1st December 2015

This issue of ODONATOLOGICA is dedicated to the memory of

Norman Winfrid Moore
(24th February 1923 – 21st October 2015)

Congratulations to

Georg Rüppell, Germany,
on his 75th birthday on 20th April 2015

and to

Eberhard G. Schmidt, Germany,
on his 80th birthday on 30th July 2015

Odonatologica gratefully acknowledges the helpful assistance during the editing of volume 44 of the following colleagues that are not part of the Editorial Board:

Cornelio A. Bota-Sierra, Colombia; Jean-Pierre Boudot, France;
Paweł Buczyński, Poland; Maria J. Gołąb, Poland; Miloš Jović, Serbia;
Vincent J. Kalkman, The Netherlands; Frederico A.A. Lencioni, Brazil;
Owen Muise, Germany; Ângelo P. Pinto, Brazil; Robby Stoks, Belgium;
Asmus Schröter, Germany.

The 2017 International Congress of Odonatology

will be convened in Annaba, Algeria, from 3rd to 6th July 2017,

followed by a post-congress tour to the El Kala National Park,
a unique Mediterranean ecosystem in the extreme north-east of the country.

Chairman of the Organizing Committee:
Prof. Dr Boudjéma Samraoui, <ICOAlgeria2017@gmail.com>
A congress homepage will be available soon and announced via:
http://worlddragonfly.org/

The 4th European Congress on Odonatology

will be convened in the village of Tyringe, Scania (Skåne County), southern Sweden, from 11th to 14th July 2016,

followed by post-congress field trips. The congress, accommodations, dinners and more will take place at the same site, Tyringe Kurhotell, under one roof.

Chairman of the Organizing Committee:
Magnus Billqvist, <magnus.billqvist@naturskyddsforeningen.se>
Congress homepage with continuously added information:
https://ecoo2016.wordpress.com/

1st December 2015

Contribution to the knowledge of the Moroccan Odonata, with first records of *Orthetrum sabina*, and an overview of first and last dates for all species

Mohamed El Haissoufi[1], Geert De Knijf[2], Johan van't Bosch[3], Nard Bennas[1] & Andrés Millán Sánchez[4]

[1] Laboratory of Ecology, Biodiversity and Environment "LEBE", Department of Biology, Faculty of Sciences, University of Abdelmalek Essâadi, Tétouan, Morocco; <med.elhaissoufi@gmail.com> <nbennas@hotmail.com>

[2] Research Institute for Nature and Forest (INBO), Kliniekstraat 25, 1070 Brussels, Belgium; <geert.deknijf@inbo.be>

[3] Newtonplein 62, 2562 JX The Hague, The Netherlands; <johanvantbosch@yahoo.co.uk>

[4] Departamento de Ecologia e Hidrologia, Facultad de Biologia, Universidad de Murcia, Murcia, España; <acmillan@um.es>

Received 29th June 2015; revised and accepted 10th September 2015

Abstract. Several field surveys between 2007 and 2014 were undertaken in Morocco. Altogether 54 species were observed during our studies, representing 86 % of the odonate fauna of the country. *Orthetrum sabina* is new for Morocco, increasing the number of species to 63. The species was found at Oued Ez-Zahar near Akhfenir, about 1 700 km off its nearest known locality at Ouargla in Algeria. Two small populations of *Erythromma viridulum* were found for the first time in the Rif, bridging the gap between populations in the Middle Atlas and the Iberian Peninsula. The third observation of *Sympetrum sinaiticum* for Morocco was recorded and we were able to significantly increase the known number of localities of the threatened Moroccan endemic *Cordulegaster princeps.* We further can show that several species (e.g., *Boyeria irene*, *Pyrrhosoma nymphula*) are more widely distributed than believed and occur also at low altitudes in the country. On the other hand, *Calopteryx exul*, *Calopteryx virgo meridionalis*, *Lestes dryas*, *Coenagrion mercuriale*, *Aeshna isoceles* and *Libellula quadrimaculata* are very rare in Morocco and their populations should be monitored to assess their potential decline. Finally, for all Moroccan dragonfly species the first and last observation dates are listed. For 17 of them we provide the earliest observation date and for seven species we prolong the observation period.

Key words. Dragonfly, damselfly, distribution, North Africa, range expansion, phenology, conservation.

Introduction

The dragonfly fauna of Morocco has been relatively well investigated (El Haissoufi 2012). An overview on all historical records of the known 58 Odonata species of Morocco was given by Jacquemin & Boudot (1999). Until then, most investigations were conducted in the more easily accessible northern and central parts of Morocco, especially in the Rif Mountains (Jacquemin 1994) and the Middle Atlas. In recent years several papers have been published on the odonatofauna of the southern and eastern parts of the country (Boudot 2008; Juillerat & Monnerat 2009; Boudot & De Knijf 2012; Mediani et al. 2012; Waldhauser 2012) but also from already relatively well investigated regions (Faucheux et al. 2005; El Haissoufi et al. 2008, 2010; Benazzouz et al. 2009; Ferreira et al. 2014, 2015), increasing the number of dragonfly species to 62.

Despite these recent publications, the knowledge on the occurrence of dragonflies from several rather inaccessible regions is still poor. To palliate this gap, between 2007 and 2014 several surveys were undertaken by us in some of these regions. The aim of this paper is to improve our understanding of the occurrence and distribution of dragonflies in Morocco. Based on our extensive dataset and on literature sources, we can also provide an overview of the first and last observation records for every species. Furthermore, this study wants to contribute to a better understanding of the ecological requirements, the phenology and the reproductive behaviour of the dragonflies in North Africa.

Material and methods

A total of 116 localities were surveyed for the presence of dragonflies from 2007 until 2014. During this period, the first author (MEH) and his research team explored most localities several times. These surveys were not randomized, but were carried out more intensively in the northern part, particularly the Rif Mountains and in southern Morocco. Eighteen localities were surveyed for the presence of dragonflies from 06–10-ix-2013 by the second author (GDK), and nine localities were investigated from 30-xii-2013 to 08-i-2014 by the third author (JVB). These twenty-seven localities were all situated in the southern part of the country. All kinds of dragonfly habitats were sampled, including standing (e.g., ponds, pools, lakes, marshes, gravel

pits) as running waters (e.g., oueds, streams, ditches, rivers). Observations by the first author were made by capturing an individual and determination on-site using Dijkstra & Lewington (2006). Species difficult to identify in the field were collected and determination was done in the laboratory. MEH and colleagues also used a kick net for collecting larvae of Odonata. Observations by GDK and JVB were made by using close-focusing binoculars or with the naked eye, with sporadical netting of individuals for hand-checking of specific characters.

The localities visited (Fig. 1) are listed below. Locality names follow primarily those in the 1:50 000 maps of Morocco. Places not indicated on maps are named according to local spelling, and are indicated in brackets where relevant. For each locality, we give the most important environmental characteristics, geographic coordinates in decimal degrees (WGS84 geodetic system), altitude above sea level and date of visit. The name of the observers is also given in brackets (see authors for initials; MEH and col. = first author and his research colleagues).

Visited localities

Western Rif

Loc. 1: Oued Martil at entry of Tétouan city, upstream bridge connecting Tétouan to Chefchaouen, large permanent oued with slow-flowing water; 35.56222°N, 5.43056°W; 10 m a.s.l.; 12-vii-2011 (MEH and col.)

Loc. 2: Coelma wetland, a complex of large swamps, old sand quarries with bulrush at Coelma, Tétouan; 35.56535°N, 5.33593°W; 30 m a.s.l.; 02-x-2010, 15-x-2010, 01-iii-2011, 15-iii--2011, 04-vi-2011, 11-vi-2011, 17-vi-2011, 06-vii-2011, 28-ix-2011 (MEH and col.)

Loc. 3: (Lamberka), spring, brook and small swamp at M'hanech, Tétouan; 35.56621°N, 5.36189°W; 26 m a.s.l.; 28-viii-2010 (MEH and col.)

Loc. 4: Oued Ez Zarka near Ez Zarka village, 5 km south of Tétouan, fast flowing river with well-developed bank vegetation; 35.5211°N, 5.34191°W; 140 m a.s.l.; 12-v-2007 (MEH and col.)

Loc. 5: (Oued Boumaâza) beyond Douar Kitane, partially dried up river bed with stagnant pools, 6 km south of Tétouan; 35.52593°N, 5.32077°W; 170 m a.s.l.; 01-xi-2009 (MEH and col.)

Loc. 6: Wide water canal with bulrush at Bouzeghlal, 3 km NW of M'diq; 35.70277°N, 5.35138°W; 2 m a.s.l.; 11-vii-2011 (MEH and col.)

Loc. 7: Smir marshes, 4 km north of M'diq; 35.71666°N, 5.3375°W; 0 m a.s.l.; 10-iii-2007, 16-v-2007, 22-v-2007, 01-vi-2007 (MEH and col.)

Loc. 8: Barrage Smir, 5 km west of M'diq, dam lake with dense riparian vegetation; 35.67°N, 5.37583°W; 45 m a.s.l.; 11-vii-2011 (MEH and col.)

Loc. 9: Oued near El Bayine, 5 km west of M'diq, small and fast flowing river with well-developed bank vegetation; 35.69773°N, 5.4051°W; 41 m a.s.l.; 23-iv-2009 (MEH and col.)

Loc. 10: Temporary pool at the Forestry House, 6 km south west of M'diq upstream of Oued Lile; 35.65782°N, 5.37652°W; 42 m a.s.l.; 13-iv-2009 (MEH and col.)

Loc. 11: Oued Belouazene, 7 km west of M'diq, small and fast flowing river with well-developed bank vegetation; 35.67347°N, 5.40515°W; 50 m a.s.l.; 13-iv-2009, 21-iv-2009 (MEH and col.)

Loc. 12: Oued near El Kouf, 8 km NW of M'diq, small and fast flowing river with well-developed bank vegetation; 35.71492°N, 5.40238°W; 43 m a.s.l.; 24-iv-2009 (MEH and col.)

Loc. 13: Oued Lile, 8 km SW of M'diq, small and fast flowing river; 35.66119°N, 5.40266°W; 39 m a.s.l.; 13-iv-2009; 21-iv-2009 (MEH and col.)

Loc. 14: Oued Boujmil small and fast flowing river, 10 km NW of M'diq; 35.76162°N, 5.40138°W; 43 m a.s.l.; 18-v-2009 (MEH and col.)

Loc. 15: Swamp in Martil, well-vegetated area with rushes and tamarisk, road from Martil to Cabo Nigro; 35.63138°N, 5.28194°W; -4 m a.s.l.; 12-vi-2011, 06-vii-2011 (MEH and col.)

Loc. 16: Oued el Kabir (= Oued Bousfiha) at bridge of Jamâa Souk Lakdim, 8 km west of Tétouan, fast flowing river with well-developed bank vegetation; 35.56138°N, 5.45916°W; 13 m a.s.l.; 12-vii-2011 (MEH and col.)

Loc. 17: Oued Ajrâz upstream of Ajrâz dam, Road N2 from Tétouan to Tangier, 11 km from Tétouan, mostly dried-up river bed with some small running sections; 35.56221°N, 5.49644°W; 44 m a.s.l.; 09-vii-2011 (MEH and col.)

Loc. 18: Oued Agla, road to Khemis Anjra with both slow-flowing sections and fast-running water; 35.66483°N, 5.50227°W; 63 m a.s.l.; 12-vii-2011 (MEH and col.)

Loc. 19: Moulay El Hassan I dam lake on Oued Rouz, near Khemis Anjra; 35.70375°N, 5.49868°W; 130 m a.s.l.; 12-vii-2011 (MEH and col.)

Loc. 20: Oued Nakhla upstream dam lake Nakhla, road N2 from Tétouan to Chefchaouen, partially dried-up river bed with sections of running as well as standing water; 35.43169°N, 5.39304°W; 209 m a.s.l.; 13-vi-2009, 18-iv-2008, 27-xi-2009 (MEH and col.)

Loc. 21: Oued Boumarouil at Ain Hamra, road N2 from Tétouan to Chefchaouen, mostly dried-up river bed with some small running sections and with well-developed bank vegetation; 35.30933°N, 5.35248°W; 516 m a.s.l.; 20-iv-2007, 15-v-2007, 17-vi-2007 (MEH and col.)

Loc. 22: Oued Moulay Bouchta near Dar Akobaâ, road N2 from Tétouan to Chefchaouen, mostly dried-up river bed with some small running sections; 35.22828°N, 5.32317°W; 278 m a.s.l.; 17-v-2007 (MEH and col.)

Loc. 23: Jbel Bouhachem around Tayenza, where twelve localities have been prospected, regrouped according the following habitats types. Loc. 23a: outlet rivulets, loc. 23b: small rivers, loc. 23c: dayas [Arabic for temporary ponds] and peat-bog, loc. 23d: complex of springs, rivulets and marshy areas; 35.2535–35.26799°N, 5.43023–5.49013°W; 950–1 210 m a.s.l.; 12--vii-2007, 28-vi-2008, 05-vi-2011 (MEH and col.)

Loc. 24: Oued Talambote upstream of village Talambote, road from Chefchaouen to Oued Laou, fast flowing river; 35.24982°N, 5.20107°W; 302 m a.s.l.; 01-vii-2008 (MEH and col.)

Loc. 25: Oued Kalaa Akoumi at Akchour, road from Chefchaouen to Oued Laou, fast flowing river with well-developed bank vegetation; 35.2383°N, 5.17516°W; 410 m a.s.l.; 17-v-2007, 17-vi-2007, 17-iv-2008 (MEH and col.)

Loc. 26: Oued Laou at Afertane, slow flowing river with near-absence of bank vegetation; 35.35358°N, 5.18238°W; 100 m a.s.l.; 17-v-2007 (MEH and col.)

Loc. 27: Oued Tassikeste, road from Oued Laou to Chefchaouen, almost dry in summer; 35.37916°N, 5.174°W; 96 m a.s.l.; 17-v-2007, 28-v-2008 (MEH and col.)

Loc. 28: Oued Laou at Tizrharine, slow flowing river with near-absence of bank vegetation; 35.39298°N, 5.1515°W; 4 m a.s.l.; 17-v-2007 (MEH and col.)

Loc. 29: Oued Laou at the bridge connecting Oued Laou to Kaâ Asras, slow running water and within the river bed some pools of standing water with aquatic vegetation; 35.42331°N, 5.11423°W; -4 m a.s.l.; 17-v-2007 (MEH and col.)

Loc. 30: Oued Bouhaya near Bou Ahmed, road from Oued Laou to El Jebha, temporary oued almost dry in summer; 35.30527°N, 4.97165°W; 30 m a.s.l.; 27-v-2009 (MEH and col.)

Loc. 31: Oued Amazithen, road from Oued Laou to El Jebha, temporary oued almost dry in summer; 35.3062°N, 4.90893°W; 75 m a.s.l.; 27-v-2009 (MEH and col.)

Loc. 32: Oued Aârkob at Arherarose, road from Oued Laou to El Jebha, temporary oued almost dry in summer; 35.26744°N, 4.840757°W; 100 m a.s.l.; 25-v-2009 (MEH and col.)

Loc. 33: Oued Jnane Niche, road from Oued Laou to El Jebha, temporary oued almost dry in summer; 35.28221°N, 4.85915°W; 60 m a.s.l.; 06-v-2009 (MEH and col.)

