNY 2012). Countries of the north-eastern region of South America have the lowest diversity of families and genera (Tables 1, 2); French Guiana and Guyana have no record with respect to seven families of Neuropterida (Sialidae, Coniopterygidae, Sisyridae, Osmylidae, Di-



**Figure 1.** Number of South American Neuropterida species described over the years. a – Fossil species; b – extant species.

laridae, Hemerobiidae and Nemopteridae) that occur in nearby countries, whereas Ecuador and Suriname have a low diversity of Neuropterida. The scarcity of records in the sub-region is probably due to the lack of studies in these countries.

Approximately 1.7 million species have been named since Linnaeus, and it is estimated that there is still about 90 % of the world biota to be described (WILSON 2000; DISNEY 2000), including part of Neuropterida fauna. There is still an unknown, presumably huge diversity of the Neuropterida in South America which needs more study. Ithonidae has records only from Chile, Nemopteridae and Berothidae have records from five South American countries, and Sialidae and Dilaridae have records from only seven countries of South America; only Corydalidae, Chrysopidae, Mantispidae and Myrmeleontidae have records from all South American countries. As to the immature stages of South American Neuropterida, probably only 10 % is known.

The South American fauna is still practically unknown. We can cite as an example recent studies of Osmylidae; in the last five years, the number of species that have been recorded in South America increased from 13 to 26, and the first Osmylidae larvae for this region were described as well (ARDILA-CAMACHO & NORIEGA 2014; MARTINS et al. 2016, 2018, 2019).

The number of fossil species of Neuropterida described grew considerably between 1976 and 2000 and has remained relatively high in the last 18 years (Fig. 1a). The greatest number of descriptions of South American Neuropterida species occurred during the years 1901–1925, probably due to the descriptions by Longinos Navás. After this period, there was a long decline in the number of descriptions in the period intermittent between the two World Wars (Fig. 1b). Recently, from the year 1975 onwards, a new increase in the number of descriptions of South American Neuropterida species (Fig. 1b) occurred which has been maintained despite the taxonomic impediment.

Forthcoming studies of South American Neuropterida should focus on data on immature stages, as well as on the fauna belonging to the countries of the north-eastern and southern sub-regions of South America. Studies with fossils should be carried out in the lower Cretaceous Crato Formation of Ceará State, Brazil, because there is a great diversity of Neuropterida fossils in that site; nevertheless, it is also important to carry out studies in other areas of other South American countries.

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# The impact of windthrow and forest fire on Neuropterida and Mecoptera

Peter Duelli<sup>1</sup>, Beat Wermelinger<sup>2</sup>, Marco Moretti<sup>1</sup> & Martin K. Obrist<sup>1</sup>

<sup>1</sup> WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Biodiversity and Conservation Biology, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland; peter.duelli@wsl.ch, marco.moretti@wsl.ch, martin.obrist@wsl.ch

<sup>2</sup> WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Forest Health and Biotic Interactions, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland; beat.wermelinger@wsl.ch

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**Abstract.** The impact of forest fires and windthrow on species compositions in the Neuroptera, Raphidioptera, and Mecoptera was assessed in Swiss forests using standardized flight interception traps. As a result, 82 % of the 50 species benefited from the disturbance and became more abundant in the years after the fire or windthrow. Only 11 species, mainly Hemerobiidae and Coniopterygidae, peaked in the undisturbed forest stands. We conclude that for Neuropterida and Mecoptera catastrophic incidences are natural ecological events which create new habitats and by this foster their occurrence and abundance.

The full manuscript to this summary has been published during the preparation of these Proceedings; see DUELLI et al. (2019).

**Further key words.** Neuroptera, Raphidioptera, natural disturbance, wind-fell, blow-down, wildfire, insects, Switzerland

## Introduction

The vast majority of European Neuropterida and Mecoptera develop and live in forests and other arboreal habitats (ASPÖCK et al 1980), with a preference for forest edges (DUELLI et al. 2002). We investigated the impact of massive disturbances such as forest fires and windthrows on the population dynamics of Neuroptera, Raphidioptera, and Mecoptera.

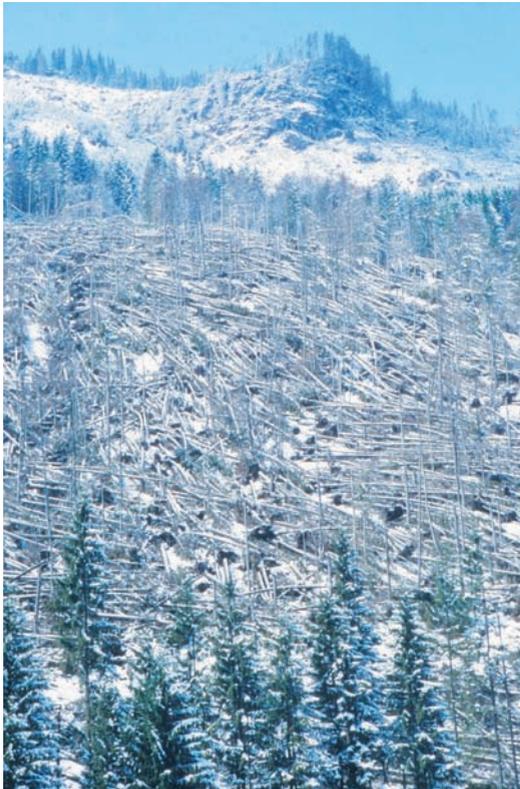
## Methods

In four independent projects carried out in Switzerland, all based on accidental natural disturbances, the differences in species composition and relative abundances of arthropod species were monitored with standardized flight interception traps (MORETTI et al. 2006; WERMELINGER et al. 2017).

In each project, two levels of disturbance were compared with controls in undisturbed forests. In the two windthrow projects (storm Vivian 1990, Figs 1–3; storm Lothar 1999, Figs 4, 5), the plots where the wind-felled trees were not removed after the storm were termed as intermediately disturbed (ID, Figs 2, 4) and the timber-harvested forest plots

as heavily disturbed (HD, Figs 3, 5). In all four projects the controls were trap stations in undisturbed forest. In the winter fire project in Ticino, the intermediately disturbed plots had only burned once in the previous 40 years (Fig. 6), while the intensely disturbed plots had burned several times. Figure 7 shows a trap station in an unburned chestnut control plot. In the summer fire project in Leuk in south-western Switzerland, where in 2003 a forest fire destroyed the forest on an entire mountain slope, the intensely disturbed plots were chosen from the center of the burned area (Fig. 8), the traps for intermediately disturbed plots stood within 10 m to the edges of unburned forest, and the control plots were chosen from areas of intact forest (Fig. 9). The windthrow plots after the storm Vivian (1990) were sampled from mid-May to late September in the years 1992, 1993, 1994, 1996. The windthrow plots after the storm Lothar (1999) were sampled from late March to late September in the years 2000, 2001, 2002. The forest fire plots in Ticino were sampled from mid-March to late September 1997. The forest fire (2003) plots above Leuk (Valais) were sampled from early May to early September in the years 2004, 2005, 2006, 2008. The traps were emptied weekly.

There were twice as many traps in disturbed plots (ID and HD) than in the control plots (FO), so the numbers of specimens in the intact forest plots (FO) had to be doubled to compare the numbers in disturbed and undisturbed plots. As an indicator for



**Figure 1.** Windthrow above Schwanden, Canton Glarus, Switzerland, caused by storm Vivian during February 1990, affecting mainly conifer forests in the Alps. Photo: © WSL (1991)



**Figure 2.** Window flight interception trap with water tray below glass screen and yellow pan trap in an uncleared Vivian windthrow (ID) plot in the Alps (Schwanden, Canton Glarus, Switzerland). Second year after the storm. Photo: © WSL (1992)



**Figure 3.** Cleared windthrow (HD) plot with trap station in the second year after storm Vivian. Even in cleared plots there is much dead wood (trunks and slash) remaining. Photo: © WSL 1992.



**Figure 4.** Storm Lothar in winter 1999 affected mainly deciduous forests in the lowlands of Switzerland. Uncleared forest (ID) plot near Habsburg, Canton Aargau, Switzerland, with combi-trap (plexiglass cross window flight interception trap above yellow funnel filled with water) and pitfall trap for epigeal arthropods. Photo: © Beat Wermelinger (2003)



**Figure 5.** Cleared windthrow plot (HD) three years after storm Lothar on the Swiss Plateau near Messen, Canton Solothurn, Switzerland. Photo: © Beat Wermelinger (1992)



**Figure 6.** Combi-trap above Locarno, Canton Ticino, Switzerland, four years after the last of several fires (HD plot), just before bud burst in spring. Regrowth in chestnut forests is very fast. Photo: © Marco Moretti (1997)



**Figure 7.** Refilling a combi-trap in an intact (FO, no fire in the previous 40 years) chestnut forest. The whole trap device can be tilted to pour the water with insects through a filter into a bucket. The insects are transferred with forceps from the filter into alcohol vials. Photo: © Denise Wyniger (1997)



**Figure 8.** Trap station in the center (HD) of a large pine forest area burned in 2003 above Leuk, Canton Valais, Switzerland. One year after the fire there is hardly any regrowth visible, but in the following years a colorful flora appeared. Photo: © Marco Moretti (2006)



**Figure 9.** Combi-trap in an unburned part (FO) of the forest above Leuk. The southerly exposed slopes of the Valais Valley are the most species-rich habitats for insects in Switzerland, including Neuropterida. Photo: © Marco Moretti (2006)

the effect of disturbance in general, the following formula was used for each species:  $\text{mean (HD + ID)} / [\text{mean (HD + ID)} + \text{FO}]$ . Species with more than 66 % are considered winners, those with less than 33 % losers. Species rating in between were not affected or considered indifferent to the midterm effects of storms or fires. A 100 % winner species means that all specimens of that species were collected in disturbed plots, while a loser species (0 %) was not caught at all in the disturbed plots in the years after the disturbances. Since the disturbances in the four projects occurred in different habitats, in different years, and in different climatic zones of Switzerland, the species composition was too variable to allow statistical treatment. Only a few species were common to all four projects.

### Results and Discussion

For the summary presented here (Table 1), all the data of the four projects were combined per species, but analyzed separately for the three disturbance categories, *i.e.*, intermediately disturbed plots (ID), heavily disturbed plots (HD), and control plots in undisturbed forest (FO).

A total of 79 species and 8 285 specimens of Neuropterida and Mecoptera were collected. However, only 50 species represented by five or more individuals were included in the analysis. The species that can be considered ‘winners’ were those with more specimens collected in disturbed plots than in the intact forest (Table 1).

In summary, 28 species above 66 % were rated as winners, 9 species were losers in the sense that their abundance was less than 33 % in the disturbed areas, and 13 species were ranking indifferent, between 33 % and 66 %. More species (20) had a higher abundance (bold print in Table 1) in intermediately disturbed (ID) plots than in heavily disturbed (HD) areas (17). Only 11 species, mainly Hemerobiidae and Coniopterygidae, peaked in the undisturbed forests (FO).

**Chrysopidae.** Almost all winners among the green lacewings are well-known forest edge species (DUELLI et al. 2002). Clear losers among the Chrysopidae were *Chrysotropa ciliata*, living in moist forests, and *Peyerimhoffina gracilis*, restricted to shady conifer forests.

**Hemerobiidae.** It was a surprise to see so many brown lacewing species ranking high up as winners after disturbances, because brown lacewings are generally known to neuropterologists to prefer the forest interior (*e.g.*, DUELLI et al. 2002). Among the losers, the genus *Symphorobius* was dominant.

**Coniopterygidae.** The dustywings showed the highest proportion of losers, also in terms of individuals.

**Myrmeleontidae.** The two antlion species were favored by the mid-term effects of fire.

**Raphidiidae.** The two most common snakefly species were winners. Dead bark of trees and trunks was an excellent habitat for their larvae.

**Panorpidae.** The two most abundant scorpionfly species were indifferent to disturbance, whereas the others were winners.

**Table 1.** List of species with five or more individuals collected in the three treatments. FO – intact forest; ID – intermediately disturbed forest; HD – heavily disturbed forest; n – Total number of specimens per species. Bold: treatment with the highest number of individuals caught. [% d.p.] – percentage of individuals caught in disturbed plots; Species >66% are considered winners, those <33% losers.

Species	[% d.p.]	n	FO	ID	HD
Neuroptera: Chrysopidae					
<i>Chrysopa formosa</i> Brauer, 1850	100 %	25		<b>17</b>	8
<i>Chrysopa pallens</i> (Rambur, [1838])	100 %	7		2	<b>5</b>
<i>Nineta flava</i> (Scopoli, 1763)	100 %	5		5	
<i>Pseudomallada prasinus</i> (Burmeister, 1839)	100 %	145		<b>76</b>	69
<i>Pseudomallada ventralis</i> (Curtis, 1834)	100 %	24		<b>16</b>	8
<i>Chrysopa perla</i> (Linnaeus, 1758)	97 %	229	4	101	<b>124</b>
<i>Chrysoperla lucasina</i> (Lacroix, 1912)	96 %	267	6	124	<b>137</b>
<i>Pseudomallada abdominalis</i> (Brauer, 1865)	85 %	12	1	3	<b>8</b>
<i>Pseudomallada flavifrons</i> (Brauer, 1851)	83 %	53	5	<b>38</b>	10
<i>Cunctochrysa albolineata</i> (Killington, 1935)	78 %	8	1	<b>4</b>	3
<i>Chrysoperla carnea</i> (Stephens, 1836)	65 %	537	113	196	<b>228</b>
<i>Hypochochrysa elegans</i> (Burmeister, 1839)	58 %	26	7	<b>10</b>	9
<i>Nothochrysa fulviceps</i> (Stephens, 1836)	43 %	5	<b>2</b>	1	<b>2</b>
<i>Chrysoperla pallida</i> Henry et al., 2002	40 %	139	<b>59</b>	39	41
<i>Chrysotropia ciliata</i> (Wesmael, 1841)	23 %	86	<b>54</b>	16	16
<i>Peyerimhoffina gracilis</i> (Schneider, 1851)	13 %	13	<b>10</b>	1	2
<b>n individuals</b>		1581	262	649	670
<b>n species with ≥5 individuals</b>		16	11	16	15
Neuroptera: Hemerobiidae					
<i>Megalomus tortricoides</i> Rambur, 1842	100 %	5		2	<b>3</b>
<i>Wesmaelius subnebulosus</i> (Stephens, 1836)	83 %	142	13	41	<b>88</b>
<i>Wesmaelius malladai</i> (Navás, 1925)	81 %	85	9	34	<b>42</b>
<i>Micromus paganus</i> (Linnaeus, 1767)	81 %	47	5	16	<b>26</b>
<i>Megalomus hirtus</i> (Linnaeus, 1758)	80 %	9	1	4	<b>4</b>
<i>Micromus angulatus</i> (Stephens, 1836)	80 %	9	1	5	3
<i>Micromus variegatus</i> (Fabricius, 1793)	78 %	73	9	<b>29</b>	<b>35</b>
<i>Hemerobius lutescens</i> Fabricius, 1793	74 %	40	6	15	<b>19</b>
<i>Hemerobius humulinus</i> Linnaeus, 1758	70 %	124	22	28	<b>74</b>
<i>Drepanopteryx phalaenoides</i> (Linnaeus, 1758)	70 %	10	3		7
<i>Hemerobius micans</i> Olivier, 1792	48 %	235	82	<b>100</b>	53
<i>Symphorobius klapaleki</i> Zelený, 1963	18 %	23	<b>16</b>	6	1
<i>Hemerobius pini</i> Stephens, 1836	13 %	16	<b>14</b>	2	
<i>Symphorobius fuscescens</i> (Wallengren, 1863)	13 %	8	7		1
<i>Symphorobius pellucidus</i> (Walker, 1853)	0 %	12	<b>12</b>		
<b>n individuals</b>		838	200	282	356
<b>n species with ≥5 individuals</b>		15	14	12	13

Species	[% d.p.]	n	FO	ID	HD
Neuroptera: Coniopterygidae					
<i>Coniopteryx esbenpeterseni</i> Tjeder, 1930	91 %	22	1	10	11
<i>Parasemidalis fuscipennis</i> (Reuter, 1894)	90 %	20	1	16	3
<i>Coniopteryx borealis</i> Tjeder, 1930	67 %	5	1	3	1
<i>Coniopteryx tineiformis</i> Curtis, 1834	57 %	66	18	30	18
<i>Coniopteryx haematica</i> McLachlan, 1868	50 %	6	2	3	1
<i>Coniopteryx drammonti</i> Rousset, 1964	33 %	10	5	4	1
<i>Semidalis aleyrodiformis</i> (Stephens, 1836)	31 %	305	161	105	39
<i>Coniopteryx pygmaea</i> Enderlein, 1906	24 %	54	33	10	11
<i>Conwentzia psociformis</i> (Curtis, 1834)	0 %	6	6		
<b>n individuals</b>		494	228	181	85
<b>n species with ≥5 individuals</b>		9	9	8	8
Neuroptera: Myrmeleontidae					
<i>Distoleon tetragrammicus</i> (Fabricius, 1798)	94 %	32	1	19	12
<i>Myrmeleon formicarius</i> Linnaeus, 1767	75 %	12	3	9	
<b>n individuals</b>		44	4	28	12
<b>n species with ≥5 individuals</b>		2	2	2	1
Raphidioptera: Raphidiidae					
<i>Phaeostigma notata</i> (Fabricius, 1781)	91 %	311	14	164	133
<i>Dichrostigma flavipes</i> (Stein, 1863)	88 %	710	46	419	245
<i>Puncha ratzeburgi</i> (Brauer, 1876)	60 %	16	4	6	6
<b>n individuals</b>		1037	64	585	381
<b>n species with ≥5 individuals</b>		3	3	3	3
Mecoptera: Panorpidae					
<i>Panorpa cognata</i> Rambur, 1842	87 %	28	2	9	17
<i>Panorpa alpina</i> Rambur, 1842	74 %	425	64	174	187
<i>Panorpa vulgaris</i> Imhoff & Labram, 1845	67 %	5	1	3	1
<i>Panorpa communis</i> Linnaeus, 1758	61 %	1904	462	673	769
<i>Panorpa germanica</i> Linnaeus, 1758	55 %	1929	555	792	582
<b>n individuals</b>		4291	1084	1651	1556
<b>n species with ≥5 individuals</b>		5	5	5	5
<b>n individuals (all taxa)</b>		8285	1647	3279	2931
<b>n species (all taxa) with ≥5 ind.</b>		50	44	46	45
<b>n species (all taxa) incl. "rare" species</b>		79	59	60	58

## Conclusion

The combined results of our four projects suggest that strong natural disturbances such as windthrow or wildfire, which humans consider to be catastrophes, are positive for most Neuroptera, Raphidioptera, and Mecoptera, by increasing their abundance in the years after fires and windthrows.

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# Raphidioptera and Neuroptera (Insecta: Neuropterida) in three National Parks in the Balkan Peninsula: Results of short collection trips

Dušan Devetak<sup>1,5</sup>, Predrag Jakšić<sup>2</sup>, Vesna Klokočovnik<sup>1</sup>, Tina Klenovšek<sup>1</sup>, Jan Podlesnik<sup>1</sup>, Franc Janžekovič<sup>1</sup>, Ana Nahirnić<sup>3</sup> & Hubert Rausch<sup>4</sup>

<sup>1</sup> Department of Biology & Institute for Biology, Ecology and Nature Conservation, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, 2000 Maribor, Slovenia

<sup>2</sup> Čingrijina 14/25, Zvezdara, 11000 Beograd, Serbia

<sup>3</sup> National Museum of Natural History, Bulgarian Academy of Sciences, Tsar Osvoboditel Blvd 1, 1000 Sofia, Bulgaria

<sup>4</sup> Naturkundliche Gesellschaft Mostviertel – ngm, Uferstrasse 7, 3270 Scheibbs, Austria

<sup>5</sup> Corresponding author: dusan.devetak@guest.arnes.si

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**Abstract.** During the course of three Balkan neuropterological expeditions in 2014, 2015 and 2017, short visits to three national parks were conducted. A survey of the collected neuropterid species (Neuropterida: Raphidioptera, Neuroptera) in the Fir of Drenova National Park, Albania, the Tara National Park, Serbia, and the Pelister National Park, North Macedonia, is presented. The distribution and ecological traits of some rare and interesting lacewing species are discussed.

**Further key words.** Nature conservation, Albania, North Macedonia, Serbia, *Phaeostigma thaleri*, *Hemerobius schedli*

## Introduction

In some parts of the Balkan Peninsula, the Neuropterida are still insufficiently known and before this study, almost no survey has been made for any national park in the Western Balkan. In the past, only the Durmitor National Park in Montenegro has been surveyed thoroughly (DEVETAK 1991). From 2014 to 2017, zoologists from the Department of Biology of the University in Maribor, Slovenia, organized four neuropterological expeditions to Albania, North Macedonia and Serbia (KLOKOČOVNIK & DEVETAK 2015; DEVETAK 2016; DEVETAK & RAUSCH 2016; DEVETAK et al. 2017).

In June 2014, a one-day visit was made to the Fir of Drenova National Park, Albania (Albanian: *Parku Kombëtar Bredhi i Drenovës*; geographic coordinates: 40°34'08"N 20°48'59"E, altitudinal range 980–1 806 m above sea level). The park with an area of 10.3 km<sup>2</sup> is located in south-eastern Albania, near Korçë (Fig. 1). Characteristic are Illyrian deciduous forests and Dinaric Alpine mixed forests, dominated by the silver fir *Abies alba* Mill. (Figs 2a, b). Prior to our study, no lacewings had been recorded in this national park.

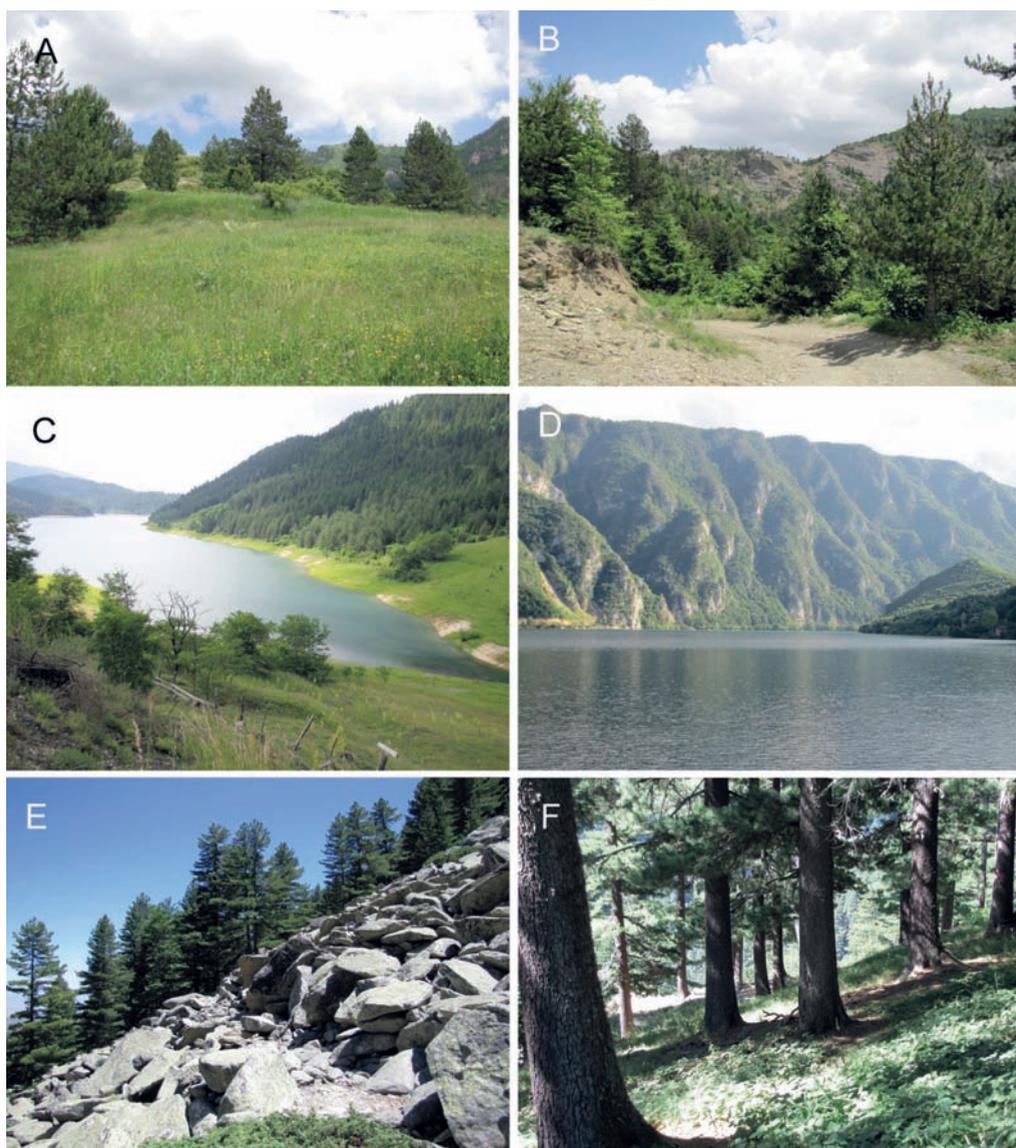
In June 2015, a two days' excursion was made to the Tara National Park, Serbia (Serbian: *Nacionalni park Tara*; 43°54'18"N 19°24'13"E; 250–1591 m a.s.l.). The park in western Serbia is delimited from Bosnia and Herzegovina by the river Drina with the Perućac lake (Perućačko jezero; Fig. 1). A large area of the park, comprising 376 km<sup>2</sup> is covered with deciduous, mixed and coniferous forests. Characteristic is the endemic "Pančić's spruce" *Picea omorika* (Pančić) Purk. (Figs 2c, d) Prior to our study, only one literature report on the presence of *Sisyra nigra* in the national park was known (PODLESNIK et al. 2017).

In July 2017, a one-day visit was conducted to the Pelister National Park, North Macedonia (Macedonian: *Nacionalen park Pelister*; 40°58'52"N 21°11'28"E; 927–2601 m a.s.l.). The park comprising 172 km<sup>2</sup> is positioned in the southern part of the country, in the Municipality of Bitola. Characteristic are coniferous forests composed mainly of five-needle pine *Pinus peuce* Griseb. (Macedonian or Balkan pine; Macedonian: Mo-



**Figure 1.** Position of the three national parks investigated in this study in the Balkan Peninsula. AL – Albania, MK – North Macedonia, SR – Serbia.

lika), endemic for the Balkan Peninsula (Figs 2e, f). Prior to our study, one single report on the occurrence of *Palpares libelluloides* in the area existed (DEVETAK 1996).



**Figure 2.** Habitats in the three National Parks. A, B – Fir of Drenova National Park, Albania; A: Coniferous trees where *Parvoraphidia microstigma* occurred; B: Pine trees, a habitat of *Phaeostigma thaleri*. C, D – Tara National Park, Serbia; C: In the surroundings of the Zaovine lake *Chrysopa gibeauxi* was found; D: Forests along the river Drina provide habitats for many lacewing species. E, F – Pelister National Park, North Macedonia; E: Endemic *Pinus peuce* is a substrate for *Hemerobius schedli*; F: *Pinus peuce*-forest was a collecting place of *Dilar turcicus*. Photos: DD

The aim of the study was to complete the knowledge on the inventory of the neuropterid fauna in Albania, North Macedonia and Serbia, which, at that time, had a sparse knowledge on their lacewing fauna.

### Material and methods

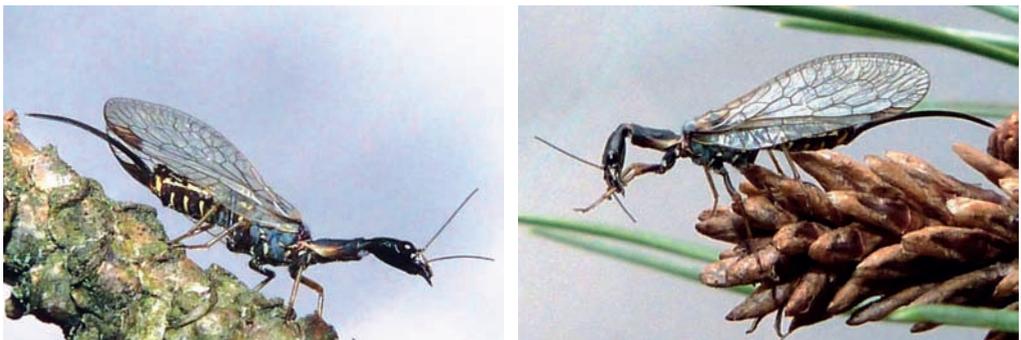
Lacewings were collected using insect net in the three national parks during short visits in a period 2014-2017 (Drenova: 27.vi.2014, Tara: 26–27.vi.2015, Pelister: 06.vii.2017). Insects are preserved in the first author's collection. We followed the nomenclature and taxonomy proposed by *Lacewing Digital Library* (OSWALD 2017). A distribution map was provided with Copernicus Land Monitoring Service.

### Results and discussion

During two-days or one-day samplings, relatively high numbers of lacewing species were collected in all three national parks, viz. 26 species in the Fir of Drenova National Park, 29 species in the Tara National Park, and 30 species in the Pelister National Park (Table 1). In all three national parks, the most abundant were green (Chrysopidae) and brown lacewings (Hemerobiidae), and solely in the Tara National Park, spongillaflies (Sisyridae) occurred in large numbers. The neuropterid fauna of the three national parks was similar in the number of species but differed in the species composition (Table 1).

In the Fir of Drenova National Park, three interesting snakefly species were noted. *Phaeostigma (Phaeostigma) pilicollis* (1♂, 1♀) was found in a mixed forest with *Abies alba* Mill., *Acer obtusatum* Willd., *Fagus sylvatica* L. and *Pinus nigra* Arnold at 1 375 m a.s.l. It is a snakefly with Balkano-Pontomediterranean distribution, known from Albania, North Macedonia, Greece, Bulgaria and European Turkey.

*Parvoraphidia microstigma* (2♀) occurred in a mixed forest and forest edge at 1 130–1 375 m a.s.l. This species with a Pontomediterranean distribution was recorded in Albania, North Macedonia and Greece.



**Figure 3.** Two females of *Phaeostigma thaleri* in the Fir of Drenova National Park, Albania. Photos: HR

**Table 1.** Neuropterida collected in three national parks in 2014, 2015 and 2017. AL – Fir of Drenova National Park, Albania; SR – Tara National Park, Serbia; MK – Pelister National Park, North Macedonia. \*See PODLESNIK et al. (2017); \*\* Collected in 1988 (DEVETAK 1996).

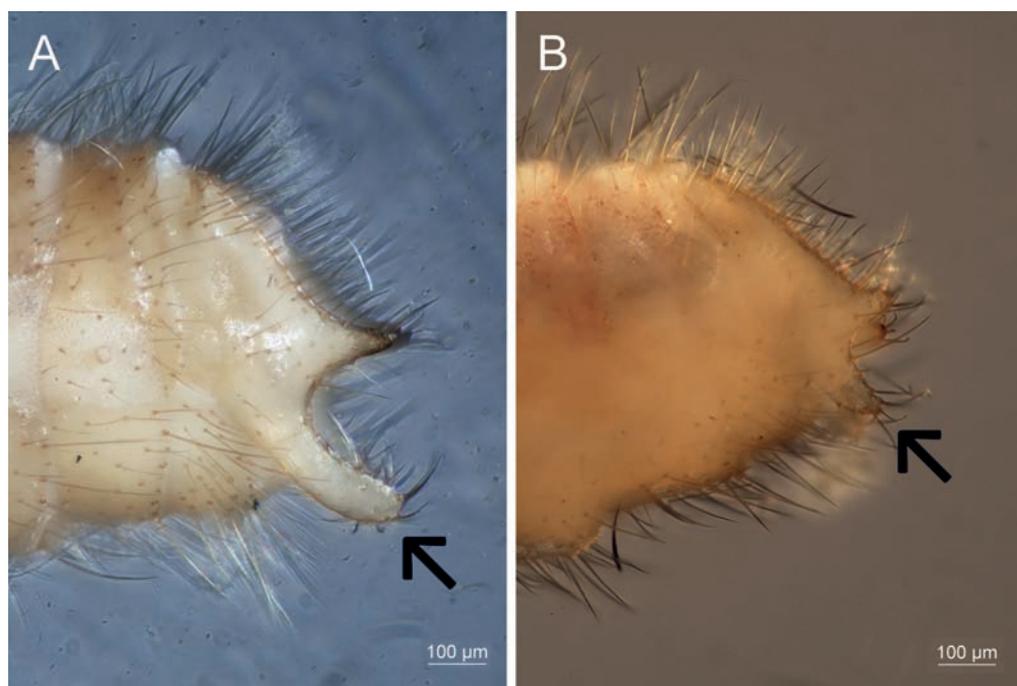
Taxon / Species	AL	SR	MK
Raphidioptera			
Raphidiidae			
<i>Phaeostigma (Phaeostigma) pilicollis</i> (Stein, 1863)	X		
<i>Phaeostigma thaleri</i> (Aspöck & Aspöck, 1964)	X		
<i>Dichrostigma flavipes</i> (Stein, 1863)	X		
<i>Parvoraphidia microstigma</i> (Stein, 1863)	X		
Neuroptera			
Osmyliidae			
<i>Osmylus fulvicephalus</i> (Scopoli, 1763)	X	X	X
Chrysopidae			
<i>Nothochrysa fulviceps</i> (Stephens, 1836)			X
<i>Nothochrysa capitata</i> (Fabricius, 1793)	X		X
<i>Hypochrysa elegans</i> (Burmeister, 1839)		X	
<i>Nineta flava</i> (Scopoli, 1763)			X
<i>Nineta principiae</i> Monserrat, 1981		X	
<i>Chrysopa perla</i> (Linnaeus, 1758)	X	X	X
<i>Chrysopa dorsalis</i> Burmeister, 1839	X	X	
<i>Chrysopa gibeauxi</i> (Leraut, 1989)		X	
<i>Pseudomallada flavifrons flavifrons</i> (Brauer, 1851)	X		X
<i>Pseudomallada prasinus</i> (Burmeister, 1839)		X	X
<i>Pseudomallada abdominalis</i> (Brauer, 1856)		X	X
<i>Pseudomallada ventralis</i> (Curtis, 1834)	X		X
<i>Cunctochrysa albolineata</i> (Killington, 1935)			X
<i>Peyerimhoffina gracilis</i> (Schneider, 1851)	X		X
<i>Chrysoperla</i> cf. <i>carnea</i> (Stephens, 1836) s.str.	X	X	
<i>Chrysoperla lucasina</i> (Lacroix, 1912)	X	X	X
<i>Chrysoperla pallida</i> Henry, Brooks, Duelli & Johnson, 2002	X		X
<i>Chrysoperla</i> cf. <i>agilis</i> Henry, Brooks, Duelli & Johnson, 2003			X
Hemerobiidae			
<i>Hemerobius humulinus</i> Linnaeus, 1758		X	X
<i>Hemerobius stigma</i> Stephens, 1836	X		X
<i>Hemerobius pini</i> Stephens, 1836		X	
<i>Hemerobius contumax</i> Tjeder, 1932	X		
<i>Hemerobius schedli</i> Hölzel, 1970			X
<i>Hemerobius handschini</i> Tjeder, 1957	X	X	
<i>Hemerobius micans</i> Olivier, 1793	X	X	X
<i>Hemerobius lutescens</i> Fabricius, 1793			X
<i>Hemerobius gilvus</i> Stein, 1863			X

Taxon / Species	AL	SR	MK
<i>Wesmaelius subnebulosus</i> (Stephens, 1836)	X		
<i>Symphorobius fuscescens</i> (Wallengren, 1863)		X	
<i>Megalomus tortricoides</i> Rambur, 1842	X	X	
<i>Micromus variegatus</i> (Fabricius, 1793)			X
<i>Micromus angulatus</i> (Stephens, 1836)		X	
<i>Micromus paganus</i> (Linnaeus, 1767)			X
<i>Micromus lanosus</i> (Zelený, 1962)		X	X
Sisyridae			
<i>Sisyra nigra</i> (Retzius, 1783)		X*	
Coniopterygidae			
<i>Aleuropteryx loewii</i> Klapálek, 1894	X	X	
<i>Helicoconis (Helicoconis) lutea</i> (Wallengren, 1871)		X	
<i>Helicoconis (Ohmopteryx) pseudolutea</i> Ohm, 1965		X	
<i>Helicoconis</i> sp.			X
<i>Coniopteryx (Coniopteryx) pygmaea</i> Enderlein, 1906	X		
<i>Coniopteryx (Metaconiopteryx) arcuata</i> Kis, 1965		X	
<i>Coniopteryx (Metaconiopteryx) esbenpeterseni</i> Tjeder, 1930		X	
<i>Coniopteryx (Metaconiopteryx) lentiae</i> Aspöck & Aspöck, 1964		X	
<i>Coniopteryx</i> sp.			X
<i>Conwentzia pineticola</i> Enderlein, 1905		X	X
<i>Semidalis aleyrodiformis</i> (Stephens, 1836)		X	
Dilaridae			
<i>Dilar turcicus</i> Hagen, 1858			X
Myrmeleontidae			
<i>Palpares libelluloides</i> (Linnaeus, 1764)			X**
<i>Myrmeleon formicarius</i> Linnaeus, 1767	X	X	X
<i>Euroleon nostras</i> (Geoffroy in Fourcroy, 1785)	X	X	
<i>Distoleon tetragrammicus</i> (Fabricius, 1798)	X		
Ascalaphidae			
<i>Libelloides macaronius</i> (Scopoli, 1763)	X		X
Total number of species	26	29	30

In the Fir of Drenova National Park, the most interesting snakefly species was *Phaestigma thaleri* (2♂, 1♀) (Fig. 3). A description of this species is based on a single male collected a century ago in Northern Albania (ASPÖCK & ASPÖCK 1964; PENTHER 1914). The recent spectacular finding (exactly 100 years after the first finding!) was the second record of the species and the first of the female (DEVETAK & RAUSCH 2016). This interesting species was collected on coniferous trees (*Pinus nigra*) and on *Salix*-bushes close to a rivulet, at an elevation of 1 015–1 425 m a.s.l.