Loc. 34: Oued Sidi Yahya Aârab, road from Oued Laou to El Jebha, temporary oued almost dry in summer; 35.28963°N, 4.88978°W; 35 m a.s.l.; 26-v-2009 (MEH and col.)

Loc. 35: Oued Laou, near bridge Sifilaou at Chefchaouen entry, wide and well vegetated river with both slow-flowing sections and fast-running water; 35.19383°N, 5.30725°W; 280 m a.s.l.; 15-v-2007 (MEH and col.)

Loc. 36: Pool Amelay characterized by aquatic vegetation at the confluence of Ras el Mae and Oued Laou; 35.16242°N, 5.31133°W; 297 m a.s.l.; 20-iv-2007, 24-iv-2009 (MEH and col.)

Loc. 37: Pool Aïn Rami near Chefchaouen, around the Forestry House, characterized by aquatic vegetation and the presence of some bushes at the edge; 35.13828°N, 5.27585°W; 505 m a.s.l.; 20-iv-2007 (MEH and col.)

Loc. 38: Ras el Mae at Chefchaouen city, fast flowing river with well-developed bank vegetation; 35.17038°N, 5.25666°W; 604 m a.s.l.; 17-vi-2007 (MEH and col.)

Loc. 39: Oued Laou at Dardara near Chefchaouen, wide and well vegetated river with both slow-flowing sections and fast-running water; 35.11877°N, 5.28817°W; 341 m a.s.l.; 05-vi-2008 (MEH and col.)

Loc. 40: Small temporary pond characterized by aquatic vegetation at the entry of Douar Khizana; 35.05113°N, 5.2135°W; 925 m a.s.l.; 05-vi-2008 (MEH and col.)

Loc. 41: Two large forest pools at (Bouztate) 18 km from Fifi, Jbel Khizana,nearly falling dry in summer; 35.02288°N, 5.20635°W; 1 200 m a.s.l.; 05-vi-2008, 01-vi-2011 (MEH and col.).

Loc. 42: Rivulet at Douar Bouztate at 16 km from Fifi, almost dry in summer, Jbel Khizana; 35.0135°N, 5.2056°W; 1 260 m a.s.l.; 10-vi-2008, 01-vi-2011 (MEH and col.)

Loc. 43: Spring rivulet at 15 km from Fifi, Jbel Khizana; 35.00687°N, 5.20165°W; 1 300 m a.s.l.; 10-vi-2008 (MEH and col.)

Loc. 44: Small pool at 10 km from Fifi, NW Douar Bouztate, Jbel Khizana; 34.98985°N, 5.20616°W; 1 320 m a.s.l.; 05-vi-2008 (MEH and col.)

Loc. 45: Spring brook at 5 km from Fifi, north of Douar Ahoundar, Jbel Khizana; 34.97412°N; 5.22016°W; 900 m a.s.l.; 10-vi-2008 (MEH and col.)

Loc. 46: Oued Majjo, north of Douar Majjo, fast flowing river with well-developed bank vegetation; 35.10342°N, 5.18501°W; 773 m a.s.l.; 16-iv-2008, 05-vi-2008, 24-iv-2009, 01-vi-2011 (MEH and col.)

Loc. 47: Oued Majjo near Douar Majjo, fast flowing river with well-developed bank vegetation; 35.09939°N, 5.18594°W; 810 m a.s.l.; 15-v-2007, 05-vi-2008 (MEH and col.)

Loc. 48: Rivulet close to Forestry House, Talassemtane National Park; 35.13253°N, 5.13641°W; 1 684 m a.s.l.; 12-vii-2008 (MEH and col.)

Loc. 49: Oued Madissouka at Talassemtane National Park, fast flowing river with well-developed bank vegetation; 35.17399°N, 5.13865°W; 1 380 m a.s.l.; 29-v-2008, 11-vii-2008 (MEH and col.)

Loc. 50: Oued near Douar Taria at Talassemtane National Park, fast flowing river with well-developed bank vegetation; 35.17095°N, 5.15838°W; 1 230 m a.s.l.; 12-vii-2008 (MEH and col.)

Loc. 51: Oued near Imezzare village at Talassemtane National Park, fast flowing river with well-developed bank vegetation; 35.17536°N, 5.16788°W; 1 039 m a.s.l.; 12-vii-2008 (MEH and col.)

Loc. 52: Oued near Tiffert village at Talassemtane National Park, fast flowing river with well-developed bank vegetation; 35.18073°N, 5.12327°W; 1 230 m a.s.l.; 11-vii-2008 (MEH and col.)

Loc. 53: Oued Beni M'hamed at Talassemtane National Park, fast flowing river with well-developed bank vegetation; 35.15883°N, 5.12922°W; 1 335 m a.s.l.; 11-vii-2008 (MEH and col.)

Loc. 54: Oued El Kanar near Beni Fenzar at Talassemtane National Park, deep and fast flowing river; 35.17646°N, 4.95365°W; 220 m a.s.l.; 13-vii-2008 (MEH and col.)

Loc. 55: Oued El Kanar near Azarhar village, fast flowing river; 35.26968°N, 5.02669°W; 240 m a.s.l.; 17-vii-2007 (MEH and col.)

Loc. 56: Pond near (Douar Yelzem) road from Bab Taza to Bab Berred; 35.01838°N, 5.0022°W; 1 390 m a.s.l.; 20-v-2011 (MEH and col.)

Loc. 57: El Anasser west of Bab Berred, deep permanent pool and marshy meadows; 35.01781°N, 4.9914°W; 1 295 m a.s.l.; 20-v-2011 (MEH and col.)

Loc. 58: Oued Oulja ech Chat at Hakkâma, road N2 from Tétouan to Tangier, with both slow-flowing sections and fast-running water; 35.6527°N, 5.68645°W; 53 m a.s.l.; 25-iv-2007 (MEH and col.)

Loc. 59: Oued Srhir, crossing road to Malloussa, with both slow-flowing sections and fast-running water and well-developed bank vegetation; 35.67719°N, 5.70345°W; 43 m a.s.l.; 26--iv-2007, 14-vii-2007 (MEH and col.)

Loc. 60: Oued Hmatoune near Crochet Blanco, with both slow-flowing sections and fast-running water; 35.5828°N, 5.64282°W; 90 m a.s.l.; 25-iv-2007 (MEH and col.)

Loc. 61: Oued el Haricha near Dar-Chaoui, with both slow-flowing sections and fast-running water; 35.53839°N, 5.69833°W; 48 m a.s.l.; 25-iv-2007 (MEH and col.).

Loc. 62: Oued el Kebir near Ahfir village, with both slow-flowing sections and fast-running water and with sandy banks; 35.46794°N, 5.82113°W; 20 m a.s.l.; 25-iv-2007, 14-vii-2007 (MEH and col.)

Loc. 63: Oued downstream Et Tleta Jbel Habib, mostly dried-up river bed with some small running section; 35.47046°N, 5.80313°W; 40 m a.s.l.; 25-iv-2007 (MEH and col.)

Loc. 64: Oued el Khoulj at Oulad Fares, with both slow-flowing sections and fast-running water; 35.56106°N, 5.91533°W; 5 m a.s.l.; 26-iv-2007, 14-vii-2007 (MEH and col.)

Loc. 65: Oued el Hachef near Blockhaus, with both slow-flowing sections and fast-running water; 35.55089°N, 5.91946°W; -2 m a.s.l.; 14-vii-2007 (MEH and col.)

Loc. 66: Oued Biada and marshy meadows near former power station; 35.64209°N, 5.95661°W; 3 m a.s.l.; 26-iv-2007 (MEH and col.)

Loc. 67: Oued at Ain-el-Assel (Oued Aâssila), fast flowing river with well-developed bank vegetation; 35.69128°N, 5.83435°W; 30 m a.s.l.; 26-iv-2007 (MHE and col.)

Loc. 68: Badriouene dam lake, shallow and overgrown by vegetation; 35.7097°N, 5.8785°W; 34 m a.s.l.; 26-iv-2007 (MEH and col.)

Central Rif

Loc. 69: Oued Taâounia near Koudiet Ajira, near Kétama village, with both slow-flowing sections and fast-running water; 34.87962°N, 4.56523°W; 1 493 m a.s.l.; 29-vi-2008 (MEH and col.)

Loc. 70: Oued Azila, near Azila village, with both slow-flowing sections and fast-running water; 34.86893°N, 4.53957°W; 1 533 m a.s.l.; 31-iii-2008 (MEH and col.)

Loc. 71: Rivulet near (Imaou-Ijdamen) in Jbel Tidghine, fast flowing small river with well-developed bank vegetation; 34.83305°N, 4.52184°W; 1 935 m a.s.l.; 31-iii-2008 (MEH and col.)

Loc. 72: Oued Sahla near Haouara village, N 8 between Taounate and Fes, well-vegetated river with both slow-flowing sections and fast-running water; 34.50115°N, 4.75159°W; 203 m a.s.l.; 05-iv-2008 (MEH and col.)

Loc. 73: Oued Aoulai at 11 km from Ghafsai, well-vegetated river with both slow-flowing sections and fast-running water; 34.57962°N, 4.96027°W; 162 m a.s.l.; 05-iv-2008 (MEH and col.)

Loc. 74: Oued Aoudour at bridge at 2 km from Tbouda, wide river with both slow-flowing sections and fast-running water; 34.74416°N, 5.13656°W; 167 m a.s.l.; 05-iv-2008 (MEH and col.)

Eastern Rif

Loc. 75: Oued Ghis near Douar Ikoubaen, well-vegetated river with both slow-flowing sections and fast-running water; 35.16716°N, 3.88594°W; 30 m a.s.l.; 01-iv-2008 (MEH and col.)

Loc. 76: Oued Kert at Ain Messaouda village, well-vegetated river with both slow-flowing sections and fast-running water; 35.02726°N, 3.26518°W; 177 m a.s.l.; 02-iv-2008 (MEH and col.)

Loc. 77: Oued Aïn Rahma near Aïn Hamra village, R 510 between Aknoul and Boured, well-vegetated river with both slow-flowing sections and fast-running water; nearly dried-up in summer with some remaining stagnant pools; 34.73222°N, 3.94909°W; 1 111 m a.s.l.; 04-iv--2008, 22-vii-2010 (MEH and col.)

Loc. 78: Oued Bou Haddoud near Douar Bou Haddoud Et Tahti, well-vegetated river with both slow-flowing sections and fast-running water, R505 (= S312) between Taza and Aknoul; 34.55081°N, 3.8759°W; 834 m a.s.l.; 17-vii-2010 (MEH and col.)

Loc. 79: Oued Broun at Feddane el Bard, R 505 between Taza and Aknoul, river with both slow-flowing sections and fast-running water; 34.51278°N, 3.89445°W; 671 m a.s.l.; 21-vii--2010 (MEH and col.)

Loc. 80: Oued Broun at Jbarna, R 505 between Taza and Aknoul, with both slow-flowing sections and fast-running water with sandy banks; 34.4956°N, 3.91329°W; 830 m a.s.l.; 21--vii-2010 (MEH and col.)

Loc. 81: Oued near Douar Lehaleha, road between Aïn Bou Kellal and Bab el Mrouj; river with both slow-flowing sections and fast-running water; 34.3691°N, 3.92858°W; 595 m a.s.l.; 21-vii-2010 (MEH and col.)

Loc. 82: Oued el Arbaâ before Aïn Bou Kellal, R505 (=S312) between Taza and Aknoul, river with both slow-flowing sections and fast-running water with near-absence of bank vegetation; 34.29194°N, 3.96771°W; 450 m a.s.l.; 23-iii-2008, 17-vii-2010 (MEH and col.)

Loc. 83: Oued Zireg at Tazzekka National Park, deep and fast flowing river with well-developed vegetation on the shore; 34.12128°N, 4.29891°W; 456 m a.s.l.; 03-iv-2008 (MEH and col.)

Middle Atlas

Loc. 84: Dayet Iffer at Ifrane; 33.60771°N, 4.90844°W; 1 500 m a.s.l.; 21-iv-2008 (MEH and col.)

Western High Atlas (west of highway Agadir-Marrakech, but including this valley)

Loc. 85: Asif n'Aït Massa, 1 km north of Timezgadiouine, partially dried-up river bed with sections of running as well as still water; 30.89438°N, 9.036°W; 930 m a.s.l.; 07-ix-2013 (GDK)

Loc. 86: Asif n'Aït Massa, 2 km south of Timezgadiouine, partially dried-up river bed with sections of running as well as still water; 30.87106°N, 9.04781°W; 890 m a.s.l.; 07-ix-2013 (GDK)

Loc. 87: Barrage Abdelmoumen near Bigoudine, reservoir with near-absence of bank vegetation, the bank is mostly quite steep, the observed dragonflies were seen on a section with a rather gentle slope; 30.70698°N, 9.20174°W; 637 m a.s.l.; 07-ix-2013 (GDK)

Loc. 88: Pond between road N8 and highway Agadir-Marrakech, near Bigoudine, characterized by aquatic vegetation and the presence of some bushes at the edge; 30.71245°N, 9.21308°W; 666 m a.s.l.; 07-ix-2013 (GDK)

Loc. 89: Asif Tamraght (= Asif Tamrhakht = Tamrhart = Taghrat) – Vallée du Paradis, cascade between Hotel Panoramique and Hotel Tifrit; fast running water, partly reduced to small irrigation channels, but also a pond just below the dried-up waterfall, all this situated in a well-vegetated river valley with many trees; 30.60057°N, 9.49615°W; 663 m a.s.l.; 08-ix-2013 (GDK)

Loc. 90: Asif Tamraght – Vallée du Paradis, running water, with both slow-flowing sections and fast-running water with some small rapids in a well-vegetated river valley with many trees, the river was investigated over a section of approximately 1.5 km upstream; 30.5832°N, 9.53366°W; 295 m a.s.l.; 08-ix-2013 (GDK)

Loc. 91: Asif Tamraght – Vallée du Paradis, running water, with both slow-flowing sections and fast-running water with some small rapids in a well-vegetated river valley with many trees; 30.57225°N, 9.53851°W; 277 m a.s.l.; 08-ix-2013 (GDK)

Loc. 92: Asif Tamraght – Vallée du Paradis, 13 km downstream from loc. 91; running water, with both slow-flowing sections and fast-running water in a well-vegetated river valley with many trees; 30.55964°N, 9.5473°W; 206 m a.s.l.; 08-ix-2013 (GDK)

Central High Atlas

Loc. 93: Rakte, Nfiss River, running water and within the riverbed a pool of standing water with well-developed bank and aquatic vegetation; 31.02111°N, 8.14278°W; 1 135 m a.s.l.; 06-ix-2013 (GDK and Boudjéma Samraoui).

Loc. 94: Gorges Moulay Ibrahim, Ighighayene river, mostly dried-up river bed with some small running sections; 31.31389°N, 7.95805°W; 990 m a.s.l.; 06-ix-2013 (GDK and Boudjéma Samraoui).

Loc. 95: Oued Ourika near Aghbalou, fast flowing river; 31.30938°N, 7.74656°W; 1 060 m a.s.l.; 01-vii-2009 (MEH and col.)