In the Tara National Park, a finding of two green lacewing species, *Nineta principiae* (3♂) and *Chrysopa gibeauxi* (1♂) represented the first record of these two species in Serbia. Despite of the fact that *Nineta principiae* does not seem to be a rare species in Europe, it was previously known in the Balkan Peninsula only from Greece (ASPÖCK et al. 2001). Another species, *Chrysopa gibeauxi*, which was only recently reinstated as a valid species (TILLIER et al. 2014; DEVETAK et al. 2015; CANARD & THIERRY 2017) was known only in a few Balkan countries.

In the Pelister National Park, a record of two species was interesting. A dilarid species, *Dilar turcicus* (1♂), occurred in a *Pinus peuce*-forest at an elevation of 1 630 m. The presence of this species in North Macedonia has been already known (for a review of distribution, see ASPÖCK et al. 2015), but the endemic *Pinus peuce* was a new plant substrate species. A surprise was the occurrence of a brown lacewing, *Hemerobius schedli*, in large numbers of individuals (35♂, 32♀). This species is well distinguished from the closely related *Hemerobius handschini* by the shape of ectoproct. In *H. schedli*, anaprocessus and cataproctus of ectoproct are equally long (Fig. 4). *Hemerobius schedli* was collected on the five-needle pine molika *Pinus peuce* at an elevation of 1 205–1 738 m a.s.l. The finding of this species in the Pelister National Park is the first report for North Macedonia and the second locality in the Balkan Peninsula (for review of distribution, see POPOV et al. 2018).



**Figure 4.** Ectoprocts of A – *Hemerobius handschini* (Jasen Reserve, North Macedonia) and B – *Hemerobius schedli* (Pelister National Park, North Macedonia). The species differ in the length of the cataproctus (arrows). Photos: DD

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# Contribution to the knowledge of the Neuroptera of the Oriental region of Morocco

Bruno Michel<sup>1</sup> & Alexandre François<sup>2</sup>

<sup>1</sup> Cirad, CBGP (INRA, Cirad, IRD, Montpellier SupAgro, Univ. Montpellier), Montpellier, France; bruno.michel@cirad.fr

<sup>2</sup> Emirates Centre for Wildlife Propagation (ECWP), Missouri, Morocco; afrancois@ecwp-ma.org

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**Abstract.** Captures of Neuroptera were performed in the Oriental region of Morocco, carried out mainly in August using a light trap to inventory the neuropterous insects of the region. During this survey, we recorded 38 species of Myrmeleontidae, four species of Ascalaphidae, three species of Chrysopidae, and one species of Mantispidae, of Hemerobiidae and of Nemopteridae, respectively.

## Introduction

In Morocco, the Emirate Centre for Wildlife Propagation (ECWP) designs and implements an overall conservation strategy aiming to restore and preserve the native populations of the Houbara Bustard, *Chlamydotis undulata* (Jacquin, 1784), of North Africa. To achieve this goal, the ECWP has implemented multi-disciplinary research in areas varied as physiology, nutrition, veterinary medicine and ecology in the Oriental (north-eastern) region of Morocco where the bustard's populations are found. The Oriental region is delimited to the East by the border with Algeria, to the West by the Middle Atlas and to the South by the High Atlas (Fig. 1). It consists of a high plateau located at an average altitude of 1 000 to 1 200 m above sea level [a.s.l.]. Temperatures can fall to between -4°C and -9°C in winter (January–February), and rise to 44°C in summer (July–August). The annual rainfall is about 160 mm with a peak drought in July and especially August.

At the ECWP located close to the town of Missouri, an investigation project has been in place for several years to determine precisely the diet of the Houbara Bustard, which is known to be omnivorous and feed on plants, small vertebrates such as lizards and invertebrates. Regarding insects, several surveys were performed to know better the entomological fauna of the Oriental region in order to determine the species preyed on by the bustard. The purpose of the survey of Neuroptera was to complete the data that had earlier focussed on other insect groups such as Coleoptera: Tenebrionidae, Hymenoptera: Formicidae or Orthoptera found in this region of Morocco.

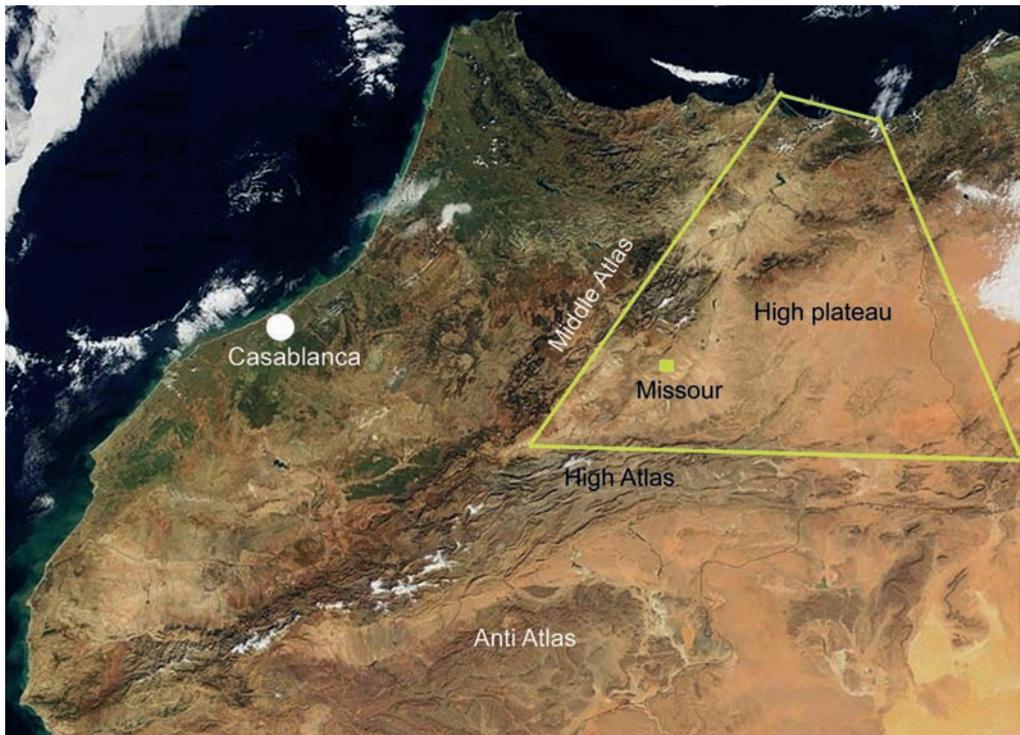
The first list of the Neuroptera of Morocco was published by MONSERRAT et al. (1990). Subsequently, several authors provided additional information (ASPÖCK & ASPÖCK 2009; ASPÖCK et al. 2001; BADANO & PANTALEONI 2012; FAUCHEUX et al. 2012; MICHEL

2013, 2014; PANTALEONI et al. 2012) and recently ABRAHAM (2017) published an updated inventory of Myrmeleontiformia including descriptions of new species. Currently, 29 species of Coniopterygidae, one species of Sisyridae, two species of Mantispidae, three species of Berothidae, nine species of Hemerobiidae, 33 species of Chrysopidae, seven species of Nemopteridae, 66 species of Myrmeleontidae and 12 species of Ascalaphidae have been recorded in Morocco (Annex 1).

### Material and methods

The survey was performed during two collecting missions carried out during the month of August. The first mission (15–22.viii.2012) took place in the south of the region and the second mission (03–12.viii.2015) followed a south-north transect from Missouri to the north region and the Moulouya River delta. Independently of these two missions, the second author (AF) carried out additional prospectings between April and October.

Neuroptera collections were mainly performed during the night using a light trap. Additional prospection and captures were carried out during the day, in particular in the search for larval stages. The larvae collected were reared at the laboratory of entomology of the ECWP.



**Figure 1.** Delimitation of the Oriental region of Morocco. Satellite image: [https://commons.wikimedia.org/wiki/File:Satellite\\_image\\_of\\_Morocco\\_in\\_January\\_2002.jpg](https://commons.wikimedia.org/wiki/File:Satellite_image_of_Morocco_in_January_2002.jpg); (Jacques Desclouetres, MODIS Land Rapid Response Team, NASA/GSFC [Public domain])

During the two missions in August, a total of 16 localities were surveyed covering a wide diversity of biotopes such as the hyper-arid areas of the southern part of the Oriental region, ungrazed meadow at the ECWP or sub-humid and humid zones in the valley and the delta of the Moulouya River.

## Results

The list below includes all the species collected during the missions in August and the additional records taken by the second author (AF).

### 1 – Myrmeleontidae

Palparini: *Palpares angustus* McLachlan, 1898, *P. hispanus* Hagen, 1860.

Dendroleontini: *Bankisus antiatlasiensis* Abraham, 2009.

Nemoleontini: *Creoleon* cf. *aegyptiacus* (Rambur, 1842), *C.* cf. *griseus* (Klug, 1834), *C. lugdunensis* (Villers, 1789), *Creoleon* spp. (6 unidentified species), *Delfimeus scriptus* Navás, 1912, *Delfimeus* sp., *Distoleon annulatus* (Klug, 1834), *D. divisus* (Navás, 1913), *Macronemurus appendiculatus* (Latreille, 1807), *M. elegantulus* McLachlan, 1898, *M. gallus* Hölzel, 1987, *Macronemurus* sp., *Mesonemurus harterti* Navás, 1919, *Neuroleon* cf. *leptaleus* (Navás, 1912), *N.* cf. *danieli* (Lacroix, 1922), *Neuroleon tenellus* (Klug, 1834), *Pseudoformicaleo gracilis* (Klug, 1834).

Myrmeleontini: *Myrmeleon fasciatus* (Navás, 1912), *M. gerlindae* Hölzel, 1974, *M. hyalinus* Olivier, 1811.

Nesoleontini: *Cueta lineosa* (Rambur, 1842).

Myrmecaelurini: *Gepus invisus* Navás, 1912, *Myrmecaelurus lachlani* Navás, 1912, *M. lepidus* (Klug, 1834), *Myrmecaelurus* spp. (2 unidentified species), *Nophis teillardi* Navás, 1912, *Solter liber* Navás, 1912, *S. francoisi* Michel, 2014, *S. leopardalis* Michel, 2014.

A total of 38 species of Myrmeleontidae were collected in the Oriental region. The most abundant species, represented by at least 20 specimens, were *Cueta lineosa* (83 specimens), *Distoleon annulatus* (59 specimens), *Neuroleon tenellus* (50 specimens), *Solter liber* (35 specimens), *Creoleon* cf. *aegyptiacus* (24 specimens) and *C. griseus* (20 specimens).

### 2 – Ascalaphidae, Ascalaphinae

*Ascalaphus barbarus* (Linnée, 1767), *Deleproctophylla blusei* Kimmins, 1949, *Libelloides ictericus* (Charpentier, 1825), *Puer algericus* van der Weele, 1908.

All the species are uncommon catches. *Ascalaphus barbarus* was collected in the humid environment of the Moulouya valley whereas the other species were collected in arid or hyper-arid areas.

### 3 – Chrysopidae

Chrysopinae: *Italochrysa stigmatica* (Rambur, 1842), *Suarius walsinghami* Navás, 1914, *Chrysoperla lucasina* (Lacroix, 1912).

The most abundant species was *S. walsinghami*, sometimes represented by very abundant population. The two other species collected during the prospectings were scarce.

### 4 – Hemerobiidae

*Wesmaelius* sp., one male.

### 5 – Mantispidae

*Mantispa aphavexelte* Aspöck & Aspöck, 1994. A single female collected at light.

### 6 – Nemopteridae

One unidentified species of Crocinae. Adults were obtained from larvae collected in rocky cavities with very fine sand on the ground.

## Conclusion

A total of 49 species of Neuroptera were collected in the Oriental region of Morocco, of which 38 belong to Myrmeleontidae and four to Ascalaphidae, representing respectively 58 % and 33 % of the species known from Morocco. Considering the other families, the ratio (number of species collected during the prospecting/number of species recorded in Morocco) is as follows: Chrysopidae 3/12, Mantispidae 1/2, Hemerobiidae 1/9 and Nemopteridae 1/7. These results indicate that the Oriental region, although located at high elevation and subject to harsh winters and very arid summers, harbours a rich and diverse Neuroptera fauna.

In August, most of the Neuroptera species collected with a light trap in the Oriental region of Morocco were Myrmeleontidae, representing 84 % of all the species found.

The study of the material collected showed that several genera are in need of revision, particularly *Creoleon*, *Myrmecaelurus* and *Neuroleon*. Regarding the Myrmecaelurini, the survey yielded two new species belonging to the genus *Solter* (MICHEL 2014).

*Bankisus antiatlasensis* was known only from the type locality in the Anti-Atlas at 1 533 m a.s.l. The capture of this species at Missouri greatly extends its area of distribution to the north and shows that it is also present at lower altitude.

*Gymnocnemia editaerevayae* Michel, 2013, described from Oukaimeden, a locality in the High Atlas Mountains at around 2 500 m a.s.l. (MICHEL 2013), was collected again in August south-east of Midelt at 1 960 m a.s.l., close to the southern limit of the Oriental region. Unlike the previous species, it seems that *G. editaerevayae* lives at high elevations and does not reach the Oriental region.

The list of Neuroptera of the Oriental region of Morocco presented here is not likely to be exhaustive and intensive surveys during other periods of the year can be expected to provide new records.

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## Annex 1

List of Neuroptera recorded from Morocco, excluding Myrmeleontiformia listed by ABRAHAM (2017).

### Coniopterygidae: Aleuropteryginae

- Aleuropteryx iberica* Monserrat, 1977  
*Aleuropteryx juniperi* Ohm, 1968  
*Aleuropteryx maculata* Meinander, 1963  
*Aleuropteryx minuta* Meinander, 1965  
*Aleuropteryx wawriake* Rausch & Aspöck, 1978  
*Helicoconis hispanica* Ohm, 1965  
*Helicoconis maroccana* (Carpentier & Lestage, 1928)  
*Helicoconis pseudolutea* Ohm, 1965

### Coniopterygidae: Coniopteryginae

- Coniopteryx arcuata* Kis, 1965  
*Coniopteryx atlantica* Ohm, 1983  
*Coniopteryx atlasensis* Meinander, 1963  
*Coniopteryx borealis* Tjeder, 1930  
*Coniopteryx drammonti* Rousset, 1964  
*Coniopteryx haematica* McLachlan, 1868  
*Coniopteryx mucrogonarcuata* Meinander, 1979  
*Coniopteryx perisi* Monserrat, 1976  
*Coniopteryx pygmaea* Enderlein, 1906

- Coniopteryx tjederi* Kimmins, 1934  
*Conwentzia pineticola* Enderlein, 1905  
*Conwentzia psociformis* (Curtis, 1834)  
*Hemisemidalis pallida* (Withycombe, 1924)  
*Nimboa espanoli* Ohm, 1973  
*Nimboa marroquina* Monserrat, 1985  
*Parasemidalis fusca* Meinander, 1963  
*Semidalis aleyrodiformis* (Stephens, 1836)  
*Semidalis candida* Navás, 1916  
*Semidalis pluriramosa* (Karny, 1924)  
*Semidalis pseudouncinata* Meinander, 1963  
*Semidalis vicina* (Hagen, 1861)
- Sisyridae  
*Sisyra iridipennis* (Costa, 1884)
- Mantispidae: Mantispinae  
*Mantispa aphavexelte* (Aspöck & Aspöck, 1994)  
*Mantispa styriaca* (Poda, 1761)
- Berothidae: Berothinae  
*Isoscelipteron glaserellum* (Aspöck, Aspöck & Hölzel, 1979)  
*Nodalla eatoni* (McLachlan, 1898)  
*Nodalla saharica* (Esben-Petersen, 1920)
- Hemerobiidae: Hemerobiinae  
*Hemerobius stigma* Stephens, 1836  
*Wesmaelius lindbergi* (Esben-Petersen, 1931)  
*Wesmaelius navasi* (Andréu, 1911)  
*Wesmaelius subnebulosus* (Stephens, 1836)
- Hemerobiidae: Sympherobiinae  
*Sympherobius pygmaeus* (Rambur, 1842)  
*Sympherobius fallax* Navás, 1908
- Hemerobiidae: Megalomiinae  
*Megalomus atomarius* Navás, 1935  
*Megalomus tineoides* Rambur, 1842
- Hemerobiidae: Microminae  
*Micromus angulatus* (Stephens, 1836)
- Chrysopidae: Chrysopinae  
*Brinckochrysa chlorosoma* (Navás, 1914)  
*Chrysopa formosa* Brauer, 1850  
*Chrysopa mimeuri* Navás, 1935  
*Chrysopa nigricostata* Brauer, 1850  
*Chrysopa pallens* (Rambur, 1838)  
*Chrysopa punctata* (Navás, 1935)  
*Chrysopa viridana* Schneider, 1845  
*Chrysoperla carnea* (Stephens, 1836)  
*Chrysoperla lucasina* (Lacroix, 1912)  
*Chrysoperla mediterranea* (Hölzel, 1972)  
*Chrysoperla mutata* (McLachlan, 1898)  
*Cunctochrysa baetica* (Hölzel, 1972)  
*Italochrysa stigmatica* (Rambur, 1842)  
*Nineta guadarramensis* (Pictet, 1865)  
*Peyerimhoffina gracilis* (Schneider, 1851)  
*Pseudomallada alarconis* (Navás, 1915)  
*Pseudomallada flavifrons* (Brauer, 1850)  
*Pseudomallada genei* (Rambur, 1842)  
*Pseudomallada granadensis* (Pictet, 1865)  
*Pseudomallada ifraninus* (Navás, 1935)  
*Pseudomallada irrorellus* (Navás, 1935)  
*Pseudomallada maghrebinus* (Hölzel & Ohm, 1984)  
*Pseudomallada picteti* (McLachlan, 1880)  
*Pseudomallada prasinus* (Burmeister, 1839)  
*Pseudomallada subcubitalis* (Navás, 1901)  
*Pseudomallada venosus* (Rambur, 1842)  
*Pseudomallada viridifrons* (Hölzel & Ohm, 1999)  
*Rexa lordina* Navás, 1919  
*Suarius caviceps* (McLachlan, 1898)  
*Suarius maroccanus* Hölzel, 1965  
*Suarius tigridis* (Morton, 1926)  
*Suarius walsinghami* Navás, 1914

## Neuroptera in two protected sand dune areas in the southern rim of the Pannonian Plain

Dušan Devetak<sup>1,3</sup>, Predrag Jakšić<sup>2</sup>, Tina Klenovšek<sup>1</sup>, Vesna Klokočovnik<sup>1</sup>, Jan Podlesnik<sup>1</sup>, Franc Janžekovič<sup>1</sup> & Danijel Ivajnsič<sup>1</sup>

<sup>1</sup>Department of Biology & Institute for Biology, Ecology and Nature Conservation, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, 2000 Maribor, Slovenia

<sup>2</sup>Čingrijina 14/25, Zvezdara, 11000 Beograd, Serbia

<sup>3</sup>Corresponding author: [dusan.devetak@guest.arnes.si](mailto:dusan.devetak@guest.arnes.si)

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**Abstract.** The Pannonian Plain is large sedimentary lowlands in Central/south-eastern Europe. Two protected sand dune areas in the southern rim of the Pannonian Plain were surveyed for the presence of Neuroptera. Đurđevac sands in Croatia is a special geographical and botanical reserve, occupying only about 0.2 km<sup>2</sup>, whereas Special Nature Reserve Deliblato sands in the Vojvodina province, Serbia, covers about 300 km<sup>2</sup>. Among other lacewings, a few rare antlion species were observed in these reserves. The green lacewing *Chrysopa commata* was recorded for the first time in Croatia. The vegetation dynamics of the study areas was determined with a multispectral LANDSAT satellite imagery. As a result of the ecological succession (in both reserves) and afforestation (in Deliblato sands) in the past, the rate of the habitat loss and degradation processes of the sand dune ecosystems have increased to a level less suitable for the antlions assemblages.

**Further key words.** Antlions, nature conservation, habitat loss, Croatia, Serbia

### Introduction

The Pannonian Plain is large sedimentary lowlands in Central to south-eastern Europe. Despite the high level of endangerment, a variety of natural habitats are still present in the plain, and one of the most characteristic is the Pannonian sand steppe. Sand steppes often occur in sand dune areas or so called windblown sands. The creation of windblown sands in the Pannonian Plain was linked to the erosion of large rivers, such as the Danube and Drava rivers in the past (e.g., KRÁLOVIČOVÁ et al. 2015). In countries where at least a part of the territory belongs to the Pannonian biogeographic region, a great deal of effort is devoted to maintaining or restoring the natural sand steppes (ŠEFFEROVÁ STANOVÁ et al. 2008).

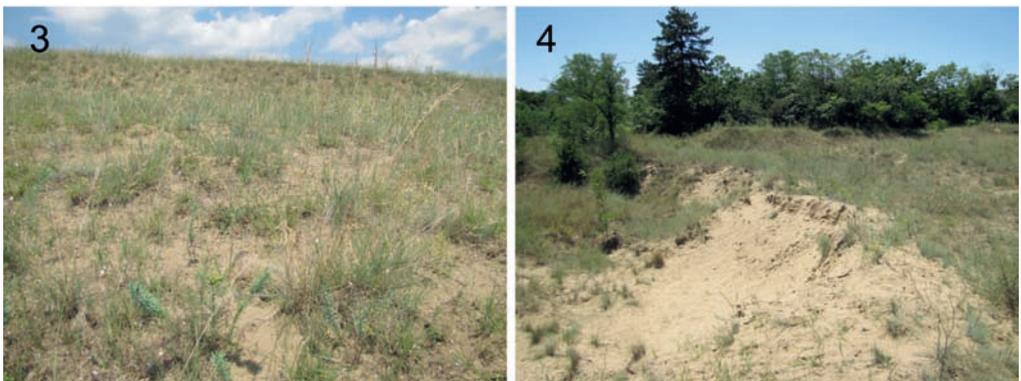
Comprehensive studies on lacewing assemblages inhabiting Pannonian sand steppes exist only for Hungary, *i.e.*, the central part of the Pannonian Plain (e.g., GEPP & HÖLZEL 1989; SZIRÁKI et al. 1992; SZENTKIRÁLYI et al. 2001, 2010; SZENTKIRÁLYI & KAZINCZY 2002; GEPP 2010). In the present study, two protected sand dune areas in the southern rim of the Pannonian Plain were surveyed for the presence of lacewings (Neuroptera).

The smaller one, Đurđevac sands (also: Djurdjevac sands; Croatian: Đurđevački pijesci, Đurđevečki peski) in Croatia, occupying about 0.2 km<sup>2</sup>, is a special geographical and botanical reserve (OZIMEC 2016) (Figs 1–2, 6). The larger area, a Special Nature Reserve Deliblato sands (Serbian: Deliblatska peščara) in the Vojvodina province, Serbia, is a geo-morphological formation of eolian origin and covers about 300 km<sup>2</sup> (Figs 3–4, 8). Prior to the present study, only old literature records on Neuroptera for the Deliblato sands existed, with the oldest record dating back to 1863 (PANČIĆ 1863; FRIVALDSZKY 1877; MOCSÁRY 1899; PONGRÁCZ 1914, PETRIK 1958; GROZDANIĆ & STEVANOVIĆ 1969; DEVETAK 1996).

The aim of the study was to describe the neuropteran fauna that could be found in order to get insight into the bio-diversity of the sand dune areas near the southern border of the Pannonian Plain. Furthermore, our aim was also to get an idea of the rate of habitat loss relevant for the endangered neuropteran species.



**Figures 1, 2.** Đurđevac sands, Croatia. 1 – Sand dunes and grasslands are successively replaced by thicket. 2 – Grassland with dominating *Festuca vaginata* grass. Photos: DD (vi.2017)



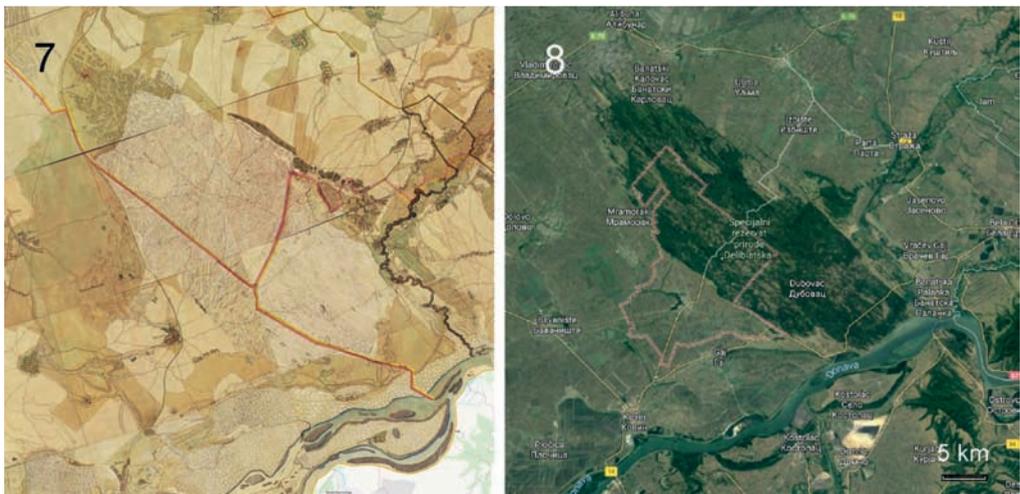
**Figures 3, 4.** Deliblato sands, Serbia. 3 – Steppe. 4 – Sand dunes afforestation with *Robinia pseudoacacia* and *Pinus nigra* trees in the background. Photos: DD (vii.2016)

### Material and methods

Insects were collected in the two protected sand dune areas during short visits in July 2016 (Deliblato sands, Serbia; two days) and July 2018 (Djurdjevac sands, Croatia; two days). Antlion larvae were excavated using a spoon. Adults were collected with insect



**Figures 5, 6.** Maps of the Đurđevac sands, Croatia. 5 – A map of the area in 19<sup>th</sup> century, The Second Military Survey (1806–1869) (ANONYMUS 1806). 6 – A contemporary map of the area (Google maps, <https://maps.google.com/>, 31.viii.2018).



**Figures 7, 8.** Maps of the Deliblato sands, Serbia. 7 – A map of the area in 18<sup>th</sup> century, The First Military Survey of the Habsburg Empire (1763–1787) (ANONYMUS 1763). 8 – A contemporary map of the area (Google maps, <https://maps.google.com/>, 31.viii.2018).

net and after identification returned to their natural habitat. A few voucher specimens of each species were deposited in the first author's collection. For identification, we used the keys in BADANO & PANTALEONI (2014). Vegetation dynamics of the study areas was determined with a multispectral LANDSAT satellite imagery, freely available on the Earth Explorer platform (<https://earthexplorer.usgs.gov/>). To evaluate the change in vegetation density, a vegetation index (NDVI) was used for each available cloud-free time window (1992–2017). Moreover, a pixel level regression tool was applied (Curve Fit) to measure the dynamics and pattern of the succession process.

## Results

### Neuroptera in the Đurđevac sands, Croatia

For the Đurđevac sands, there is no record in the literature of prior lacewing collection. Despite the fact that the sand dune reserve is a small area occupying only about 0.2 km<sup>2</sup>, a relatively high number (17) of lacewing species was detected during the two-days of sampling (Table 1). Antlions were the most abundant and four species were collected in the sandy habitat. The most numerous antlion species was *Myrmeleon bore*, and all collected individuals were in larval stage (Fig. 9). The finding of this species was the second record for Croatia. Interestingly, the first finding place of *M. bore* in



**Figure 9.** Pits of *Myrmeleon bore* larvae in the Đurđevac sands, Croatia. Photo: DD (vi.2017)

**Table 1.** Lacewing species recorded in 2018 in the Đurđevac sands, Croatia. Abundance: sporadic – 1–4 individuals observed; frequent – 10–49 individuals observed; very frequent – 50 individuals or more observed.

Taxon	Abundance
Chrysopidae	
<i>Chrysopa perla</i> (Linnaeus, 1758)	sporadic
<i>Chrysopa dorsalis</i> Burmeister, 1839	sporadic
<i>Chrysopa commata</i> Kis & Újhelyi, 1965	sporadic
<i>Chrysopa formosa</i> Brauer, 1851	sporadic
<i>Chrysopa gibeauxi</i> (Leraut, 1989)	sporadic
<i>Pseudomallada flavifrons</i> (Brauer, 1851)	sporadic
<i>Pseudomallada prasinus</i> (Burmeister, 1839)	frequent in nearby forest
<i>Pseudomallada abdominalis</i> (Brauer, 1856)	sporadic
<i>Pseudomallada ventralis</i> (Curtis, 1834)	sporadic
<i>Chrysoperla carnea</i> (Stephens, 1836) s.str.	sporadic
<i>Chrysoperla agilis</i> Henry, Brooks, Duelli & Johnson, 2003	sporadic
<i>Chrysoperla lucasina</i> (Lacroix, 1912)	frequent
Hemerobiidae	
<i>Hemerobius humulinus</i> Linnaeus, 1758	sporadic
Myrmeleontidae	
<i>Myrmeleon inconspicuus</i> Rambur, 1842	frequent
<i>Myrmeleon bore</i> (Tjeder, 1941)	very frequent – dominant
<i>Euroleon nostras</i> (Geoffroy in Fourcroy, 1785)	sporadic
<i>Creoleon plumbeus</i> (Olivier, 1811)	frequent

Croatia (ÁBRAHÁM 2008) was in the Drava river basin as well. We noted twelve green lacewing species. The green lacewing *Chrysopa commata* was recorded in Croatia for the first time.

### Neuroptera in the Deliblato sands, Serbia

In contrast to the Đurđevac sands, a number of older literature records of Neuroptera exist for the Deliblato sands. In 2015, we collected 13 lacewing species, but there were a further nine species known from the literature that we did not find (Table 2). The antlion *Megistopus flavicornis* was collected in the Deliblato sands in 1988 (DD unpubl.). Similarly to the finding in the Đurđevac sands, antlions were the most abundant neuropterans also in the Deliblato sands. When old literature records were taken into account, ten species of antlions were listed altogether. Among them, three antlion species, namely *Palpares libelluloides*, *Acanthaclisis occitanica*, and *Nohoveus punctulatus*, are suspected to be extinct in Serbia due to the fact that records only older than 1983 exist.

**Table 2.** Lacewing species listed for the Deliblato sands, Serbia. X – Presence confirmed during this study in 2016.

<b>Taxon</b>	<b>Historical reports (&lt; 1920)</b>	<b>Contemporary reports (1950 &gt;)</b>	<b>Col- lected in 2016</b>
<b>Chrysopidae</b>			
<i>Chrysopa perla</i> (Linnaeus, 1758)		PETRIK (1958)	
<i>Chrysopa formosa</i> Brauer, 1851	FRIVALDSZKY (1877); MOCSÁRY (1899)	PETRIK (1958)	
<i>Chrysopa phyllochroma</i> Wesmael, 1841	FRIVALDSZKY (1877); MOCSÁRY (1899); PONGRÁCZ (1914)	PETRIK (1958)	
<i>Pseudomallada flavifrons flavifrons</i> (Brauer, 1851)			X
<i>Pseudomallada prasinus</i> (Burmeister, 1839)			X
<i>Pseudomallada abdominalis</i> (Brauer, 1856)			X
<i>Chrysoperla</i> cf. <i>carnea</i> (Stephens, 1836) s.str.			X
<i>Chrysoperla</i> cf. <i>agilis</i> Henry, Brooks, Duelli & Johnson, 2003			X
<i>Chrysoperla lucasina</i> (Lacroix, 1912)			X
<i>Chrysoperla pallida</i> Henry, Brooks, Duelli & Johnson, 2002			X
<b>Hemerobiidae</b>			
<i>Hemerobius humulinus</i> Linnaeus, 1758			X
<i>Symphorobius elegans</i> (Stephens, 1836)	MOCSÁRY (1899); PONGRÁCZ (1914)		
<b>Myrmeleontidae</b>			
<i>Palpares libelluloides</i> (Linnaeus, 1764)		DEVETAK (1996)	
<i>Acanthaclisis occitanica</i> (Villers, 1789)	FRIVALDSZKY (1877); MOCSÁRY (1899); PONGRÁCZ (1914)		
<i>Myrmecaelurus trigrammus</i> (Pallas, 1771)	FRIVALDSZKY (1877); MOCSÁRY (1899)	GROZDANIĆ & STEVANOVIĆ (1969)	X
<i>Nohoveus punctulatus</i> (Steven in Fischer v. Waldheim, 1822)	FRIVALDSZKY (1877); PONGRÁCZ (1914)		
<i>Myrmeleon formicarius</i> Linnaeus, 1767		PETRIK (1958); GROZDANIĆ & STEVANOVIĆ (1969)	X
<i>Myrmeleon inconspicuus</i> Rambur, 1842		GROZDANIĆ & STEVANOVIĆ (1969)	X
<i>Euroleon nostras</i> (Geoffroy in Fourcroy, 1785)		GROZDANIĆ & STEVANOVIĆ (1969)	X

Taxon	Historical reports (< 1920)	Contemporary reports (1950 >)	Col- lected in 2016
<i>Distoleon tetragrammicus</i> (Fabricius, 1798)	FRIVALDSZKY (1877); MOCSÁRY (1899); PONGRÁCZ (1914)		
<i>Creoleon plumbeus</i> (Olivier, 1811)	FRIVALDSZKY (1877); MOCSÁRY (1899); PONGRÁCZ (1914)	GROZDANIĆ & STEVANOVIĆ (1969)	X
<i>Megistopus flavicornis</i> (Rossi, 1790)	PANČIĆ (1863); MOCSÁRY (1899); PONGRÁCZ (1914)	DD unpubl. (1988)	

### Endangerment of Neuroptera in both sand dune areas

Maps of the southern part of the Pannonian Plain depicted in the 18<sup>th</sup> and 19<sup>th</sup> century reveal that at that time sand dominated in both dune areas and they were devoid of woody plants (Anonymus 1763, 1806); cf. Figs 5, 7). Later, in the late 19<sup>th</sup> and the first half of the 20<sup>th</sup> century, intense afforestation was conducted in order to control soil erosion (for Đurđevac sands reviewed by PETRIĆ 2009, 2014). Consequently, former sandy areas were successively transformed into agricultural landscape or forest and only sporadic or mosaic sandy areas were left (Figs 6, 8). In both reserves, additionally, ecological succession – *i.e.*, overgrowth – occurred. The result of the ecological succession (in both reserves) and afforestation in the past (in Deliblato sands) is habitat loss.

Habitat loss is the greatest threat to antlions in both sand dune reserves. In the Deliblato sands, three antlion species have not been recorded for the last few decades (Table 2). A multispectral LANDSAT satellite imagery applied in the Deliblato sands revealed that the succession process increased to a level less suitable for the antlions assemblages. Results of the satellite imagery will be presented in a separate paper.

### Discussion

Lacewings assemblages in the two sand dune areas (Deliblato sands, Đurđevac sands) in the southernmost parts of the Pannonian Plain are composed of a significantly large number of species with an antlion composition comparable to antlion assemblages in similar habitats in Hungary (*e.g.*, SZENTKIRÁLYI *et al.* 2001, 2010; SZENTKIRÁLYI & KAZINCZY 2002). Sand dune reserves are important refuges for rare species, such as the rare antlion, *Myrmeleon bore*, and the typical sandy grassland inhabiting green lacewing *Chrysopa commata*. The consequence of afforestation is the occurrence of two pine-linked species, *Chrysopa dorsalis* and *Chrysopa gibeauxi*, in Đurđevac sands. At least two neuropteran species, *Acanthaclisis occitanica* and *Nohoveus punctulatus*, which were not collected during this survey and which have not been recorded in Serbia for over one hundred years (FRIVALDSZKY 1877; MOCSÁRY 1899; PONGRÁCZ 1914) are suspected to be extinct in the country.

Both sand dune areas are recognized as fragile ecosystems. The main threats to the two sand dune ecosystems in the southernmost parts of the Pannonian Plain are the ecological succession, afforestation, and disturbances such as overgrazing, animal and human treading, weed spreading, or devastating moto- and autocross. In the Deliblato sands, the rate of the habitat loss increased to a level less suitable or even unsuitable for some antlion species.

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# On owlfly larvae from Costa Rica, with emphasis on *Haploglenius luteus* Walker, 1853 (Neuroptera, Ascalaphidae)

Johannes Gepp

Institute for Nature Conservation, Herdergasse 3, 8010 Graz, Austria;  
j.gepp@naturschutzzinstitut.at

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**Abstract.** Twelve larvae of Ascalaphidae – in four similar forms – were found in different regions of Costa Rica. Behaviour and external morphology are briefly described. The flat larvae are camouflaged in coloration and exceedingly inactive. They spend weeks sitting on the surface areas of large leaves where, in a cautiously selective manner, catching insects which are climbing past them. The larval development takes between one and two years. Larval rearing was only successful in the case of *Haploglenius luteus* Walker, 1853.

## Introduction

Neuroptera larvae of the family Ascalaphidae (owlflies) are still largely unknown and were first investigated in the 1970s. Excellent descriptions of the larval stages of *Ulu-lodes* and *Ascaloptynx* from Arizona are given by HENRY (1976) and HENRY (1977) was the first to notice that larvae of Haplogleniini reside in leaf litter. According to GEPP (1984), larval stages of 24 species have been described worldwide only before 1980. For European Ascalaphidae, there is an excellent compilation by BADANO & PANTALEONI (2014). What regards the Neotropics, the knowledge on ascalaphid larvae in general and on the genus *Haploglenius* in particular is little. CAMACHO & JONES (2012) published a photo of *Haploglenius* sp. from the Colombian region Orinoquía. A revision of the genus *Haploglenius* by JONES (2014) yielded 23 valid species. To date, 17 species of the family of Ascalaphidae have been described from Costa Rica (PENNY 2002), however none in larval stages yet (PENNY 1981, 2002; HECKMAN 2017).

Searching on internet forums for ascalaphid larvae from Costa Rica resulted in a handful of photos of unidentified species – the majority was from Nicaragua, however. Nevertheless, in comparison there weren't many more results, and as far as one could recognize from existing publications, no new larval forms were shown.

## Material and methods

Some rainforests and their peripheries as well as deciduous dry forest of Costa Rica were visited during two study trips (February 2010 and February 2012) of Austrian entomologists. An intensive search for ascalaphid larvae was carried out during these stays. Areas especially visited and with larval finding were:

- Boca Tapada, Alajuela (rainforest): form A, D
- La Gamba, Puntarenas (rainforest): form A
- Rincon de la Vieja National Park, Guanacaste (deciduous dry forest): form A, B, C
- Tortuguero National Park, Limon (rainforest): form D.

Larvae were collected alive, and as far as possible, they were kept alive after returning to Austria for up to 15 months.

## Results

Twelve larvae of the Ascalaphidae family – in four similar forms (A–D) – were discovered in the course of targeted searches in the four visited regions of Costa Rica. However, their occurrence was rare. The author's visual observation showed that on average only one medium-sized larva a day was found sitting on large leaves approximately 1 m above the ground. The larvae usually nestled in small cavities of leaf axes. They were also attracted by UV light, which is used for scientific insect traps: The larvae could be seen to climb in the middle of the night from a height of 3 to 4 m from dense bushes onto the gauze fabric (Rincon de la Vieja National Park, 24.ii.2012). Despite intensive searches no egg clutches were found near the larvae.

### Ascalaphid larvae found in Costa Rica

The owlfly larvae were found during the two trips to four destinations in 2010 and 2012. During the day they were found sitting on large leaves. In nature they spent some days and in laboratory weeks sitting motionless on the surface areas of large leaves where, in a cautiously selective manner, they catch insects climbing past them. The flat larvae are camouflaged in colour and are extremely inactive. The following interpretations are also typically similar to all of the owlfly larvae that had been collected.

An example of a description of a location where we found a larva of *Haploglenius luteus* Walker, 1853, in the third stage (larval form A: Figs 1–7, 28–31) is provided in the 'Rainforest of the Austrians', La Gamba (N08°41'56" E83°12'22", 70 m a.s.l.), Puntarenas, 21.ii.2010: This ascalaphid larva in the third stage (17–22 mm) was pressed against the midrib surface of a heavily moss-grown and highly structured leaf, surrounded by several light brown and dead parts of leaves as well as by lichens and particularly mosses. The larva pressed itself against the leaf in such a way that its lateral scoli formed a kind of fence and hardly any animal was able to climb under the larva. From the head the larva defended itself with its mandibles, which are also pressed firmly onto the leaf surface in resting position. Passing insects were occasionally ignored motionless, but probably precisely selected. The larvae were found on the third lower level of the rainforest so to speak, whereas the fourth level would have been the ground. The larva was located about three quarters of a meter above the ground in a big sloping leaf, above it was the leafy canopy of the dense rainforest. In the immediate vicinity there was a stream which had been cleared upwards on the one hand, and a cleared garden culture

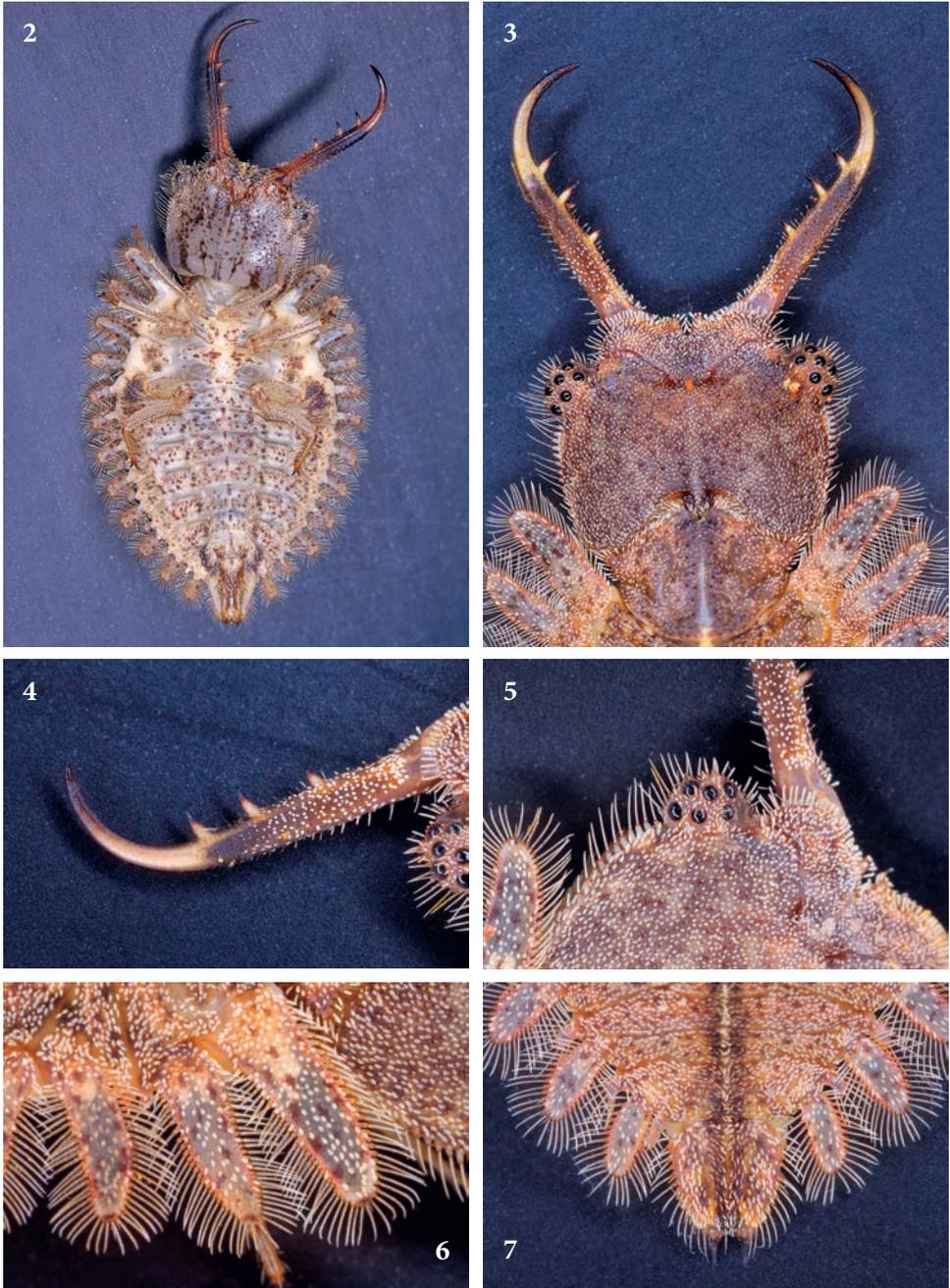
of the tourist lodge on the other. The locality was rather shady but not completely. There were numerous similar moss-covered leaves on different tree levels. A larva lying on its back will have difficulty turning back into its former position. Therefore it must twist its head and use the laterally protruding mandibles as levers. Otherwise, the larva is very well fixed to the leaf surface and can only be separated from it with great difficulty. This larva was observed just before heavy rainfall, and also during the rain it had stayed at the place where it was found.

The surrounding location, where the larva had been found was thoroughly searched. The older leaves of large-leaved plants were already covered by lichens and mosses on top while they were practically clean on the bottom sides. It can therefore be assumed that especially the mossy-topsides are inhabited by the larvae. Could the larvae possibly be suited for mossed and lichen-covered trunks? But there are extremely many ants everywhere! Of course, there would be plenty of rolled up, fallen leaves and stems with structural diversity where the larvae could stay. Here, even the protruding roots of large trees are heavily mossy and show similar colour structures to the larva. However, in this area a lively concentration of predators can be observed at night. One method of collection may be to pile numerous large leaves in heaps on top of each other, wait for the larvae to climb from the bottom leaves to the uppermost leaves and search there. Large *Heliconia* leaves, which are mossy on the upper side, seem to be ideal.

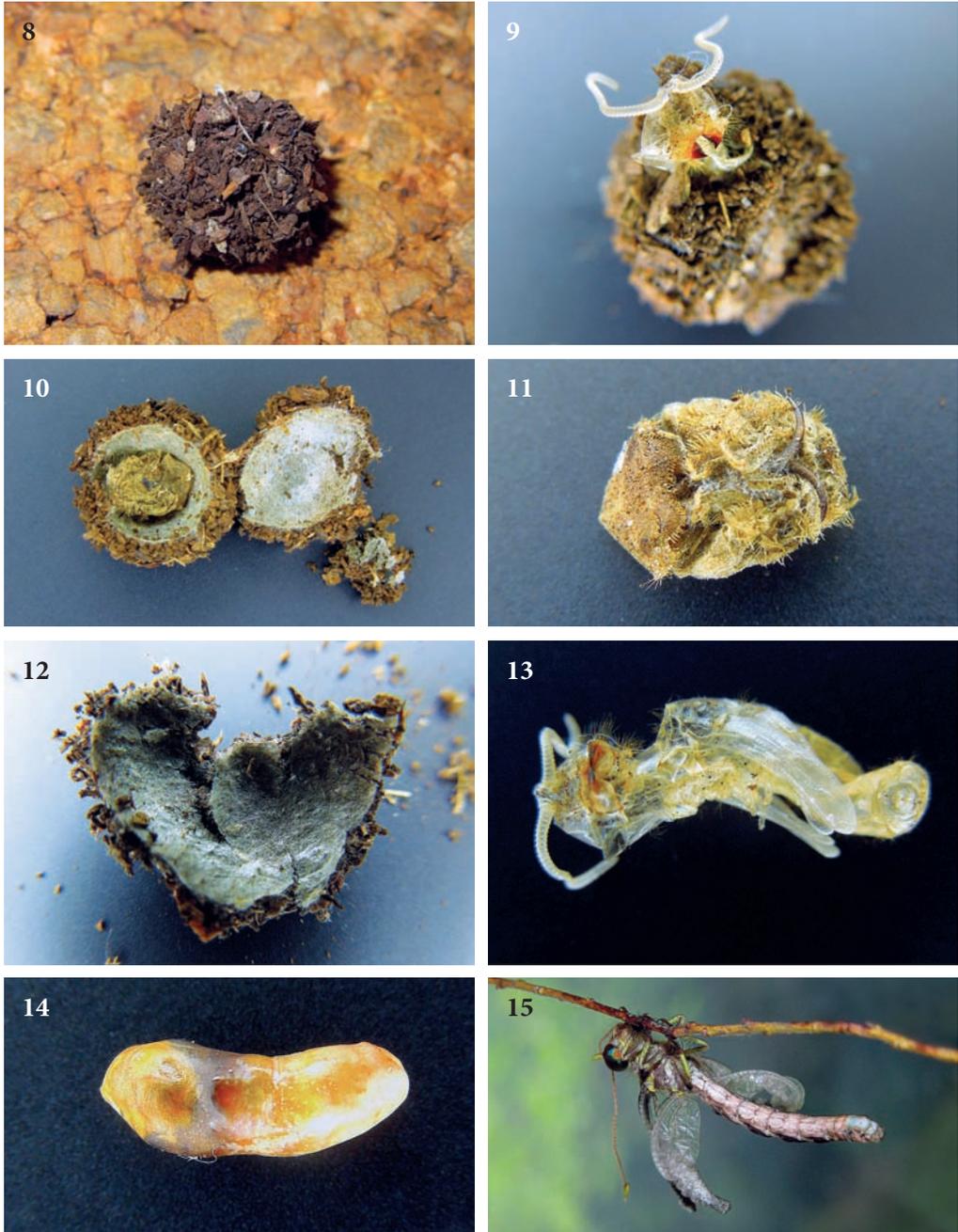
The imago to this larva emerged after two weeks of development (Fig. 15) in the cocoon (Figs 8–10) in detritus and was determined as *Haploglenius luteus* 13 months after the larva had been collected.



**Figure 1.** Mature 3<sup>rd</sup> larval stage of *Haploglenius luteus* Walker, 1853, (form A) found in the rain forest of La Gamba, Puntarenas, Costa Rica, February 2012 (natural length 22 mm). Photo: JG



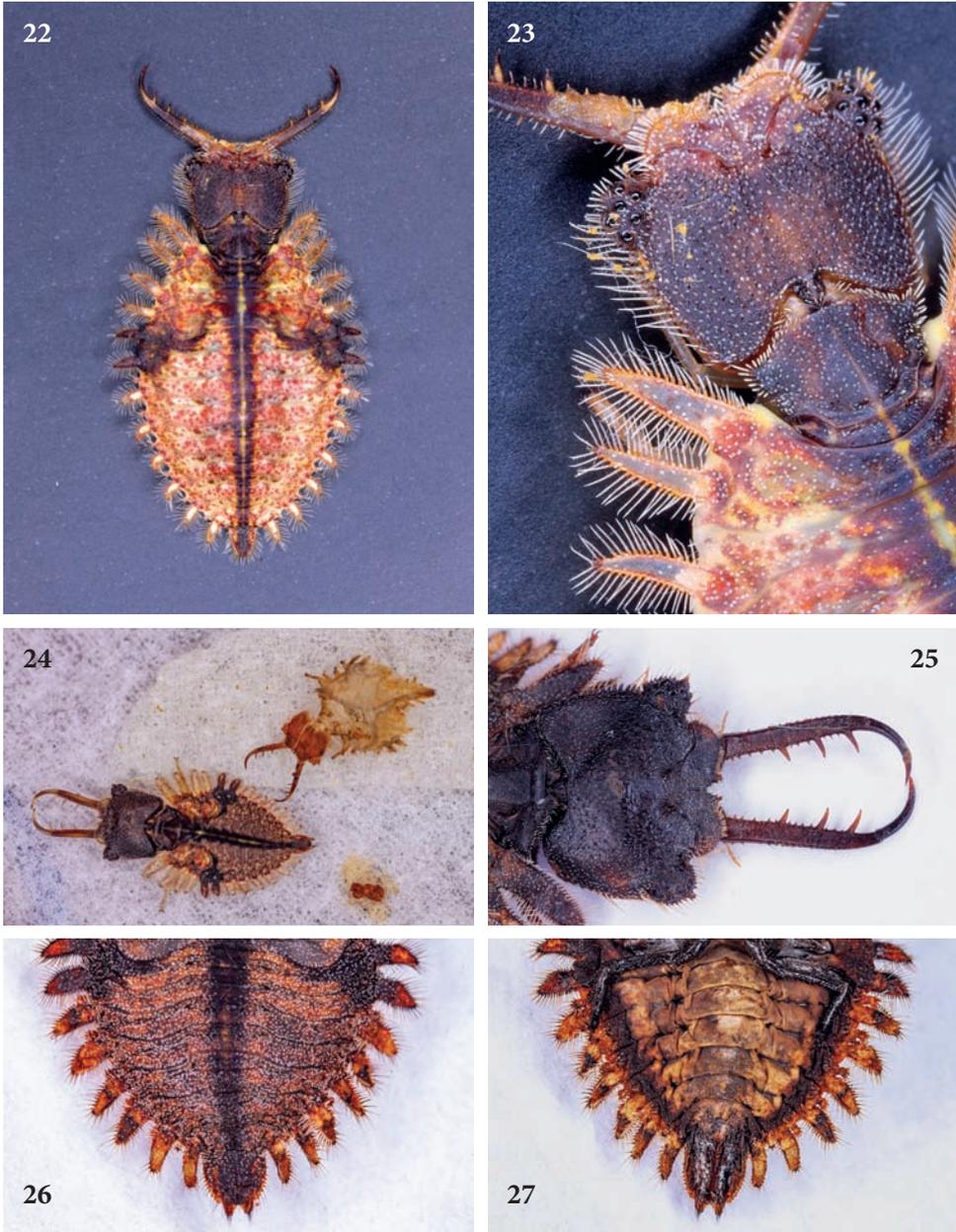
**Figures 2–7.** *Haploglenius luteus* Walker, 1853; third larval stage (form A) from Rincon de la Vieja National Park, NW Costa Rica; details of depicted body parts. 2 – ventral side; 3 – head capsule; 4 – mandibles; 5 – part of the head with ocular tubercle; 6 – meso- and metathoracic scoli; 7 – last abdominal segments. Photos: JG



**Figures 8–15.** Cocoon of *Haploglenius luteus* Walker, 1853, reared in captivity; diameter of the cocoon 14.5 mm; 8 – cocoon covered with detritus; 9 – cocoon with pupal exuvia; 10 – artificially opened cocoon; 11 – exuviae of the 3<sup>rd</sup> instar; 12 – silky interior of the cocoon; 13 – pupal exuvia; 14 – meconium (length 3 mm); 15 – imago of *H. luteus* shortly after emergence. Photos: JG



**Figures 16–21.** Third stage of similarly coloured but unidentified larvae (green form B: Figs 16, 21; yellow form C: Figs 17–20) of Ascalaphidae from Rincon de la Vieja National Park, NW Costa Rica; 16 – dorsal side of a green specimen; 17 – dorsal side of a yellow specimen; 18 – ventral side of the 3<sup>rd</sup> stage of yellow specimen; 19 – head capsule of yellow specimen; 20 – lateral scoli of form C; 21 – last abdominal segments of form B. Photos: JG



**Figures 22–27.** Second and third stage (Figs 25–27: desiccated, dead specimen) of an unidentified larva of Ascalaphidae (form D) from Boca Tapada, 1 km E Lagarto Lodge, NE Costa Rica, reared in laboratory; 22 – second instar, dorsal (natural length 9 mm); 23 – head capsule (dorsal) of a green variation of 2<sup>nd</sup> instar (form D, but cf. Fig. 16); 24 – emerged larva in 3<sup>rd</sup> stage with exuviae of 2<sup>nd</sup> instar; 25 – head capsule of 3<sup>rd</sup> instar; 26 – abdomen of 3<sup>rd</sup> instar, dorsal; 27 – abdomen of 3<sup>rd</sup> instar, ventral. Photos: JG



**Figures 28–31.** Ascalaphid larvae (form A) from Rincon de la Vieja National Park, NW Costa Rica; 28, 29 – larvae in the third stage of *Haploglenius luteus* Walker, 1853, in a sitting position on the surface of a leaf, surrounded by dead parts of leaves, and sucking on prey in the laboratory; 30, 31 – larvae of *H. luteus* in the second stage in a lurking position and sucking on prey. Photos: JG

### Behaviour in the laboratory

Placed in a 10 cm-cup with diverse structures, the third instar (L3) of *Haploglenius luteus* climbed up a small dark twig from morning until noon and was ideally positioned with its head down in the cavity of a leaf (e.g., Figs 28, 30). When photographed with flash it appeared slightly silvery and slightly green, giving it an ideal camouflage for mossy surroundings. The larva sometimes sat on the surface of leaves in the laboratory. Even when several leaves were placed in the rearing cup, the larvae climbed laboriously on the surface of the uppermost leaf. Sitting in a lurking position, the larva's mandibles were opened exactly 180° (Fig. 30). The body was colour-camouflaged and pressed to the leaf surface; thereby also filling in small cavities of the leaf. It preferred a position in the corner and liked to climb from underneath the leaves onto the top side.

When placed on its back, the larva was able to turn back on its legs by turning its head sideways and tilting the mandibles back dorsally. The larval head is attached to the thorax by only a relatively small neck. The larva was able to climb slowly, but it could go a long way (20 to 30 cm in 2 to 3 minutes). When the larva moved on a flat surface and its mandibles touched on a fissure-area, it turned round and tried to squeeze into the fissure with the abdominal end ahead. In all movements, the larva obviously relied on its camouflage and did not try to move rapidly or to escape.

### Prey and rearing

During the study trips, small termite mounds were also taken along for feeding. In laboratory rearing in Austria, feeding of the larvae turned out to be very difficult. They accepted almost none of the typical food animals such as vinegar flies, fly maggots, aphids, etc. Among hundreds of potential prey insects that had been offered, some of the larvae accepted not more than one prey in the course of two to three weeks (Figs 29, 31). So the larvae were very selective. PENNY (2002) mentioned a preference for slow-moving insects, such as Pseudococcidae.

Further rearing of the collected larvae lasted months and was particularly characterized by feeding problems. Within months most of the larvae starved to death, although they had been offered numerous insect larvae. Rearing larvae from the larval stage to the imago apparently is highly difficult and rarely succeeds.

The larvae were sometimes rather aggressive toward prey animals (Fig. 31), although they sometimes had the prey placed several times in front of their mandibles before they grabbed it. We observed the behaviour in seizing the prey. The larva snapped when a cricket was held above or in front of its head, impaling the body of the cricket from both sides with the upward-pointing mandibles. The folding of the mandibles occurred unexpectedly, jerkily and quickly. If the mandibles didn't penetrate into the prey, but only held it, after a short moment of waiting one mandible was raised and opened slightly; the mandible tip then penetrated into the soft parts of the body. After a few seconds the other mandible did the same.

Smaller crickets were completely sucked out, meaning that their skins remained compressed and empty. When fed with a cricket during rearing, the larva threw the cricket placed in front of the mandibles over its head twice, just as antlions throw sand. The third time the larva seized the cricket with its mandibles and held up the impaled prey, its head raised by 60°. After five minutes the ascalaphid larva completely turned in its sitting position by approximately 120° and lifted the prey up again before it began to suck it out. The thorax was also raised dorsally about 30°. The larvae produced dark, yellow coloured liquid droplets (very likely via the mandibles) after they sucked out larger preys. These drops were found 1–2 cm away from the location of the larva.

After three days of starvation, the first prey to be grabbed by the larva was another relatively large cricket. *Acheta domestica*, which was two thirds the size of the ascalaphid larva, was immediately seized by the larva after it had been placed in front of the animal's mandibles with the help of tweezers. A single ascalaphid larva sucked on a large cricket for more than three hours.

The particularity of the larvae is their slow growth, which lasts one or two years and takes even longer in the laboratory. The length of the process introduces the risk that the larvae will dry out. If, however, the larvae are kept too moist, the environment and eventually even the larvae will be covered with mildew. As a result, rearing them in captivity to the imago-stage is challenging and has rarely been successful.

### Identification

Early in our observations, the difference in colouring between the larvae found seemed to be a possible differentiating factor. However, the morphological similarity of some larvae suggests that some of them could also be colour variants of one species (Fig. 16, green form B, and Fig. 17, yellow form C). In the laboratory, some larvae appear to be even more colourful for a few days than they were originally in Costa Rica, having perfectly adapted to the surface of the dry leaf on which they sat. This may or may not be due to active colour adjustment as there have been observations that individual larvae can at least adapt themselves in nuances to the colouring of their environment. If further material were to be available in the future, genetic investigation is conceivable. However, this will require the availability of multiple samples of imagoes in future years. Since the colour patterns of the larvae also vary depending on the larval stage (cf. Figs 28 and 30), it is difficult to create a textual identification key for the present. Only the larvae form A of the species *Haploglenius luteus* have been successfully reared until the imago-stage and could therefore be identified. We therefore do not yet know the larvae of the other 16 species of Costa Rican Ascalaphidae.

### Chaetotaxy

Excellent photographs of Ascalaphidae larvae from the Mediterranean region of Europe can be seen in BADANO & PANTALEONI (2014). Although the species are related, the

differences between the Mediterranean larvae and those from Central America are too significant. The conspicuous protuberances at the lateral sides of the body also seemed typical of European Ascalaphids, but not of Costa Rica's Ascalaphids. The pedunculated setiferous processes can be of high diagnostic value. BADANO & PANTALEONI (2014) mention on chaetotaxy that the larvae are covered by dolichasters, the typical setae of larval Myrmeleontiformia, which cover the whole body, including mouthparts; this also applies to the 11 larvae from Costa Rica. The existing material on larvae collected from Costa Rica that were kept alive was not sufficient to elaborate differentiations. The collected larvae of Costa Rica have so far been undeterminable and were thus marked with the letters A, B, C and D in four colour-groups.

We drew a short morphological description of a larva of form D (Figs 22–27, type 'dark sides') from Boca Tapada, February 2012. The larva was found sitting on the leaf scar of a large-leaved, man-high plant. Surrounded by lichens, algal growth and dried parts of leaves, the larva firmly pressed itself against the leaf scar area and, although partly camouflaged, it could nonetheless be easily identified. The larva was 16 mm long and pale brown in colour, its head and the middle third of the mandibles were slightly darker. Medially, a dark brown stripe was divided into three parts by two light elongated spots. Semidorsally, at the 4<sup>th</sup> and 5<sup>th</sup> segment, two small dark longitudinal spots were pointing outwards to the rear. Semilaterally, the abdomen showed a thin, wavy dark brown line on either side. It was noticeable that the larva was characterized laterally by 12 skin protuberances which were covered with different setal types. The 5<sup>th</sup> and 6<sup>th</sup> scoli were dark brown in colour, while all the others were translucent but had dark bristles. The abdomen was dark in colour like the body, its pointed end protruding further than the lateral, surrounding bristle humps. The digital photo shows a certain dorsal fluorescence with a play of bluish colour. On the bottom side, the larva was significantly lighter in colour, only the two lateral skin protrusions 5 and 6 as well as the tips of the abdominal ends were dark brown. Laterally, the bottom side of the larva was somewhat darker than the rest of the body. The legs were light to translucent throughout. The head capsule displayed a dark brown W-shaped pattern close to the body, otherwise it was pale brown. The mandibles were largely dark brown, especially the tips, partly white in between. CAMACHO & JONES (2012) published a photo of *Haploglenius* sp. from the region of the Colombian Orinoco similar to *H. luteus* (coloured like the 'dark sides'-type of this larva No 4 from Tortuguero) but with shorter lateral scoli.

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# Crucial first steps toward a revision of the *Pseudomallada prasinus* group in Europe (Neuroptera: Chrysopidae)

Peter Duelli

Swiss Federal Institute of Forest, Snow & Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland; peter.duelli@wsl.ch

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**Abstract.** Three sympatric morphs of *Pseudomallada prasinus* were hybridized in search of reproductively separated species. The full manuscript to this summary has been published during the preparation of these Proceedings; see DUELLI & OBRIST (2019).

**Further key words.** Species validation, cross-breeding, hybridization, morphotype, lacewings, *Chrysopa aspersa*, *Chrysopa mariana*

## Introduction

The identity of some of the green lacewing species in the *Pseudomallada prasinus* group (e.g., ASPÖCK et al. 2001; HÖLZEL 1973, 1995, 1998) was always uncertain. Prasinoid morphs, i.e., specimens that key out as *Pseudomallada prasinus* (Burmeister, 1839) in current keys, have costal cross-veins with a green center in most or at least one of the cross-veins (Figs 2–5). Other species in the *prasinus* group have completely black costal cross-veins, including *P. abdominalis* (Brauer, 1856) (Fig. 6), *P. zelleri* (Schneider, 1851) (Fig. 7), and *P. ventralis* (Curtis, 1834).

## Methods

In Switzerland and neighboring countries samples of prasinoid morphs from nature or museum collections were analyzed morphologically to find consistent traits for separating sympatric morphs. With a focus on the most widespread and most abundant species, three morphs of *P. prasinus* were reared and hybridized in search of reproductively separated species. “Greenhead” and “sulfurhead” are small to medium sized morphs that deposit eggs singly, without obligatory diapause in the second instar. A third morph, “*marianus*”, is large, deposits bundled eggs (Fig. 1), and is characterized by an obligatory diapause in about half of the second instar larvae. Virgin specimens of the three prasinoid morphs were cross-bred in search of pre- and post-copulatory reproductive isolation. The three morphs were compared to prasinoid type specimens in the collections of the following European museums: Museu de Ciències Naturals de Barcelona, Catalonia, Spain (MCNB); Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRNSB); Martin-Luther-Universität Halle-Wittenberg, Halle, Germany (MLUH); and Naturhistorisches Museum Wien, Vienna, Austria (NHM).

## Results and Discussion

### Hybridization

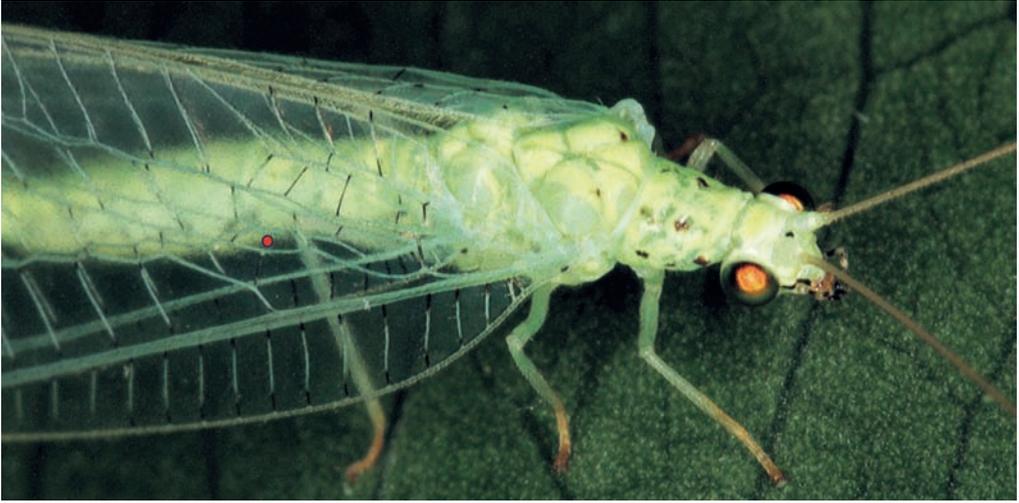
In cross-breeding experiments, the prasinoid morph “*marianus*” turned out to be reproductively isolated from the two other morphs, “greenhead” and the Mediterranean “sulfurhead”. While control couples (virgin male and female of the same morph) started to deposit viable eggs 5–10 days after being put together, hybrid couples took much longer and most did not produce any viable eggs. Only some of the crosses between “greenhead” females and “*marianus*” males (of about equal size) produced numerous eggs, but less than 2.2% of these eggs yielded healthy larvae. The rest were unfertilized (eggs green, dry) or the larva died before or while emerging (eggs grey or black).