Loc. 96: Oued R'Mat south of Amanouz, this small river runs north away from the High Atlas; nearly dried-up river bed with some remaining stagnant pools and some scattered rocks, near the road; 31.49275°N, 7.72574°W; 643 m a.s.l.; 30-xii-2013 (JVB)

Loc. 97: Asif Tifnoute near Tanmitert, small stream, with partially dried-up river bed with sections of running as well as still water, investigated over a length of 500 m downstream this point; 30.95578°N, 7.83289°W; 1 540 m a.s.l.; 09-ix-2013 (GDK)

Loc. 98: Asif Tifnoute near Aït Kalla, small stream, with partially dried-up river bed with sections of running as well as still water, investigated over a length of 500 m downstream this point; 30.93539°N, 7.857°W; 1 470 m a.s.l.; 09-ix-2013 (GDK)

Loc. 99: Archbar, small stream before flowing into the Nfiss River, just north of village; partially dried-up stream bed; 30.90503°N, 8.40494°W; 1 615 m a.s.l.; 10-ix-2013 (GDK)

Loc. 100: Archbar, Nfiss River, just west of village; fast flowing river, with well-developed bank vegetation; 30.90164°N, 8.40967°W; 1 658 m a.s.l.; 10-ix-2013 (GDK)

Loc. 101: Mouldikht, Nfiss River valley, along route R203 from Tizi-n'Test towards Marrakech; 30.9065°N, 8.31739°W; 1 812 m a.s.l.; 10-ix-2013 (GDK)

South of High Atlas

Loc. 102: Barrage Ahle Souss east of Aït-Baha, eutrophic dam lake with aquatic and bank vegetation; 30.06387°N, 9.12307°W; 608 m a.s.l.; 08-ix-2013 (GDK)

Loc. 103: Oued Sous just below dam lake, east of Idrgane, river bed with sections of running as well as still water with well-developed vegetation on the shore; 30.73728°N, 7.98561°W; 880 m a.s.l.; 09-ix-2013 (GDK)

Loc. 104: Oued Sous, northeast of Aoulouz, wide open river valley, with only a broad channel of slowly flowing water; 30.69733°N, 8.15472°W; 697 m a.s.l.; 10-ix-2013 (GDK)

Loc. 105: Oued Rheris, Erfoud, river with partially dried up river bed, with sections of running and still water, some bushes, small trees and reeds along and in the river, 50–100 m of the river investigated, south of the road; 31.43012°N, 4.30411°W; 783 m a.s.l.; 02-i-2014 (JVB)

Loc. 106: Merzouga, dry riverbed in stony plains, approximately 17 km north of the village; 31.24167°N, 4.08139°W; 746 m a.s.l.; 03-i-2014 (JVB)

Loc. 107: Drâa River just west of Tamnougalt, along the road near the river; 30.67451°N, 6.40741°W; 910 m a.s.l.; 04-i-2014 (JVB)

Loc. 108: Drâa River southeast of Tamnougalt, partially dried-up river bed with stagnant pools and nearby agricultural land; 30.67169°N, 6.37372°W; 905 m a.s.l.; 04-i-2014 (JVB)

Loc. 109: Tazzarine, palm grove, 3 km northwest of village along road R108; 30.79356°N, 5.57804°W; 876 m a.s.l.; 04-i-2014 (JVB)

Loc. 110: Oued Massa north of Tikioute, well-vegetated pools, with a lot of reed and many low trees and bushes; 30.00404°N, 9.65635°W; 3 m a.s.l.; 07-i-2014 (JVB)

Loc. 111: Oued Massa near Zaouid Massa, well vegetated small river with reeds, trees and bushes; 30.03108°N, 9.64456°W; 3 m a.s.l.; 07-i-2014 (JVB)

Loc. 112: Estuary of Oued Sous near Inezgane, sparsely to well-vegetated flood plain with a few remaining small pools; loc.112a: 30.36409°N, 9.59048°W; loc. 112b: 30.357565°N, 9.574301°W.; 3 m a.s.l.; 08-i-2014 (JVB)

Loc. 113: Oasis Oued Sayad (= Seyyâd) at Aït Bekkou (Aït Boukka); 28.93723°N, 9.90348°W; 304 m a.s.l.; 02-iv-2007 (MEH and col.)

Loc. 114: Oued Darâa, entry of Tan Tan, N 1 between Tan Tan and Laâyoune, partially dried-up river bed with stagnant pools; 28.52826°N, 10.948°W; 16 m a.s.l.; 03-iv-2007 (MEH and col.)

Loc. 115: Oued Ez Zehar near Akhfennir (= Oued el Ouaâr), Khnifiss National Park, N1 between Tan Tan and Laâyoune; well vegetated river with reeds, trees and bushes; 27.96531°N, 11.94816°W; 90 m a.s.l.; 05-iv-2007 (MEH and col.)

Loc. 116: Oued Al Mwilah, Khnifiss National Park; 27.78°N, 12.08°W; 242 m a.s.l.; 04-iv--2007 (MEH and col.)

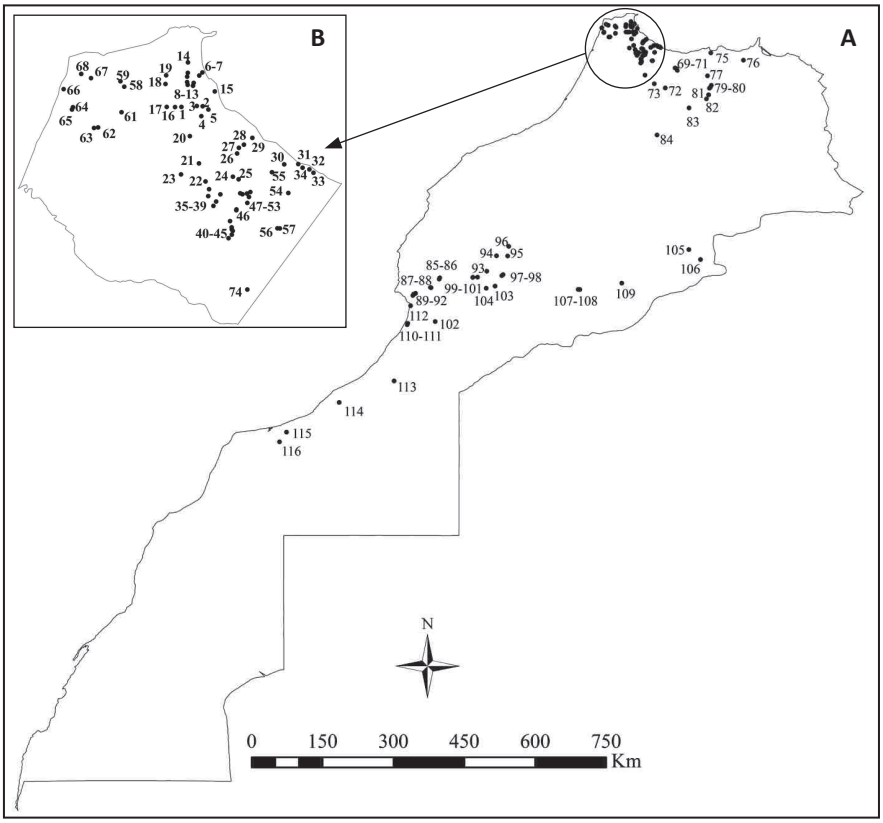


Figure 1. A – Localities investigated in Morocoo during this study; B – Detailed map of sampling localities in northwestern Morocco.

Results

List of recorded species and subspecies

Abbreviations used: ad – adult, la – larva(e), ex – exuvia(e), co – coupling, ov–oviposition or egg-laying, ta – tandem, ten – teneral(s).

Zygoptera

Lestidae

Chalcolestes viridis (Vander Linden, 1825)

Loc. 5 (10♂, 5♀, 5 ta), **loc. 14** (2 la), **loc. 15** 12-vi-2011 (1♀), **loc. 17** (>10♂, >10♀, co, ta, ov), **loc. 20** 13-vi-2009 (12♂, 5♀), **loc. 21** 17-vi-2007 (>40♂, >20♀), **loc. 22** (1 la), **loc. 23c** 28--vi-2008 (4♂, 3♀), **loc. 58** (3 la), **loc. 59** 26-iv-2007 (3 la), 14-vii-2007 (>20♂, >20♀), **loc. 60** (1 la), **loc. 61** (1 la), **loc. 63** (1 la), **loc. 64** (3 la), **loc. 66** (3 la), **loc. 67** (3 la), **loc. 74**(2 la), **loc. 77** 22-vii-2010 (5♂)

Lestes barbarus (Fabricius, 1798)

Loc. 2 (3♂, 1♀), **loc. 15** 12-vi-2011 (4♂, 1♀), 06-vii-2011 (5♂, 2♀), **loc. 20** 27-xi-2009 (2♂, 2♀), **loc. 23c** 28-vi-2008 (4♂, 2♀), **loc. 40** (>20♂, >10♀), **loc. 41** 01-vi-2011 (>50 ten)

Lestes dryas Kirby, 1890

loc. 23c 05-vi-2011 (1♂, 1♀), 28-vi-2008 (3♂, 5♀), **loc. 23d** 28-vi-2008 (1♂, 2♀), **loc. 36** 20--iv-2007 (1 la), **loc. 37** (1 la), **loc. 40** (1♂, 2♀), **loc. 41** 01-vi-2011 (5♂, 3♀), **loc. 44** (3♂, 2♀), **loc. 56** (2♂, 6♀)

Lestes virens virens (Charpentier, 1825)

Loc. 2 04-vi-2011 (2♂), 11-vi-2011 (6♂), 17-vi-2011 (7♂), 06-vii-2011 (5♂, 1♀), **loc. 15** 12--vi-2011 (3♂), **loc. 23c** 28-vi-2008 (3♂, 1♀), **loc. 41** 5-vi-2008 (>20♂, >10♀)

Sympecma fusca (Vander Linden, 1820)

Loc. 2 11-vi-2011 (2♂, 1♀), **loc. 14** (1♂), **loc. 15** 12-vi-2011 (2♂), **loc. 37** (1♀), **loc. 77** 04--vi-2008 (1♂)

Calopterygidae

Calopteryx exul Selys, 1853

Loc. 20 (5♂, 2♀)

Calopteryx haemorrhoidalis (Vander Linden, 1825)

Loc. 4 (5♂, 3♀), **loc. 5** (3♂, 1♀), **loc. 13** (2♂, 1♀), **loc. 16** (7♂, 2♀), **loc. 20** (>20♂, >10♀), **loc. 21** (23♂, 12♀), loc. **23b** 12-vii-2007 (>20♂, >10♀, 2 ta), 29-vi-2008 (20♂, >10♀), **loc. 23d** (20♂, >10♀), **loc. 25** (10♂, 5♀, 2 ta), **loc. 31** (1♂, 1♀), **loc. 38** (4♂, 3♀), **loc. 39** (5♂, 2♀), **loc. 45** (3♂, 2♀), **loc. 50** (3♂, 1♀), **loc. 51** (3♂, 2♀), **loc. 54** (4♂, 3♀), **loc. 55** (5♂, 2♀), **loc. 77** (5♂, 3♀), **loc. 113** (>30♂, >20♀)

Calopteryx virgo meridionalis Selys, 1873
Loc. 23b 29-vi-2008 (7♂, 4♀), **loc. 23d** 28-vi-2008 (5♂, 3♀), 05-vi-2011 (3♂, 2♀)

Platycnemididae
Platycnemis subdilatata Selys, 1849
Loc. 1 (>20♂, >20♀, co, ov), **loc. 2** 11-vi-2011 (5♂, 2♀), **loc. 16** (13♂, 11♀, co, ta, ov), **loc. 18** (6♂, 4♀, 2 co, 1 ov), **loc. 20** 13-vi-2009 (>20♂, >20♀, co, ov), **loc. 21** 17-vi-2007 (7♂, 1♀), **loc. 24** (3♂, 2♀), **loc. 29** (1 la), **loc. 60** (2 la), **loc. 62** 25-iv-2007 (1 la), 14-vii-2007 (2♂, 2♀), **loc. 72** (1 la), **loc. 77** 22-vii-2010 (2♂), **loc. 82** 23-iii-2008 (2 la), **loc. 83** (2 la), **loc. 89** (1♂), **loc. 98** (1♀), **loc. 113** (1♂, 2 la)

Coenagrionidae
Ceriagrion tenellum (Villers, 1789)
Loc. 23b 29-vi-2008 (6♂, 3♀), **loc. 23d** 05-vi-2011 (4♂, 3♀), 28-vi-2008 (>20♂, >20♀, 5 co), 05-vi-2011 (3♂, 3♀, 1co), **loc. 23c** 28-vi-2008 (1♂), **loc. 43** (1♂)

Coenagrion caerulescens (Fonscolombe, 1838)
Loc. 23a 12-vii-2007 (1♀), **loc. 23b** 29-vi-2008 (2♂, 2♀), **loc. 55** (6♂, 4♀, 1 co, **loc. 56** (1♂, 1♀), **loc. 69** (5♂, 3♀), **loc. 76** (4♂, 3♀, co, ta, 1 ov in tandem), **loc. 77** 04-iv-2008 (4♂, 5♀), 22-vii-2010 (6♂, 5♀), **loc. 78** (3♂, 2♀), **loc. 80** (2♂, 1♀), **loc. 85** (15♂, 3♀, ov), **loc. 93** (>50 ad, 10 ov, 5 ten), **loc. 97** (3♂), **loc. 98** (2♂)

Coenagrion mercuriale (Charpentier, 1840)
Loc. 46 05-vi-2008 (2♂), 01-vi-2011 (1♂)

Coenagrion puella (Linnaeus, 1758)
Loc. 23d 28-vi-2008 (10♂), **loc. 53** (1♂)

Coenagrion scitulum (Rambur, 1842)
Loc. 23c 05-vi-2011 (2♂)

Erythromma lindenii (Selys, 1840)
Loc. 1 (7♂, 5♀, 3co, 1ov), **loc. 16** (6♂, 3♀, 1 co, 1 ov), **loc. 18** (>10♂, >10♀, co, ta, ov), **loc. 20** 13-vi-2009 (4♂, 3♀, co), **loc. 62** 14-vii-2007 (8♂, 5♀, 2 co), **loc. 64** 26-iv-2007 (8♂, 5♀); 14-vii-2007 (8♂, 4♀), **loc. 68** (2♂), **loc. 72** (>10♂, >10♀), **loc. 73** (1♂, 1♀), **loc. 74** (1♂, 1♀), **loc. 82** 17-vii-2010 (4♂, 4♀), **loc. 88** (1♂), **loc. 90** (2♂)

Erythromma viridulum (Charpentier, 1840)
Loc. 2 11-vi-2011 (4♂, 2♀), 06-vii-2011 (6♂, 2♀, co, ov), 10-vii-2012 (4♂, 2♀, co, ov)

Ischnura graellsii (Rambur, 1842)
Loc. 1 (5♂, 2♀), **loc. 2** 04-vi-2011 (9♂, 5♀), 11-vi-2011 (>50♂, 50♀), 06-vii-2011 (>50♂, >50♀, co, ov), 28-ix-2011 (3♂, 4♀), **loc. 3** (5♂, 3♀), **loc. 6** (6♂, 2♀), **loc. 7** 10-iii-2007 (9♂, 2♀), 16-