### Morphology

For live and preserved specimens of most European species in the *prasinus* group, 26 morphological and two biological (oviposition and diapause) traits were recorded. The easiest way to separate the “*marianus*” morph from the two others is size, measured here as forewing length. The average wing lengths of females and males in the “*marianus*” morph ( $n=65$ ) were significantly ( $P<0.01$ ) larger than those of the smaller morphs, “greenhead” ( $n=67$ ) and “sulfurhead” ( $n=30$ ). But there is an overlap zone, as in all morphological traits recorded for these taxa. A combination of traits that are different in a majority of specimens per trait allows an almost safe identification (see below).



**Figure 1.** Bundled eggs of the “*marianus*” morph, *i.e.*, the real *Pseudomallada prasinus*. No other species of the *prasinus* group or prasinoid morph deposits eggs in bundles. Female is from Agarone, Switzerland. Photo: PD



**Figure 2.** The real *Pseudomallada prasinus* (“*marianus*” morph) has costal cross-veins with more green than black, the intramedian cell (im, red dot) is surrounded by more than 90% green veins, and the head is green without a red or brown suture below the antennae. Dots on the abdomen are rare. Female is from Follatères, Switzerland. Photo: PD



**Figure 3.** The “greenhead” morph (likely to be the real *P. aspersus*) has costal cross-veins with variable portions of green between the black ends. The intramedian cell (red dot) is surrounded by 10–25% black veins. Dots on the abdominal tergites are common, but usually small. Female is from La Spezia, Italy. Photo: PD



**Figure 4.** The Mediterranean “sulfurhead” morph also has variable portions of green in its costal cross-veins, and the im cell (arrow) is surrounded by 10–30 % black veins. Dots on abdominal tergites are often restricted to the distal half of the segments. Female is from Follonica, Italy. Photo: PD



**Figure 5.** *Pseudomallada benedictae*, restricted to hot and dry Mediterranean habitats, is extremely pale green, has a bright yellow vertex, and a dot on the caudal side of the scape (barely visible on this picture). The costal cross-veins are mainly green and the im cell is framed by only green veins. The “sulfurhead” morph, living in the same habitat, mainly evergreen oaks, is bright green and never has dots on the scape. Male is from Forêt de Palayson, France. Photo: PD



**Figure 6.** In *Pseudomallada abdominalis*, mainly found on conifers, the costal cross-veins (arrow) are usually completely black and in most individuals the intramedian cell (red dot) is surrounded by only black veins. The abdominal tergites often bear two rows of black dots per segment. Male is from Zürich, Switzerland. Photo: PD



**Figure 7.** The Mediterranean *Pseudomallada zelleri* is the smallest species in the *prasinus* group. The costal cross-veins are completely black, and all cross-veins are often shaded. The intramedian cell (red dot) is surrounded by 40–75% black, but not completely black, veins. The characteristic two reddish brown dots on the vertex are often combined with lateral black stripes on the scape. Here the brown suture between antennal base and genal black stripe is visible, as well as the abdominal dots. Female is from Agarone, Switzerland. Photo: PD

The range of the female fore wing length in the “*marianus*” morph was 15.0 to 17.5 mm. The type specimen of *Chrysopa prasina* Burmeister, 1839, in Halle, Germany (coll. MLUH), with a wing length of 16.5 mm, is clearly within the range of the “*marianus*” morph. The same is true for the type specimen of *Chrysopa coerulea* Brauer, 1851, in Vienna (coll. NHM), which is reported to have deposited bundled eggs (BRAUER 1851) and has a wing length of 17 mm. It was synonymized with *C. prasina* (BRAUER 1856). The type of *C. mariana* Navás, 1905, in Barcelona (coll. MCNB) has a wing length of 16 mm and also was synonymized with *P. prasinus* (HÖLZEL 1973). All three types are females well within the range of the “*marianus*” morph (15.0–17.5 mm) and barely touching the range of the two other, smaller morphs (12.5–16.0 mm).

*Chrysopa aspersa* was described by WESMAEL (1841) but had been synonymized by BRAUER (1856) with *C. prasina*. The type specimen of *C. aspersa* in Brussels (coll. IRNSB) has a wing length of 12.5 mm and thus is far out of the range of the “*marianus*” morph. The conclusion is that the “*marianus*” morph is the real *P. prasinus*, and because the two other morphs are not the same species as the “*marianus*” morph, they cannot be *P. prasinus*.

*Pseudomallada marianus* (Navás, 1905) is confirmed as a junior synonym of *P. prasinus*, depositing bundled eggs, whereas the smaller “greenhead” morph, depositing single eggs, corresponds in all visible traits to the type specimen of *C. aspersa*. *Pseudomallada aspersus* (Wesmael, 1841) is thus a valid species, but it is premature to link it to



**Figure 8.** A male “greenhead” morph from Agarone, Switzerland. Many, but not all, individuals of “greenheads” have a red suture between the base of the antennae and the black genal stripe. In “sulfurheads” that suture is more brownish, in *P. zelleri* it is brown or black. No colored suture was found in any of the real *Pseudomallada prasinus*. Photo: PD

**Table 1.** Key for separating *Pseudomallada prasinus* from “greenhead” and “sulfurhead”. For all morphological measurements there is an overlap (center column). Start on top with fore wing size. With overlap measures go down one step, until a decision for left or right is possible. *Pseudomallada prasinus* never has a yellow vertex.

<i>P. prasinus</i>	overlap	“green”- or “sulfurhead”
	wing size females	
>16.0 mm	15.0–16.0 mm	<15.0 mm
	wing size males	
>14.0 mm	13.0–14.0 mm	<13.0 mm
	v	
	subantennal suture	
	pale	red or brown (Fig. 8)
	v	
	veins of intramedian cell	
<10 % dark (Fig. 2)	10–25 % dark	>25 % dark
	v	
97 % have no or few dots	abdominal tergites	80–89 % have dots

one of the tested morphs. The species identity of the third morph, the Mediterranean “sulfurhead,” is not yet clear.

With the help of Table 1 it should be possible to recognize almost all “real” *P. prasinus* from live samples and well-preserved museum collection specimens. Discovering and documenting potential reproductive isolation between “greenhead”, *P. abdominalis*, “sulfurhead”, and possibly other European morphs is the goal of ongoing research.

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## The current state of knowledge of Polish Chrysopidae: Research history, distribution and present-day problems

Roland Dobosz

Upper Silesian Museum in Bytom, Department of Natural History, pl. Jana III Sobieskiego 2, Bytom 41-902, Poland; dobosz@muzeum.bytom.pl

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**Abstract.** Neuropterida are represented in Poland to date by 103 species from nine families. Chrysopidae (31 species) is one of the two largest families, second only to Hemerobiidae (34 species). The first studies from the early 19<sup>th</sup> century (Perthées' MS – Weigel 1806) described two species of green lacewings from the area of present-day Poland. Between 1802 and 2017, fifty-six authors (as the only or the first co-author) published 134 papers on the subject of Chrysopidae. On the basis of bibliographical data and unpublished studies, green lacewings have been found to occur at 542 sites in 455 UTM squares.

**Further key words.** History of neuropterology, faunistics, Poland

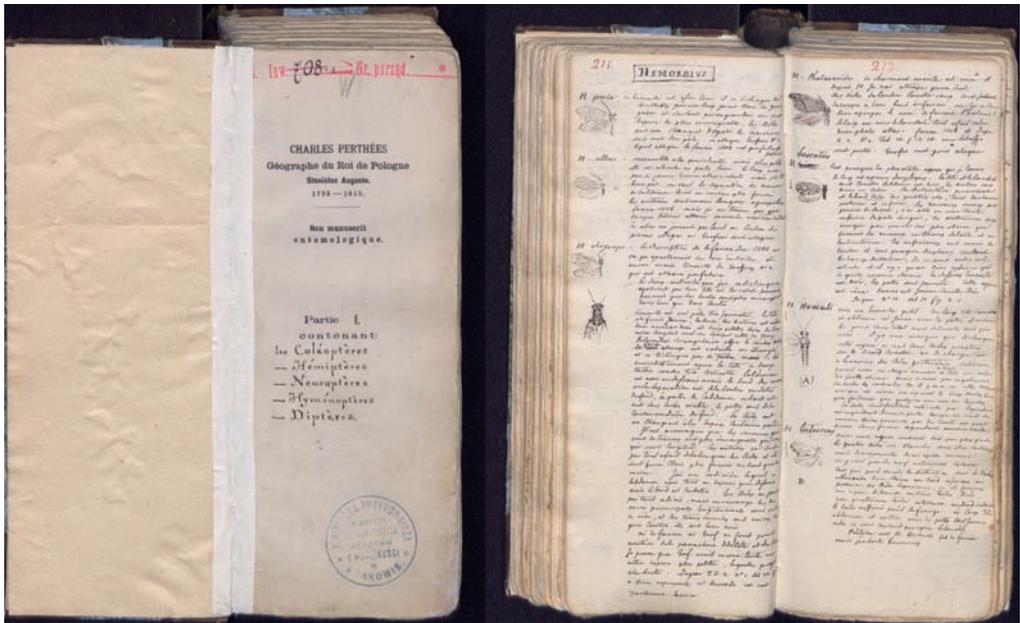
### First data, prior to 1795

The very first, albeit unpublished, information on green lacewings from Poland (within the country's post-1945 borders) comes from the beginning of the 19<sup>th</sup> century (1802–03) in the first volume of a manuscript by Karol Perthées, cartographer at the court of King Stanisław August. Besides compiling maps, he had a great passion for collecting and describing insects. He caught them mainly in the area around Warsaw, but he also possessed specimens from other parts of the country which he had been given by friends and colleagues. His manuscript, preserved in the library of the Institute of Systematics and Evolution of Animals (Polish Academy of Sciences) in Kraków (Fig. 1), contains information on eleven species of Neuropterida, including three lacewings, *Hemerobius albus*, *H. chrysops* and *H. perla*. The species mentioned in this work can be identified from their descriptions, the last-mentioned one also from the detailed morphological drawings. Perthées' collection has two common species: *Chrysopa perla* (*H. perla* and *H. chrysops*) and *Chrysotropia ciliata* (*H. albus*). The next references to green lacewings from Poland were in a list of animals of Silesia published by Weigel in 1806. Among the twelve taxa which he listed under the genus *Hemerobius* there are two that are now classified as green lacewings: *Chrysopa perla* and *Chrysotropia ciliata*. The others belong to the family Hemerobiidae (7) or to the order Psocoptera (2). All these species were stated as being from Silesia: no specific localities were given.

For general information on the old literature on and particularly illustrations of Chrysopidae see ASPÖCK & ASPÖCK (2007).

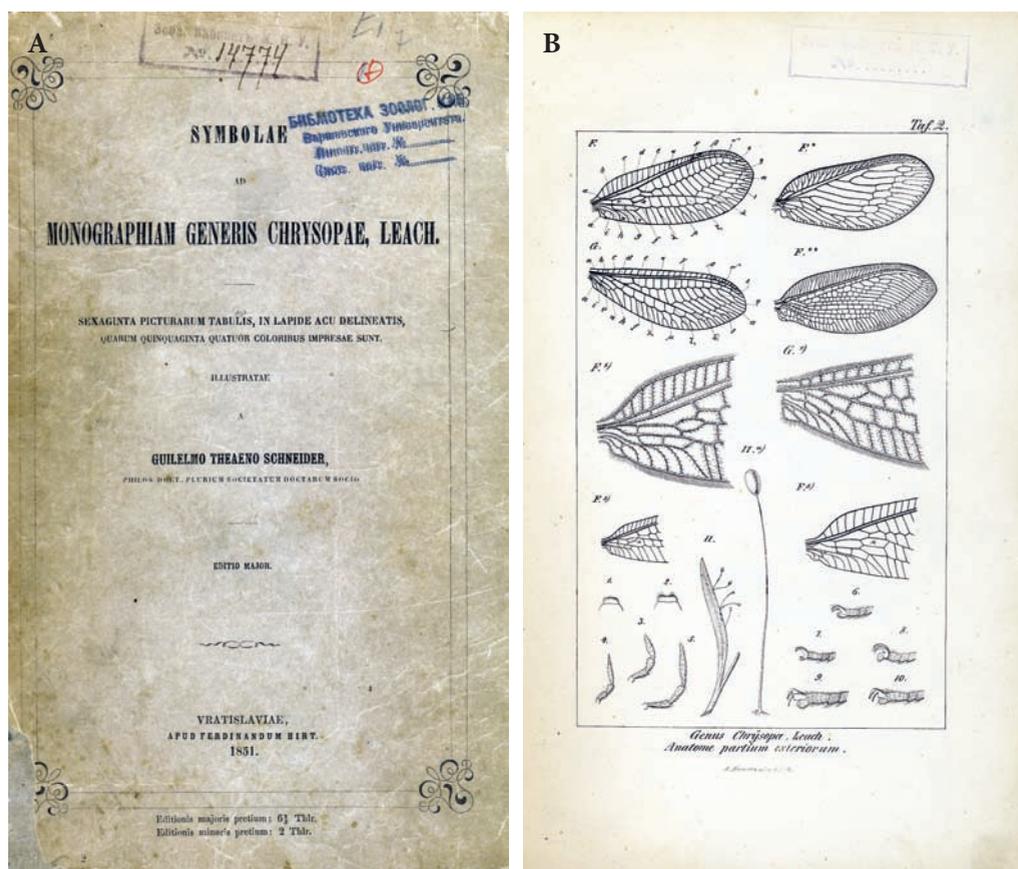
### The era of the partitions of Poland (1795–1918)

Some forty years later, a group of entomologists from Wrocław (Breslau) undertook a systematic study of Neuroptera in Silesia. One of them, Wilhelm Gottlieb Schneider, made a major contribution to knowledge of Chrysopidae. He not only compiled a list of species and provided new localities for some of them; he also described three taxa from the region that were new to science: *Chrysopa pallida*, *Ch. stenoptila* and *Ch. tenella* (SCHNEIDER 1845, 1846, 1851a, 1851b). Schneider was also the author of the first worldwide monograph on Chrysopidae (1851a; Fig. 2). This book is a milestone in the history of Neuropterology (ASPÖCK & ASPÖCK 2007). It contains data on 15 green lacewing species from Silesia. The conclusion of his studies of Silesian neuropterans was a critical checklist together with localities and comments on their phenology (SCHNEIDER 1885) containing data on 14 green lacewing species. At the same time as Schneider was working in Silesia, a number of faunistic works covering neuropterans, including green lacewings, were published in Galicia, the Austro-Hungarian partition of Poland. Lists of Galician insects contain information on the occurrence and phenology of eight green lacewing species (NOWICKI 1864, 1865). Some of the data in those works relate to areas now beyond the present-day borders of Poland (Podole, Bukowina). In a separate paper NOWICKI (1867a) published phenological and bionomic data on many groups of insects, including neuropterans and one green lacewing. It was during this period that he began studying the insect fauna of the Tatra Mountains, and a little later, of the Pi-



**Figure 1.** Front page and page 211 f. of the »Manuscrit entomologique. Partie I« by Karol Perthées, cartographer at the court of King Stanisław August (PERTHÉES 1802–1803), preserved in the library of the Institute of Systematics and Evolution of Animals PAS in Kraków.

eniny Mountains. Detailed reports of these entomological explorations, also containing information on green lacewings, were published in the Reports of the Physiographical Commission (NOWICKI 1867b, 1868, 1870). In the second half of the 19<sup>th</sup> century, faunistic material on green lacewings, including those from Galicia, were published by WIERZEJSKI (1868, 1883), and from the mid-1850s we have a report of a naturalists' expedition to Ojców, near Kraków, in 1854 (WAGA 1857). They did not find many neuropteran species, but some of their voucher specimens are preserved at the Natural History Museum of the Institute of Systematics and Evolution of Animals (Polish Academy of Sciences) in Kraków. Among other things, that report contains the description by an unknown author of a green lacewing that had been discovered just a few years earlier, described in SCHNEIDER'S (1851a) monograph on Chrysopidae under the name of *Chrysopa gracilis* (currently placed in the genus *Peyerimhoffina*; Fig. 3).



**Figure 2.** The first worldwide monograph on Chrysopidae, by Wilhelm Gottlieb [here G.T.] Schneider (1851), »Symbolae ad Monographiam generis Chrysopae, Leach«. A – Title page, B – plate 2 (Library R. Dobosz)

In the late 19<sup>th</sup> century there appeared a great many summaries and checklists of species based on bibliographic data published in Germany, Austria and Warsaw, relating to areas within the present-day borders of Poland (BRAUER 1876, 1878; MAJEWSKI 1882, 1885; ROSTOCK 1881, 1888). The 1880s saw the start of research into the insects of central Pomerania, including green lacewings (BRISCHKE 1887, 1888, 1889, 1891, 1894). Carl Gustav Alexander Brischke's studies yielded a great deal of original faunistic and phenological information on several green lacewing species, and ENDERLEIN (1908) published an extensive biological-faunistic study of the Baltic coast and its hinterland from Władysławowo to Hel. Besides many species from different insect orders, this compilation mentions neuropterans, including five green lacewing species. At the same time as Brischke was working in Pomerania, the first publications were appearing by one of the most outstanding late 19<sup>th</sup>- century Polish neuropterologists, Józef Dziędzielewicz, a pupil of Marian Łomnicki, who continued the studies started by Maksymilian Nowicki. He published his first work while yet a student (DZIĘDZIELEWICZ 1867) – an extensive description of the insects from his first research and collecting expeditions to Galicia. His next work, entitled »Przegląd fauny krajowej owadów siatkoskrzydłych (Neuroptera, Pseudoneuroptera)« [A review of the nation's neuropteran insects] (DZIĘDZIELEWICZ



**Figure 3.** *Peyerimhoffina gracilis* (Schneider, 1851), from the A. Waga collection in the Institute of Systematics and Evolution of Animals PAS in Kraków.

1891), included a critical discussion of the national bibliography on neuropterans, which also covered other systematic groupings such as caddisflies, dragonflies, mayflies and stoneflies. Unlike his earlier works, this contained original, hitherto unpublished data. His subsequent publications dealt with his research into neuropterans and gave lists of these insects from the eastern Carpathians, the Tatra Mountains, the Podkarpackie region and Silesia. Only the work pertaining to the Tatras contained information on green lacewings (DZIĘDZIELEWICZ 1895). While he was on the staff of the Natural History Museum in Lwów [now Lviv in western Ukraine; also known in German as Lemberg], he carried on a lively correspondence with the most eminent specialists on neuropteran insects in Europe of the time: Günther Enderlein from Szczecin, František Klapálek from Prague and Friedrich Brauer from Vienna. By exchanging scientific material with these experts, he had access to rich, verified sources of comparative materials. As Dziędzielewicz's scientific interests at the beginning of the 20<sup>th</sup> century began to focus mainly on caddisflies and dragonflies, he did not publish much more on neuropterans – only a single paper containing data on *Chrysopa flavifrons*, a rare species from Zawoja on the foot of the Babia Góra mountain in the western Carpathians (DZIĘDZIELEWICZ 1911). His crowning achievement was the publication in two parts of a checklist of neuropteran insects from Poland; the second part (DZIĘDZIELEWICZ 1918) contains a list of 18 green lacewings.

In the late 19<sup>th</sup> century, M.G. Lurié published some of the results of his research on the biology and larval structure of green lacewings of the genus *Chrysopa* sp. (LURIÉ 1897b) and described *Chrysopa polonica* from the Lublin area (LURIÉ 1897a), a species new to science. Despite exhaustive searches, I was unable to locate the type of this species, either in the collections of the Museum and Institute of Zoology (Polish Academy of Sciences) in Warsaw, or in St. Petersburg or Moscow. Judging by LURIÉ's description (1897a), it may in fact have been *Ch. viridana*, a species described by W.G. Schneider (DOBOSZ 1992).

The work by the Hungarian entomologist A. PONGRÁCZ (1919), who described the neuropterans collected by Zamoyski and deposited at the National Museum in Budapest, was of great importance as regards knowledge of the distribution ranges of these insects. Most of the data in his body of work come from localities situated in the then Russian partition (Kielce, Radom, Puławy, Lubartów, Lublin). The author mentioned 12 species of green lacewings, adding that he had no knowledge of *Ch. polonica*.

In the early 20<sup>th</sup> century, SCHILLE (1902) published materials relating to the neuropteran fauna of the Poprad valley, which included four species of green lacewings (when working up these data he received invaluable assistance from Dziędzielewicz).

### The inter-war period

The works by DZIĘDZIELEWICZ (1918) and PONGRÁCZ (1919) were published after the restoration of Poland's independence, but as they had been written and prepared for publication when Poland was still partitioned, they were discussed in the previous section. MIKULSKI (1931) refers to SCHILLE's (1902) work in the Poprad valley; besides other neuropteran families, he mentions eight green lacewing species.

In the late 1930s, intensive entomological research was taking place in German eastern Pomerania. KARL (1937) published materials relating to orthopteran, psocopteran and neuropteran species, including green lacewings, from the Słupsk area (the present-day Polish province of Pomerania), and ENGEL (1938) issued a list of insects caught at Bielinek nad Odrą (Polish western Pomerania) that included six neuropterans, two of which were green lacewings.

ZACWILICHOWSKI (1938a, 1938b, 1939) published faunistic papers and a summary of the state of research into neuropterans within the borders of pre-World War II Poland, stating that 68 neuropteran species were known from the country, including 20 green lacewing species. He based his publications on materials from his own collections, as well as those in Kraków and Warsaw.

### The period after 1945

During the period of World War II (1939–1945), nothing was published on neuropterans from Poland; for obvious reasons, no systematic fieldwork was possible. Small additions were made to the neuropteran collections at the Oberschlesisches Landesmuseum Beuthen (now Muzeum Górnośląskie w Bytomiu), some of which survived the wartime destruction. Nor were papers on neuropterans published in the years immediately after the war. There is just a mention of the green lacewing *Chrysopa vulgaris* in a paper by RIABININ (1954) dealing with the secondary entomofauna of insect foraging areas.

The first information from Wielkopolska comes from the second half of the 1950s (BURKÓWNA 1957). This list contains seven green lacewing species, plus another one that she was unable to identify on the basis of the bibliography available to her at that time. Unfortunately, the material from her fieldwork in 1955 has been lost. In the 1960s, a good many biological and ecological papers were published containing snippets of faunistic information on single common green lacewings, usually *Chrysopa vulgaris* (now *Chrysopa carnea* s.l.), or very general data without species being named. On the other hand, interesting biological and ecological data can be gleaned from published results of field and laboratory studies (ANASIEWICZ & MICZULSKI 1962; KARPIŃSKI 1963, 1967; KOEHLER & SCHNEIDER 1966; NIEMCZYK 1966; WIĄCKOWSKI 1968; WIĄCKOWSKI & DRONKA 1966; WIĄCKOWSKI & WIĄCKOWSKA 1968; GAŁECKA & ZELENÝ 1969). The last-mentioned of these papers, dealing with the frequency of aphid predators from the genus *Chrysopa* sp. in farmland communities, reports a new species for the Polish fauna – *Chrysopa commata* Kis & Ujhelyi, 1965.

There is little faunistic information in the majority of papers published in the 1970s (BURZYŃSKI 1971, 1979; STROJNY 1971; STARZYK 1974; BAŃKOWSKA et al. 1975, 1978; BAŃKOWSKA & MIKOŁAJCZAK 1976; KACZMAREK 1977). It was at this time that a series of papers written by Tatiana KOWALSKA (1971, 1973, 1978; KOWALSKA & SZCZEPAŃSKA 1973) appeared, in which, besides biological information from laboratory studies or breeding, she summarized the state of knowledge of the biology of the predaceous green lacewings occurring in Poland at that time. Also worthy of mention from that period are the faunistic publications describing the neuropteran fauna of the Kampi-

noski National Park (12 green lacewing species) and the Wielkopolski National Park (9 green lacewings) (PLEWKA 1974, 1981; WOŹNIAK 1974). These were the first papers dealing with neuropterans in protected areas in Poland. In the 1980s and 1990s research continued into the ecology and biology of Neuroptera (WINIARSKA & CHOLEWICKA 1990). There were also papers addressing their use in biological pest control (GARBARCZYK & MIKOŁAJCZYK 1982; KOT & PLEWKA 1982; MISZCZAK 1982; CHŁODNY 1983). Research that had begun in the 1970s was continuing into the fauna inhabiting birds' nests (KACZMAREK 1981, 1984, 1990, 1991b; KACZMAREK & PAJKERT 1987); these papers contained information on green lacewings, mainly *Chrysopa carnea* (s.l.). Scraps of information on Chrysopidae can be found in papers on the insect fauna of inhabited beehives (BANASZAK 1980; KACZMAREK 1984, 1991a), dead insects found on the tourist trails in the Bieszczady National Park (STARZYK & KOSIOR 1985) and in popular science descriptions (STROJNY 1986).

In the mid-1980s, an extensive work was published on the neuropterans of the Bory Tucholskie pine forests in northern Poland (BERNDT 1984): it lists 31 species including 11 green lacewings. During the same period, intensive research into neuropterans was started at scientific centres in Warsaw and Bytom. A comprehensive ecological survey run by the Institute of Zoology (Polish Academy of Sciences) in Warsaw yielded much new faunistic and bionomic information on the neuropterans of the province of Mazovia (Mazowsze) – 56 species from nine families, including 17 green lacewings, particularly those species associated with various types of woodland in the region and with the urbanized areas of Warsaw (CZECHOWSKA 1982, 1985, 1986, 1990, 1994, 1997, 2002). An extensive project in the Białowieża Primeval Forest (Puszcza Białowieska) (north-eastern Poland) concluded with a lengthy monograph on secondary succession in fresh coniferous woodland, which recorded 23 neuropterans (among them, seven green lacewings) (TROJAN et al. 1994).

In the 1990s, the centres in Kielce (WERSTAK 1990, 1994, 1998) and Bytom joined in the field and laboratory work. In the latter case, some of the work involved the description of museum collections (DOBOSZ 1989, 1991b). At the same time, there appeared a series of papers summarizing and updating lists of neuropterans in Polish national parks and other naturally valuable areas (DOBOSZ & LIS 1990; DOBOSZ 1993, 1996a, 1996b, 1998, 1999a, 2000a, 2000b, 2001, 2003, 2010, 2015; DOBOSZ & BLAIK 2008; BLAIK & DOBOSZ 2010). Other papers focused on dipteran ectoparasites (Ceratopogonidae) of green lacewings (DOBOSZ 1991a, 1994, 1999b) and on faunistic and bionomic information on rare species or species new to Poland (DOBOSZ 2005; DOBOSZ & SZCZEPAŃSKI 2011; TILLIER et al. 2014; DOBOSZ & ZAMORSKI 2015). In the early 21<sup>st</sup> century, entomologists from the University of Opole initiated studies of Neuroptera, publishing papers on these insects from the Opole region and the mountains of south-western Poland (BLAIK 2007; BLAIK et al. 2007; BLAIK & KOREK 2008). Some of this work was done in collaboration with the Bytom museum.

Apart from the centres already mentioned, not much work has been done anywhere else on Neuropterida, and on Chrysopidae in particular; the bibliography in their re-

spect is sparse and those papers that have been published focus mainly on common species or species from the *Chrysoperla carnea*-complex (BARCZAK 1994; DYSARZ & WIŚNIEWSKI 1996; THIERRY et al. 1998; PANKANIN-FRANCZYK & BILEWICZ-PAWIŃSKA 2000; PAWŁOWSKI 2009; SOSZYŃSKA-MAJ 2008; ZYCH 2004).

The upsurge in research on the neuropterans of Poland since the early 1980s also bore fruit in the form of review papers summarizing the state of knowledge of Polish neuropterans or critically analysing bibliographic data published in earlier papers (CZECHOWSKA & DOBOSZ 1990; DOBOSZ 1992; DOBOSZ 1997; ASPÖCK et al. 1980, 2001; CZECHOWSKA 2007). The first checklist of the Neuropterida of Poland, published in 1990, gave 89 species, 25 of which were green lacewings.

### Distribution and current problems

To date, 103 species of neuropteran insects have been recorded in Poland, 31 of which belong to Chrysopidae. The relevant literature consists of 134 papers citing original data or summaries relating to green lacewings in Poland. On the basis of bibliographic data and the author's own materials, a total of 31 species of green lacewings have so far been recorded at 542 localities.

Despite the many years of research, the state of knowledge of the distribution of green lacewings in Poland remains rather poor. At least one green lacewing has been recorded in only 455 of the 3200 UTM (Universal Transverse Mercator) squares covering Poland (Fig. 4). The distributions of green lacewings in Poland broken down into the regions applied in the Catalogues of Polish Fauna (Katalogi Fauny Polski) are shown in Table 1. Only three of the 31 species of green lacewings – *Chrysopa perla*, *Chrysoperla carnea* (s.l.) and *Chrysopa phyllochroma* – have been recorded in 20 or more of the 24 regions specified. There are localities of seven species – *Nineta vittata*, *Chrysotropia ciliata*, *Chrysopa abbreviata*, *Ch. pallens*, *Pseudomallada prasinus*, *Ps. ventralis* and *Cunctochrysa albolineata* – in 15 to 19 regions, and another eight species – *Nothochrysa capitata*, *Nineta flava*, *Chrysopa commata*, *Ch. dorsalis*, *Ch. formosa*, *Ch. gibeauxi*, *Pseudomallada abdominalis* and *Peyerimhoffina gracilis* – have been recorded in ten to 14 regions. The other 13 species have hitherto been recorded in less than ten regions, and five are known from only a single locality in one to three regions: *Hypochrysa elegans* (3), *Chrysopa nigricostata* (2), *Ch. dasyptera* (1), *Ch. hummeli* (1) and *Ch. walkeri* (1).

The best researched regions of Poland with regard to green lacewings are the Wielkopolska-Kujawy Lowland with 24 species, the Baltic Coast and Upper Silesia with 22 species and the Pomeranian Lakeland and the Mazovian Lowland with 21 species. There are 20 species each from the Kraków-Wieluń Upland, the Małopolska Upland and the Świętokrzyskie Mountains. The regions with the fewest number of species are all the mountainous regions and the Lublin Upland. Nevertheless, as far as the number of species recorded nationally is concerned, the state of knowledge is undoubtedly good compared with that of countries bordering Poland (Czech Republic 24, Germany 28, Russia 28, Slovakia 26). In the coming years, field work and revisions of museum collections will be necessary, especially with regard to species only recently recorded in Poland,

**Table 1.** Distribution of green lacewings (Chrysopidae) in Poland, according to the physiographical regions applied in the Catalogues of Polish Fauna (Katalogi Fauny Polski). ● – bibliographic data; ○ – unpublished data; 1 – Baltic Coast; 2 – Pomeranian Lakeland; 3 – Mazurian Lakeland; 4 – Wielkopolska-Kujawy Lowland; 5 – Mazovian Lowland; 6 – Podlasie; 7 – Białowieża Primeval Forest; 8 – Lower Silesia; 9 – Trzebnickie Hills; 10 – Upper Silesia; 11 – Kraków-Wieluń Upland; 12 – Małopolska Upland; 13 – Świętokrzyskie Mountains; 14 – Lublin Upland; 15 – Roztocze; 16 – Sandomierz Lowland; 17 – West Sudetes; 18 – East Sudetes; 19 – West Beskid; 20 – Nowy Targ Valley; 21 – East Beskid; 22 – Bieszczady Mountains; 23 – Pieniny Mountains; 24 – Tatra Mountains.

L.-p.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Σ	
1	<i>Nothochrysa fulviceps</i> (Stephens, 1836)	●	●										●	●	●	●	●	●	●	●	●	●	●	●	●	6	
2	<i>Nothochrysa capitata</i> (Fabricius, 1793)	●	○		●								●	●	●	●	●	●	●	●	●	●	●	●	●	10	
3	<i>Hypochrysa elegans</i> (Burmeister, 1839)										●															3	
4	<i>Nineta flava</i> (Scopoli, 1763)	●	●	○	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	12	
5	<i>Nineta vittata</i> (Wesmael, 1841)	●	●	○	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	17
6	<i>Nineta impunctata</i> (Reuter, 1894)			○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	8
7	<i>Nineta pallida</i> (Schneider, 1846)				●				●																	7	
8	<i>Chrysotropia ciliata</i> (Wesmael, 1841)	●	○	○	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19	
9	<i>Chrysopa perla</i> (Linnaeus, 1758)	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	23	
10	<i>Chrysopa walkeri</i> McLachlan, 1893																									1	
11	<i>Chrysopa dorsalis</i> Burmeister, 1839	●	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	12	
12	<i>Chrysopa abbreviata</i> Curtis, 1834	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	17	
13	<i>Chrysopa dasyptera</i> McLachlan, 1872								●																	1	
14	<i>Chrysopa formosa</i> Brauer, 1850	●	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	10	
15	<i>Chrysopa phyllochroma</i> Wesmael, 1841	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	20
16	<i>Chrysopa commata</i> Kis et Ujhelyi, 1965			○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	12
17	<i>Chrysopa hummeli</i> Tjeder, 1936	●																								1	
18	<i>Chrysopa viridana</i> Schneider, 1845		○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	4
19	<i>Chrysopa nigricostata</i> Brauer, 1850				●																					2	
20	<i>Chrysopa pallens</i> (Rambur, 1838)	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19	
21	<i>Chrysopa gibeauxi</i> (Leraut, 1989)	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	12
22	<i>Pseudomallada flavifrons</i> (Brauer, 1850)			○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	8
23	<i>Pseudomallada prasinus</i> (Burmeister, 1839)	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19	
24	<i>Pseudomallada abdominalis</i> (Brauer, 1856)	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	10	
25	<i>Pseudomallada ventralis</i> (Curtis, 1834)	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19	
26	<i>Peyerimhoffia gracilis</i> (Schneider, 1851)	●	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	13	
27	<i>Chrysoperla carnea</i> (Stephens, 1836) s.l.	●	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	23	
28	<i>Chrysoperla lucasina</i> (Lacroix, 1912)	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	7	
29	<i>Chrysoperla pallida</i> Henry et al., 2002				○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	5	
30	<i>Chrysoperla carnea</i> (Stephens, 1836) s.str.	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	21	
31	<i>Cunctochrysa albolineata</i> (Killington, 1935)	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	15	
32	<i>Cunctochrysa cosmia</i> (Navás, 1918)	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	6	
Σ		22	21	14	24	21	12	16	15	4	22	20	20	20	8	16	12	15	11	21	7	16	12	9	4		



**Figure 4.** Records of green lacewings in Poland in UTM (Universal Transverse Mercator) squares

such as *Ch. walkeri*, separated from the *Chrysoperla carnea* s.l. complex, and also those restored to species status, such as *Ch. gibeauxi*, *Cu. cosmia* and *Ps. abdominalis*. In addition, intensive revision of the *Ps. prasinus* complex may lead to an increase in the number of green lacewing species identified in Poland.