-iii-2007 (8♂, 3♀), **loc. 10** (2♂, 3♀), loc. **13** 13-iv-2009 (2♂), **loc. 15** 12-vi-2011(4♂, 6♀), 06-vii--2011 (>50♂, >50♀), **loc. 16** (>20♂, >20♀, co), **loc. 17** (>20♂, >20♀, co, ov), **loc. 18** (3♂, 6♀), **loc. 19** (4♂, 2♀), **loc. 20** 13-vi-2009 (6♂, 3♀), **loc. 21** 17-vi-2007 (5♂, 3♀, co), **loc. 23c** 28-vi--2008 (4♂, 2♀), **loc. 36** 24-iv-2009 (>20♂, >20♀), **loc. 37** (1♂), **loc. 46** 24-iv-2009 (1♂), **loc. 56** (7♂, 4♀), **loc. 57** (5♂, 5♀), **loc. 59** (14-vii-2007 (6♂, 2♀), **loc. 64** 26-iv-2007 (5♂, 3♀), 14-vii--2007 (8♂, 6♀), **loc. 65** (8♂, 6♀, ov), **loc. 66** (1♀), **loc. 67** (4♂, 2♀), **loc. 68** (7♂, 2♀), **loc. 72** (5♂, 2♀), **loc. 74** (3♂, 2♀), **loc. 75** (1♂), **loc. 77** 22-vii-2010 (6♂, 4♀), **loc. 78** (1♂, 2♀), **loc. 79** (3♂, 4♀), **loc. 80** (5♂, 4♀), **loc. 81** (>20♂, >20♀, co), **loc. 82** 17-vii-2010 (6♂, 3♀), **loc. 93** (1♀)

Ischnura pumilio (Charpentier, 1825)
Loc. 2 04-vi-2011 (1♂), **loc. 77** 22-vii-2010 (2♂)

Ischnura saharensis Aguesse, 1958
Loc. 88 (5♂), **loc. 104** (3♂, 1♀), **loc. 115** (>50♂, >50♀)

Pyrrhosoma nymphula (Sulzer, 1776)
Loc. 4 (5♂, 2♀), **loc. 23a** 12-vii-2007 (6♂, 4♀), **loc. 23b** 29-vi-2008 (3♂, 2♀), **loc. 23c** 28-vi--2008 (1♂, 2♀), **loc. 23d** 5-vi-2011 (5♂, 2♀), 28-vi-2008 (8♂, 3♀, co), **loc. 25** 17-vi-07 (7♂, 4♀, co), **loc. 52** (2 la)

Anisoptera
Aeshnidae
Aeshna affinis Vander Linden, 1820
Loc. 15 06-vii-2011 (1♂), **loc. 17** (6♂, 2♀), **loc. 23a** 12-vii-2007 (1♂), **loc. 36** 17-iv-2007 (2 la); 24-iv-2009 (1 la), **loc. 37** (2 la), **loc. 72** (1 la)

Aeshna isoceles (Müller, 1767)
Loc. 7 16-v-2007 (>10♂, >10♀)

Aeshna mixta Latreille, 1805
Loc. 2 15-x-2010 (2♂, 2♀), 01-iii-2011 (1♂), **loc. 5** (>20♂, >20♀), **loc. 23d** 05-vi-2011(1♂), **loc. 50** (1♂), **loc. 64** 26-iv-2007(2 la)

Anax ephippiger (Burmeister, 1839)
Loc. 2 17-vi-2011 (1♂, 2 ex), **loc. 106** (1 ad), **loc. 107** (1 ad), **loc. 108** (2 ad), **loc. 109** (1 ♀), **loc. 110** (5♂, 12 ad), **loc. 111** (4 ad), **loc. 112a** (23 ad), **112b** (1 ad), **loc. 114** (1♀), **loc. 116** (1♂).

Anax imperator Leach, 1815
Loc. 2 02-x-2010 (1♂), 17-vi-2011 (1♂), 06-vii-2011(1♂), **loc. 7** 17-v-2007 (1♀), **loc. 13** 21--iv-2009 (1♂), **loc. 16** (1♂), **loc. 17** (1♂), **loc. 20** 13-vi-2009 (1♂), **loc. 21** 17-vi-2007 (1♂), **loc. 23c** 28-vi-2008 (2♂), **loc. 23d** 28-vi-2008 (1♂, 1♀), **loc. 25** 17-vi-2007 (1♂, 3 ex), **loc. 40** (1♂), **loc. 41** (1♂), **loc. 51** (1♂), **loc. 64** 14-vii-2007 (1♂), **loc. 68** (1 la), **loc. 72** (1♂), **loc. 76** (1♂), **loc. 77** 04-iv-2008 (1♂), 22-vii-2010 (1♂), **loc. 78** (1♂, 1♀), **loc. 80** (1♂), **loc. 84** (2 la)

Anax parthenope Selys, 1839
Loc. 2 15-iii-2011 (1♂), **loc. 23c** 28-vi-2008 (1♂), **loc. 77** 22-vii-2010 (1♂), **loc. 88** (1 ♂, 1 ♀, ov)

Boyeria irene (Fonscolombe, 1838)
Loc. 4 (1 la), **loc. 11** (2 la), **loc. 12** (1 la), **loc. 13** (1 la), **loc. 14** (2 la), **loc. 20** 13-vi-2009 (2♂), **loc. 21** 20-iv-2007 (1 la), **loc. 23b** 09-vi-2008 (1♂), **loc. 25** 17-v-2007 (1 la), 17-iv-2008 (2 la), **loc. 31** (1 la), **loc. 32** (2 la), **loc. 33** (2 la), **loc. 46** 05-vi-2008 (2 la), **loc. 47** 05-vi-2008 (2 la), **loc. 84** (2 la)

Gomphidae

Gomphus simillimus maroccanus Lieftinck, 1966
Loc. 12 (2 la), **loc. 20** 13-vi-2009 (2♂, 2♀), **loc. 25** 17-vi-2007 (1♂, ten), **loc. 55** (1♂), **loc. 113** (2 la)

Onychogomphus costae Selys, 1885
Loc. 27 17-v-2007 (2 la), **loc. 28** (1 la), **loc. 73** (1♂), **loc. 82** 17-vii-2010 (1♂), **loc. 113** (2 la)

Onychogomphus forcipatus unguiculatus (Vander Linden, 1823)
Loc. 14 (1 la), **loc. 20** 18-iv-2008 (1 la), 13-vi-2009 (2♂, 2 ex), **loc. 21** 17-iv-2007 (3♂, 2♀, 1 la), 15-v-2007 (3 la), **loc. 22** (1 la), loc. 26 (2 la), **loc. 27** 17-v-2007 (2 la), 28-v-2008 (2 la), **loc. 28** (2 la), **loc. 30** (1 ex, 1 la), **loc. 31** (2 la), **loc. 33** (1 la), **loc. 35** (2 la), **loc. 83** (3 la)

Onychogomphus uncatus (Charpentier, 1840)
Loc. 4 (1 la), **loc. 9** (3 la), **loc. 11** 21-iv-2009 (2 ex), **loc. 12** (2 la), **loc. 13** 21-iv-2009 (2♂, 2 la), **loc. 14** (3 la), **loc. 23a** 12-vii-2007 (1♂), **loc. 23b** 12-vii-2007(1♂, 2♀), 29-vi-2008 (6♂, 2♀, 1 ex), **loc. 23d** 28-vi-2008 (2♂, 2♀), **loc. 25** 17-vi-2007 (1♂, 2♀), 17-v-2007(3 la), **loc. 30** (2 la, 1 ex), **loc. 31** (3 la), **loc. 33** (3 la), **loc. 34** (2 la), **loc. 42** 10-vi-2008 (7♂, 4♀), **loc. 45** (5♂, 5♀), **loc. 47** 15-v-2007 (1 la), **loc. 50** (8♂, 6♀), **loc. 51** (7♂, 6♀), **loc. 53** (9♂, 6♀), **loc. 54** (2♂, 2 la), **loc. 55** (1♂), **loc. 95** (2♂)

Paragomphus genei (Selys, 1841)
Loc. 16 (1♂, 1♀), **loc. 22** (1♂), **loc. 35** (1 la), **loc. 62** 17-vii-2007 (2 la), **loc. 72** (1♂, 1 la), **loc. 74** (1 la), **loc. 76** (1 la)

Cordulegastridae

Cordulegaster boltonii algirica Morton, 1916
Loc. 23a 12-vii-2007 (7♂, 5♀, co), **loc. 23b** 29-vi-2008 (5♂, 4♀), **loc. 23d** 05-vi-2011 (1♂), 28-vi-2008 (4♂, 3♀, co), **loc. 25** 17-vi-2007 (6♂, 3♀, 2 la), 17-iv-2008 (2 la), **loc. 31** (2 la), **loc. 32** (2 la), **loc. 33** (1 la), **loc. 38** (5♂, 2♀), **loc. 46** 05-vi-2008 (2♂, 2 la), **loc. 47** 05-vi-2008 (2♂, 2♀), **loc. 48** (1♂), **loc. 49** (2 la), **loc. 50** (2♂, 2♀), **loc. 51** (1♂), **loc. 53** (2♂, 2♀), **loc. 54** (2♂), **loc. 70** (2 la), **loc. 71** (2 la)

Cordulegaster princeps Morton, 1916
Loc. 95 (2♂, 1♀), **loc. 99** (1♂), **loc. 100** (2♂), **loc. 101** (1 ad)

Libellulidae

Brachythemis impartita (Karsch, 1890)

Loc. 62 14-vii-2007 (>20♂, >20♀), **loc. 87** (3♂, 5♀, 2 ta), **loc. 102** (2♂)

Crocothemis erythraea (Brullé, 1832)

Loc. 1 (17♂, 15♀), **loc. 2** 15-x-2010 (1♂), 11-vi-2011(>20♂, >20♀); 28-ix-2011 (6♂, 7♀), **loc. 3** (12♂, 13♀), **loc. 6** (4♂, 2♀), **loc. 7** 16-v-2007 (8♂, 7♀), **loc. 15** 12-vi-2011(>20♂, >20♀), 06-vii- 2011 (7♂, 3♀), **loc. 16** (5♂, 4♀), **loc. 17** (8♂, 3♀), **loc. 18** (2♂), **loc. 20** 22-v-2007 (1♂), **loc. 21** 15-v-2007 (1 la), **loc. 55** (1♂), **loc. 76** (1♂), **loc. 68** (2 la), **loc. 85** (1♂), **loc. 86** (1♂), **loc. 102** (5♂), **loc. 104** (15♂, 3♀, 1 ov)

Diplacodes lefebvrii (Rambur, 1842)

Loc. 2 02-x-2010 (>20♂, >20♀), 11-vi-2011 (25♂, 21♀), 06-vii-2011 (25♂, 12♀, 8 ten, 5 co), 28-ix-2011 (>20♂, >20♀, ma, ten), **loc. 3** (1♂, ten), **loc. 6** (22♂, 20♀), **loc. 15** 12-vi-2011 (23♂, 20♀, ten), **loc. 64** 14-vii-2007 (1♂)

Libellula quadrimaculata Linnaeus, 1758

Loc. 23d 28-vi-2008 (9♂, 7♀), 05-vi-2011 (8♂, 4♀), 28-vi-2008 (9♂, 6♀) **loc. 23c** 05-vi-2011 (25♂, 21♀), **loc. 84** (2 la)

Orthetrum brunneum (Fonscolombe, 1837)

Loc. 7 16-v-2007 (1♀), 22-v-2007 (4♂, 2♀, 1 co), **loc. 82** 17-vii-2010 (1♂)

Orthetrum cancellatum (Linnaeus, 1758)

Loc. 8 (>20♂, >20♀)

Orthetrum chrysostigma (Burmeister, 1839)

Loc. 3 (7♂, 3♀), **loc. 7** 22-v-2007 (1♂), **loc. 16** (>20♂, >20♀, co), **loc. 17** (5♂, 3♀, 2co), **loc. 18** (7♂, 4♀), **loc. 20** 13-vi-2009 (5♂, 2♀), **loc. 21** 17-vi-2007 (8♂, 2♀), **loc. 25** 17-vi-2007(14♂, 3♀), **loc. 77** 22-vii-2010 (16♂, 5♀), **loc. 78** 17-vii-2010 (5♂, 4♀), **loc. 85** (2♂), **loc. 86** (4♂, 2 ov), **loc. 89** (3♂, 1 ov), **loc. 90** (15♂), **loc. 91** (2♂), **loc. 92** (1♂, 1♀, 1 ov), **loc. 93** (5♂), **loc. 94** (1♂, 3 ex), **loc. 98** (1♂), **loc. 99** (2♂, 1 ta, 1 ten), **loc. 103** (1♂), **loc. 104** (10♂, 1♀, 1 ov, 2 ten)

Orthetrum coerulescens anceps (Schneider, 1845)

Loc. 3 (5♂, 2♀), **loc. 4** (8♂, 3♀), **loc. 6** (2♂, 1♀), **loc. 17** (2♂, 2♀), **loc. 23a** 12-vii-2007(>20♂, 2♀), **loc. 23b** 29-vi-2008 (9♂, 5♀, 2co), **loc. 23c** 28-vi-2008 (>20♂, 5♀), **loc. 23d** 28-vi-2008 (4♂, 2♀), **loc. 54** (1♀), **loc. 77** 22-vii-2010 (8♂, 3♀), **loc. 85** (5♂, 1 ov), **loc. 86** (1♂), **loc. 90** (2♂), **loc. 93** (2♂)

Orthetrum nitidinerve (Selys, 1841)

Loc. 55 17-vii-2007 (2♂), **loc. 103** (1♂)

Orthetrum sabina (Drury, 1773)

Loc. 115 (>20♂, >20♀)

Orthetrum trinacria (Selys, 1841)
Loc. 2 02-x-2010 (1♀), 15-x-2010 (5♂, 2♀, 1 co), 11-vi-2011 (2♂), **loc. 15** 12-vi-2011 (1♂), 06-vii-2011 (1♂), **loc. 64** 14-vii-2007 (4♂, 2♀)

Sympetrum fonscolombii (Selys, 1840)
Loc. 2 02-x-2010 (5♂, 3♀), 15-x-2010 (8♂, 3♀, 2 co), **loc. 3** (7♂, 2♀), **loc. 7** 10-iii-2007(7♂, 6♀), **loc. 10** (5♂, 3♀), **loc. 17** (5♂, 2♀), **loc. 59** 14-vii-2007 (5♂, 2♀), **loc. 65** (6♂, 2♀), **loc. 66** (1♀), **loc. 72** (2♂, 2♀), **loc. 73** (1♂), **loc. 74** (1♂), **loc. 82** 17-vii-2010 (4♂, 2♀), **loc. 108** (1♀), **loc. 110** (6♂), **loc. 112a** (1♂)

Sympetrum meridionale (Selys, 1841)
Loc. 23d 28-vi-2008 (1♀)

Sympetrum sanguineum (Müller, 1764)
Loc. 23d 28-vi-2008 (1♂)

Sympetrum sinaiticum Dumont, 1977
Loc. 105 (6♂, 2 ta)

Sympetrum striolatum (Charpentier, 1840)
Loc. 2 02-x-2010 (>20♂, >20♀), 15-x-2010 (>20♂, >20♀, co), **loc. 5** (15♂, 8♀), **loc. 21** 20--iv-2007 (1 la), 15-vi-2007 (3 la), **loc. 22** (1 la), **loc. 23a** 12-07-2007 (2♂, 2♀), **loc. 37** (2 la), **loc. 58** (3 la), **loc. 59** 26-iv-2007 (2 la), **loc. 60** (2 la), **loc. 67** (3 la), **loc. 84** (2 la), **loc. 96** (2♂)

Trithemis annulata (Palisot de Beauvois, 1807)
Loc. 1 (>20♂, >20♀), **loc. 2** 17-vi-2011 (>20♂, >20♀), 06-vii-2011 (>20♂, >20♀), 28-ix-2011 (5♂, 2♀), **loc. 3** (1♀), **loc. 8** (>20♂, >20♀, co), **loc. 16** (>20♂, 5♀), **loc. 18** (>20♂, 5♀, 3 co), **loc. 19** (>20♂, 5♀), **loc. 25** 17-vi-2007 (4♂, 2♀), **loc. 55** (2♂), **loc. 82** 17-vii-2010 (3♂, 2♀), **loc. 86** (2♂), **loc. 88** (15♂), **loc. 90** (2♂), **loc. 92** (1♂), **loc. 93** (3♂, 1♀), **loc. 102** (10♂), **loc. 103** (10♂), **loc. 104** (10♂), **loc. 113** (1♂)

Trithemis arteriosa (Burmeister, 1839)
Loc. 85 (1♂), **loc. 86** (2♂), **loc. 87** (2♂), **loc. 88** (2♂), **loc. 89** (3♂), **loc. 90** (20♂), **loc. 91** (5♂, 2♀, 1 ov), **loc. 92** (2♂), **loc. 93** (1♂), **loc. 103** (5♂)

Trithemis kirbyi Selys, 1891
Loc. 16 (8♂, 3♀), **loc. 20** 13-vi-2009 (2♂), **loc. 75** (1♂), **loc. 77** 22-vii-2010 (2♂), **loc. 78** (9♂, 3♀), **loc. 79** (2♂), **loc. 80** (3♂, 2♀), **loc. 85** (3♂, 1 ov), **loc. 86** (10♂, 2 ov), **loc. 88** (10♂), **loc. 90** (5♂), **loc. 91** (10 ad), **loc. 92** (4♂), **loc. 93** (10♂), **loc. 96** (1♂, 1♀), **loc. 102** (4♂), **loc. 103** (3♂)

Zygonyx torridus (Kirby, 1889)
Loc. 89 (1♀), **loc. 90** (>1 500 ad, 10 ta, 10 ov, 2 ex), **loc. 91** (25♂), **loc. 92** (2♂)

Discussion

During several surveys 116 freshwater localities, with either standing or running water or both, were investigated regarding the presence of their local dragonfly fauna. These localities were widely distributed over Morocco, ranging from the Deep South to the Rif Mountains in the north. These surveys resulted in the observation of 54 dragonfly species, or 86 % of the Moroccan Odonata fauna. *Orthetrum sabina* was found for the first time, increasing the number of species recorded from Morocco to 63. Two small populations of *Erythromma viridulum* were found for the first time in the Rif. Our surveys yield also a new observation of *Sympetrum sinaiticum* for Morocco and significantly increase the known number of localities of the threatened Moroccan endemic *Cordulegaster princeps.* Several species such as *Calopteryx exul*, *C. virgo meridionalis*, *Lestes dryas*, *Coenagrion mercuriale*, *Aeshna isoceles* and *Libellula quadrimaculata* are very rare in Morocco. On the contrary, *Boyeria irene* or *Pyrrhosoma nymphula* were frequently observed, also at low altitudes.

Comments to some rare species

Orthetrum sabina was found as new for Morocco. It is an Indo-Malayan species with a huge range stretching from Australia and Japan to North Africa, where it is already long-time known from Egypt, Tunisia and from eastern Algeria (Boudot et al. 2009). On 05-iv-2007, a population of *O. sabina* was discovered at the Oued Ez-Zahar near Akhfenir. The species was observed again at the same wadi in August and October 2013, respectively, by S. Zegres and C. Glen (http//morocco.observado.org/waarneming/view/79899506). Another unpublished Moroccan locality, where *O. sabina* was recorded by R. Gabb and N. Stones in 2011, is reported without further details by Mediani et al. (2014). Oued Ez-Zahar is a salty stream dominated by *Salicornia* vegetation and some bushes on the river bank, situated in an open desert valley near the Atlantic coast in southern Morocco. We saw more than 40 adults flying over and near the water. The nearest known population of *O. sabina* is at Ouargla in eastern Algeria (Samraoui & Menaï 1999), about 1 700 km from the Moroccan site. The species may have taken advantage of past pluvial periods to spread across North Africa (Dijkstra & Boudot 2010). However, as this is also a very mobile species adapted to temporary and brackish

water, it remains unclear whether *O. sabina* only recently colonised the area or if it has been present already for long. Throughout its area, *O. sabina* can be found in a broad range of both slow flowing as still water habitats, from ponds and lakes to paddy fields, irrigation ditches and marshes.

Erythromma viridulum is very rare in Morocco and populations occur only at seven localities in the Middle Atlas between 1 400 and 1 700 m a.s.l.; Dumont (1972) mentions *E. viridulum* also for Allal Tazi in the Gharb plain on the Atlantic littoral, but this locality could not be traced back by Jacquemin & Boudot (1999). They doubt if the species occurs in the Rif as they consider that the habitat requirements are missing there. We found *E. viridulum* at two small ponds surrounded by dense vegetation (loc. 2, Fig. 2), especially of bulrush. These ponds are part of the Coelma wetlands complex, situated at only 30 m a.s.l. These populations are the first for northern Morocco and thus filling the gap between the populations in southern Spain and the Middle Atlas, and are also the first at low altitudes. The Coelma wetlands complex is only few kilometres away from the major city of Tétouan and as a consequence of this proximity, it underwent strong alterations due to urban and industrial expansion (Fig. 2). Another new species for the Rif is *Brachythemis impartita*. Several dozens of individuals were found along a slow wadi, Oued el Kebir (loc. 62), with wide sandy banks. Until now, *B. impartita* was mainly distributed along the Atlantic coast, the Saharan fringe in the South and the Oriental region of Morocco.

Our observation of *Sympetrum sinaiticum* is only the third for Morocco. This species was first found on 23-iv-2007 by Juillerat & Monnerat (2009), extending its known geographic range in North Africa by 1 200 km to the west and filling the gap with the populations in Spain. A second observation was included in the Atlas of the Mediterranean and North Africa (Boudot et al. 2009). Subsequently *S. sinaiticum* has been observed several times on the Italian island of Lampedusa (Corso et al. 2012), where it is considered a migrant. This species has a remarkable phenology and is known for its long aestivation period. Emergences take place in May and June and sexual maturation is postponed until late autumn or early winter (Jödicke et al. 2000b; Dumont 2007). After emergence, immature individuals spend sometimes several months very far away from water and aestivate in Mediterranean forest, steppe and desert habitats (Dumont 1978;

Jödicke et al. 2000b). Reproductive behaviour has been observed in Tunisia from October to March (Jödicke et al. 2000b), synchronizing the reproductive period with the rainy season. The species is known to breed in streams, ditches, ponds and swampy depressions, situated either in Mediterranean forests, steppe or desert environments (Dijkstra & Lewington 2006). Exuviae have also been found in concrete water reservoirs in Spain (Corso et al. 2012). Our observation of six males and at least two copulae at the beginning of January in Oued Rheris on the northern fringe of the Sahara (loc. 105) supports the species' breeding in a partially dried up sandy river bed with residual sections of running and standing water. Both the banks and the middle of the river contained some bushes and small trees. Emergent vegetation was present in the remaining water and on the dry parts of the river. We saw individuals and copulae resting only on the sandy soil or in the vegetation in the dry river bed. All individuals of *S. sinaiticum* were old and rather dark, making identification in the field less straightforward than for fresher individuals, and increasing the risk of confusion with similar species (mostly *S. striolatum* and *S. meridionale*).

Cordulegaster princeps is one of the two known endemic dragonfly species for Morocco, the other being the only recently described *Onychogomphus boudoti* (Ferreira et al. 2014). *Cordulegaster princeps* is restricted to the High and Middle Atlas, where it is found at altitudes between 1 000 and

Figure 2. Pond in the Coelma wetlands near Tétouan, Morocco. This habitat of the scarce *Erythromma viridulum* is highly endangered due to backfill by nearby brick factories. Photo: MEH (06-vii-2011)

Figure 3. Habitats of *Cordulegaster princeps* in the High Atlas, Morocco; a – Small rivulet before flowing into the Nfiss River near the village of Archbar; b – Nfiss River just upstream of Archbar. Photos: GDK (10-ix-2013)

Figure 4. Asif Tamraght near Immouzer, Morocco, a site where *Zygonyx torridus* is omnipresent. On that day >1 500 adults were observed along a 13 km stretch of the river. Photo: GDK (08-ix-2013)

2 600 m a.s.l. (Boudot 2008; Boudot & De Knijf 2012). In the High Atlas, most sites are situated in the Jebel Toubkal region and in the surroundings of the Tizi-n-Test Pass (Boudot 2008; Boudot & De Knijf 2012). The latter site was considered for a long time as the westernmost for this species (Lieftinck 1966). Waldhauser (2012) discovered *C. princeps* at eight new localities west of the Tizi-n-Test within the uppermost River Nfiss basin, as well as west of the Tizi-n-Aslim Pass. We found the species at three localities, all clustering well within the previously known localities of the Nfiss basin. In recent years the species was also found at two new localities in the eastern High Atlas and at one locality in the Middle Atlas (Boudot & De Knijf 2012). Together with our three localities, the total number of published localities increases to 35 for this endemic species. *Cordulegaster princeps* has been assessed as »Near threatened« in the regional Red List of North Africa (Samraoui et al. 2010). Our observations during mid-September are probably of the latest in the flight season. At one locality (loc. 99, Fig. 3a), the species was found at a tiny stream fully exposed to sunshine, 50 cm wide, <10 cm deep and nearly dry at some parts. At locality 100, the river was fast running, >3 m wide and >80 cm deep and the riverbank was nearly fully overgrown by *Nerium oleander* providing a lot of shade (Fig. 3b). This confirms the descriptions of the known habitat range of this species, which encompass more variability than given by Jacquemin & Boudot (1999).

Zygonyx torridus is an Afrotropical-Oriental species, its range extending over the southern parts of the Palaearctic, where it has a fragmented occurrence (Kunz et al. 2006). It is assessed as »Near Threatened« in the regional Red List of North Africa (Samraoui et al. 2010) and as »Vulnerable« in the European Red List (Kalkman et al. 2010). In the western part of the Mediterranean it occurs in Sicily, Spain, Portugal, Morocco and Tunisia, and, further to the west, on the Canary Islands (Kunz et al. 2006; Boudot et al. 2009; De Knijf & Demolder 2009). The species is rare in Morocco and occurs at very few localities from Agadir to the Rif and the Moulouya River, all west and north of the Atlas (Jacquemin & Boudot 1999; Boudot & De Knijf 2012). It was already mentioned by Jacquemin & Boudot (1999) to occur in the Asif Tamraght, which was additionally considered to be the same river than which was denoted as 'near Agadir' by Ocharan (1992). Kunz et al. (2006) mention three additional records, including exuviae,

from Asif Tamraght. On 08-ix-2013, we observed more than 1 500 adults flying over the Asif Tamraght (Fig. 4) along a total distance of 13 km. We also found two exuviae and several freshly emerged individuals. The species already appears in April (Kunz et al. 2006; Juillerat & Monnerat 2009), suggesting that it either has a minimum of two generations per year or that emergences occur continuously during most of the year. Both Jacquemin & Boudot (1999) and Dijkstra & Lewington (2006) state that the flight period of *Z. torridus* in the Western Palaearctic extends until August. In an intensive survey of the population of *Z. torridus* along the Rio Cabriel in Spain, Grand (2010) found exuviae until the end of July and the last three adults were observed on 26 September, two months after the last emergence. The huge numbers seen on the wing at mid-September, together with several freshly emerged individuals, suggest that, like in the Canary Islands (Bemmerle 2005), in the westernmost part of Morocco the flight period extends all year round due to mild winter conditions.

During our visit to Asif Tamraght, the first individuals appeared soon after 09 h WEST (UTC+1). From 14 h onwards the numbers dropped rapidly. Males were mostly seen along the river, while females were mostly noticed further away, especially among scattered bushes and trees exposed to the sun. Oviposition was mostly performed in tandem flight, during which the female touched the water with the abdomen. In some cases, we also observed that the female was ovipositing alone, on other occasions, guarded by the male. Such plasticity in this species' egg-laying behaviour has also been observed on Mauritius by Martens (2015).

Several species have their main distribution in Europe and occur only marginally in North Africa. It is generally believed that *Pyrrhosoma nymphula* and *Boyeria irene* mostly occur in North Africa at higher altitudes (Jacquemin & Boudot 1999; Samraoui & Alfarhan 2015). Our results show that *Boyeria irene* is also common at low altitudes (locs 4, 11, 12, 13, 14, 20, 25, 32, 33) but always at rapidly flowing wadis. Due to its crepuscular flight, *B. irene* remains often unnoticed, which is probably the reason for the low number of records of this species from Morocco. Our search for larvae and exuviae yielded 27 new localities of *B. irene* from the western Rif. We also found larvae at Dayet Iffer in the Middle Atlas (loc. 84), a pool at 1 500 m a.s.l., proving the reproduction of *B. irene* at high altitude stagnant waters.

Morocco constitutes the southern limit of the range of *Pyrrhosoma nymphula*, a species which is known from a dozen of localities in the Rif, Middle Atlas and the Oriental region, all at higher altitudes (Jacquemin 1994; Jacquemin & Boudot 1999; Boudot 2008; Melhaoui & Boudot 2009). Our surveys revealed seven new localities for this species from the Rif, two of which were lowland running waters (loc. 4 at 140 m and loc. 25 at 410 m).