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# Mesozoic Mantispidae: A review of the current state of knowledge

James E. Jepson<sup>1,2</sup> & Michael Ohl<sup>1</sup>

<sup>1</sup> Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr. 43, 10115 Berlin, Germany; e-mail: michael.ohl@mfn-berlin.de

<sup>2</sup> Current address: School of Biological, Earth and Environmental Science, University College Cork, North Mall, Cork, Ireland; e-mail: james.jepson@ucc.ie

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**Abstract.** The majority of fossil Mantispidae (Neuroptera) are known from the Mesozoic, including the oldest mantispid from the Lower Jurassic of Germany as well as others recorded from the Mid-Upper Jurassic, and Lower and Upper Cretaceous. They are currently represented by 37 specimens, with described specimens representing 13 species, 11 genera, and two subfamilies. Most are placed within the extinct subfamily Mesomantispinae, with others being placed within the extant Drepanicinae. The current knowledge of Mesozoic Mantispidae is reviewed.

**Further key words.** Cretaceous, Drepanicinae, Jurassic, Mesomantispinae

## Introduction

Mantispidae are a specialized family of Neuroptera, easily recognized by the following characters: raptorial fore legs (connected to the anterior end of the prothorax), and an elongate pronotum (elongation posterior to the leg connection). Today there are approximately 410 valid species-group taxa of mantispids, divided into four subfamilies: Drepanicinae, Symphrasinae, Mantispinae, and Calomantispinae. They are distributed in the Nearctic, Australasian Region, Oriental Region, Afrotropics, and Palearctic (OHL 2004; LIU et al. 2015). Mantispids are rare in the fossil record with only 48 individual specimens recorded; see JEPSON (2015) for a review of fossil record, with additions in JEPSON et al. (2018) and herein. The earliest fossils are recorded from the Jurassic, with others known from the Cretaceous, Palaeogene and Neogene (JEPSON 2015).

Most fossil mantispids are from the Mesozoic (Jurassic and Cretaceous), with 11 genera and 13 species described (Table 1). The earliest fossil Mantispidae is from the Lower Jurassic of Germany. Most Mesozoic mantispids are from Asia (China and Kazakhstan), where they show variation in their body morphology, particularly their raptorial fore legs, ranging from slender to clubbed. Their wing venation, however, is very similar making it difficult to determine taxonomic affinity by wings alone. Most of the Mesozoic taxa are placed in the subfamily Mesomantispinae, the exceptions are *Liassochrysa* and *Promantispia*, placed in Drepanicinae.

## Jurassic mantispids

*Liassochrysa stigmatica* (Fig. 1A), represented by an isolated fore wing, is the oldest fossil record of Mantispidae (Lower Jurassic, Germany). The species was recently placed within Drepanicinae (LIU et al. 2015). The first fossil record of Mantispidae with body

**Table 1.** Table of the known Mesozoic Mantispidae. Number of specimens for each species is one, unless stated.

<b>Taxon</b>	<b>Subfamily</b>	<b>Deposit</b>	<b>Age</b>
<i>Doratomantispa burmanica</i> Poinar & Buckley 1990	<i>Incertae sedis</i>	Burmese amber	Upper Cretaceous
Unnamed species (12 specimens) (Lu pers. comm. 2018)	–	Burmese amber	Upper Cretaceous
Larva (HAUG et al. 2018)	–	Burmese amber	Upper Cretaceous
<i>Gerstaeckerella asiatica</i> Makarkin, 1990	Drepanicinae	Kzyl-Zhar, Kazakhstan	Upper Cretaceous
<i>Sinomesomantispa microdentata</i> Jepson et al. 2013	Mesomantispinae	Yixian Formation, China	Lower Cretaceous
<i>Archaeodrepanicus acutus</i> Jepson et al. 2013	Mesomantispinae	Yixian Formation, China	Lower Cretaceous
<i>Archaeodrepanicus nuddsi</i> Jepson et al. 2013 (3 specimens)	Mesomantispinae	Yixian Formation, China	Lower Cretaceous
<i>Archaeodrepanicus</i> sp. (Jepson et al. 2013)	Mesomantispinae	Yixian Formation, China	Lower Cretaceous
Unnamed species (5 specimens) (Makarkin et al. 2012)	Mesomantispinae	Yixian Formation, China	Lower Cretaceous
<i>Mesomantispa sibirica</i> Makarkin 1997 (2 specimens)	Mesomantispinae	Baissa, Siberia, Russia	Lower Cretaceous
<i>Promantispa similis</i> Panfilov 1980 (2 specimens)	Drepanicinae	Karatau, Kazakhstan	Upper Jurassic
<i>Karataumantispa carnaria</i> (Khramov 2013)	Mesomantispinae	Karatau, Kazakhstan	Upper Jurassic
<i>Longipronotum benmaddoxi</i> (Jepson et al. 2018)	Mesomantispinae	Karatau, Kazakhstan	Upper Jurassic
<i>Ovalofemora monstrosa</i> (Khramov 2013)	Mesomantispinae	Karatau, Kazakhstan	Upper Jurassic
<i>Ovalofemora abbottae</i> Jepson et al. 2018	Mesomantispinae	Karatau, Kazakhstan	Upper Jurassic
Mesomantispinae gen et sp. indet (Jepson et al. 2018)	Mesomantispinae	Karatau, Kazakhstan	Upper Jurassic
<i>Clavifemora rotundata</i> Jepson et al. 2013	Mesomantispinae	Jiulongshan Formation, Daohugou, China	Mid-Upper Jurassic
<i>Liassochrysa stigmatica</i> Ansorge & Schlüter 1990	Drepanicinae	Dobbertin, Germany	Lower Jurassic

parts is *Clavifemora rotundata* (Fig. 1B), from the Mid-Upper Jurassic of China with the characteristic raptorial fore legs attached to the anterior of the prothorax. Its fore legs, however, are quite different to those of other mantispids and are enlarged and club-like

(JEPSON et al. 2013). This species represents the earliest record of the extinct subfamily Mesomantispinae. The Upper Jurassic of Kazakhstan (Karatau) yields a good diversity of mantispids (Figs 2, 3), with four genera and five species. The majority of these belong to Mesomantispinae. The mantispids with body parts show diversity in the shape of their fore legs, with genus *Ovalofemora* having oval shaped femora (Figs 2C, 3A), and others having slender shaped femora (*Longipronotum benmaddoxi*, *Karataumantispia carnaria*; Figs 2A, B; see JEPSON et al. 2018). Although there is much variation in their fore legs, the mesomantispines, both Jurassic and Cretaceous, have very similar wing venation making it difficult to determine genera on venation alone. This problem is highlighted by an isolated fore wing (Fig. 3B) which could only be placed in Mesomantispinae (JEPSON et al. 2018). Another Karatau mantispid, *Promantispia similis* (Fig. 3C), is represented by an isolated fore wing. *Promantispia* is thought to be closely related to *Liassochrysa*, based on characters such as the structure of the pterostigma (WEDMANN & MAKARKIN 2007), and has also been placed within Drepanicinae (LIU et al. 2015).

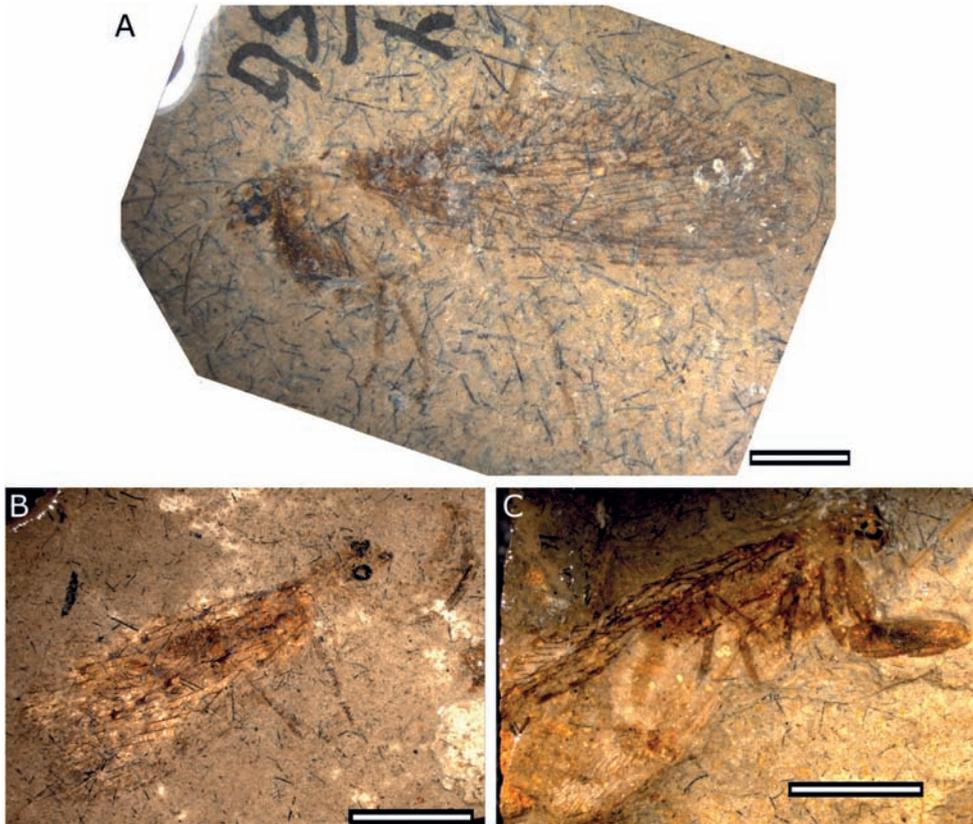


**Figure 1.** Jurassic Mantispidae. A – *Liassochrysa stigmatica*, holotype, Lower Jurassic, Germany. Scale bar 2 mm. B – *Clavifemora rotundata*, holotype, Mid-Upper Jurassic, China. Scale bar 5 mm.

### Cretaceous mantispids

Cretaceous fossils of Mantispidae are currently only known from Asia. The Lower Cretaceous has yielded fossils from Russia (Baissa) and China. *Mesomantispa sibirica* (Fig. 4A) (Baissa) is represented by two specimens of isolated fore wings (MAKARKIN 1997; WEDMANN & MAKARKIN 2007). This is the type species of the subfamily Mesomantispinae. In the Yixian Formation, China, there are other members of Mesomantispinae, with body parts, *Archaeodrepanicus nudsi* (Fig. 4B), *A. acutus* (Fig. 4C), *Archaeodrepanicus* sp., and *Sinomesomatispa microdentata* (Fig. 4D) as well as other undescribed specimens. Again these mantispids show some variation in their fore leg morphology, e.g., the size of their spines.

In the Upper Cretaceous an isolated hind wing (Fig. 5A) from Kzyl-Zhar, Kazakhstan is attributed to the extant genus *Gerstaeckerella* (Drepanicinae) due to having an almost identical venation with extant taxa (MAKARKIN 1990). However, it has been suggested that this similarity could be due to convergence (WEDMANN & MAKARKIN 2007). If it is



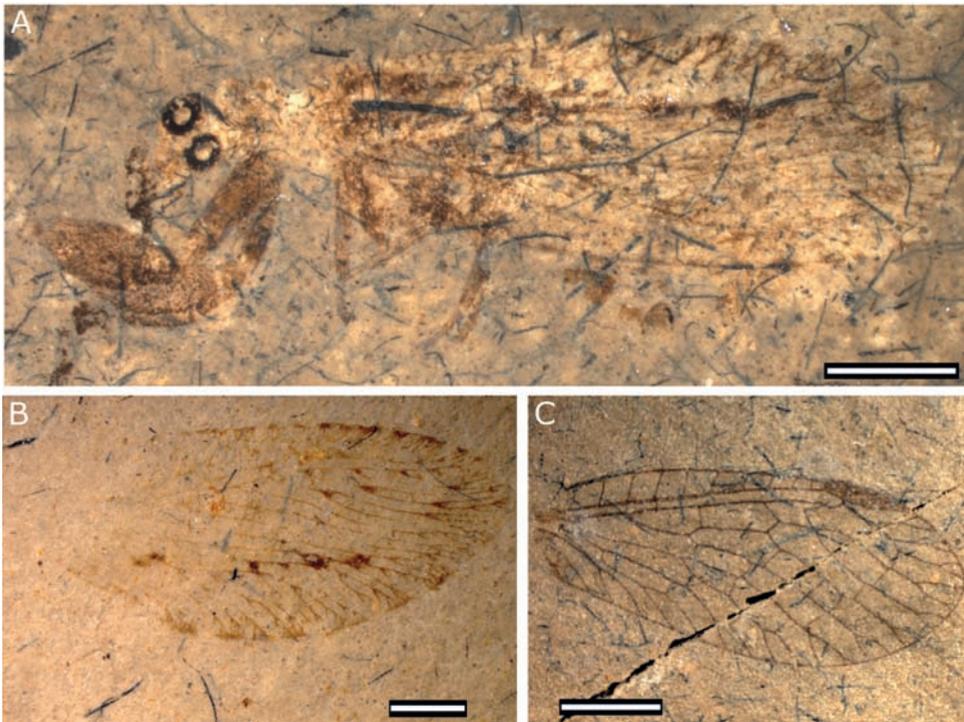
**Figure 2.** Upper Jurassic Karatau Mantispidae. A – *Lonipronotum benmaddoxi*, holotype. Scale bar 1 mm. B – *Karataumantispa carnaria*, holotype. Scale bar 5 mm. C – *Ovalofemora monstruosa*, holotype. Scale bar 5 mm.

a true member of this genus, *Gerstaeckerella asiatica* would represent the only known occurrence of the genus outside of South America, suggesting a more widespread distribution in the past.

Most described Mesozoic mantispids are known from fossils in rock with few described in amber. One species from Upper Cretaceous Burmese amber (Fig. 5B) has been described, *Doratomantispa burmanica* (POINAR & BUCKLEY 2011). In LIU et al.'s (2015) phylogeny it was considered to be Mantispidae *incertae sedis*. Recently, a mantispid larva associated with a spider (HAUG et al. 2018) and 12 adult specimens of Mantispidae (X. Lu pers. comm. 2018) have been discovered in Burmese amber. These new specimens will hopefully give a greater insight into Upper Cretaceous mantispids.

### Mantispid-like neuropterans

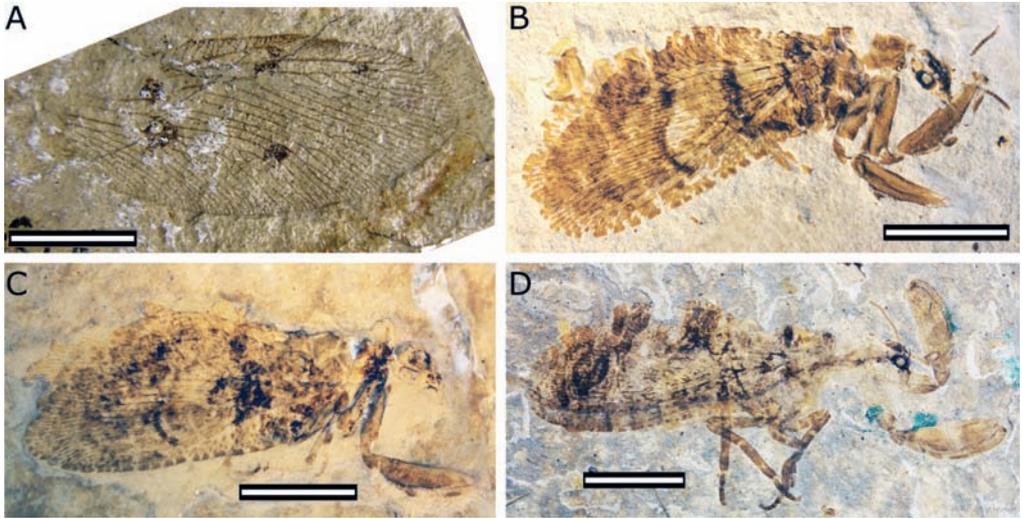
Some Mesozoic fossil neuropterans have a striking similarity to Mantispidae, with characters such as raptorial fore legs, elongate pronotum, and similar wing venation. These similarities have led to some of these specimens being described as Mantispidae, e.g., *Mesithone* Panfilov, 1980 (KHRAMOV 2013) and *Micromantispa* (SHI et al. 2015). These however can be separated from Mantispidae by characters such as their fore legs being



**Figure 3.** Upper Jurassic Karatau Mantispidae. A – *Ovalofemora abbottae*, holotype. Scale bar 1 mm. B – Mesomantispinae gen et sp. indet. Scale bar 2 mm. C – *Promantispa similis*, holotype. Scale bar 2 mm.

attached to the posterior of their prothorax, their pronotum being elongated anterior to this connection, an absence of prostrate setae on fore legs, the fore femur spines being densely packed, and a long pectinate CuA running parallel to the wing margin in hind wing. These taxa have now been placed within Berothidae, in either the subfamily Mesithoninae or Paraberothinae (MAKARKIN 2015; JEPSON 2015).

In addition, there are enigmatic mantispid-like neuropterans with halteres, described from the Cretaceous (USA and China). These were originally considered to be mantispids (GRIMALDI 2000; ENGEL & GRIMALDI 2008), but are now placed within their own family Dipteromantispidae (MAKARKIN et al. 2013; LIU et al. 2017).



**Figure 4.** Lower Cretaceous Mantispidae. A – *Mesomantispa sibirica*, paratype. B – *Archaeodrepanicus nuddsi*, holotype. C – *Archaeodrepanicus acutus*, holotype. D – *Sinomesomantispa microdentata*, holotype. All scale bars 5 mm.



**Figure 5.** Upper Cretaceous Mantispidae. A – *Gerstaeckerella asiatica*, holotype. Scale bar 5 mm. B – *Doratomantispa burmanica*, holotype. Scale bar 1.5 mm.

## Discussion

The majority of described Mesozoic mantispids, especially mesomantispines, are diagnosed on characters from their raptorial fore legs, or other body parts, *e.g.*, the long pronotum of *Longipronotum benmaddoxi*, with few diagnostic characters being taken from their wing venation. This is problematic when isolated wings, which are often more common, are found, *e.g.*, an isolated fore wing that could only be placed at sub-family level (JEPSON et al. 2018). However, some venation characters can be used to narrow specimens down to a genus or a group of genera, *e.g.*, cross-veins present in the cubital area, observed in just *Mesomantispa*, and the structure of CuP in the fore wing, *e.g.*, pectinate (*Clavifemora*, *Sinomesomantispa*, *Archaeodrepanicus*) or non-pectinate (*Karataumantispa*, *Ovalofemora*, *Longipronotum*). This venation problem may be due to many fossil taxa only having a partial venation preserved, and for most no hind wing venation has been described. It is hoped that discovery of more complete specimens in the future will help in finding taxonomically useful wing venation characters.

To date there has been no cladistic analysis of both extant and all fossil Mantispidae – LIU et al. (2015) included only a few fossils in their analysis – together with Berothidae, Rhachiberothidae, and Dipteromantispidae. Such an analysis would be interesting to see the relationships of these families, especially with regard to early Mesozoic taxa. However, problems of wing venation (mentioned above) and the fact that many fossils are still awaiting description (mantispids and especially berothids), it may be premature to consider such an analysis at this time.

With regard to the distribution of Mesozoic mantispids, all but one is from Asia, the exception being *Liassochochrysa stigmatica* from the Lower Jurassic of Germany. Other than this record, nothing is known of fossil mantispids in Europe until the Eocene, where fossils are known from Germany, UK, and Baltic amber (JEPSON 2015). This lack of knowledge could be due to a lack of fossil localities of this age in Europe, however, there are many well studied deposits, *e.g.*, Lower Cretaceous of the UK (Purbeck Limestone Group, Wealden Supergroup) and Spain (El Montsec, Las Hoyas, Spanish amber), therefore this is probably not the case. Therefore, it is most likely that either specimens are awaiting discovery, or mantispids were much rarer in Europe than Asia at this time.

## Postscriptum

Since acceptance, two publications have described new Cretaceous mantispids, increasing the known Mesozoic genera to 14 and species to 16 (PÉREZ-DE LA FUENTE & PEÑALVER 2019: *Aragomantsipa lacerata* from Spanish amber; SHI et al. 2019: *Archaeosymphrasis pennyi* and *Habosymphrasis xiai* from Burmese amber).

## Acknowledgements

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# Preliminary results of NEUIT (Barcoding of Italian Neuropterida) project

Agostino Letardi

ENEA, Lungotevere Thaon di Revel, 76, 00196 Roma, Italy; agostino.letardi@enea.it

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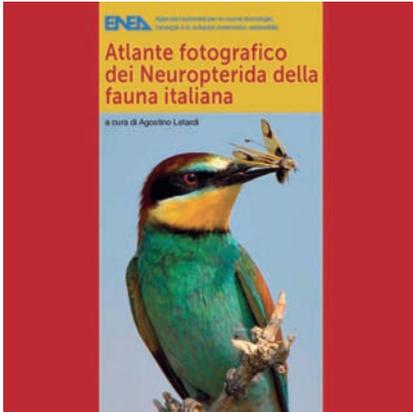
**Abstract.** This publication provides the first comprehensive DNA barcode data set for the Neuropterida of Italy, including 67 of the 195 species (34%) recorded from this country. Seventeen species represent a ‘unique presence’ in the database. The present DNA barcode library not only allows the identification of adult stages, but also provides valuable information for alpha-taxonomy, in addition to ecological and evolutionary research.

## Introduction

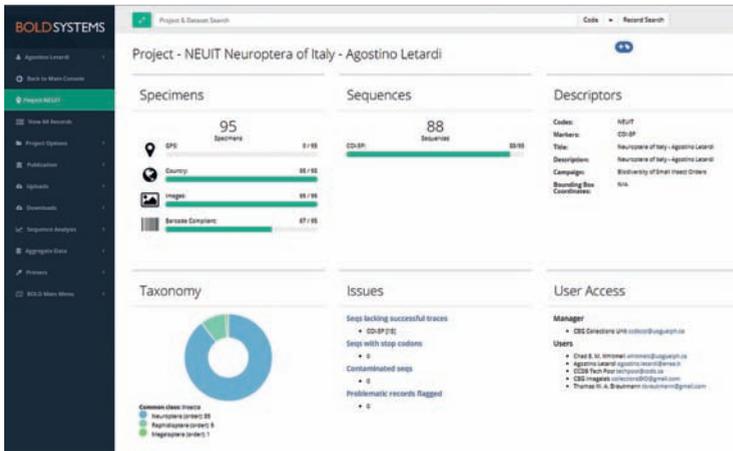
DNA barcoding aims at providing an efficient method for species level separation using a partial sequence of the mitochondrial COI gene. But DNA barcoding represents just one important descriptor in the framework of the multidimensional species approach (HEBERT et al. 2016). A huge effort of morphological and faunal studies has been realized for the Neuropterida of Italy (LETARDI 2016; Fig. 1): the goal of the present project is to create a DNA barcode library for a significant number of Italian species (Fig. 2).

## Material and methods

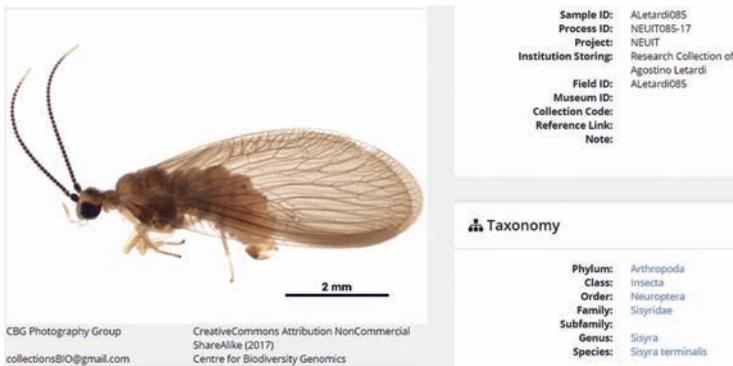
Along the lines of a study conducted in Germany (MORINIÈRE et al. 2014), in 2017, I started a close collaboration with the Biodiversity Institute of Ontario (‘BIO’, Guelph, Canada) to assemble a DNA barcode library for all Neuropterida known to occur in Italy in the framework of the International Barcode of Life Initiative (‘iBOL’) (Figs 3–4). Specimens derive from public collections (La Specola Museum, Florence; Museum “E.Caffi”, Bergamo) and from my private collections housed in the ENEA Casaccia Research Centre in Rome. In order to also get an image of each specimen for the ‘Barcode of Life Data System’ database (<http://www.boldsystem.org>), 95 complete specimens, representing 85 species of Neuropterida of the Italian fauna (mostly male specimens, some females and with few both females and males) were sent to the Canadian Center for DNA Barcoding (CCDB). There a single leg was removed from each specimen for standardized, high-throughput DNA extraction, PCR amplification and bidirectional Sanger sequencing ([www.dnabarcoding.ca/page/research/protocols](http://www.dnabarcoding.ca/page/research/protocols)). The amplified target region has a length of 658 bp, starting from the 59 end of the mitochondrial cytochrome oxidase c (COI) gene, which includes the 648 bp barcode region (HEBERT et al. 2003).



**Figure 1.** Book cover of the photographic atlas of the Italian Neuropterida fauna (LETARDI 2016).



**Figure 2.** Actual data in NEUIT project in May 2018 ([http://www.boldsystems.org/index.php/MAS\\_Management\\_DataConsole?codes=NEUIT](http://www.boldsystems.org/index.php/MAS_Management_DataConsole?codes=NEUIT)).



**Figure 3.** *Sisyra terminalis* Curtis, 1854, as an example of image elaboration in NEUIT project ([http://www.boldsystems.org/index.php/Public\\_BarcodeCluster?clusteruri=BOLD:AAU3101](http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:AAU3101)).

## PUBLIC DATA PORTAL - BIN PAGE

BINS ▾
SEARCH

**Barcode Index Number Registry For BOLD:ADI6611**  
Go to public records in this BIN

### BIN DETAILS

BIN URI:	BOLD:ADI6611	Average Distance:	N/A
DOI:	<a href="#">REQUEST DOI</a>	Maximum Distance:	N/A
Member Count:	1 [0 Public]	Distance to Nearest Neighbor:	10.33% (p-dist)
Barcode Compliant Members:	1		
Founding Record:			

### NEAREST NEIGHBOR (NN) DETAILS

Nearest BIN URI:	BOLD:ACT3826	Average Distance:	0.16% (p-dist)
Member Count:	2	Maximum Distance:	0.16% (p-dist)
Nearest Member:	FBNE472-15	Distance Variance:	0% (p-dist)

Nearest Member Taxonomy: Arthropoda, Insecta, Raphidioptera, Inocelliidae, Inocelliinae, Inocellini, Inocella, Inocella crassicornis

### TAXONOMY

- Phylum: Arthropoda [1] ↻
- Class: Insecta [1] ↻
- Order: Raphidioptera [1] ↻
- Family: Inocelliidae [1] ↻
- Subfamily: Inocelliinae [1] ↻
- Genus: Fibla [1] ↻
- Species: Fibla maclachlani [1] ↻

Subspecies:

Tags + -

Comments  +

### TREE RECONSTRUCTION OF BIN & NEAREST NEIGHBOR

No tree is generated when there are less than 3 or more than 1000 public records.

### COLLECTION LOCATION

Countries:

- Italy - [1] ↻

### DATA MANAGERS

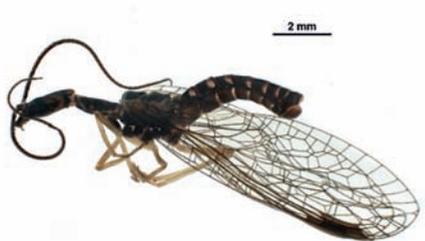
Public Data:	Private Data:
	CBG Collections Unit - [1]

**Specimens:** [DWC](#) [XML](#) [TSV](#)  
**Sequences:** [FASTA](#) [TSV](#)  
**Combined:** [XML](#) [TSV](#)

[Back to Last Page](#)

BIN COMPLIANT WITH METADATA REQUIREMENTS

Specimen Images:



### NEUIT027-17 (*Fibla maclachlani*)

License: Creative Commons Attribution NonCommercial ShareAlike (2017) [CC BY-NC-SA](#)

License Holder: CBG Photography Group, Centre for Biodiversity Genomics

Tags + -

Comments  +

Literal



Collection Sites: N/A

Tags + -

Comments  +

### Attribution

Specimen Depositories:

- Research Collection of Agostino Letardi - [1] ↻

Sequencing Centers:

- Biodiversity Institute of Ontario - [1]

Photography:

- CBG Photography Group - [1]

Collectors:

- Nappini S. - [1]

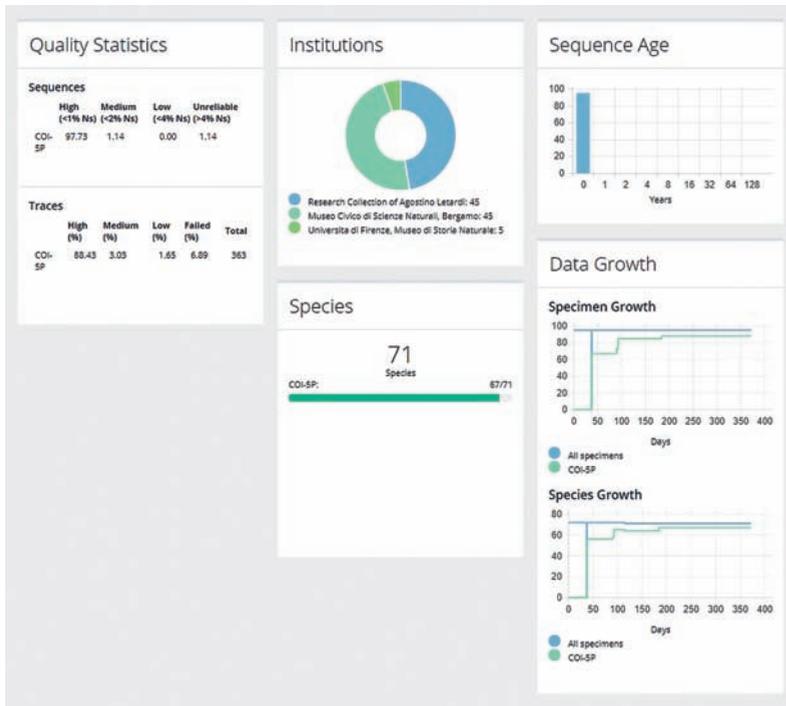
Specimen Identification:

- Agostino Letardi - [1]

**Figure 4.** *Fibla maclachlani* (Albarda, 1891), as an example for a species sheet in the ‘Barcode of Life Data System (v4)’ ([http://www.boldsystems.org/index.php/Public\\_BarcodeCluster?clusteru ri=BOLD:ADI6611](http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteru ri=BOLD:ADI6611)).

### Results and discussion

At present, 195 species, 66 genera and 14 families represent the known biodiversity of Italian Neuropterida. This preliminary report (Fig. 5) shows COI barcode sequences for 67 of these species, including representatives of 30 genera and 10 families. Seventeen species represent a ‘unique presence’ in the database (Fig. 6). Further analysis will be implemented in order to get data concerning all families of the Italian fauna and, at least, 80 % of the whole biodiversity of Neuropterida of my country.



**Figure 5.** Synthesis of presently available data in the ‘Barcode of Life Data System (v4)’

BIN Details			
Unique Bins (17) - Members 21			
BIN	TotalMembers	Taxa	Count in Project
BOLD:ADI5678	1	Megalomus tineoides	1
BOLD:ADI5703	2	Parasemidalis fuscipennis	2
BOLD:ADI6611	1	Fibla maclachlani	1
BOLD:ADI7417	1	Megalomus pyraloides	1
BOLD:ADI7485	1	Chrysopa viridana	1
BOLD:ADI7723	2	Pseudomallada clathratus	2
BOLD:ADJ2437	1	Ornatoraphidia flavilabris	1
BOLD:ADJ3535	1	Neuroleon nemausensis	1
BOLD:ADJ3874	1	Helicoconis sp.	1
BOLD:ADJ4765	2	Macronemurus appendiculatus	2
BOLD:ADJ5121	1	Semidalis aleyrodiformis	1
BOLD:ADJ5205	1	Symphorobius elegans	1
BOLD:ADJ5513	1	Neuroleon microstenus	1
BOLD:ADK9415	1	Pseudomallada genei	1
BOLD:ADK9478	2	Parainocellia bicolor	2
BOLD:ADK9613	1	Coniopteryx lentiae	1
BOLD:ADM7974	1	Coniopteryx pygmaea	1

**Figure 6.** Unique data in the ‘Barcode of Life Data System (v4)’ from the Italian specimens.

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# Mantispidae of the Área de Conservación Privada (ACP) Panguana, Peru

Axel Gruppe<sup>1,3</sup>, Michael Gebhardt<sup>1</sup> & Ernst-Gerhard Burmeister<sup>2</sup>

<sup>1</sup> Chair of Zoology – Entomology group, Department of Animal Sciences, Technical University of Munich (TUM), Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; [gruppe@wzw.tum.de](mailto:gruppe@wzw.tum.de); [michael.gebhardt@posteo.de](mailto:michael.gebhardt@posteo.de)

<sup>2</sup> The Bavarian State Collection of Zoology, Münchhausenstraße 21, 81247 München, Germany; [burmeister@zsm.mwn.de](mailto:burmeister@zsm.mwn.de)

<sup>3</sup> Corresponding author: [gruppe@wzw.tum.de](mailto:gruppe@wzw.tum.de)

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**Abstract.** Mantispidae are among the most familiar but least studied Neuroptera worldwide. Recent reviews of Mantispidae have enabled the determination of many species from the Neotropics. So far, no summary of Mantispidae of Peru has been published, however, according to HECKMAN (2017), six species are known to occur. We studied Mantispidae collected in the ACP Panguana in the Peruvian lowland primary rainforest. In the last two decades, 78 specimens have been collected around the ACP Panguana, most of which from light traps. However, with the exception of two field trips in 2015, Neuroptera have never been the primary focus of study. Altogether, 16 species have been collected, with *Dicromantisa gracilis* (Erichson, 1839) (52.2%) and *Zeugomantisa virescens* (Rambur, 1842) (16.6%) being most abundant. Nine out of 16 species are represented by only one specimen. Thirteen species have been recorded for the first time in Peru. Therefore, 19 species of Mantispidae are now currently known from Peru.

## Introduction

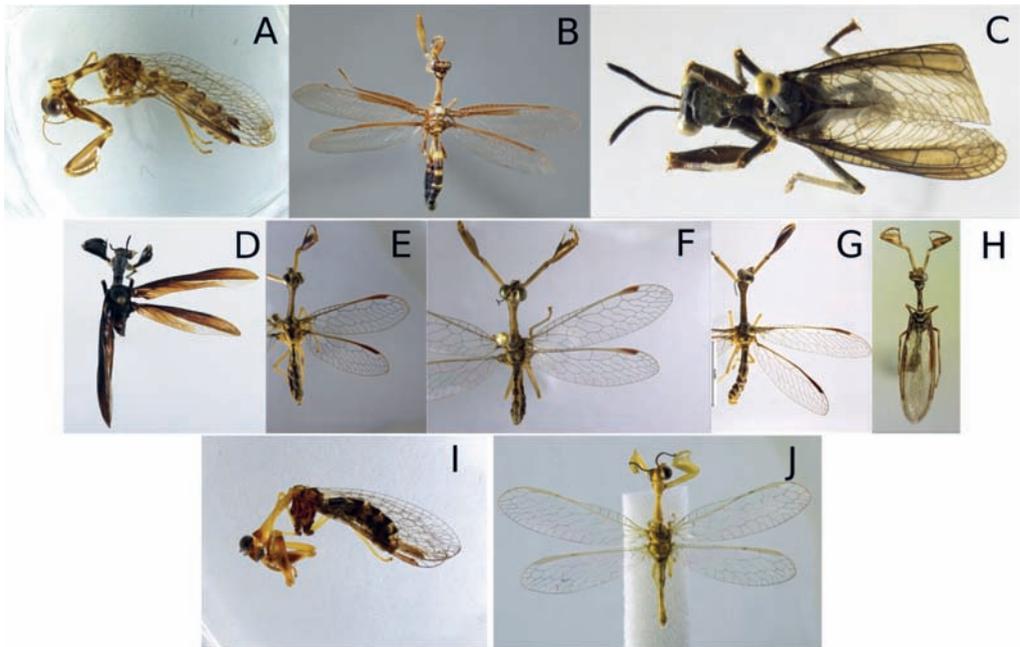
Mantispidae is a small family of Neuroptera of nearly worldwide distribution. Although they are very attractive with remarkable characteristics, such as raptorial forelegs and prolonged prothorax, their taxonomy and systematics have not been treated for most faunas. OHL (2004), in his worldwide review of Mantispidae, listed 410 extant species, of which 95 species of 16 genera of all four subfamilies have been recorded in the Neotropics. However, in the last decade several new species from the Neotropics have also been described (MACHADO & RAFAEL 2007, 2010; ARDILA-CAMACHO & GARCIA 2015; ARDILA-CAMACHO et al. 2018). A comprehensive work on Mantispidae of the Neotropics was first published by PENNY (1982) for the Amazon Basin. MACHADO & RAFAEL (2007, 2010) and ARDILA-CAMACHO et al. (2018) present well-illustrated keys of Mantispidae for Brazil and Colombia, respectively. HECKMAN (2017) provides keys for the South American Mantispidae and also states that the revision of most taxa is urgently needed.

The Área de Conservación Privada (ACP) Panguana research station was established in the primary lowland rainforest in the province Huanuco, Peru, by Maria and Hans-

Wilhelm Köpke in 1968 (PANGUANA FOUNDATION 2018). Many researchers have collected insects here during the last two decades. Although Neuroptera have never been the main focus of these entomologists, many specimens have been collected and the majority of these are deposited in the Bavarian State Collection of Zoology in Munich, Germany. In 2015, Neuroptera were the focus of two collecting trips to the ACP during spring and autumn.

MARTINS (2019) mentions seven species currently known from Peru. However, Peruvian Mantispidae have hitherto never been collected or studied in detail. Thus, the collection from the ACP Panguana, with many representatives from the lowland rainforest, is an important source for Peruvian species.

This paper deals with Mantispidae collected over the last two decades around the ACP Panguana. It represents the first detailed work on a local mantispid fauna in the Peruvian lowland rainforest. A major result of this study is the increase of known Peruvian Mantispidae species from seven to 19.



**Figure 1.** Mantispidae (Mantispidae) species collected in the Área de Conservación Privada (ACP) Panguana, Huánuco, Peru. A – *Buyda phthisica* (Gerstaecker, 1885) (9.9 mm), B – *Entanoneura batesella* (Westwood, 1867) (19.4 mm), C – *Climaciella obtusa* Hoffman in Penny, 2002 (7.1 mm), D – *Climaciella semihyalina* (Le Peletier de Saint Fargeau & Audinet-Serville in Latreille et al., 1825) (17.3 mm), E – *Dicromantispa debilis* (Gerstaecker, 1888) (8.7 mm), F – *Dicromantispa gracilis* (Erichson, 1839) (9.1 mm), G – *Dicromantispa moulti* (Navás, 1909) (9.5 mm), H – *Entanoneura batesella* (Westwood, 1867) (17.2 mm), I – *Leptomantispa* sp. (10.2 mm), J – *Zeugomantispa virescens* (Rambur, 1842) (6.6 mm). Numbers in parentheses denote fore wing length.

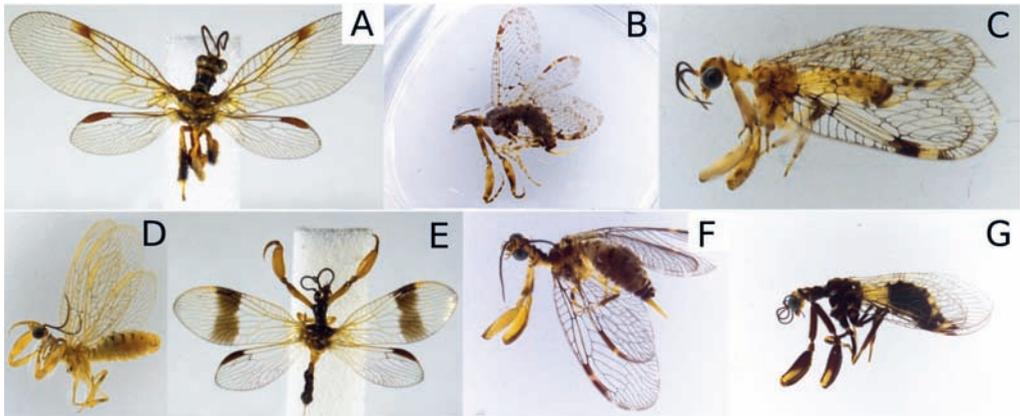
### Material and methods

Mantispidae were collected in the Área de Conservación Privada Panguana, Huánuco, Peru (9.63°S, 74.93°W, 260 m a.s.l.). The conservation area today covers an area of approximately 16 km<sup>2</sup> and is located between the Peruvian Cordillera Oriental of the Andes and the Sira Mountains at the Rio Yuyapichis, a tributary to the Rio Pachitea and thus the Amazonas system. The forest is largely a primary Amazonian Lowland Rainforest with only minor areas that had been logged extensively in the past. This land use increases dramatically in the surroundings of the protected area.

About 90 % of all mantispid specimens were collected close to the Panguana research station, located on a clearing at the riverbank of the Rio Yuyapichis. Here, a high-pressure mercury lamp (160 W) with a white sheet (5 × 2 m) was permanently installed on the waterside of the clearing, about 100 m from the Rio Yuyapichis (at normal water level) and about 50 m from the edge of the rain forest. Several fruit trees have been grown on the clearing and the river bank was covered by small bushes and herbal vegetation.

Teams of entomologists have collected here most years between April and June and September and October. The light trap was run nearly every night between 2000 and 2017, when entomologists were present at the station. Mantispidae specimens were either pinned or stored in alcohol. All types and half of the collected animals will be transferred to the Museum of Natural History, Lima, Peru; the remaining material will be stored in the Bavarian States Collection of Zoology in Munich, Germany.

We used the keys provided by PENNY (1982), MACHADO & RAFAEL (2007, 2010) ARDILA-CAMACHO & GARCIA (2015), HECKMAN (2017) and ARDILA-CAMACHO et al. (2018) for species determination.



**Figure 2.** Symphrasinae (Mantispidae) species collected in the Área de Conservación Privada (ACP) Panguana, Huánuco, Peru. A – *Anchieta eurydella* (Westwood, 1867) (6.7 mm), B – *Plega hagenella* (Westwood, 1867) (6.4 mm), C – *Trichoscelia anae* Penny, 1983 (7.4 mm), D – *Trichoscelia iridella* (Westwood, 1867) (8.0 mm), E – *Trichoscelia* sp. 1 (5.0 mm), F – *Trichoscelia* sp. 2 (7.6 mm), G – *Trichoscelia* sp. 3 (9.8 mm). Numbers in parentheses denote fore wing length.

**Table 1.** Species of Mantispidae collected at light in the Área de Conservación Privada Panguana (ACP), Huánuco, Peru, and their abundance.

Subfamily/ Species	n specimens
Symphrasinae	
<i>Anchieta eurydella</i> (Westwood, 1867)	1
<i>Plega hagenella</i> (Westwood, 1867)	1
<i>Trichoscelia anae</i> Penny, 1983	1
<i>Trichoscelia iridella</i> (Westwood, 1867)	1
<i>Trichoscelia</i> sp. 1	1
<i>Trichoscelia</i> sp. 2	2
<i>Trichoscelia</i> sp. 3	1
Mantispinae	
<i>Buyda phthisica</i> (Gerstaecker, 1885)	5
<i>Climaciella obtusa</i> Hoffman in Penny, 2002	1
<i>Climaciella semihyalina</i> (Le Peletier de Saint Fargeau & Audinet-Serville in Latreille et al., 1825)	3
<i>Dicromantispa debilis</i> (Gerstaecker, 1888)	2
<i>Dicromantispa gracilis</i> (Erichson, 1839)	43
<i>Dicromantispa moulti</i> (Navás, 1909)	5
<i>Entanoneura batesella</i> (Westwood, 1867)	3
<i>Leptomantispa</i> sp.	1
<i>Zeugomantispa virescens</i> (Rambur, 1842)	13
Total number of specimens	78
Total number of species	17

## Results

A total of 78 specimens representing 17 species of nine genera of Mantispidae have so far been collected (Table 1). Symphrasinae amounts to 13 specimens of seven species, representing 10% of specimens and 41% of all collected species (Fig. 2). The other 65 individuals and 10 species belong to Mantispinae, representing approximately 60% of known Peruvian mantispid diversity (Fig. 1). The most abundant species were *Dicromantispa gracilis* and *Zeugomantispa virescens*, representing 52% and 17% of all collected specimens, respectively. About 70% of all species (100% of Symphrasinae) were represented by only one or two specimens (Table 1).

## Discussion

In his most recent review, MARTINS (2019) mentions seven species known from Peru. However, Peruvian Mantispidae have never been studied in detail. We found 17 species in the collections of the ACP Panguana from the lowland rainforest, representing about 20% of the known Neotropical mantispid species (OHL 2004). It is a surprise to find so

many species in one small Peruvian area, which represents only one biome, especially if one takes into account that the specimens were only occasionally collected.

Mantispinae represented about 90% of all specimens collected and *Dicromantispa gracilis* and *Zeugomantispa virescens* were the most abundant species. This dominance has also been recorded in Colombia and Brazil (PENNY 1982; MACHADO & RAFAEL 2010; ARDILA-CAMACHO et al. 2018). In contrast, Symphrasinae – comprising about 40% of mantispid species – were less abundant, but this taxon seems to be much more diverse than previously observed. Four individuals have not been assigned to a species because morphological characters did not fully fit the existing descriptions in the literature (PENNY 1982; ARDILA-CAMACHO & GARCIA 2015; HECKMAN 2017; ARDILA-CAMACHO et al. 2018).

We expect that more mantispid species occur in the ACP Panguana and they should be discovered in future surveys dedicated to Mantispidae. The number of species in Peru should be much higher; this is due to the presence of many different biomes. In the present study specimens were only collected from the lowland rainforest biome. Last but not least, in agreement with HECKMAN (2017), this study has highlighted the urgent need of a revision of Neotropical Mantispidae in general and of Symphrasinae in particular.

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## What is the supposed owlfly illustrated in Aldrovandi's *De animalibus insectis* (1602)?

Rinaldo Nicoli Aldini

Dipartimento di Scienze delle Produzioni Vegetali Sostenibili (DI.PRO.VE.S.), Area Protezione Sostenibile delle Piante e degli Alimenti, Facoltà di Scienze Agrarie, Alimentari e Ambientali, Università Cattolica del Sacro Cuore, Piacenza, Italy; rinaldo.nicoli@unicatt.it

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**Abstract.** With his work, *De animalibus insectis* (1602), Ulisse Aldrovandi occupies a prominent place in the history of entomology. Of particular interest in this volume are the many original descriptions and woodcuts of insects. Partly due to the 'Tavole di animali' [Tables of animals] – illustrations drawn and watercoloured by hand, made by the author previously for the realization of the woodcuts for the printed book – some of them can be identified at genus or species level. For a large number of insects, Aldrovandi's descriptions and illustrations are the oldest in the entomological literature. Three adult antlions and one adult green lacewing are recognizable in the book and have already been studied; hypothetical larvae of green lacewings can be added and are recorded here. Among the butterflies and moths, there is another rather enigmatic insect, which could be an owlfly (ascalaphid), though there is some uncertainty due to discrepancies between its colouring in the 'Tavole di animali' and its description in the book. This paper deals with the possible identification of this insect as an ascalaphid and outlines the origin and meaning of the term 'ascalaph'.

### Historical preamble

Despite their medium or large size and showy aspect, owlflies seem to have made their first appearance rather late in entomological literature of the past centuries. Insects apparently related to dragonflies or halfway between dragonflies and butterflies, as in the case of the genus *Libelloides* Schaffer, 1763, with brightly coloured wings, represented for some of the early taxonomists a puzzle for purposes of classification. Proof of this is the fact that both Giovanni Antonio Scopoli in his *Entomologia Carniolica* published in 1763 and Michael Denis and Ignaz Schiffermüller in their anonymous work of 1775, usually known as *Wiener Verzeichnis*, ascribed the current *Libelloides macaronius* and *L. coccajus*, described by them, to the genus *Papilio* Linnaeus, 1758 (LETARDI 1995). Not so, however, Linnaeus, who in the 1764 edition of his *Systema Naturae* had already recognized the true affinity of such insects, placing the current *L. longicornis* described by him in that year in his (at that time widely comprehensive) genus *Hemerobius* and later, in the 1768 edition, improving the attribution by assigning it to the genus *Myrmeleon*, which he instituted in the same work (PANTALEONI & LORU 2018); these authors also present an overview of the 18th century authors who dealt with owlflies. For the subsequent century, see the monograph by VAN DER WEELE (1908: 7 ff.).

As regards the 18<sup>th</sup> century, the following authors are briefly mentioned here: James Petiver, who seems to have been the first, in 1711, to provide a certain illustration of an owlfly, the current *L. macaronius* (Scopoli, 1763), using the name »Smyrna Butter-bolt« in his *Gazophylacium* (PETIVERUS 1711); Jacob Christian Schäffer, who in his monographic study *Das Zwiefalter oder Afterjungferchen*, published in 1763, dealt with the current *L. coccajus* ([Denis & Schiffermüller], 1775), calling it »*Libelloides seu Libellula spuria*« (SCHÄFFER 1763); and Albertus Seba, who in his *Locupletissimi rerum naturalium thesauri accurata descriptio*, published in 1765, also provided illustrations of owlflies (SEBA 1765).

It is therefore in the 18th century, especially the second half, that with the onset of the great period of systematic classification of insects that blossomed in the cultural context of the Enlightenment, the presence of today's owlflies or ascalaphids appears with certainty in entomological literature. These insects had apparently escaped the consideration of the most eminent entomologists active in England, France and Central Europe in the 16<sup>th</sup> and 17<sup>th</sup> centuries, from Mufet to Ray and from Réaumur to Roesel von Rosenhof. Perhaps this was due to the distribution in Europe of owlflies being mostly to the south, in the northern Mediterranean region, and also because they are often localized or rare insects, whose biology and holometabolic development were still unknown at that time.

It is noteworthy, therefore, that Aldrovandi, an Italian author active in the second half of the 16<sup>th</sup> and the very early 17<sup>th</sup> century, left an indication in his work of a hypothetical owlfly, even if the elements provided by him give rise to some uncertainty. The following notes aim to focus principally on this particular aspect of his work, a very small tessera in the large mosaic of the encyclopaedic production of this giant in the history of natural sciences and forerunner in the systematic study of insects; but a tessera perhaps of some interest for the history of neuropterology.

### Ulisse Aldrovandi and his neuropterans

Ulisse Aldrovandi (Bologna 1522–1605; Fig. 1) is an important representative of scientific humanism of the late Renaissance and one of the greatest naturalists of the 16<sup>th</sup> century. He was a professor at the University of Bologna for many years and began publishing his monumental work only at the age of 77 (BERLESE 1909; BODENHEIMER 1928–29; MONTALENTI 1978; NICOLI ALDINI 2005). The many volumes of Aldrovandi's manuscripts and original watercolour illustrations of naturalistic subjects pertinent to his observations, dating back to the second half of the 16th century and preserved in the University Library of Bologna (BUB 2019), are a precious reference source for a deeper analysis of his way of thinking and working (ALESSANDRINI & CERAGATO 2007; NICOLI ALDINI 2007, 2008). His work *De animalibus insectis libri septem* (ALDROVANDUS 1602; Fig. 2) is the first printed book dedicated entirely to insects and stands out in the history of entomology; after the *editio princeps* published in 1602, there were several posthumous editions: Frankfurt, 1618, 1623; Bologna 1620, 1634, 1638–44 (MONTALENTI 1978), testifying to its quality, novelty, and the interest it aroused for posterity. It is in

large part an ample and accurate compilation, a true mine of quotations and notions taken from previous authors, especially from classical antiquity, but also containing a classification schema, many original observations and a large number of woodcuts of



**Figure 1.** Engraving portrait of Ulisse Aldrovandi, eighty years old, from the first pages of his book *De animalibus insectis libri septem* (Bononiae 1602) (private library, Bologna).

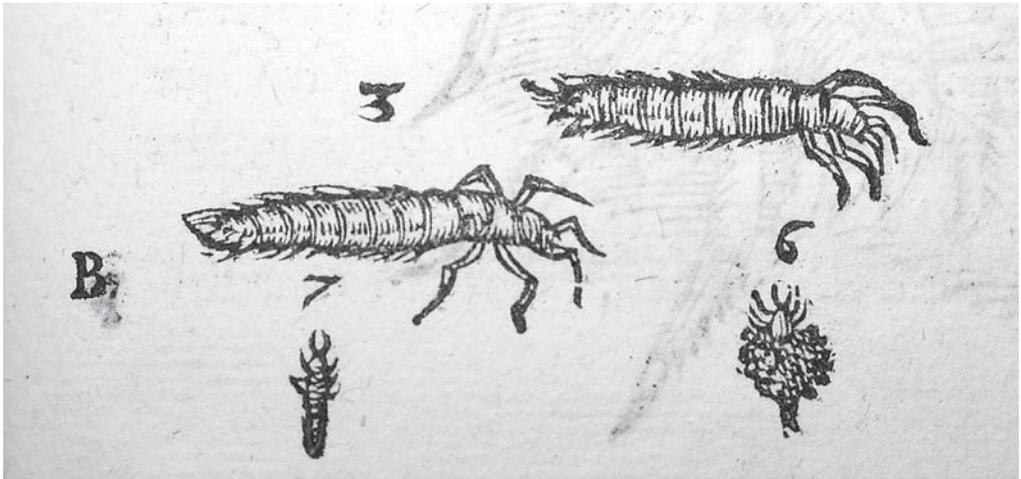


Figure 2. Ulisse Aldrovandi, *De animalibus insectis libri septem* (BONONIAE 1602): frontispiece.

insects, almost all present in Italy and observed by the author. A certain number of these woodcuts and descriptions are identifiable today at genus or species level, thanks partly to the series of 'Tavole di animali' [Tables of animals] drawn and watercoloured by hand, which the author had prepared previously for the future realization of the woodcuts for his zoological books (BUB, *Tavole acquerellate di Ulisse Aldrovandi*). However, the woodcuts of insects in the printed book are more numerous than the watercolours of insects in the Tables. For a good number of genera or species of insects, Aldrovandi's descriptions and illustrations are the oldest in entomological literature.

Of the many insects considered in the *De animalibus insectis*, only a few are now classified as neuropterans, recognizable at family level. The adults of one green lacewing (Chrysopidae) and three different antlions (Myrmeleontidae) have been briefly treated (ASPÖCK & ASPÖCK 2007; NICOLI ALDINI 2007), but only one of the latter is identifiable with certainty at genus level, thanks above all to the 'Tavole di animali', in which there is also an antlion larva not included in the printed work (NICOLI ALDINI 2007). Aldrovandi treated adult antlions, dragonflies and damselflies together, mixing them under the Latin name of '*Perlae*'.

For a more complete analysis of Aldrovandi's neuropterological work, it should be added that in the printed book there are also two woodcuts of a hypothetical debris-carrying larva of a green lacewing (Chrysopidae), drawn respectively with and without debris and placed among the insects named (in the singular) '*Xylophthoros*' or '*Ligniperda*' or '*Phryganium*', i.e., larvae of the current caddis-flies and psychid moths provided with cases of plant material. Aldrovandi wrote: »*Item [habes hic iconem] alterius [Xylophthori] minimi cum suis festucis, et sine festucis nimirum n. 6, et 7*« [Similarly [you have here the image] of another [Xylophthoros], very small, with its straws and without straws, i.e., nos. 6 and 7] (ALDROVANDUS 1602: 763 and woodcuts 6–7; Fig. 3).



**Figure 3.** Ulisse Aldrovandi, *De animalibus insectis* (1602), two hypothetic larvae of green lacewings, one of which (right) is a debris-carrier (woodcut at p. 763).

BODENHEIMER (1928–29: II, 345) did not attempt an identification, qualifying these illustrations simply as »Insekten-Larven«. The hypothesis that at least one could be a debris-carrying larva of a green lacewing (e.g., a species of the current genus *Pseudomallada* Tsukaguchi, 1995) is supported by its mouthparts which are forceps-like; the other larva, with similar mouthparts, but without debris and with a slender body, could belong to another green lacewing genus rather than to the same debris-carrying species.

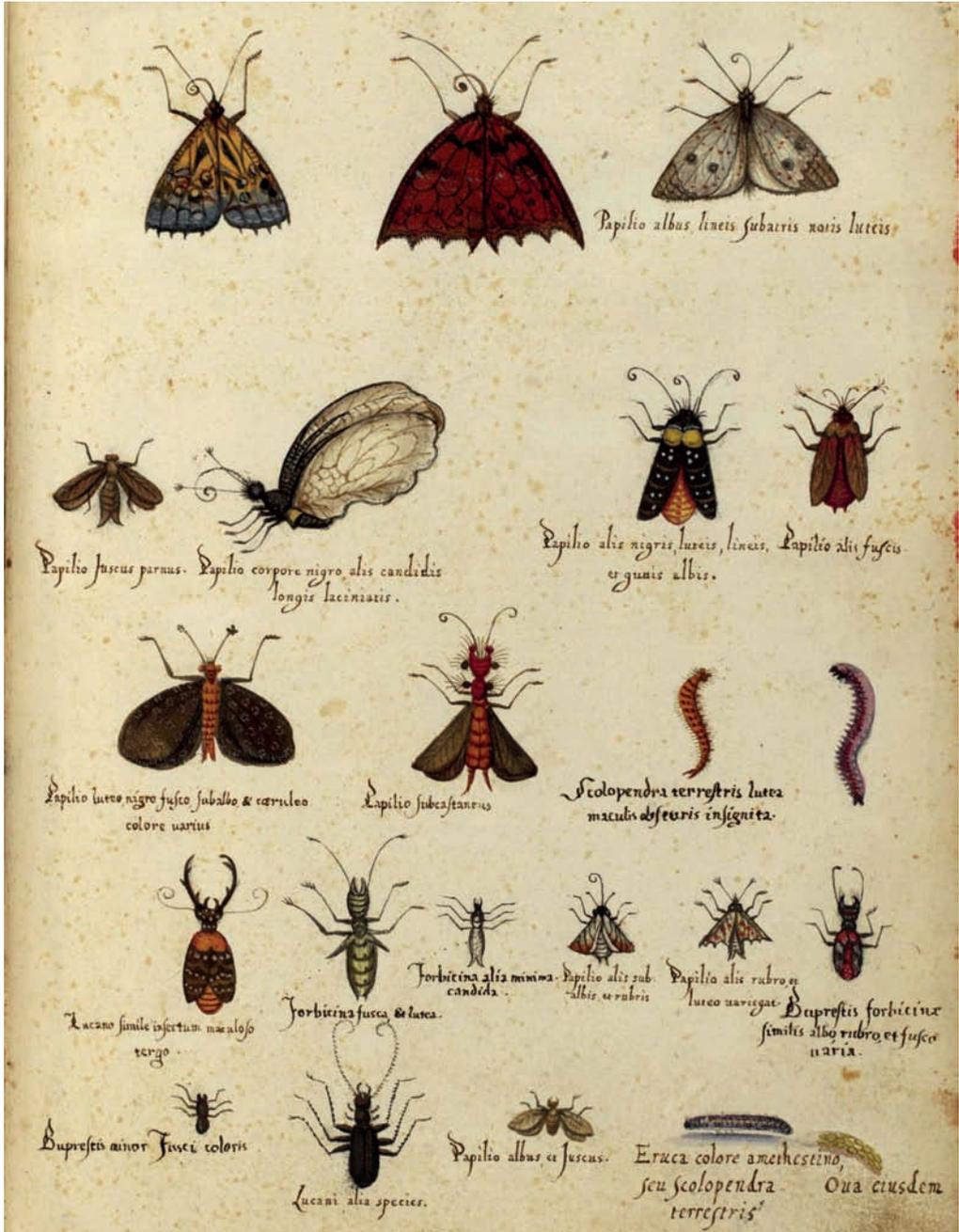
Aldrovandi's neuropterans are also later considered in the work *Historiae naturalis de insectis libri tres*, published in 1653 (first edition) by the naturalist of Scottish origin, John Jonston (Johannes Jonstonus), who explicitly took into account the many insects previously treated in the *De animalibus insectis* by Aldrovandi and in the *Insectorum sive minimorum animalium theatrum* (1634) by Moufet, reproducing descriptions and woodcuts of both these forerunners (JONSTONUS 1653).

### Is Aldrovandi's insect really an owlfly?

Among Aldrovandi's butterflies and moths, there is an enigmatic insect, perhaps an owlfly, although there is some uncertainty, partly due to the discrepancy between its colouring as it appears in the Tables of animals, where it is referred to as »*Papilio subcastaneus*« (BUB, *Tavole acquerellate di Ulisse Aldrovandi, Tavole di animali*, tomo VII, c. 119; Figs 4, 5) and its description in the printed book. The combination of the chromatic features described, which seem only partially compatible with the current genus *Libelloides* or with other genera of owlflies, is perplexing. BODENHEIMER (1928–1929: II, 340), basing himself on the illustration in the printed book, qualified this insect as »(*Ascalaphus* sp.)«, the use of parentheses denoting doubt. Among the many insects treated by Aldrovandi, this is only one of several insects giving rise to uncertainty regarding identification. Here is Aldrovandi's Latin description from his book, and a translation:

»*Insolentis profecto formae caput obtinet quinto loco pictus, a cuius lateribus duo sunt tubercula rotunda, nigra multis capillamentis nigris hirta, et in extremo alia duo, sed quae eiusdem cum capite sunt coloris nimirum ruberrimi, a cuius quoque lateribus duo alia sunt tubercula nigra, ut priora. Alae ex infima tergoris parte exoriuntur, colore fere nigricante, luteis aureisque lineis et guttis refertae. Alvus est bifurcata, tota lutea rubris zonis interstincta. Pedes et antennae nigricant*« [The one illustrated at place five undoubtedly has an unusually-shaped head, with two round black tubercles on the sides, bristling with many black hairs, and another two on the front, which however are of the same colour as the head – i.e., intensely red – on the sides of which there are two more tubercles, black like the first mentioned. The wings sprout from the lower extremity of the back and they are of rather blackish colour, with golden-yellow lines and stains. The abdomen is bifurcated, all yellowish, and spotted here and there with red areas. The legs and the antennae are blackish] (ALDROVANDUS 1602: 252 f., woodcut 5).

The watercolour of this insect (Fig. 5) and the derived woodcut in the *De animalibus insectis* (Figs 6, 7) as for other illustrations by Aldrovandi of insects present some fanciful elements, examples of artistic licence. In all likelihood, some features in the picture are not faithful to the model, especially as regards long legs: in the 'Tavole di animali',



**Figure 4.** Tavole acquerellate di Ulisse Aldrovandi, Tavole di animali, tomo VII, carta 119 with, in the centre, the hypothetic owlfly («*Papilio subcastaneus*»). From BUB (2019); printed with permission of the Biblioteca Universitaria, Bologna (© BUB); any further reproduction or duplication by any means is forbidden.

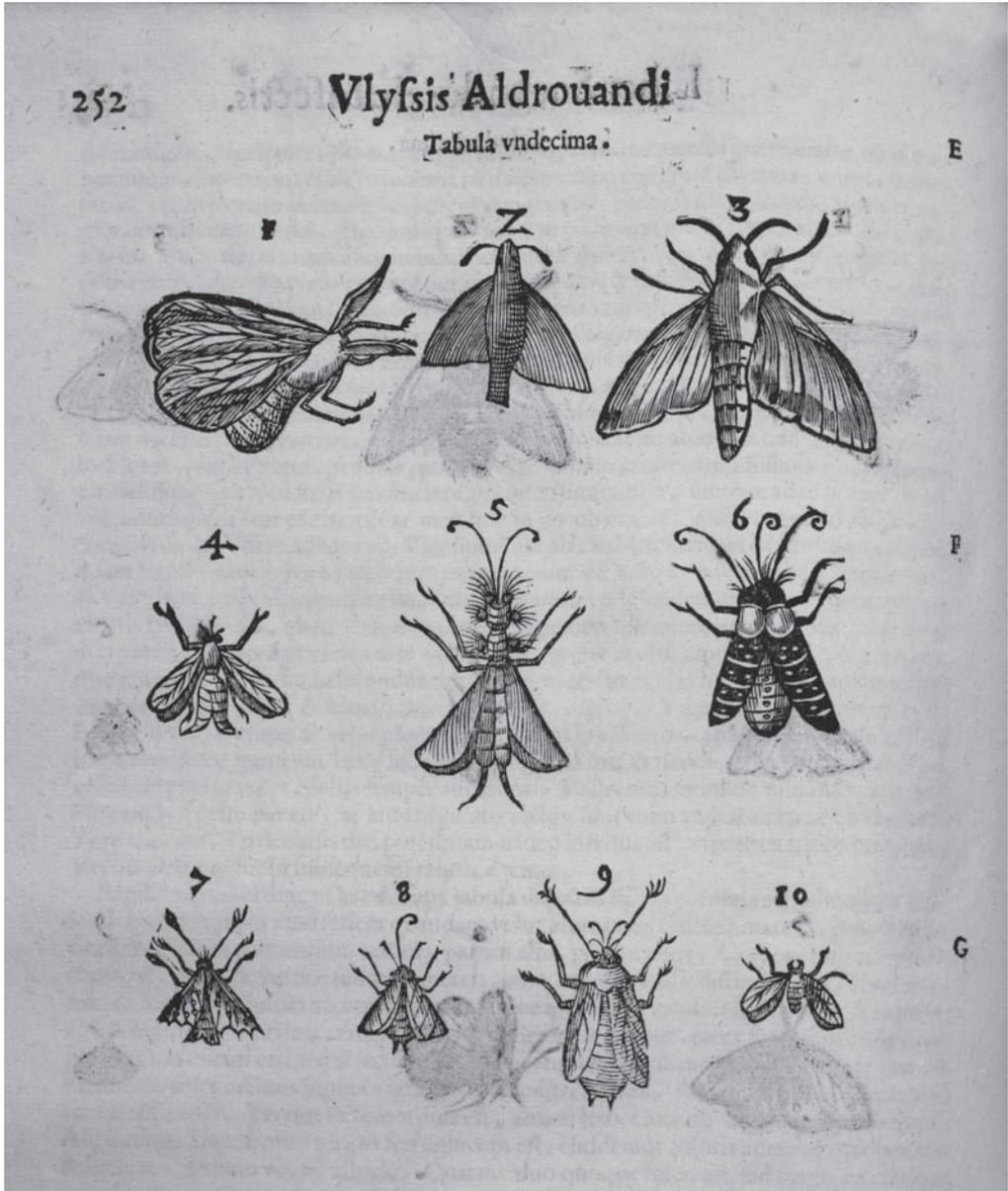
and consequently in the printed book, there are various examples of genera and species, especially butterflies and moths, which are easily recognizable, but illustrated with long legs (instead of short thin legs) based on imagination rather than reality. The uniformly dark colour of the wings of »*Papilio subcastaneus*« in the same 'Tavole' can also be seen in watercolours of other insects with membranous wings (for example, dragonflies identifiable at species level, with hyaline wings), where a silvery colour was probably used which subsequently oxidized, becoming darker; this uniformly dark colouring of the hypothetical owlfly does not, moreover, correspond to its description in the book, which seems to suggest the pigmentation and wing venation of a species of *Libelloides*, dark but with golden-yellow spots and lines. The very simple "fish bone" wing veins, present in the watercolour and in the woodcut, may also be due to imagination. The colour of the abdomen, both in the watercolour and in the description, yellowish and red, as well as the rest of the body, intensely red with some black tubercles, does not correspond with the colour of a *Libelloides* and is rather closer to that of the current genus *Deleproctophylla* Lefèbvre, 1842, if we refer to Italian and Mediterranean owlflies, but the latter genus does not coincide with other descriptive elements. The head and the thorax with thick and erect black hairs, instead, are very suggestive for the attribution to a *Libelloides*. The abdominal formations could be male cerci, even though imperfectly drawn, if the insect was indeed an owlfly. Was the model of the enigmatic insect perhaps a specimen of *Libelloides* with the colour of the body (not red) altered and lightened by many years of exposure to light? Or was it an immature adult, with the body incompletely pigmented? Or were errors made by the author of the watercolour? It is not possible to say.

Evidence in favour of the hypothesis that the mysterious insect is in any case a neuropteran is given by Aldrovandi himself further on in the same book, when he comments on the woodcut of an unquestionable *Palpares* Rambur, 1842 (NICOLI ALDINI 2007), erroneously inserted in a table including locusts and mantids: »*Papilionis icon est, quam supra dedimus inter papiliones*« [It is the image of a butterfly or moth, which we have provided above among them] (ALDROVANDUS 1602: 414 f., woodcut 5). BODENHEIMER (1928–29: II, 345) seemed to identify without doubt this insect as »*Ascalaphus* sp.«, but



**Figure 5.** Detail of Figure 4, with the insect enlarged. From BUB (2019); printed with permission of the Biblioteca Universitaria, Bologna (© BUB); any further reproduction or duplication by any means is forbidden.

erroneously. In fact, among Aldrovandi's '*Papiliones*' there is no woodcut of *Palpares* or other current neuropterans, except the hypothetical owlfly, which also corresponds as regards dimensions. In Aldrovandi's work, there are generally no precise size indications, but the figures in the tables are roughly to scale between themselves.



**Figure 6.** Ulisse Aldrovandi, *De animalibus insectis* (1602), woodcuts at p. 252 with the hypothetical owlfly in the centre.

A different hypothesis is that proposed as definitive by Roberto A. Pantaleoni (*in litt.*): the enigmatic insect could be a male *Palaeococcus* Cockerell, 1894 (Homoptera, Orthozioidea, Margarodidae); in Europe this genus includes one species – *P. fuscipennis* (Burmeister, 1839) – which corresponds in shape and in the dark-grey colour of the only pair of wings developed (however, Aldrovandi’s insect has two pairs of wings), in the bright red colour of the whole body and blackish colour of the antennae and legs, as well as in the presence of dorsal reliefs on the thorax, while the antennal scapus may seem from either side an anterior tubercle, and the posterior end of the abdomen has two elongated red processes (*cf.* GAVRILOV-ZIMIN 2018). The chromatic similarities with the watercolour are undoubtedly suggestive, but the presence of only one pair of wings, the rather small overall dimensions of the males of “giant scales”, slightly less than one centimetre, and the absence of the many erect black hairs on the head and thorax are less convincing.