Phenology

Our surveys resulted in several extreme seasonal records (Table 1) and especially provided the earliest observation date for no less than 17 of the 54 observed species, i.e., nearly one third of them. Our data were sometimes so far from previously known extreme seasonal records that we could extend the flying period in Morocco for six species, namely: *Lestes barbarus* (27-xi), *Lestes dryas* (12-vii), *Calopteryx haemorrhoidalis* (01-xi), *Coenagrion puella* (11-vii), *Trithemis kirbyi* (30-xii) and *Zygonyx torridus* (08-ix). The most important reason for this high proportion is without doubt the many surveys that were undertaken over several years and nearly year-round by resident odonatologists. By contrast, many of the past surveys were undertaken by foreigners during several weeks of holidays, mostly from spring to early summer. As our data were collected over the different regions of Morocco, each with its own climate, it is difficult to compare them. To have a full appreciation of the extent of the flight season, more surveys are necessary throughout the year. Van Schalkwyk et al. (2014) found that air temperature and associated low humidity is highly positively associated with flying activity and survival rate of overwintering dragonflies. This emphasizes that the species were opportunistic during the winter and only took to the air on clear, sunny and warm winter days. We suppose that several species, especially of the genera *Anax*, *Aeshna*, *Crocothemis*, *Sympetrum* and *Trithemis* can be found all year-round along the Atlantic Coast and the fringes of the Sahara in the south of Morocco, where these weather conditions occur. One record of *Trithemis kirbyi* was taken on 30-xii-2013 in the foothills north of the High Atlas (loc. 96) and not in a desert oasis. This suggests that the species shifts from univoltine to multivoltine development according to local climate, which could contribute to its rapid expansion in the Iberian Peninsula (Márquez-Rodríguez 2011; Romero Porrino 2012; Obregón-Romero et al. 2013).The long flight

period of some Zygoptera also indicates at least a bivoltine, or even a multivoltine life-cycle in Morocco. This has already been suggested for *Coenagrion caerulescens* by Conesa García (1995) and Jödicke et al. (2000a), but seems also to happen in *Platycnemis subdilatata* and *Ischnura saharensis.*

Conservation

Lestes dryas, *Calopteryx exul*, *C. virgo meridionalis*, *Aeshna isoceles*, *Libellula quadrimaculata* and *Coenagrion mercuriale* are rare species in Morocco but also in the rest of North Africa, with only a handful known populations, respectively. All these species are listed on the North African Red List (Samraoui et al. 2010). *Calopteryx v. meridionalis* is assessed as »Critically endangered«, *C. exul* and *C. mercuriale* as »Endangered«, and *L. dryas*, *A. isoceles* and *L. quadrimaculata* as »Vulnerable«. The current conservation status of many aquatic habitats in the Rif is deteriorating very fast, especially due to on-going urban development and road construction. This has led to the destruction (e.g., Smir marshes, wetland of Coelma), alteration, and degradation of water quality or changes of hydrology (e.g., upstream river Martil, Oued Moulay Bouchta) of many freshwater habitats. The localities were these North African Red List species occur are urgently in need of protection through Natural Parks or reserves and species protection plans. Hence, conservation measures should be taken to restore these habitats and their aquatic fauna, including the dragonfly community. The conservation of these sites, which are part of the natural heritage not only of Morocco but also of North Africa, should be done at the hydro-basin level as suggested by Holland et al. (2012), in order to integrate and coordinate the basin activities and management plans. In addition, population monitoring of these very rare species could allow us to control the efficiency of the conservation measures that will be undertaken.

Acknowledgement

The second author would like to thank Violeta Barrios (IUCN) for the organization of the fieldtrip on 6 September 2013 to some of the valleys in the High Atlas. Boudjéma Samraoui was of great help while searching for dragonflies during this organized fieldtrip on 6 September. Spanish AECI partially supported this study.

Table 1. List of Odonata taxa from Morocco recorded during this study, with the hitherto earliest and latest observation dates during the year. Numerals in parentheses refer to the following references: 1 – Aguesse & Pruja (1958); 2 – Lieftinck (1966); 3 – Dumont (1972); 4 – Lavergne-Viala & Thiery (1983); 5 – Jacquemin (1987); 6 – Jacquemin (1994); 7 – Jacquemin & Boudot (1999); 8 – Faucheux et al. (2005); 9 – Juillerat & Monnerat (2009); 10 – El Haissoufi et al. (2010); 11 – Boudot & De Knijf (2012); 12 - Mediani et al. (2014).

Taxon	First recording date	Last recording date
Lestes barbarus	02-iii-1985 (5)	27-xi-2009 (this work, loc. 20)
Lestes dryas	20-v-2011 (this work, loc. 56)	12-vii-2007 (this work, loc. 23c)
Lestes virens virens	01-vi-2012 (this work, loc. 41)	23-ix-1984 (6)
Lestes viridis	05-v-2005 (10)	23-xii-1983 (6)
Sympecma fusca	10-iii-1985 (6)	22-xii-1984 (6)
Calopteryx exul	05-v-2005 (10)	02-viii-85 (6)
Calopteryx haemorrhoidalis	20-iii-1938 (1)	01-xi-2009 (this work, loc. 5)
Calopteryx virgo meridionalis	05-vi-2011 (this work, loc. 23a)	23-ix-85 (6)
Platycnemis subdilatata	02-iv-2007 (this work, loc. 113)	23-ix-1984 (6)
Ceriagrion tenellum	07-iv-1985 (6)	23-ix-1984 (6)
Coenagrion caerulescens	02-iv-2008 (this work, loc.76)	26-ix-1983 (6)
Coenagrion mercuriale	05-iii-1984 (6)	22-ix-1984 (6)
Coenagrion puella	07-iv-1984 (6)	11-vii-2008 (this work, loc. 53)
Coenagrion scitulum	17-v-1966 (2)	25-vii-1971 (3)
Erythromma lindenii	10-iii-1985 (6)	24-x-1983 (6)
Erythromma viridulum	11-vi-2011 (this work, loc. 2)	22-vii-2010 (11)
Ischnura graellsii	30-iii-1985 (5)	22-xii-1984 (5)
Ischnura pumilio	09-iii-1983 (6)	26-ix-1983 (6)
Ischnura saharensis	05-iv-2017 (this work, loc. 115)	30-i-2014 (12)
Pyrrhosoma nymphula	12-v-2007 (this work, loc. 4)	26-vii-1971 (3)
Aeshna affinis	21-vi-1983 (6)	19-ix-1983 (6)
Aeshna isoceles	04-iv-1985 (6)	01-viii-1985 (7)
Aeshna mixta	01-iii-2011 (this work, loc. 2)	12-xii-1984 (5)
Anax ephippiger	03-i-2014 (12)	09-xii-2014 (12)
Anax imperator	01-iv-1984 (5)	19-xii-1984 (5)

Taxon	First recording date	Last recording date
Anax parthenope	15-iii-2011 (this work, loc. 2)	12-xi-1983 (5)
Boyeria irene	13-vi-2009 (this work, loc. 20)	09-x-2006 (9)
Gomphus simillimus maroccanus	07-iv-1985 (6)	27-vii-1971 (3)
Onychogomphus costae	15-iv-2011 (11)	03-viii-1984 (6)
Onychogomphus forcipatus unguiculatus	24-v-1983 (6)	08-viii-1984 (6)
Onychogomphus uncatus	21-iv-2009 (this work, loc. 13)	31-viii-1971 (3)
Paragomphus genei	05-iv-2008 (this work, loc. 72)	22-x-1983 (6)
Cordulegaster boltonii algirica	28-v-1985(7)	08-viii-1985 (6)
Cordulegaster princeps	22-v-1966 (2)	24-ix-1946 (1)
Brachythemis impartita	18-iv-1985 (5)	22-x-1984 (5)
Crocothemis erythraea	02-iv-2008 (this work, loc. 76)	04-i-2014 (12)
Diplacodes lefebvrii	14-iv-1985 (6)	07-x-1953 (1)
Libellula quadrimaculata	21-v-1966 (2)	01-viii-1985 (7)
Orthetrum brunneum	15-iv-2003 (9)	04-viii-1985 (7)
Orthetrum cancellatum	01-iv-1985 (5)	22-vii-1971 (3)
Orthetrum chrysostigma	12-iii-1949 (1)	22-xi-1984 (7)
Orthetrum coerulescens anceps	07-iv-1999 (8)	28-ix-1983 (6)
Orthetrum nitidinerve	14-iv-2011 (11)	02-x-1983 (6)
Orthetrum sabina	05-iv-2007 (this work, loc. 115)	x-2013 (C. Glen)
Orthetrum trinacria	01-iv-1984 (5)	22-x-1983 (5)
Sympetrum fonscolombii	02-iii-1985 (5)	04-i-2014 (12)
Sympetrum meridionale	03-v-1985(5)	20-x-1983 (7)
Sympetrum sanguineum	21-vi-1983 (6)	27-ix-1983 (6)
Sympetrum sinaiticum	02-i-2014 (this work, loc. 105)	29-ix-2007 (9)
Sympetrum striolatum	03-v-1985 (7)	01-iv-1985 (7)
Trithemis annulata	02-iv-2007 (this work, loc. 113)	03-i-2014 (12)
Trithemis arteriosa	10-iv-2004 (9)	x-1982 (4)
Trithemis kirbyi	01-iv-2008 (this work, loc. 75)	30-xii-2013 (this work, loc. 96)
Zygonyx torridus	28-iv-2007 (9)	08-ix-2013 (this work, locs 89–92)

References

Aguesse P. & Pruja J.P. 1958. Odonates récoltés par M. Ch. Rungs au Maroc, au Sahara, en Mauritanie et au Sénégal. *Comptes rendus des Séances mensuelles de la Société des Sciences naturelles et physiques du Maroc* 24 (5): 103-106

Bemmerle B. 2005. *Zygonyx torridus* auf La Gomera, Kanarische Inseln (Odonata: Libellulidae). *Libellula* 24: 249-256

Benazzouz B., Mouna M., Amezian M., Bensusan K., Perez C. & Cortes J. 2009. Assessment and conservation of the dragonflies and damselflies (Insecta: Odonata) at the marshes of Smir. *Bulletin de l'Institut scientifique* (Sciences de la Vie) 31: 79-84

Boudot J.-P. 2008. *Selysiothemis nigra* (Vander Linden, 1825), nouveau pour le Maroc, et autres observations sur les Odonates du Maghreb nord-occidental (Odonata: Anisoptera: Libellulidae). *Martinia* 24: 3-29

Boudot J.-P. & De Knijf G. 2012. Nouvelles données sur les Odonates du Maroc oriental et méridional (Odonata). *Martinia* 28: 1-28

Boudot J.-P., Kalkman V.J., Azpilicueta Amorín M., Bogdanović T., Cordero Rivera A., Degabriele G., Dommanget J.-L., Ferreira S., Garrigós B., Jović M., Kotarac M., Lopau W., Marinov M., Mihoković N., Riservato E., Samraoui B. & Schneider W. 2009. Atlas of the Odonata of the Mediterranean and North Africa. *Libellula Supplement* 9: 1-256

Conesa García M.A. 1995. Notes on infraspeciation in *Coenagrion caerulescens* (B. de Fonscolombe, 1839), with description of *C. c. isabelae* ssp. nov. from Morocco (Zygoptera: Coenagrionidae). *Odonatologica* 24: 425-440

Corso A., Janni O., Pavesi M., Sammut M., Sciberras A. & Vigano M. 2012. Annotated checklist of the dragonflies (Insecta Odonata) of the islands of the Sicilian Channel, including the first records of *Sympetrum sinaiticum* Dumont, 1977 and *Pantala flavescens* (Fabricius, 1798) for Italy. *Biodiversity Journal* 3: 459-478

De Knijf G. & Demolder H. 2010. Odonata records from Alentejo and Algarve, southern Portugal. *Libellula* 29: 61-90

Dijkstra K.-D.B. & Boudot J.-P. 2010. First update of the Atlas of the Odonata of the Mediterranean and North Africa: *Orthetrum machadoi* new to the Palaearctic and *Agriocnemis sania* new to the Egyptian Nile Valley. *Libellula* 29: 107-125

Dijkstra K.-D.B. & Lewington R. 2006. Field guide to the dragonflies of Britain and Europe. British Wildlife Publishing, Gillingham

Dumont H.J. 1972. Contribution à la connaissance des odonates du Maroc. *Bulletin de la Société des Sciences naturelles et physiques du Maroc* 52: 149-179

Dumont H.J. 1978. Odonates d'Algérie, principalement du Hoggar et d'oasis du Sud. *Bulletin et Annales de la Société royale belge d'Entomologie* 114: 99-106

Dumont H.J. 2007. Odonata from the Mouydir Plateau (North Central Sahara, Algeria). *Bulletin de la Société royale belge d'Entomologie* 143: 164-168

El Haissoufi M. 2012. Les Odonates du Maroc: Atlas, Etat de Conservation et Outils de Gestion. Thèse nationale. Université Abdelmalek Essaâdi, Faculté des Sciences, Tétouan

El Haissoufi M., Lmohdi O., Bennas N., Melládo A. & Millán A. 2008. Les odo-

nates du Bassin versant du Laou (Rif Occidental). *Travaux de l'Institut scientifique*, Rabat (Série générale) 5: 47-59

El Haissoufi M., Bennas N., Lmohdi O. & Millán A. 2010. Analyse préliminaire de la vulnérabilité des Odonates (Odonata) du Rif Occidental (Nord du Maroc). *Boletín de la Sociedad entomológica aragonesa* 46: 345-354

Faucheux M.J., Meurgey F. & El Wahbi Y. 2005. Odonates des environs d'Essaouira (Maroc méridional). *Bulletin de la Société des Sciences naturelles, Ouest de la France* 27: 122-130

Ferreira S., Velo-Anton G., Brochard C., Vieira C., Célio Alves P., Thompson D.J., Watts P.C. & Brito J.C. 2014. A Critically Endangered new dragonfly species from Morocco: *Onychogomphus boudoti* sp. nov. (Odonata: Gomphidae). *Zootaxa* 3856: 349-365

Ferreira S., Martínez-Freiría F., Boudot J.-P., El Haissoufi M., Bennas N., Célio Alves P., Watts P.C., Thompson D.J. & Brito J.C. 2015. Local extinctions and range contraction of the endangered *Coenagrion mercuriale* in North Africa. *International Journal of Odonatology* 18: 137-152; DOI: 10.1080/13887890.2015.1017846

Grand D. 2010. *Zygonyx torridus* (Kirby, 1889) sur le rio Gabriel, provinces de Albacete, Cuenca et Valencia (Espagne): distribution et observations biologiques (Odonata, Anisoptera, Libellulidae). *Martinia* 26: 138-150

Holland R.A, Darwall W.R.T. & Smith K.G. 2012. Conservation priorities for freshwater biodiversity: The Key Biodiversity Area approach refined and tested for continental Africa. *Biological Conservation* 148: 167-179

Jacquemin G. 1994. Odonata of the Rif, northern Morocco. *Odonatologica* 23: 217-237

Jacquemin G. & Boudot J.-P. 1999. Les libellules (Odonates) du Maroc. Société française d'Odonatologie, Bois d'Arcy

Jödicke R., Arlt J., Kunz B., Lopau W. & Seidenbusch R. 2000a. The Odonata of Tunisia. *International Journal of Odonatology* 3: 41-71

Jödicke R., Borisov S.N., Haritonov A.Y. & Popova O. 2000b. Additions to the knowledge of *Sympetrum sinaiticum* Dumont (Odonata: Libellulidae). *International Journal of Odonatology* 3: 131-140

Juillerat L. & Monnerat C. 2009. Odonata in southern Morocco, with first records of *Orthetrum ransonnetii* and *Sympetrum sinaiticum* (Odonata: Libellulidae). *Libellula* 28: 97-115

Kalkman V.J., Boudot J.-P., Bernard R., Conze K.-J., De Knijf G., Dyatlova E., Ferreira S., Jović M., Ott J., Riservato E. & Sahlén G. 2010. European Red List of dragonflies. Office for Official Publications of the European Union, Luxembourg

Kunz B., Ober S.V. & Jödicke R. 2006. The distribution of *Zygonyx torridus* in the Palaearctic (Odonata: Libellulidae). *Libellula* 25: 89-108

Lavergne-Viala M., & Thiery A. 1983. Les Odonates de Marrakech: inventaire et clé de détermination à base de ptérographies. *Bulletin de la Faculté des Sciences de Marrakech* (Sciences de la Vie) 2: 63-74

Lieftinck M.A. 1966. A survey of the dragonfly fauna of Morocco (Odonata). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 42: 1-63

Márquez-Rodríguez J. 2011. *Trithemis kirbyi ardens* (Gerstaecker, 1891) (Odona-

ta: Libellulidae); datos de campo sobre su ecología en el Sur de España y primeros registros para la provincia de Sevilla (España). *Métodos en Ecología y Sistemática* 6: 10-20

Martens A. 2015. Alternative oviposition tactics in *Zygonyx torridus* (Kirby) (Odonata: Libellulidae): modes and sequential flexibility. *International Journal of Odonatology* 18: 71-80

Mediani M., Boudot J.-P., Benazzouz B. & El Bella T. 2012. Two dragonfly species (Insecta: Odonata) migrating at Dakhla (region of Oued Ad-Dahab Lagouira, Morocco). *International Journal of Odonatology* 15: 293-298

Mediani M., Boudot J-P., Chevalier F., Qninba A. & Rodrigues J.C.C. 2014. Nouvelles données sur les Odonates dans le Grand Sud marocain, avec *Ischnura saharensis*, *Anax parthenope*, *Crocothemis erythraea* et *Trithemis annulata* nouveaux pour le Sahara Atlantique (Odonata: Coenagrionidae, Aeshnidae, Libellulidae). *Martinia* 30: 11-22

Melhaoui M. & Boudot J.-P. 2009. Diagnostic de la biodiversité aquatique dans le Bassin Hydraulique de la Moulouya. Projet ABHM/UICN. Rapport d'expertise. IUCN, Málaga

Obregón-Romero R., Cano-Villegas F.J., Tamajón-Gómez R. & López Tirado J. 2013. Primeras citas de *Trithemis kirbyi* Sélys, 1891 (Odonata, Libellulidae) en las provincias de Ciudad Real y Huelva, y nuevas aportaciones para la provincia de Badajoz (Espańa). *Boletín de la Sociedad andaluza de Entomología* 22: 88-93

Ocharan F.J. 1992. Odonata collected in Morocco and southern Andalucia, Spain. *Notulae odonatologicae* 3: 143-145

Romero Porrino R. 2012. Odonatos de Sierra Morena: algunas citas de interés en el período 2010-2011. *Boletín Rola* 1: 22-29

Samraoui B. & Alfarhan A.H. 2015. Odonata in streams on Mount Edough, Algeria, and in Kroumiria, Tunisia. *African Entomology* 23: 173-179

Samraoui B. & Menaï R. 1999. A contribution to the study of Algerian Odonata. *International Journal of Odonatology* 2: 145-165

Samraoui B., Boudot J.-P., Ferreira S., Riservato E., Jović M., Kalkman V.J. & Schneider W. 2010. Chapter 5. The status and distribution of dragonflies. In: Garcia N., Cuttelod A. & Abdul Malak D. (Eds), The status and distribution of freshwater biodiversity in Northern Africa: 51-70. IUCN, Gland, Cambridge, & Málaga

Van Schalkwyk J., Samways M.J. & Pryke J.S. 2014. Winter survival by dragonfly adults in the Cape Floristic Region. *International Journal of Odonatology* 17: 17-30

Waldhauser M. 2012. Dragonflies from the Western High Atlas, Morocco, with the first records of *Pyrrhosoma nymphula* in the High Atlas (Odonata: Coenagrionidae). *Libellula* 31: 243-250

1st December 2015

Cordulegaster heros and *Somatochlora meridionalis* in Ukraine: solving the zoogeographical puzzle at their northern range limits (Odonata: Cordulegastridae, Corduliidae)

Rafał Bernard[1] & Bogusław Daraż[2]

[1] Department of Nature Education and Conservation,
Adam Mickiewicz University, Umultowska 89, PL-61-614 Poznań, Poland;
<rbernard@amu.edu.pl>

[2] Kościelna 41, PL-35-505 Rzeszów, Poland

Received 29th May 2015; revised and accepted 18th September 2015

Abstract. The first records of *Cordulegaster heros* and *Somatochlora meridionalis* in Ukraine completed their distribution picture, thereby allowing the zoogeography of Balkan Odonata species at their northern range limit in Eastern Europe to be better understood. Five localities of *C. heros* in the Khotyn and Chernivtsi Uplands showed the eastern colonisation route to have proceeded north through the eastern Subcarpathians and adjacent hilly areas in Romania and southern Ukraine. A habitat and zoogeographical analysis mostly solved the *Cordulegaster*-puzzle in Ukraine and drew a picture of a northern *C. boltonii*-zone divided from a southern *C. heros*-zone by the extensive Podolian Upland. The population of *S. meridionalis* found in the extreme southwestern Ukraine completed the northernmost range limit in Eastern Europe between the known Slovakian and Romanian localities. It occurs in the Transcarpathian Lowland, i.e., the northernmost part of the Great Hungarian Plain in the direct foreground of the Carpathian foothills. Thus, it perfectly follows the species distribution pattern largely based on an extensive border zone of great basins and low foothills of the adjacent mountain ranges of the Carpathians and Alps. The situation and habitat of Ukrainian and eastern Slovakian localities suggest the Tisa River system as the main colonisation route of *S. meridionalis* for Central and Eastern Europe. Clear differences in the population sizes between streams suggested the optimal, acceptable, and marginal habitats of *C. heros*, which differed in the grain size of the bottom sediments, the stream morphology, and water current. *Somatochlora meridionalis* occurred in a several-metre-broad slow flowing and largely shaded canal-like river where specific habitat conditions were responsible for the concentration of species activity near the levee and pipe culvert.

Key words. Dragonfly, Anisoptera, Balkan fauna, Eastern Europe, zoogeography, habitat selection.

Introduction

Records of *Cordulegaster heros* Theischinger, 1979 and *Somatochlora meridionalis* Nielsen, 1935 from Slovakia (David 2000; Blaškovič et al. 2003; Holuša & Kúdela 2010; David 2011; Holuša & Holušova 2012b) and the Czech Republic (Holuša 2007, 2009; Staufer & Holuša 2010; Holuša et al. 2011) showed that range limits of these species are situated much farther north than had earlier been known. That discovery referred to the western parts of the species' ranges, but the extent of their distribution in eastern parts has mostly remained an open question. Additionally, misleading information has been included in European literature as a consequence of the late description of *C. heros* and species misidentifications in the genus *Cordulegaster* Leach, 1815 in Central and Eastern Europe. In the area of potential misidentification, *Cordulegaster boltonii* Donovan, 1809 was reported from Austria (Raab & Pennerstorfer 2006), Hungary (Dévai et al. 1976), Romania (Cîrdei & Bulimar 1965), the Czech Republic (Dolný & Holuša 2007), Slovakia (Straka 1990), and Ukraine (Gorb et al. 2000). The last quarter-century has shown that the data collected in Hungary and Slovakia must have concerned *C. heros* or *Cordulegaster bidentata* Selys, 1843 (Ambrus et al. 1992; Janský & David 2008). However, the "Field guide to the dragonflies of Britain and Europe" shows how complicated the situation still remains. On the *boltonii*-map (van Pelt 2006), there are still several points drawn with question marks in Romania and Ukraine. To solve these puzzles and answer questions about the Balkan species ranges, we organised an expedition to southern Ukraine in June 2013 and analysed all known data. On this basis, the current article presents the concept of the northern range limits of *C. heros* and *S. meridionalis* in Eastern Europe and the issue of the allopatric distribution of *C. heros* and *C. boltonii* there as a result of naturally conditioned postglacial colonisation and possibly also human induced habitat changes.

Study area and methods

Studies were carried out in three selected geographical regions of southern Ukraine: mainly in the Transcarpathian Lowland (Zakarpats'ka nyzovyna) and the Khotyn Upland (Khotyns'ka vysochyna) and additionally in the Chernivtsi Upland (Chernivets'ka vysochyna).

The Transcarpathian Lowland, the northeasternmost part of the Great Hungarian Plain, is situated west and south of the adjacent Carpathians, mostly at an elevation of 100–130 m a.m.s.l. [above mean sea level] in the Tisa River Basin with the major rivers: the Tisa and its tributaries, the Borzhava and the Latorica. This low-relief region is relatively warm and humid and is mostly deforested and anthropogenically impacted.

The Khotyn Upland is an undulating hilly ridge reaching 350–515 m a.m.s.l., situated east of the Carpathians and forming a watershed between the Prut and Dniester River Basins. It consists of central plateau-like elevations and their slopes separated by deep ravines with streams. The warm and humid upland is more than in 75 % overgrown with oak-hornbeam and beech forests (Kunytsya 1994).

In the southwest, the Khotyn Upland almost directly borders the Chernivtsi Upland. The latter is the easternmost part of the Ukrainian Subcarpathians (Peredkarpattya), which extend south towards the Romanian Subcarpathians. The Chernivtsi Upland consists of groups of hills, ridges and plateau-like elevations, mostly reaching 250–400 (up to 537) m a.m.s.l. and partly covered with oak-hornbeam and fir-beech forests.

Localities selected on detailed maps were examined for both imagines and larvae (exuviae) of *Cordulegaster* spp. and *Somatochlora* spp. in the second decade of June 2013. Only localities where those dragonflies were recorded are briefly characterised below. Localities 1–4 were situated in the Khotyn Upland, Loc. 5 in the Chernivtsi Upland, and Locs 6–7 in the Transcarpathian Lowland. Names of villages and water bodies are transliterated from Ukrainian and (in parentheses) sometimes from Russian, as Russian names still exist on many maps. Bottom deposits were collected at a locality with a stem population of *C. heros* (Loc. 1) and analysed texturally with the use of a sieve method to segregate grain sizes between -3.5 and 4.0 phi, with 0.5 phi intervals.

In the prepared maps (Figs 5 and 6), distribution of previously published records of *Cordulegaster heros* and *Somatochlora meridionalis* was based on information from numerous literature sources (e.g., Bernard et al. 2009; Buczyński et al. 2012; Cîrdei & Bulimar 1965; David 2011; Dijkstra & Koese 2001; Ermolenko & Tytar 2009; Gorb 1991; Grzędzicka 2010, 2013; Holuša & Kúdela 2010; Kutera & Woźniak 2010; Lehrer & Buli-

mar 1979; Manci 2011, 2012; Miszta & Cuber 2009; Sheshurak & Berest 2003; Sheshurak & Parkhomenko 2005; Trylis 1988; Tymochko 2013; Zabłocki & Wolny 2012).

Localities

Loc. 1. 48°28'39–40"N, 26°14'10–11"E, *ca* 264 m a.m.s.l., UTM 35UMP 46; 0.4 km S of the southern border of Polyana village, to the E of the road Polyana-Mlynky; a small, 0.8–1.2 m broad stream (Fig. 1) meandering below a low cascade on a locally gently inclined plateau in a dark deciduous forest, consisting mainly of *Carpinus betulus* with admixtures of *Acer pseudoplatanus* and *Fagus sylvatica*; deeply shaded with small light gaps; basic bottom sediments sandy-gravelly (sand 79.6 %, gravel 15.6 %) with a small admixture of silt (4.8 %) and with flat rocky debris and stones; the sediment was very fine gravelly fine sand with the following grain size distribution: very coarse silt (4.8 %), very fine sand (11.8 %), fine sand (25.6 %), medium

Figure 1. Stream south of Polyana (Loc. 1), optimal habitat of *Cordulegaster heros* in the Khotyn Upland, Ukraine. Photo by BD (17-vi-2013)

sand (20.7 %), coarse sand (12.4 %), very coarse sand (9.1 %), very fine gravel (7.5 %), fine gravel (5.8 %), medium gravel (2.3 %); local accumulations of fallen tree branches modified the breadth and strength of the water current.

Loc. 2. 48°29'18"N, 26°17'22"E, *ca* 245 m a.m.s.l., UTM 35UMP 47; *ca* 0.7 km SSW of the crossroads Nedoboivtsi-Rashkiv-Hordivtsi, 4.1 km ENE of Loc. 1, in the same stream basin; a forest brooklet (Fig. 2) situated in a 6–9 m deep ravine in deciduous forest consisting mainly of *Carpinus betulus* with admixtures of *Quercus robur*, *Q. petraea*, *Acer campestre*, *A. pseudoplatanus*, and *A. platanoides*; shaded with many small light gaps; small, mostly 0.3–0.4 m and locally up to 1 m broad; very shallow, with a small amount of trickling water; not meandering and steeper than the stream at Loc. 1, with many low cascades and shelves; basic bottom sediments sandy-gravelly with a large admixture of silt (movement makes the water very cloudy) and with many stones and flat rocky debris.

Figure 2. Brooklet in a ravine, SSW of the crossroads Nedoboivtsi-Rashkiv-Hordivtsi (Loc. 2), example of an acceptable, but not optimal habitat of *Cordulegaster heros* in the Khotyn Upland, Ukraine. Photo by BD (18-vi-2013)

Loc. 3. 48°30'06"N, 26°20'35"E, 151 m a.m.s.l., UTM 35UMP 57; at the Rukshyn-Hordivtsi road, 0.7 km ESE of Hordivtsi, 4.8 km ENE of Loc. 2; a quite shaded, fast-flowing forest stream with many small cascades and rapids, and with rocky shelves and a stony bottom with only a small amount of gravelly-sandy bottom deposits locally, but a greater amount beneath the road bridge.

Loc. 4. 48°27'56"N, 26°09'36"E, 375 m a.m.s.l., UTM 35UMP 36; the upper reach of the Rynhach (Ryngach) stream, *ca* 0.35 km SW of the Malyntsi-Blyshchad' road, 1.1 km SSE of the crossroads to Korneshty, 5.8 km WSW of Loc. 1; a forest shaded stream, meandering in a deep ravine in a *Carpinus betulus* forest; slowly flowing with dominating fine silty bottom deposits, only locally more gravelly-sandy, with some stones and flat rocky debris.

Loc. 5. 48°08'27"–09'12"N, 26°01'42"–02'06"E, 230–248 m a.m.s.l., UTM 35UMP 23; the Nevil'nytsya (Nevol'nitsa) stream above, i.e., to the south of Valya Kuz'myna (Valya Kuz'mina); fairly fast-flowing in deciduous forest (*Quercus*, *Fraxinus*, *Acer*, and *Salix*) with a narrow deforested clearing along all its western shore, therefore, only partly shaded; bottom sediments with silt dominating in the lower reaches and slightly more sandy-gravelly in the upper reaches.

Loc. 6. 48°11'52"N, 22°46'01"E, 119 m a.m.s.l., UTM 34UFU 33; the Mala Borzhava (Malaya Borzhava) River 1 km N of Kvasovo; a canal-like, from several to 10 m wide river (Fig. 3), running through and along the edge of a forest; shaded with only a few sunny clearings; very slow with a recognisable current only near a pipe-culvert connecting the river course before and behind a levee; water transparent, but dark-looking with a yellowish tint in sunny places; vegetation only very local: *Phalaris arundinacea*, *Sparganium* sp., a patch of *Nuphar lutea*.