Uncertainty therefore prevails regarding this apparent chimera. Future careful research into Aldrovandi’s entomological manuscripts may be helpful in solving this puzzle.



**Figure 7.** Detail of Figure 6, with the insect enlarged.

The illustration of this hypothetical owfly was later (1653) reproduced by Jonston, merely reporting faithfully the description provided by Aldrovandi (JONSTONUS 1653: 56, pl. VI n. 5).

### **Ascalaphids, the weight of a name**

If the insect treated by Aldrovandi was in fact an ascalaphid, it would be the earliest representative of this neuropteran family in entomological literature, anticipating by more than a century its unquestionable and well-known illustrations of the 18<sup>th</sup> century. However, it took over a century and a half for the current term 'ascalaph' to appear in entomological literature.

Indeed, this noun appeared scientifically thanks to Johann Christian Fabricius, who in 1775 instituted the genus *Ascalaphus* (VAN DER WEELE 1908; ASPÖCK et al. 1980). The Latin word derives from the ancient Greek ἀσκάλαφος (*askálaphos* – sort of owl or barn owl), the name used by Aristotle for an unspecified nocturnal bird of prey; but Ἀσκάλαφος (*Askálaphos*) is, in Greek mythology, a son of Ares, quoted in the Iliad; or, according to other myths, a suitor of Helen, or a son of Acheron transformed by Persephone into an owl (BONAVILLA & MARCHI 1819; FERRARI 1999). A particularly euphonic and meaningful name, due to its double value in expressing, on the one hand, similarity of the 'face' of these lacewings with that of the well-known nocturnal birds of prey and, on the other hand, in transposing mythological figures of ancient Hellas into the world of insects, in the wake of Linnaeus.

Many more decades passed before Alexandre Louis Lefèbvre de Cérisy instituted the family Ascalaphidae in 1842 (VAN DER WEELE 1908; ASPÖCK et al. 2001), and from this family name sprang the more wide-ranging term 'ascalaphid', used in many modern languages for indicating all species of this family of voracious predators, whether they are on the wing during the sunniest hours of the day, or on the contrary, in common with owls, have twilight or nocturnal habits.

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# On some morphological abnormalities found in Neuroptera

Rinaldo Nicoli Aldini

Dipartimento di Scienze delle Produzioni Vegetali Sostenibili (DI.PRO.VE.S.), Area Protezione Sostenibile delle Piante e degli Alimenti, Facoltà di Scienze Agrarie, Alimentari e Ambientali, Università Cattolica del Sacro Cuore, Piacenza, Italy; rinaldo.nicoli@unicatt.it

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**Abstract.** Cases of morphological abnormalities concerning Neuropterida have been published only rarely. If we neglect the deformities observable less rarely in the wings of the three orders of these insects (Megaloptera, Raphidioptera, Neuroptera), which result from defective adult emergence, or certain modest and recurrent anomalies in wing venation, it seems that these abnormalities are more rare than in other insects, such as Coleoptera, for which particularly striking teratological cases have been reported. The present contribution summarizes records of morphological anomalies in the literature concerning Neuropterida and illustrates three unpublished cases observed by the author in Neuroptera (Myrmeleontidae and Chrysopidae); of special interest is a case of unilateral antennal aplasia.

## Introduction

Morphological abnormalities in Neuropterida (Raphidioptera, Megaloptera, Neuroptera) have been described and illustrated in the entomological literature only very rarely. Modest symmetrical or asymmetric anomalies in wing venation, which can be ascribed to individual variability, have been observed to be relatively common (see, e.g., LACROIX 1917, 1920; OHM 1961; GREVE 1969; ZELENÝ 1969, 1971; NICOLI ALDINI & BAVIERA 2001; CANBULAT & KIYAK 2004). Similarly, some non-specific malformations (above all in wings) resulting from disturbances during the delicate phase of adult emergence have been observed not rarely. If we neglect to address these anomalies, it will seem that in the three orders of Neuropterida such abnormalities occur more infrequently than in insects of other orders, such as Coleoptera. For the latter, particularly relevant cases of real monstrosities are known, but these are apparently never observed in Neuropterida. Panoramic or at least extensive reviews on this subject have been published on both exopterygote and endopterygote insects of various systematic groups, sometimes also accompanied by experimental investigations: Phasmatodea (CAPPE DE BAILLON 1927, 1931), orthopteroid insects (BALAZUC 1955), Rhynchotha and related orders (BALAZUC 1952), Coleoptera (BALAZUC 1948, 1969), Strepsiptera and Hymenoptera (BALAZUC 1958). However, there is nothing inclusive as regards Neuropterida.

The pathomorphology of insects is due to various causes and ranges from very modest structural anomalies to highly conspicuous abnormalities, which fall fully within the sphere of teratology. Consequently, the field of study of insect pathomorphology is

broad and heterogeneous with respect to the different types of abnormalities that can occur and with respect to the factors responsible. Any abnormality may occur to different degrees, notably in the exoskeleton (body and appendages), in the adult as well as in pre-imaginal stages. Factors implicated in the etiopathogenesis may be intrinsic or extrinsic (environmental) factors that may act singularly or in combination. They include, among others, a range of genetic and endocrine factors, chemical and toxicological causes, mechanical, traumatic and other physical causes, climatic and microclimatic factors, and microbial and parasitic agents, which can interfere during embryonic or postembryonic development (see, e.g., CAPPE DE BAILLON 1927, 1931; BALAZUC 1948).

As regards Neuropterida, a short review, not claiming to be complete, includes, for the Megaloptera, the phenomenon of metathetely in Sialidae (DU BOIS & GEIGY 1935) and cases of male gynomorphic mandibles (BOWLES et al. 2007) and other abnormalities (schistomely; atrophy of a leg with symphysopody) (ELZINGA 1968; FERREIRA 2016) in Corydalidae; for the Raphidioptera, metathetely in Raphidiidae (ASPÖCK et al. 2018); and for the Neuroptera, various fairly significant abnormalities: anomalies, asymmetric or symmetrical, concerning only wing venation (LACROIX 1920), or both wing venation and wing shape (LACROIX 1934), or both wing venation and chaetotaxy (PRINCIPI 1985) in Chrysopidae; significant anomalies in the terminalia of an Emerobiidae (PRINCIPI 1958) and again in Chrysopidae (female with two spermathecae) (NEW 1987); and marked alterations in wing pigmentation in an Osmylidae (ASPÖCK & Aspöck 1964); as well as others.

The present preliminary contribution describes and illustrates some unpublished cases observed by the author in adult Neuroptera. A wider unpublished survey will be published with further contributions. The terminology used for the abnormalities mainly follows BALAZUC (1948). Discussion of the possible causes of the anomalies presented here is omitted. The specimens are preserved, dry and pinned, in the author's collection. The measurements reported were all made on dry specimens, without carrying out microscopic preparations.

### **Description and discussion of three cases**

#### **Unilateral antennal aplasia**

*Neuroleon* Navás, 1909 sp., ♀ (Figs 1, 2).

South African Republic: Cape Town, 5.iii.1972, Bassi leg.

The left antenna is completely missing and there is no trace of its insertion on the head (no torulus is observed, the corresponding surface of the head is rather smooth, without obvious depressions or reliefs). The vertex, seen from above, is slightly asymmetrical, more prominent at the border with the frons on the left side. No other anomalies can be observed on the head or other regions of the body (however the author does not have access to conspecific specimens for comparison and checking of any modest associated symmetrical anomaly). The right mesothoracic leg is almost completely missing, but this absence is clearly due to trauma.

This is the most interesting teratological case of those illustrated here. Cases of antennal aplasia, bilateral or unilateral, are very rare in insects and are more often associated with other anomalies, for example evident head deformity, or absence or malformation of the compound eye on the same side as the single missing antenna; they have been reported for example in Hymenoptera and Coleoptera (RODEK 1943; BALAZUC 1948, 1958; SOKOLOFF 1972).

The term “aplasia” (*i.e.*, complete lack of formation, as well as its synonym “agenesia”), of wider use in biological sciences, is preferred here, rather than the term “ectromelia” used by BALAZUC (1948, etc.) to indicate the total absence of development of an appendage. An alternative term is also “amelia”.



**Figure 1.** *Neuroleon Navás sp.*, female (South Africa): the specimen *in toto*.



**Figure 2.** *Neuroleon Navás sp.*, female (South Africa): detail of the head, view from the front.

### Unilateral atrophy of metathoracic leg with symphysopody

*Distoleon tetragrammicus* (Fabricius, 1798), ♂ (Figs 3–5).

Greece: Chalkidiki, Athos: Ag. Pavl., 18.viii.2008, L. Fancello leg.

The development of the left metathoracic leg is very much reduced starting from the femur (the coxa and trochanter are normally developed): the femur and tibia are each little more than  $\frac{2}{3}$  the length of the corresponding segments of the right metathoracic leg (which is normally developed), the tibial spurs are shorter, the tarsus is about half as long as the right one and made up of four recognizable tarsomeres (all shortened, especially the distal ones) instead of five; the second and third tarsomeres are very short and fused together ventrally; the fourth tarsomere is either completely fused with the fifth, or absent. The claws are shorter than those of the right metathoracic leg. The pigmentation and chaetotaxy of the femur, tibia and tarsus in the left metathoracic leg are rather different (modification in dark pigmentation, bristle reductions). Measurements (length) [mm]: right metafemur 2.7, left 2.0; right metatibia 2.9, left 2.0; right metatarsus (+ pretarsus) 2.0, left (+ pretarsus) 1.2.

According to the literature (see, e.g., BALAZUC 1948, 1952, 1969; SOKOLOFF 1972) and based on the author's experience, the more or less marked atrophy of a leg is one of the most common abnormalities (probably, the most common) observed in insects of both exopterygote and endopterygote orders (e.g., Odonata, Dermaptera, Rhynchota, Coleoptera, etc.). Its association with symphysopody (fusion of tarsomeres) is rarer. Reports for Neuropterida seem in any case to be extremely scarce; FERREIRA (2016) recently illustrated a case of atrophy of a leg with symphysopody in Corydalidae.



**Figure 3.** *Distoleon tetragrammicus* (Fabricius), male (Greece): the specimen *in toto*.

**Figure 4.** *Distoleon tetragrammicus* (Fabricius), male (Greece), detail of the metathoracic legs.



**Figure 5.** *Distoleon tetragrammicus* (Fabricius), male (Greece): detail of the left metathoracic leg, at higher magnification (the four arrows indicate the recognizable tarsomeres).



### Unilateral atrophy of metathoracic leg and of hind wing with anomalous venation

*Chrysoperla* Steinmann, 1964 sp. (? *pallida* Henry, Brooks, Duelli & Johnson, 2002), ♀ (Figs 6–8).

Italy: Lombardy: Brescia: Sellero m. 480 a.s.l., 12.viii.1978, R. Nicoli Aldini leg.

This specimen presents more abnormalities, all concerning the right appendages of the metathorax.

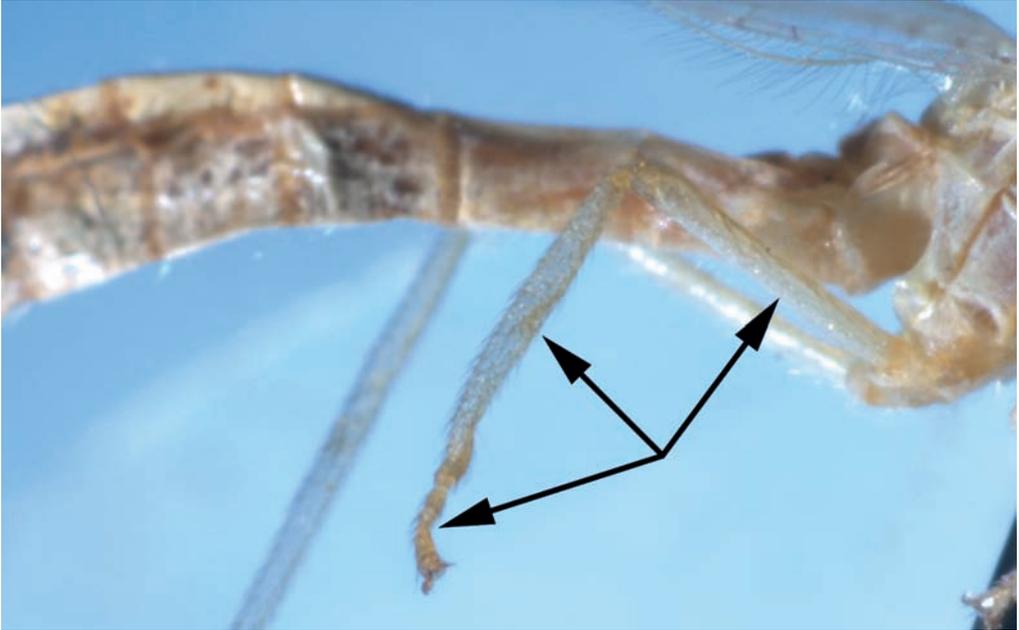
The right metathoracic leg is markedly reduced in its development starting from the femur (the coxa is normal, the trochanter is very slightly shortened): the femur is approx.  $\frac{2}{3}$  the length of the corresponding one in the left metathoracic leg (which is normally developed), the tibia is a little more than half the length of the corresponding one, and slightly deformed (curved) at the distal end; the tarsus (+ pretarsus) is little more than half the length of the corresponding one and provided with five tarsomeres, all shortened, but separated from each other (there is no symphysopody); the pretarsus has normal claws. Measurements (length) [mm]: right metafemur 1.5, left 2.2; right metatibia 1.9, left 3.5; right metatarsus (+ pretarsus) 0.5, left (+ pretarsus) 0.9.

The right hind wing presents modest atrophy accompanied by evident anomalies in the venation, which concern the radial sector and some cross-veins close to it. Measurements [mm]: length of the right fore wing 13.7, of the left 13.7; maximum width of the right fore wing 4.6, of the left 4.5; length of the right hind wing 11.0, of the left 12.3; maximum width of the right hind wing 3.5, of the left 4.0.

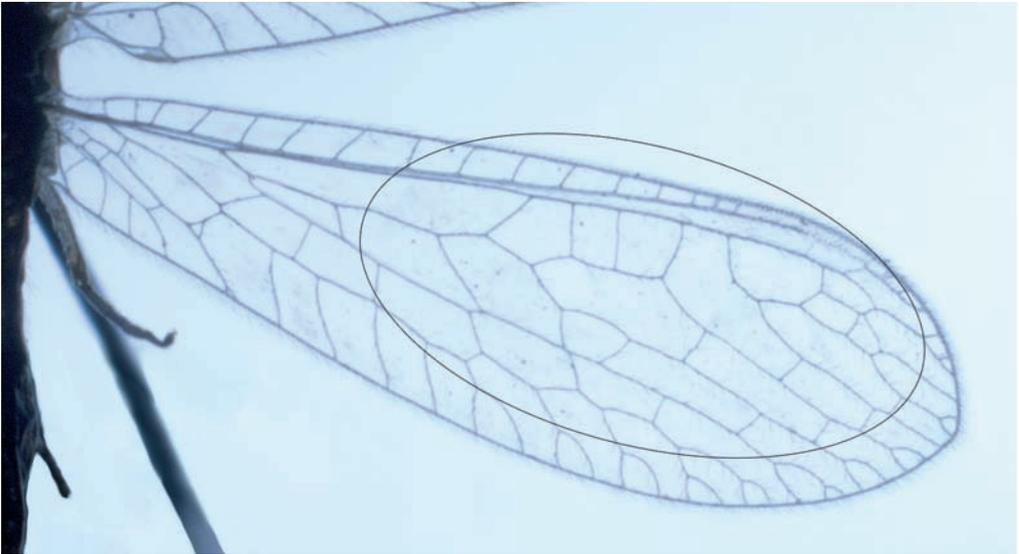
Significant anomalies in the venation of single fore wings have been described in Chrysopidae as regards the current genera *Pseudomallada* Tsukaguchi, 1995, and *Chrysoperla* Steinmann, 1964 (LACROIX 1920, 1934), and concern mostly the radial sector and some related cross-veins.



**Figure 6.** *Chrysoperla* Steinmann sp. (? *pallida* Henry et al.), female (Italy): the specimen *in toto*.



**Figure 7.** *Chrysoperla* Steinmann sp. (? *pallida* Henry et al.), female (Italy): detail showing the right metathoracic leg (the three arrows indicate tarsus, tibia and femur, respectively).



**Figure 8.** *Chrysoperla* Steinmann sp. (? *pallida* Henry et al.), female (Italy): right hind wing (the oval circumscribes the portion of the wing with anomalous venation).

The association of anomalous hind wing venation with a certain degree of wing atrophy, as well as their combination with marked atrophy of the homolateral metathoracic leg, accentuate the interest of this case.

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# Contribution to the study of the fine structure of the egg in the genus *Pseudomallada* Tsukaguchi, 1995 (Neuroptera, Chrysopidae)

Rinaldo Nicoli Aldini

Dipartimento di Scienze delle Produzioni Vegetali Sostenibili (DI.PRO.VE.S.), Area Protezione Sostenibile delle Piante e degli Alimenti, Facoltà di Scienze Agrarie, Alimentari e Ambientali, Università Cattolica del Sacro Cuore, Piacenza, Italy; rinaldo.nicoli@unicatt.it

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**Abstract.** The pattern of egg deposition, the morphology of the eggs and particularly the fine structure of the chorion surface examined by means of the scanning electron microscope (SEM) can provide useful elements for discriminating subfamilies, genera and species in green lacewings (Neuroptera, Chrysopidae). Observations are now available in the world literature on the fine structure of the exochorion for various genera and at least a dozen green lacewing species. The present work deals principally with the surface structures (exochorion surface, micropylar area) of the egg – examined by means of SEM – of some species belonging to the genus *Pseudomallada* Tsukaguchi, 1995 (Chrysopinae), which in Europe includes about two dozen taxa of specific or subspecific rank, some of which are difficult to discriminate and problematic as regards their systematic level. The species considered are: *P. prasinus* (Burmeister, 1839), *P. inornatus* (Navás, 1901), *P. clathratus* (Schneider, 1845), and *P. cf. picteti* (McLachlan, 1880). To date, the observations available in the literature on the egg features in these species are quite limited or absent. The pattern of the exochorion sculpturing provides more or less evident discriminating features between at least some of the species examined. It seems to be more difficult to find easily recognizable differences between species in the structure of the micropylar area. Other differences are to be found in the length of the egg and its stalk and in the shape of the egg itself, which can nevertheless change a little in relation to embryonic development.

## Introduction

The pattern of egg deposition, the size and colour of the eggs, the length of the egg stalk and the fine structure of the exochorion surface can provide useful elements for discriminating subfamilies and even genera and species in green lacewings (Neuroptera, Chrysopidae). The advent of the scanning electron microscope (SEM) has considerably increased the potential for investigation and has provided information on the external morphology of the egg of a good number of chrysopids, particularly as regards the fine structure of the exochorion surface and the micropylar area. Progressive improvements to the SEM and related techniques now result in images of increasingly better quality. To date, worldwide observations are available for various genera and approximately a dozen species of green lacewings (GEPP 1984a, 1984b, 1990; MONSERRAT et al. 2001). As pointed out by GEPP (1990), investigations on the fine morphology of the exochorion by

means of SEM in different, but closely related species within the Neuroptera can provide discriminating features; this research therefore deserves to be developed as far as is possible for ootaxonomy purposes, an aspect of undoubted interest although very poorly, or never considered for most taxa of many genera.

The first SEM observations concerning green lacewing eggs were carried out by MAZZINI (1974, 1976) on two taxa belonging, respectively, to the current genera *Chrysopa* Leach, 1815, and *Chrysoperla* Steinmann, 1964 (Chrysopinae). This pioneering research aimed above all to study the micropylar area, but also highlighted the basic features of the exochorion (fine sculpturing of a waxy-like nature). The micropylar area in these chrysopids is a circular structure, with a spongy appearance, located at the anterior (cephalic) pole of the egg and projecting above the exochorion; it is rather concave in the center. The margin of the micropylar area is scalloped, having many indentations, each of which corresponds to a micropylar orifice; by means of the SEM it is often possible to observe on the cephalic pole the flagellum of one spermatozoon penetrated through a micropylar orifice. Excluding the micropylar area, the exochorion reveals a rather uniform surface sculpturing, consisting in a reticulum of more or less thickly intersecting sinuous 'filaments' provided with a great number of more prominent projections which are more or less dense, irregularly shaped, slightly convex, vaguely fungiform; this set of 'filaments' and projections gradually disappears near the posterior (caudal) pole of the egg, where the stalk begins (MAZZINI 1974, 1976). Such a micro-sculpturing creates a characteristic pattern on the egg surface.

This general structure, which seems to be common at least to the main European genera of Chrysopinae, is also found in the genus *Pseudomallada* Tsukaguchi, 1995. In Europe this genus includes about two dozen taxa of specific or subspecific rank, some of which are difficult to discriminate or problematic as regards their systematic level. DUELLI et al. (2017) identified four main groups within the genus *Pseudomallada* by means of genital morphology and molecular genetics. Three of these groups are represented in Europe, and also in this survey. The present, preliminary work deals with the external morphology of the egg of four species of *Pseudomallada*: *P. prasinus* (Burmeister, 1839), a member of the *prasinus* group, *P. clathratus* (Schneider, 1845), a member of the *venosus* group, *P. cf. picteti* (McLachlan, 1880), a member of the *flavifrons* group, and finally *P. inornatus* (Navás, 1901), which does not fit into any of the four groups (DUELLI et al. 2017). The fine structure of the exochorion surface and the micropylar area are illustrated and discussed. Egg shape, size and colour, and length of egg stalk as well as the pattern of egg deposition are also recorded.

### Material and methods

The observations were made on eggs laid in the laboratory by gravid females collected by the author by the common methods used for the sampling of green lacewings on plants, or at artificial light sources in the evening. The females collected were introduced into transparent plastic or glass tubes, closed, some provided with twigs and leaves inside and some not, and kept there for a few days, generally without providing food,

until egg deposition. The laid eggs were taken off, together with their stalks by removing them at their base with the help of the tip of a pin and then were attached to specimen holders for metallization with gold and subsequent observation for taking SEM micrographs. When it was not possible to metallize and examine them within 1–3 days of deposition, the eggs were placed in a refrigerator at  $T = +4 \pm 1^\circ\text{C}$ , to slow down or to stop the embryonic development until preparation for the SEM observations. In no case were eggs temporarily stored in ethanol. The observation of eggs very soon after deposition allows one to obtain images of the eggs *in toto* without the depressions and deformations of the chorion easily caused by fixation in ethanol and subsequent steps until drying to the critical point.

The micrographs of the surface of the exochorion were made, for each species, at two different magnifications ( $3\,700\times$  and  $7\,000\times$  for *P. inornatus*;  $5\,000\times$  and  $10\,000\times$  for *P. clathratus*;  $5\,000\times$  and  $15\,000\times$  for *P. prasinus* and *P. cf. picteti*) and on three different areas of the egg: i) at a short distance from the front pole; ii) at approximately the equator; iii) at a short distance from the rear pole. The micrographs of the micropylar area were taken both in front view and from the side. As regards the magnifications of other micrographs, the reader is referred to the scale bar shown in the images themselves.

The females of *Pseudomallada* used to produce the eggs for the SEM observations were all collected in Italy, as follows: *P. prasinus* (Burmeister, 1839), Emilia Romagna: Piacenza, San Lazzaro, ix.2012 (1 female) and (same locality) vii.2018 (1 female); *P. inornatus* (Navás, 1901), Emilia Romagna: Piacenza: Gazzola: Momeliano, vii.2005 (1 female); *P. clathratus* (Schneider, 1845), Marche: Ancona: Osimo, vii.2011 (1 female); *P. cf. picteti* (McLachlan, 1880), Emilia Romagna: Piacenza, San Lazzaro, vii.2012 (1 female) and Campania: Napoli, vii.2018 (1 female).

Because of the well-known taxonomic problems and discrimination difficulties within the genus *Pseudomallada*, it is appropriate to specify here that the species in this research called *P. prasinus*, common and widespread throughout Italy and its major islands, is rather similar to *P. abdominalis* (Brauer, 1856) and *P. marianus* (Navás, 1905), but differs from the latter species on the basis of both the morpho-chromatic features of the adult and the pattern of egg deposition: in *P. prasinus* the eggs are laid singly and not – as occurs in the other two species – arranged in clusters with stalks more or less close each other (personal observations; see also LACROIX 1923; DUELLI 1984; PANTALEONI 1990; HÖLZEL 1998; ASPÖCK et al. 2001; LETARDI 2016). The species indicated here as *P. cf. picteti*, which occurs in peninsular and insular Italy, is similar to *P. flavifrons* (Brauer, 1850), from which it differs in some morpho-chromatic features; the male pronotum is not dilated on the sides and the male terminalia are as in *P. picteti* (McLachlan, 1880), but the chromotaxy is a little different from the latter (BULLINI et al. 1983; PANTALEONI 1990; BERNARDI IORI et al. 1995; LETARDI 2016).

The SEM used was an X L 30 ESEM FEI for *P. inornatus* and *P. clathratus*, and a Quanta FEG 250 ESEM FEI for *P. prasinus* and *P. cf. picteti*, both in the Laboratorio di Microscopia Elettronica, Facoltà di Scienze Agrarie, Alimentari e Ambientali, Uni-

versità Cattolica del Sacro Cuore, Piacenza. For each species, 2–5 eggs were examined. Measurements of the egg and stalk length were made on SEM micrographs, based on the magnification scale.

### Results and discussion

The observations and original data on the four species are reported below.

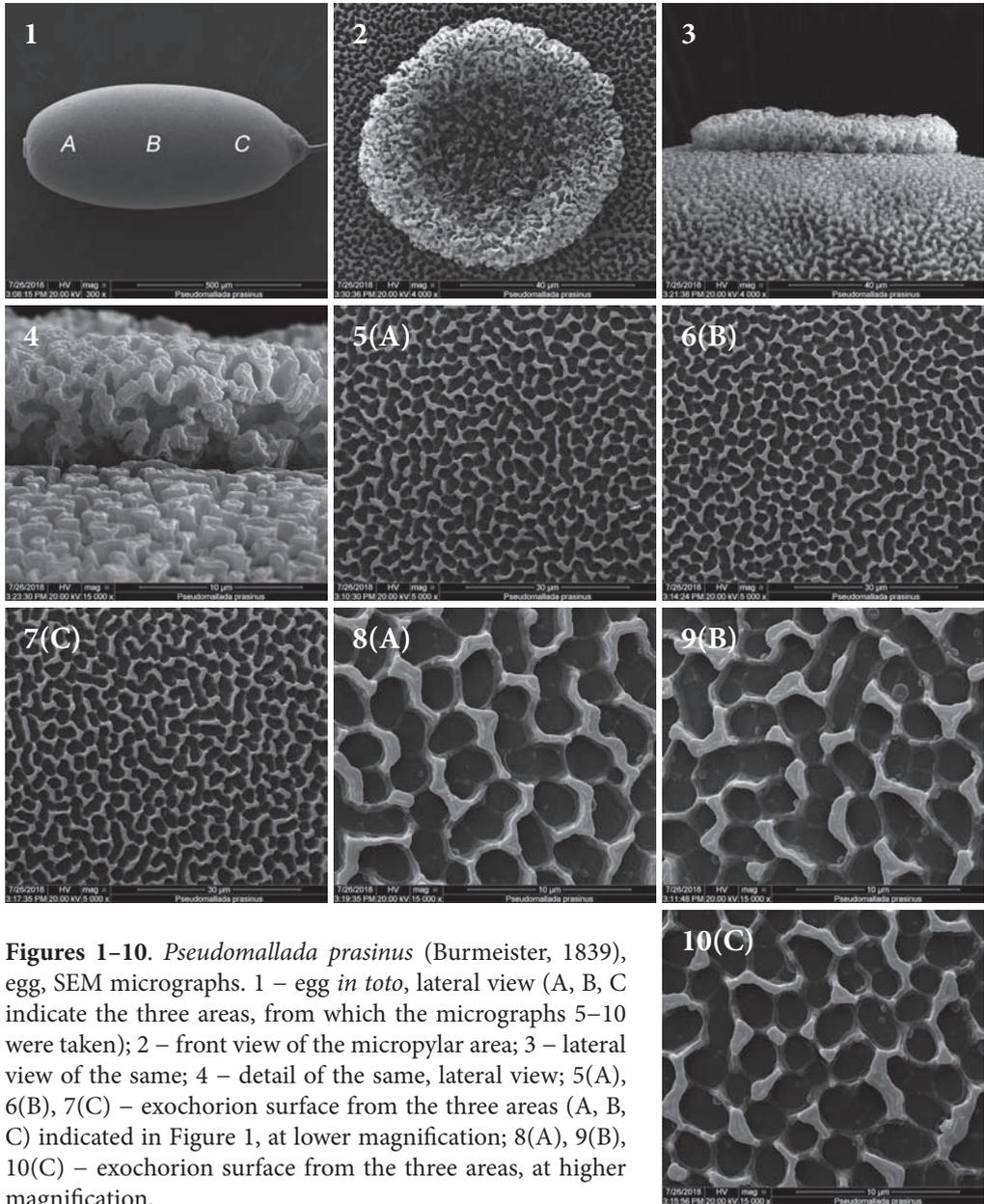
*Pseudomallada prasinus* (Burmeister, 1839) – Pattern of egg deposition: eggs laid singly and, when more than one, rather far apart. Colour of freshly laid eggs: light green. Length [mm]: egg (Fig. 1) 1.0 approx.; stalk 5.75 approx. Micropylar area and its details as in Figures 2–4. Exochorion surface: fungiform projections densely distributed and varied in shape; a good number of them elongated and quite wide. Meshes of the underlying reticulum mostly covered by these fungiform processes. The areas delimited by the reticulum are, mostly, irregularly rounded or quadrangular. The minimum distance between two nearby fungiform projections almost always corresponds to a single area (rarely to two) of the reticulum (Figs 5A, 6B, 7C; 8A, 9B, 10C).

*Pseudomallada inornatus* (Navás, 1901) – Pattern of egg deposition: eggs laid singly and, when more than one, rather far apart. Colour of freshly laid eggs: very light yellowish green, almost whitish. Length [mm]: egg (Fig. 11) 0.82–0.85 approx.; stalk 7.4 approx. Micropylar area and its details as in Figures 12–14. Exochorion surface: fungiform projections densely distributed and varied in shape, sometimes narrower and more angular than in *P. prasinus*. Meshes of the underlying reticulum largely covered by these fungiform processes; when recognizable, the reticulum is not very evident and the areas delimited by it are mostly irregularly ovoid and elongated. The minimum distance between two nearby fungiform projections corresponds to a single large area of the reticulum (Figs 15A, 16B, 17C; 18A, 19B, 20C).

*Pseudomallada clathratus* (Schneider, 1845) – Pattern of egg deposition: eggs laid singly and, when more than one, rather far apart. Colour of freshly laid eggs: light green. Length [mm]: egg (Fig. 21) 0.96 approx.; stalk 4.7 approx. Micropylar area and its details as in Figures 22–24. Exochorion surface: fungiform projections dense, very numerous, often rather thinner at both ends; these processes are larger than in *P. prasinus* and much wider than in *P. inornatus*. Meshes of the underlying reticulum well evident, delimiting irregularly round or almost square areas. The minimum distance between two nearby fungiform projections often corresponds to two areas of the reticulum and even more rarely to three (Figs 25A, 26B, 27C, 28A, 29B, 30C).

*Pseudomallada* cf. *picteti* (McLachlan, 1880) – Pattern of egg deposition: eggs laid in clusters (5–8 in each cluster in the present observations), whose stalks are very close to each other. Colour of freshly laid eggs: whitish. Length [mm]: egg (Fig. 31) 0.89 approx.; stalk 4.4–4.5 approx. (Piacenza San Lazzaro), 6.5–6.6 approx. (Napoli). Micro-

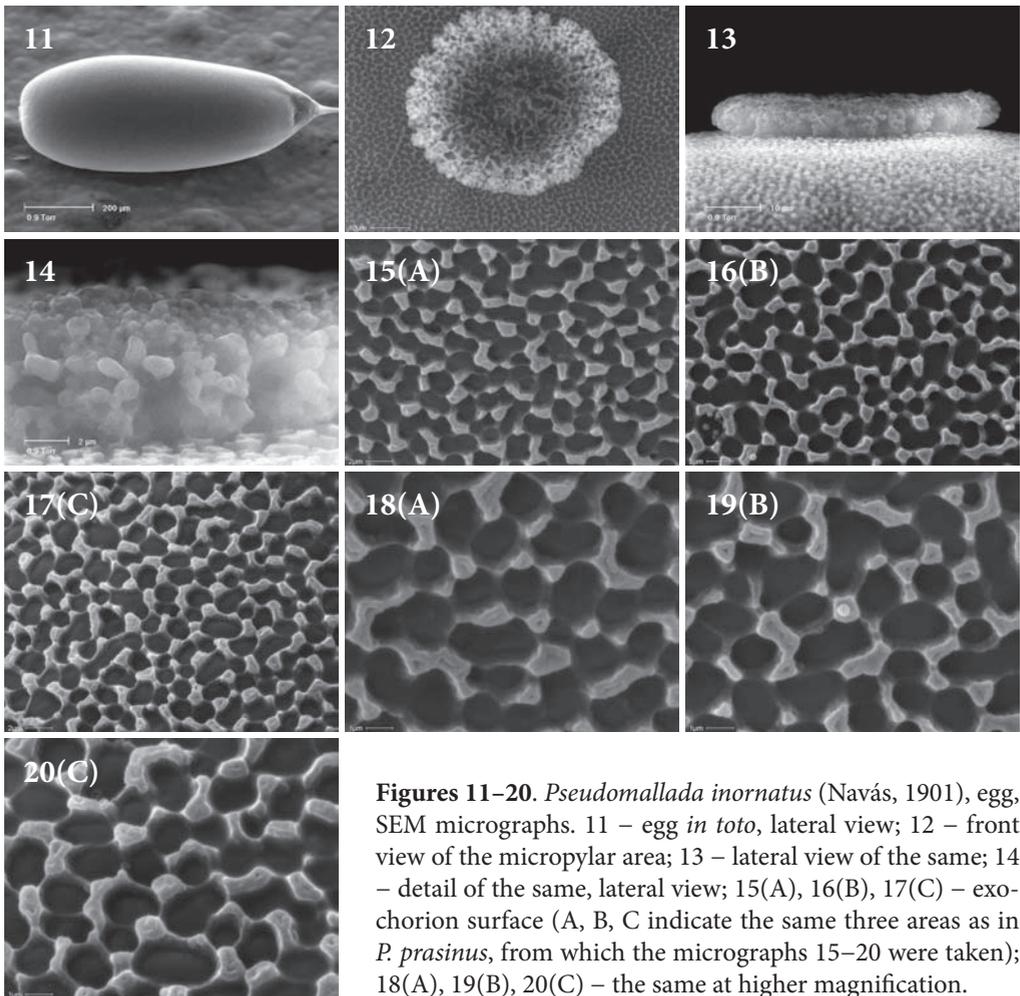
pylar area and its details as in Figures 32–34. Exochorion surface: fungiform projections almost triangular or sinuous, often with clearly thinned ends or provided with thin, elongated offshoots, more distant from each other than in *P. prasinus* and *P. inornatus*,



**Figures 1–10.** *Pseudomallada prasinus* (Burmeister, 1839), egg, SEM micrographs. 1 – egg *in toto*, lateral view (A, B, C indicate the three areas, from which the micrographs 5–10 were taken); 2 – front view of the micropylar area; 3 – lateral view of the same; 4 – detail of the same, lateral view; 5(A), 6(B), 7(C) – exochorion surface from the three areas (A, B, C) indicated in Figure 1, at lower magnification; 8(A), 9(B), 10(C) – exochorion surface from the three areas, at higher magnification.

narrower and thinner than in *P. clathratus*. Meshes of the underlying reticulum evident and numerous, delimiting irregularly rounded or slightly ovoid or almost square areas. The minimum distance between two nearby fungiform projections often corresponds to two, three or sometimes even four areas of the reticulum (Figs 35A, 36B, 37C, 38A, 39B, 40C). The comparison between the SEM micrographs of eggs laid by a female of *P. cf. picteti* from Piacenza (San Lazzaro) and by a female from Napoli evidenced a good similarity in the exochorion pattern.

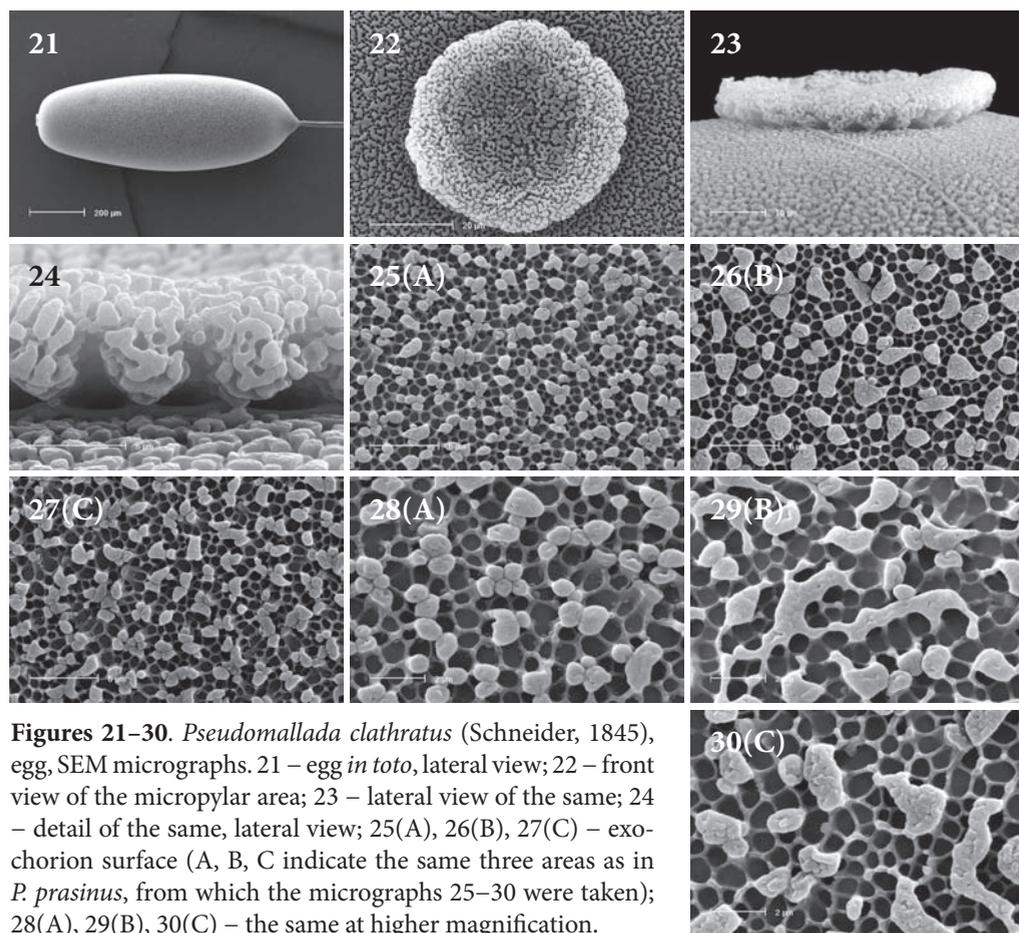
As far as the pattern of egg deposition is concerned, from a general point of view the present data confirm already well-known observations (*e.g.*, LACROIX 1923; PRINCIPI



**Figures 11–20.** *Pseudomallada inornatus* (Navás, 1901), egg, SEM micrographs. 11 – egg *in toto*, lateral view; 12 – front view of the micropylar area; 13 – lateral view of the same; 14 – detail of the same, lateral view; 15(A), 16(B), 17(C) – exochorion surface (A, B, C indicate the same three areas as in *P. prasinus*, from which the micrographs 15–20 were taken); 18(A), 19(B), 20(C) – the same at higher magnification.

1956). As regards the colour of the freshly laid eggs, the colour in *P. cf. picteti*, whitish instead of pale green, is similar to that in *P. flavifrons* (Brauer, 1850) and, together with the similar pattern of egg deposition, denotes affinity between these two taxa. This close relationship is only partially confirmed, however, by the pattern of the exochorion surface (RNA unpubl.) observed in oviposition by different females of *P. flavifrons* from the same locality of Italian Alps (in one oviposition the pattern seems to recall *P. clathratus* more than *P. cf. picteti*).

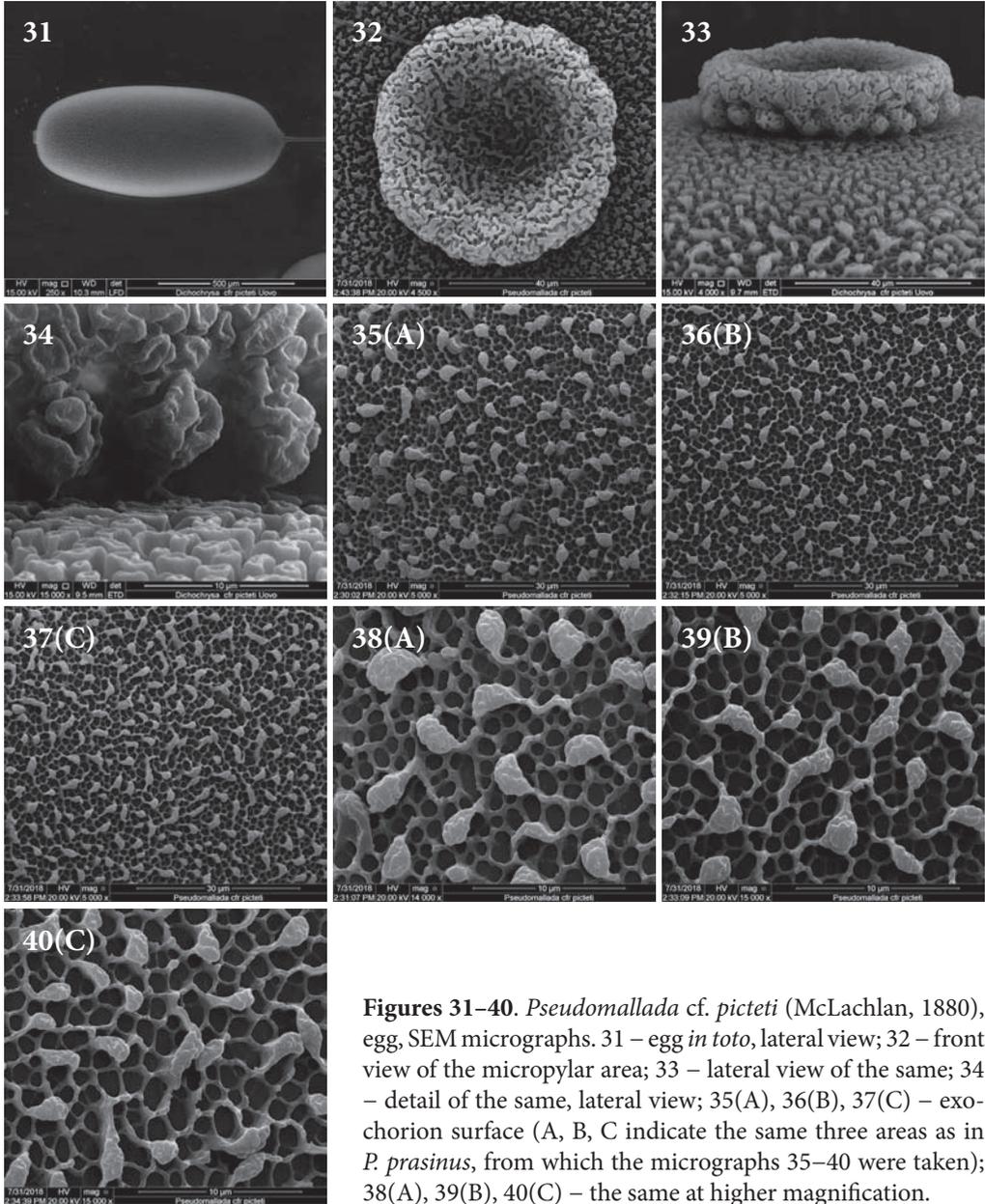
From a general point of view, the pattern of the exochorion sculpturing, as highlighted above, can provide more or less evident discriminating features between at least some of the species examined. It seems to be more difficult, however, to find easily recognizable differences between species in the structure of the micropylar area. Other



**Figures 21–30.** *Pseudomallada clathratus* (Schneider, 1845), egg, SEM micrographs. 21 – egg *in toto*, lateral view; 22 – front view of the micropylar area; 23 – lateral view of the same; 24 – detail of the same, lateral view; 25(A), 26(B), 27(C) – exochorion surface (A, B, C indicate the same three areas as in *P. prasinus*, from which the micrographs 25–30 were taken); 28(A), 29(B), 30(C) – the same at higher magnification.

differences are to be found in the length of the egg and its stalk and in the shape of the egg itself, which can nevertheless change a little in relation to embryonic development.

The comparison of the sculpturing of the three (A, B, C) areas of the exochorion in each species does not seem to show significant differences between these distinct points of the egg surface.



**Figures 31–40.** *Pseudomallada cf. picteti* (McLachlan, 1880), egg, SEM micrographs. 31 – egg *in toto*, lateral view; 32 – front view of the micropylar area; 33 – lateral view of the same; 34 – detail of the same, lateral view; 35(A), 36(B), 37(C) – exochorion surface (A, B, C indicate the same three areas as in *P. prasinus*, from which the micrographs 35–40 were taken); 38(A), 39(B), 40(C) – the same at higher magnification.

Bibliographic data on the eggs of the species considered here concern, mainly or exclusively, the pattern of egg deposition as well as the egg colouring. Thus, there are no previous data obtained by means of the SEM micrographs comparable with the present results. It is desirable, for *Pseudomallada* (as well as for other genera of chrysopids) that this research (measurements included) be extended to all the taxa of the genus and also, for each taxon, to more populations of different geographical origin within the respective areal, as well as to more eggs for each species, to verify the existence of constant similarities or, to the contrary, of differences.

These investigations seem therefore useful for ootaxonomic purposes; in particular they can contribute to the detection of more or less close levels of phylogenetic relationship between different taxa and groups of taxa within this lacewing genus.

### Acknowledgements

Heartfelt thanks to Andrea Roverselli, in charge of the Laboratorio di Microscopia Elettronica, Università Cattolica del Sacro Cuore, Piacenza, for his valuable collaboration in the observations and especially for the carrying out and management of the SEM micrographs.

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# A targeted survey of Neuropterida diversity in natural areas of eastern Bavaria, Germany – Results of the Post-Symposium excursion

Joshua R. Jones<sup>1</sup>, Lukas Kirschey<sup>2</sup> & Axel Gruppe<sup>3</sup>

<sup>1</sup> Utah Valley University, Dept of Biology, 800 W. University Pkwy, Orem, UT 84058, USA; doc.jonesresearch@gmail.com

<sup>2</sup> Museum für Naturkunde, Invalidenstraße 43, 10115 Berlin, Germany; lukas.kirschey@mfk-berlin.de

<sup>3</sup> Lehrstuhl für Zoologie – Entomologie, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; gruppe@wzw.tum.de

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**Abstract.** During the 13<sup>th</sup> International Symposium of Neuropterology in Bavaria, Germany, two field excursions to natural areas of south-eastern Bavaria were conducted, one on 19.vi.2018 and a second on 22–25.vi.2018. Sites visited included Laufen on river Salzach and environs; Nature Reserve Weitsee-Lödensee; Schönrammer Filz; Frauenberg Hostel and environs, near the municipality of Haidmühle; Bavarian Forest National Park; and the Nature Reserve ‘Donauleiten von Passau bis Jochenstein’. Range extensions were recorded for *Aleuropteryx lowii*, *Osmylus fulvicephalus*, *Sialis fuliginosa*, *Nineta flava*, and *Chrysopidia ciliata*, and the first records of Neuropterida were made from Laufen, Weitsee-Lödensee and Schönrammer Filz. A participant list, collection site descriptions, maps and photos, and a table of species collected at each site are presented.

## Introduction

During the 13<sup>th</sup> International Symposium of Neuropterology in Bavaria, Germany, two field excursions to natural areas of south-eastern Bavaria were conducted, a midterm excursion on 19.vi.2018 to two sites, and the post-symposium excursion, which took place from 22–25.vi.2018 at four sites. Bavaria, at over 70 500 km<sup>2</sup>, is the largest German federal state, and is situated in the south-eastern part of the country, adjacent to Austria and the Czech Republic (Fig. 1), with which it shares a border. Two major rivers flow through the state, the Danube, tributary to the Black Sea, and the Main, tributary to the Rhine and thus the North Sea. Along Bavaria’s border with Austria are the Bavarian Alps, which include the Zugspitze (2962 m a.s.l.), the highest peak in Germany. In this region, at the foothills of the Alps, the mid-term excursion was held. The Bavarian Forest, a geological unit with the Bohemian Forest, forms the vast majority of the frontier with the Czech Republic. This was the target of the post-symposium excursion.

Bavaria, with a warm temperate climate, lies in the transitional area of the maritime climate of Western Europe to the northwest and the continental climate of Eastern Eu-

rope in the east. Whereas the maritime climate is characterized by mild winters, cool summers and high humidity, the continental climate tends to be characterized by cold winters, hot summers, and low humidity (WEATHER & CLIMATE 2018). Due to the extremely dynamic configuration of the landforms in eastern Bavaria, and localized extremes in elevational relief, cool (boreal, alpine: sites 2, 4, 5) and warm (Mediterranean: sites 1, 3, 6) sites occurred in close proximity to one another.

The six excursion sites visited were chosen by the organizers to provide symposium participants the opportunity to collect in diverse places and altitudes (Fig. 2): [1] Laufen on river Salzach, and environs; [2] Nature Reserve Weitsee-Lödensee; [3] Schönramer Filz; [4] Frauenberg Hostel and environs; [5] Bavarian Forest National Park; and [6] Nature Reserve 'Donauleiten von Passau bis Jochenstein' (Fig. 2). The city of Laufen, where the symposium was held [1], and the two collecting sites of the midterm collection trip [2, 3], are near to the border with Austria. The collecting sites of the post-symposium excursion are located at the border with Austria [6] and the Czech Republic [4, 5]. Each of these sites is treated in more detail below.

The following individuals participated in the post-symposium excursion (Fig. 3; see also Appendix 1): Horst Aspöck, Ulrike Aspöck, Davide Badano, Caleb Califre Martins, Peter Duelli, Odile Frank, Axel Gruppe, James Jepson, Joshua Jones, Seulki Kim, Lukas Kirschey, Xingyue Liu, Zhiqi Liu, Xiumei Lu, Yanan Lyu, John Oswald, André Prost, Dong Ren, Chaofan Shi, Yongjie Wang, and Han Xu.

Overall, the excursions were very pleasant, with many interesting Neuropterida collected, despite the weather not always being on our side. To our misfortune, the light trappings during dusk and night were confounded by rain and weren't very successful. Additional to the rain, which started nearly every evening, sometimes heavily, we experienced strong winds and a noticeable decrease in temperature. Nonetheless, these nights became quite productive, as they were used instead to discuss talks and posters presented during the symposium, or joint projects that hopefully will cumulate in fruitful new works and collaborations and enhance old ones.

This paper summarizes the events of the excursions and largely follows the formats presented already by JONES et al. (in press, 2013) and MANSELL & ASPÖCK (1990).

### **Materials and methods**

The post-symposium excursion took place in south-eastern Germany, in the state of Bavaria (Fig. 1).

Maps were adapted from files downloaded at <https://d-maps.com> (DALET 2018) and were optimized in Adobe Photoshop CS3. Reference coordinates were first mapped in Google Earth (version 7.3.2.5491).

All images were captured by the authors, except the group photo (Fig. 3), which was contributed by H. Aspöck. Plates and the group photo key were prepared in Adobe Photoshop and Illustrator.



**Figure 1.** Map of Germany. The post-symposium excursion took place in south-eastern Germany, in the state of Bavaria. The inset rectangle marks the bounds of Figure 2.



**Figure 2.** Bavaria and post-symposium excursion field sites. Six sites were surveyed: [1] Laufen on river Salzach (also the site of the symposium, marked with a star), and environs; [2] Nature Reserve Weitsee-Lödensee; [3] Schönramer Filz; [4] Frauenberg Hostel and environs; [5] Bavarian Forest National Park; and [6] Nature Reserve 'Donauleiten von Passau bis Jochenstein'.

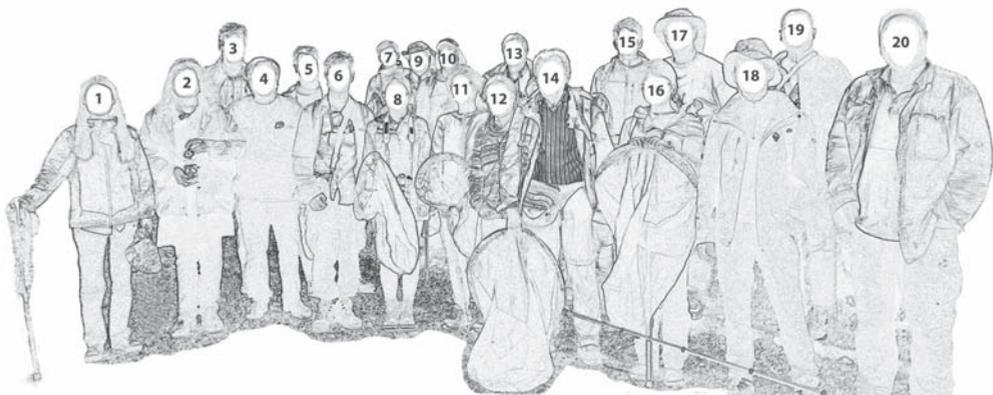
Collection took place at the following field sites (see Fig. 2):

[1] Laufen: Kapuzinerhof, river Salzach, and environs (47.938°N, 12.936°E, 390–410 m a.s.l., 16–21.vi.2018; Figs 5–7)

At the symposium's venue in Laufen, participants collected mainly in the garden of the former monastery 'Kapuzinerhof', located in the center of the town. The garden included vegetables, ornamental plants, fruit trees, and tall, broad-leaved trees. The habitat was very diverse in structure and plant species, with a park-like layout. Laufen is located



**Figure 3.** Group photo of the post-symposium excursion. Taken at Bavarian Forest National Park, Lusensteig, 23.vi.2018. Photo: Horst Aspöck



**Figure 4.** Key to group photo (Fig. 3); see Appendix for participant information.

in the easternmost part of Germany in the foothills of the Alps (subalpine upper moraine), and is touched by the river Salzach, a tributary to the Danube. The river is largely dammed in its course, as a protection against high water during snow melt in the Alps. Insects were collected on all plants in the garden, as well as in the bushes and herbal vegetation of the banks of river Salzach in the town. They were also collected along forested paths on the shores of the river.

[2] Nature Reserve Weitsee-Lödensee (47.697°N, 12.604°E, 750–780 m a.s.l., 19.vi.2018; Figs 8–10)

The Lödensee is the easternmost of three modern lakes formed during the last glaciation. The lake is about 10 ha in area and 6 m deep. It is surrounded by high mountains reaching 1 500 m a.s.l. Collections were made from the lake's eastern shoreline to beyond the car park (<1 km), along the bottom of the valley, which is covered by low vegetation and some trees (Norway spruce, willows) because of the gravel subsurface. Some additional collecting took place at the valley's edges, where the floor meets the mountain slopes. Here, Montane mixed forests grew, with Norway spruce, European beech and sycamore as the dominant tree species. The shrub layer was dominated by hazelnut and regenerating trees.

[3] Schönramer Filz (47.896°N, 12.849°E, 460 m a.s.l., 19.vi.2018, evening and light trapping; Figs 11–12)

The 'Schönramer Filz' is a protected area with the status of a Natural Forest Reserve and of an Area of Conservation under the EU Habitats Directive. Due to impermeable layers under the ground, moor land has developed. This moor is fed by the river Sur. In the open areas, the vegetation consisted of small bushes of blueberry, heather and others. In the forested areas, Scots pine was the dominant tree species, but Norway spruce, beech and willow were also common. No forest management had occurred in the area for 40 years before.

At this site we had a nice barbecue for dinner, organized by colleagues of the ANL in Laufen, and we set up four light traps. However, as it was very cold, very few lacewings (primarily hemerobiids) came to the lights.

[4] Frauenberg Hostel (48.794°N, 13.760°E, 850–870 m a.s.l., 22–24.vi.2018; Figs 13, 14)

The Haidmühle-Frauenberg Hostel is located in the eastern part of the Bavarian Forest, near the small municipalities of Haidmühle and Frauenberg. This heavily forested region is close to the border of both Czech Republic and Austria, and forms one of the largest wooded areas remaining in Europe. The predominant mountain of the region is often called 'Böhmerwald', or 'Šumava' in the Czech language, because of its old Paleozoic bedrock. The area has high rainfall, with a total annual precipitation of more than 1 000 mm. During our stay, the weather was wet and rainy, with low temperatures. Collections were done in the managed forest close to the hostel, which represented a typical nearly pure spruce assemblage of the Bavarian Forest. Admixed in were individual trees



**Figures 5–10, excursion sites.** 5, 6 – Internal courtyard and gardens of Kapuzinerhof, where the symposium was held; 7 – Salzach River, between Laufen, Germany (left) and Oberndorf bei Salzburg, Austria (right); 8–10 – Nature Reserve Weitsee-Lödensee.

of European beech and sycamore, and, close to the small creek, willows and alder. We set up light traps over two nights, but collected only very few specimens due to the cold and rainy weather.

[5]: Bavarian Forest National Park, Lusensteig (48.944°N, 13.543°E, 920–1 000 m a.s.l., 23.vi.2018; Figs 3, 4, 15–18)

Lusensteig is named after the Lusen (1 373 m a.s.l.), one of the highest mountains in the Bavarian Forest. It is located in the easternmost part of the Bavarian Forest National Park and is well known for its characteristic gravel top that is devoid of vegetation. The hiking path starts at about 900 m a.s.l. The forest in the Park was pure Norway spruce and had not been managed since the creation of the National Park in 1970. Outbreaks of spruce bark beetle (mainly *Ips typographus*) have killed many hectares of mature spruce trees in the surrounding areas since 1980.

The Lusensteig follows a small creek, where we collected mainly on Norway spruce and in the understory, but also in some meadow pockets. The weather was sunny with clouds, but windy.



**Figures 11–14, excursion sites.** 11 – Schönrammer Filz; 12 – Light-trapping at Schönrammer Filz; 13 – Haidmühle-Frauenberg municipal region, near the Frauenberg Hostel; 14 – Bavarian Forest adjacent to Frauenberg Hostel.

[6]: Nature Reserve ‘Donauleiten von Passau bis Jochenstein’ (48.520°N 13.710°E, 290–520 m a.s.l., 24.vi.2018; Figs 19–22)

Jochensteiner Hänge is part of the large Nature Reserve ‘Donauleiten von Passau bis Jochenstein’, which covers the northern slope of Danube valley close to the border with Austria. The slope is very steep and southerly exposed, resulting in a Mediterranean climate. It is a heat island situated in the migratory route along the Danube. The slope was covered by woodland interrupted by rocks and cliffs. In the forest many thermophilic tree species grew that are known primarily from the Mediterranean area.

We started collecting close to the banks of Danube and climbed up the slope on different hiking paths.

### Results

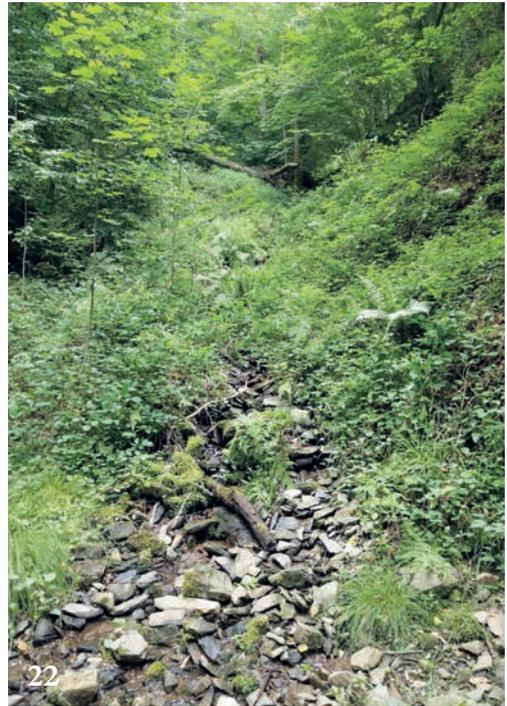
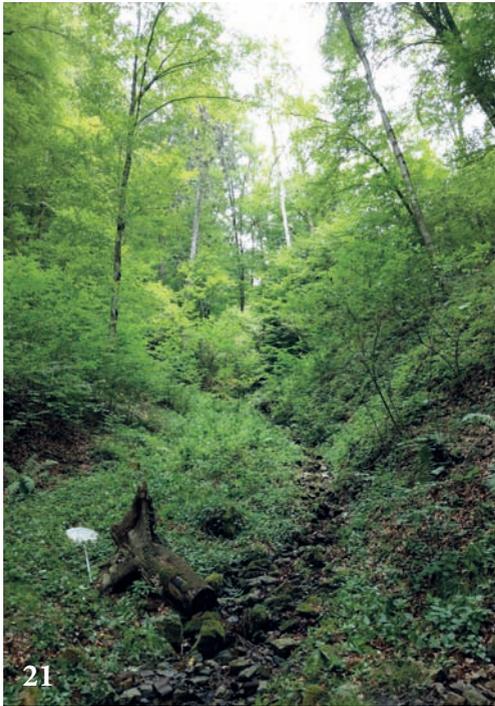
As a result of collecting activities, 37 species (not including those identified only to genus) were collected representing Raphidioptera (1 sp.), Megaloptera (1 sp.) and Neuroptera (35 spp.). Neuroptera comprised 14 species of Chrysopidae, 7 Coniopterygidae, 10 Hemerobiidae, 1 Myrmeleontidae, 1 Osmylidae and 2 Sisyridae. A list of species collected is given in Table 1.



**Figures 15–18, excursion sites.** Bavarian Forest National Park, Lusensteig.

### Discussion

Most species recorded during the excursions are common in Bavaria, though no comprehensive species list of Bavarian Neuropterida has been published recently (PRÖSE & GRUPPE 2003). The record of *Aleuropteryx lowii* is notable because this species was recorded at seven sites in Bavaria before, but not in the eastern part of the country (GRUPPE & DOCZKAL 2017). The occurrence of *Osmylus fulvicephalus* at nearly all sites, except Nature Reserve Weitsee-Lödensee, is also of importance. The species has previously been recorded only rarely in Bavaria, but this seems to be due to low collecting activity. The data presented here suggest that it is much more common.



**Figures 19–22, excursion sites.** 19 – Danube\_River, near Nature Reserve, ‘Donauleiten von Passau bis Jochenstein’; 20–22 – Jochensteiner Hänge.

**Table 1.** Neuropterida collected during the post-symposium excursion. Table includes families, genera and species encountered. Species names follow OSWALD (2018).

Taxon	Laufen	Weitsee-Lödensee	Schönramer Filz	Frauenberg Hostel	Lusensteig	Jochensteiner Hänge
<b>Raphidioptera: Raphidiidae</b>						•
<i>Dichrostigma flavipes</i> (Stein, 1863)						•
<b>Megaloptera: Sialidae</b>					•	
<i>Sialis fuliginosa</i> Pictet, 1836					•	
<b>Neuroptera: Chrysopidae</b>	•	•	•	•	•	•
<i>Chrysopa perla</i> (Linnaeus, 1758)		•	•	•		•
<i>Chrysoperla affinis</i> (Stephens, 1836)						•
<i>Chrysoperla carnea</i> (Stephens, 1836)	•					•
<i>Chrysoperla lucasina</i> (Lacroix, 1912)	•					•
<i>Chrysoperla pallida</i> Henry et al., 2002	•	•	•			•
<i>Chrysopidia (Chrysotropia) ciliata</i> (Wesmael, 1841)	•	•	•	•	•	•
<i>Cunctochrysa albolineata</i> (Killington, 1935)						•
<i>Hypochrysa elegans</i> (Burmeister, 1839)	•					•
<i>Nineta flava</i> (Scopoli, 1763)				•	•	
<i>Nothochrysa capitata</i> (Fabricius, 1793)					•	
<i>Peyerimhoffina gracilis</i> (Schneider, 1851)					•	
<i>Pseudomallada abdominalis</i> (Brauer, 1856)		•	•			•
<i>Pseudomallada flavifrons</i> (Brauer, 1851)			•			•
<i>Pseudomallada ventralis</i> (Curtis, 1834)		•	•	•		•
<b>Neuroptera: Coniopterygidae</b>	•	•		•	•	•
<i>Aleuropteryx (loewii) loewii</i> Klapálek, 1894		•				
<i>Coniopteryx (Coniopteryx) borealis</i> Tjeder, 1930						•
<i>Coniopteryx (Coniopteryx) pygmaea</i> Enderlein, 1906					•	
<i>Coniopteryx (Coniopteryx) tineiformis</i> Curtis, 1834	•			•		•
<i>Coniopteryx (Metaconiopteryx) esbenpeterseni</i> Tjeder, 1930	•					•
<i>Coniopteryx</i> sp.				•	•	
<i>Conwentzia psociformis</i> (Curtis, 1834)		•				
<i>Semidalis aleyrodiformis</i> (Stephens, 1836)	•					
<i>Semidalis</i> sp.				•		

Taxon	Laufen	Weitsee-Lödensee	Schönramer Filz	Frauenberg Hostel	Lusensteig	Jochensteiner Hänge
<b>Neuroptera: Hemerobiidae</b>	•	•	•		•	•
<i>Hemerobius atrifrons</i> McLachlan, 1868					•	
<i>Hemerobius contumax</i> Tjeder, 1932		•			•	
<i>Hemerobius fenestratus</i> Tjeder, 1932					•	
<i>Hemerobius humulinus</i> Linnaeus, 1758	•	•				•
<i>Hemerobius lutescens</i> Fabricius, 1793					•	
<i>Hemerobius marginatus</i> Stephens, 1836					•	•
<i>Hemerobius micans</i> Olivier, 1793	•		•		•	•
<i>Hemerobius pini</i> Stephens, 1836	•	•			•	•
<i>Hemerobius stigma</i> Stephens, 1836			•			
<i>Hemerobius</i> sp.					•	
<i>Micromus variegatus</i> (Fabricius, 1793)			•			•
<b>Neuroptera: Myrmeleontidae</b>					•	
<i>Myrmeleon formicarius</i> Linnaeus, 1767					•	
<b>Neuroptera: Osmyliidae</b>	•		•	•	•	•
<i>Osmylus fulvicephalus</i> (Scopoli, 1763)	•		•	•	•	•
<b>Neuroptera: Sisyridae</b>			•			•
<i>Sisyra nigra</i> (Retzius, 1783)			•			•
<i>Sisyra terminalis</i> Curtis, 1854						•

Several species were here recorded for the first time in the altitudinal range of Lusensteig, Bavarian Forest National Park, namely *Sialis fuliginosa*, *Nineta flava*, *Chrysopidia ciliata*, and *O. fulvicephalus*; see GRUPPE (2011) for a previous accounting of Neuropterida in the Park.

The species collected in Laufen, Weitsee-Lödensee and Schönramer Filz are the first records of Neuropterida in those regions, and represent the first known collecting events from those sites.

Though few in number, these new records greatly augment the known distribution of Neuropterida in Bavaria.

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We would like to thank the staff of The Bavarian Academy for Nature Conservation and Landscape Management (ANL), in particular Christian Stettmer and Marianne Krause, who organized the mid-term excursion, secured the bus for the post-symposium excursion and assisted in

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**Appendix 1.**

Post-symposium excursion participant information, sorted by family name.

<b>Name</b>	<b>Country</b>	<b>Institution or hometown</b>	<b>Contact</b>	<b>Key # (Fig. 3)</b>
Horst Aspöck	Austria	Medical University of Vienna	horst.aspoeck@meduniwien.ac.at	14
Ulrike Aspöck	Austria	Naturhistorisches Museum Wien	ulrike.aspoeck@nhm-wien.ac.at	12
Davide Badano	Italy	University of Genoa	davide.badano@gmail.com	15
Caleb Califre Martins	Brazil	Universidade de São Paulo	calebcalfre@gmail.com	10
Peter Duelli	Switzerland	Swiss Federal Institute for Forest, Snow and Landscape Research WSL	peter.duelli@wsl.ch	13
Odile Frank	France	Loisia	Andre.prost@free.fr	2
Axel Gruppe	Germany	Technische Universität München	gruppe@wzw.tum.de	3
James Jepson	England	University College Cork	james.jepson@ucc.ie	6
Joshua Jones	USA	Utah Valley University	doc.jonesresearch@gmail.com	not pictured
Seulki Kim	South Korea	Chungbuk National University	neurosk84@gmail.com	9
Lukas Kirschey	Germany	Museum für Naturkunde	lukas.kirschey@mfn-berlin.de	5
Xingyue Liu	China	China Agricultural University	xingyue_liu@yahoo.com	18
Zhiqi Liu	China	China Agricultural University	liuzhiqi@cau.edu.cn	11
Xiumei Lu	China	China Agricultural University	xiumeilu@cau.edu.cn	1
Yanan Lyu	China	China Agricultural University	lyyanan214@cau.edu.cn	16
John Oswald	USA	Texas A&M University	j-oswald@tamu.edu	17
André Prost	France	Loisia	prostloisia@gmail.com	4
Dong Ren	China	Capital Normal University	rendong@mail.cnu.edu.cn	19
Chaofan Shi	China	Sun Yat-sen University	paleobioscf@gmail.com	8
Yongjie Wang	China	Capital Normal University	wangyjosmy@gmail.com	20
Han Xu	China	China Agricultural University	hanny_90@163.com	7







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