Loc. 7. 48°17'55"N, 22°56'07"E, 127 m a.m.s.l., UTM 34UFU 45; a stream crossing the Mukacheve-Khust road 2 km N of Kam'yans'ke (Kamenskoe), 16.5 km NE of Loc. 6, in the same river basin; a small sunny stream running between meadows, flanked with 2–3 m high slopes; with diverse sections, from shallow, fairly fast and mostly clayey to deeper, slow and more muddy,

with some stones and rocky debris; vegetation in moderate amounts: *Glyceria* sp., *Sparganium erectum*, *Alisma plantago-aquatica*, *Mentha aquatica*, *Phalaris arundinacea*; different conditions beneath the bridge: totally shaded, shallow, with a lot of rubble remaining from road construction and a small amount of other bottom deposits locally between stones.

Results

Cordulegaster heros was recorded at five localities, four (Locs 1–4) in the Khotyn Upland and one (Loc. 5) in the Chernivtsi Upland of the Subcarpathians. Localities 1–3 were situated in the Dniester River Basin and localities 4 and 5 in the Prut River Basin.

Loc. 1: 17–18-vi-2013, *Cordulegaster heros*; a very large population with continuously patrolling males (several collected), one exuvia, extremely abundant larvae of diverse size present almost in each sample, up to six per sample. Accompanying species: *Cordulegaster bidentata*; rare (1 larva).

Figure 3. The Mala Borzhava River north of Kvasovo (Loc. 6), a habitat of *Somatochlora meridionalis* in the Transcarpathian Lowland, Ukraine. Photo by BD (20-vi--2013)

Abundant scuds *Gammarus* sp. (Amphipoda) and fairly abundant larvae of *Ephemera danica* Müller, 1764 (Ephemeroptera).

Loc. 2: 17–18-vi-2013, *Cordulegaster heros*; uncommon but regularly patrolling males (2 collected), 1 larva. Accompanying species: *Cordulegaster bidentata*; one male, one ovipositing female with only upper parts of eyes green and the rest dark grey.

Loc. 3: 18-vi-2013, *Cordulegaster heros*; three exuviae on the walls beneath the bridge, 1–2.5 m above the water surface. Accompanying species: *Onychogomphus forcipatus* (Linnaeus, 1758); three individuals (1 collected male) above the road and in a small glade near the stream. Apart from these residents, three other species were recorded from the road and glade, *Calopteryx splendens* (Harris, 1780), *Orthetrum coerulescens* (Fabricius, 1798), and *Libellula depressa* Linnaeus, 1758; they must have originated from another, calmer and sunnier section of this stream or its tributary.

Loc. 4: 18-vi-2013, *Cordulegaster heros*; uncommon but regularly patrolling males (1 collected) and three larvae (per many samples). Accompanying dragonfly species on a glade near the stream: *Calopteryx virgo* (Linnaeus, 1758), *Calopteryx splendens*, *Libellula depressa*. Rare scuds *Gammarus* sp. (Amphipoda) and uncommon larvae of *Ephemera danica* (Ephemeroptera) in more gravelly sites.

Loc. 5: 19-vi-2013, *Cordulegaster heros*; rare and local, only two larvae in a section with coarser sediments, possibly its main population inhabited the unvisited uppermost reach of the stream if it is more shaded and with less silty sediments. Accompanying species: *Cordulegaster bidentata* (1 exuvia), *Calopteryx virgo* (several males). Additionally, single or uncommon individuals of three other species, *Libellula depressa*, *Orthetrum coerulescens*, and *Pyrrhosoma nymphula* (Sulzer, 1776), which must have originated from a small marshy trickle and puddles. Abundant larval mayflies (Ephemeroptera).

Somatochlora meridionalis was recorded at two localities (Locs 6–7) in the Borzhava River Basin in the Transcarpathian Lowland.

Loc. 6: 20-vi-2013, *Somatochlora meridionalis*; associated with the close proximity of the bridge, where males sometimes patrolled along shores, but spent most of the time flying within a very small area near the levee and culvert and even flew through the pipe to the other side of the levee. One, or sometimes two, males were present, and almost as soon as they were caught, they were replaced by other males. In total, five males were collected and new ones still appeared and patrolled up to 20:53 h EEST, i.e., 40 minutes before sunset. One female oviposited in a shallow film of water on the detritus covered bottom near the shore. She was flying very fast and seemingly chaotically in a very restricted area and often rapidly changed flight direction. Generally, she subsequently moved between land and water, many times repeating a similar ovipositing sequence; i.e., she touched the earth surface with the end of her abdomen and after 2–3 rapid changes in flight direction touched the water surface. In the late afternoon, up to 20:51 h, three females intensively foraged in erratic rapid flight on the adjacent meadow. Five exuviae were found on large rocky stones used for construction of the levee and on a fallen tree trunk, four of them characteristically situated – attached to overhanging parts of stones or wood over mud or shallow water. Accompanying species: *Calopteryx splendens*.

Loc. 7: 15-vi-2013, *Somatochlora meridionalis*; six exuviae dispersed beneath the bridge, high (1.5–3 m) on its walls, in each case just at the top of the wall. Accompanying species occurring in the open stream: *Calopteryx splendens*, *Platycnemis pennipes* (Pallas, 1771), *Pyrrhosoma nymphula*, *Orthetrum albistylum* (Selys, 1848), *Orthetrum brunneum* (Fonscolombe, 1837), *Libellula depressa*.

Discussion

Zoogeography of *Cordulegaster heros* in the north of its range

Cordulegaster heros is a southeastern European endemic with its core distribution in the Balkans (van Pelt 2006). Considering the glacial refugia and dispersal centres, it could be described as a Ponto-Mediterranean faunal element (sensu de Lattin 1967 and Dévai 1976). The term »East Mediterranean species« (Holuša & Kúdela 2010) is much too broad as *C. heros* does not occur in most of the Eastern Mediterranean where it is replaced by other species of *Cordulegaster*.

First of all, it is necessary to say that at some point in the Holocene *Cordulegaster heros* theoretically could have reached the northern borderlands of its present range occasionally migrating over large flat lowlands or high mountain ranges. However, taking the species' biology and specialized habitat requirements into consideration, it is much more probable that its postglacial northward colonisation proceeded in a 'jumping' manner through appropriate hilly areas, e.g., along the mountain edges. We are convinced of this explanation, so we used it as an assumption in further considerations.

The present range of the species reaches far into southern Central Europe, through western Hungary and eastern Austria up to the southeastern Czech Republic and four regions in southern Slovakia (van Pelt 2006; Schweighofer 2008; Holuša & Kúdela 2010; Holuša et al. 2011; Holuša & Holušova 2012b; Rozner et al. 2012). It most probably reflects the westernmost postglacial colonisation route that went around the Great Hungarian Plain, to the west of it (Fig. 4). It still remains unknown whether the species also colonised the northern part of its range through the central

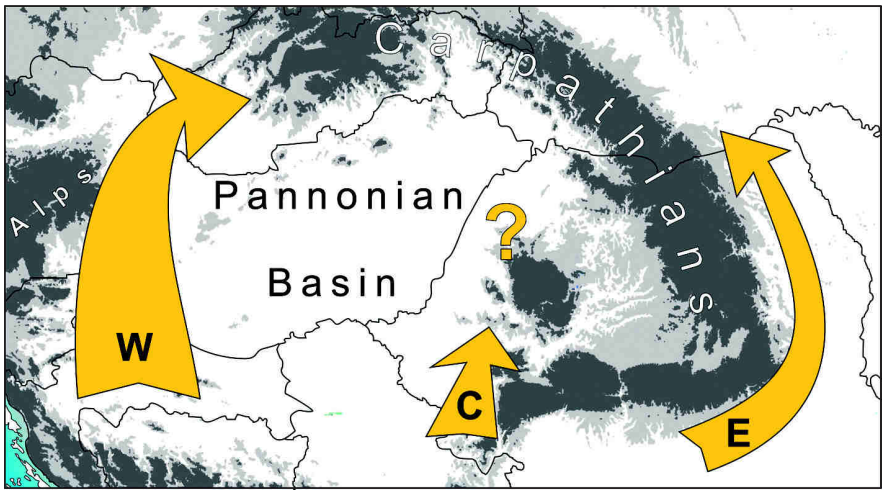


Figure 4. Hypothetical postglacial colonisation routes of *Cordulegaster heros* in the Pannonian-Carpathian zone. The arrows, described as W, C, and E, roughly show a possible western, central and eastern route, respectively. The question mark refers to a potential but so far unknown occurrence of the species in a northward projection of the central route.

route between the Great Hungarian Plain and the Carpathians as its localities have been recorded no farther north in that direction than mid-western Romania (Manci 2012; Figs 4, 5). The third potential route, i.e., the one running east of the Carpathians (Fig. 4) has become known only recently after two localities near Iași (NE Romania, Fig. 5) were published on the basis of data collected between the 1970s and 1990s (Manci 2011). The localities found by us have shown that the eastern 'branch' of the *C. heros*-range reaches even much farther north, as far as southern Ukraine (Figs 4, 5). Theoretically, this eastern route with seemingly lacking geographical barriers has offered a much better possibility of northward colonisation for the Balkan/Eastern Mediterranean fauna than the central or western routes, which are limited by the Carpathians (Figs 4, 5). However, it was unclear

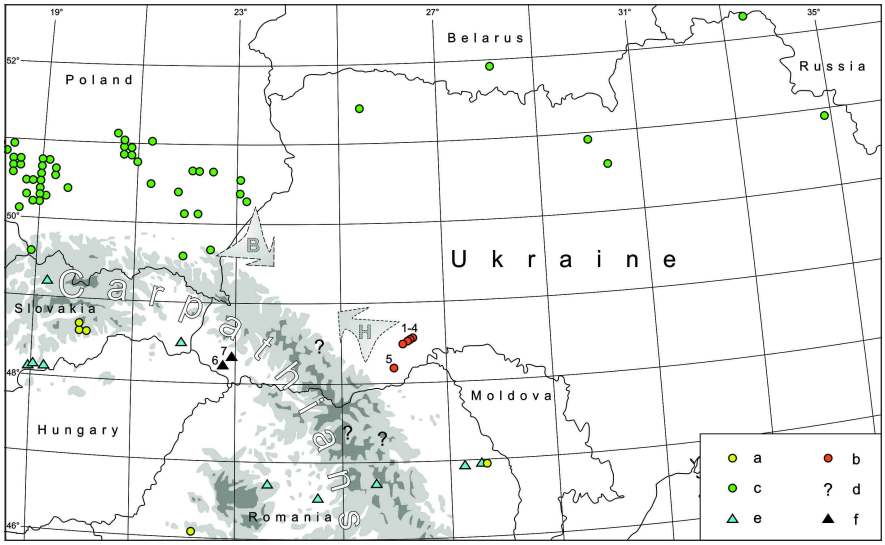


Figure 5. Distribution of *Cordulegaster heros* (a, b) and *Somatochlora meridionalis* (e, f) in the northeast of their ranges and in relation to the distribution of *Cordulegaster boltonii* (c) in the neighbouring areas. a, c, e – previously published data (see references in the chapter "Study area and methods"); b, f – new data collected in Ukraine; d – suggested misidentifications, i.e., published records of *C. boltonii*, considered to be *C. heros* and/or *C. bidentata*. A single point shows a locality or a group of localities either situated closely to each other or situated in one UTM 10x10 km square. Dashed arrows show theoretically possible projections of distribution ranges of *C. boltonii* (B) and *C. heros* (H).

how far north the distribution ranges of the Balkan Odonata species could have reached through the eastern 'passage'. To answer this question, it is necessary to analyse the puzzle of *C. heros* and *C. boltonii* in Eastern Europe in the light of our new data.

The puzzle of *C. heros* and *C. boltonii* in Eastern Europe

Cordulegaster heros was recognized as a separate species within the *C. boltonii*-complex quite late (Theischinger 1979). Together with the limited knowledge of diagnostic features and the general deficiency in the literature, this fact led to misidentifications of *Cordulegaster* species in Central and Eastern Europe. The problem concerned not only the theoretically problematic pair *C. heros*-*C. boltonii* but surprisingly even *C. bidentata*. In consequence, *C. boltonii* was reported from some localities in Hungary (Dévai et al. 1976), Romania (Cîrdei & Bulimar 1965; Lehrer & Bulimar 1979), and Slovakia (Straka 1990) while at present, it is clear that only *C. heros* and *C. bidentata* occur in these countries. For example, an individual of '*C. boltonii*' from the western Hungarian borderlands was proved to be *C. heros* (Ambrus et al. 1992). In Slovakia, all the checked '*boltonii*' individuals in collections turned out to have been misidentified. In fact, they mostly turned out to be *C. bidentata* with some additional *C. heros* (Janský & David 2008). In Romania, individuals of *C. boltonii* have not been found in collections, and its occurrence there has been diagnosed as questionable (Manci 2012). Four old localities of '*boltonii*' records (Cîrdei & Bulimar 1965; Lehrer & Bulimar 1979), drawn with question marks in van Pelt (2006), might have pertained to *C. heros*. However, in our opinion, *C. bidentata* should also be considered at least at one of these localities, Poiana Stampei. It is situated deep in the mountains, at about 900 m a.m.s.l., and both this fact and the clearly mountainous characteristics of this site suggest *C. bidentata* rather than *C. heros*.

The situation in Ukraine has been even more complicated as *C. boltonii* could potentially occur there, and *C. heros* was unknown prior to our current studies. This confusion is reflected in the *boltonii*-map in the European field guide (van Pelt 2006) where only question marks are given for Ukraine in both southern and northern parts. The southern question mark covers two old records in Klishkivtsi (Klishkovtsy) and Kolinkivtsi (Ko-

lenkovtsy), originally reported for *C. boltonii* (Brauner 1910; Gorb 2000). They are situated in the Khotyn Upland, in exactly the same stream systems where our current studies were undertaken. Our careful search yielded mostly *C. heros* and, additionally, *C. bidentata*, making it most likely that these old records actually referred to *C. heros*, which was still undescribed in the early 20th century.

In contrast to the southern location, the northern question mark must be replaced by dot(s) for *C. boltonii*. In fact, *C. boltonii* has been reported in northern Ukraine from several localities, not only in the Kyiv region (Trylis 1988; Gorb 1991), but also from Sumy (Sheshurak & Parkhomenko 2005), from the northernmost borderland with Russia (Sheshurak & Berest 2003), and the far northwest of the country (Ermolenko & Tytar 2009; Fig. 5). At all these localities, the occurrence of *C. heros* is improbable. Our certainty is based on two sets of arguments (see below) concerning the habitat conditions that prevail along the potential route of colonisation and the habitat and climatic conditions in northern Ukraine.

The situations in both southern Ukrainian and northeastern Romanian localities suggest that *C. heros* most probably colonised these areas proceeding along the eastern edge of the Eastern Carpathians. However, it must have proceeded not through the higher mountains but within a zone of the low eastern foothills, locally penetrating adjacent regions through hilly and forest 'projections' such as fragments of the Moldavian Plateau (Iași Ridge) and the Khotyn Upland (Figs 5, 6). In the northeastern part of its range, the species clearly requires hilly and mostly forested submontane/upland areas with undisturbed upper reaches of small streams. They provide the necessary microclimatic and habitat conditions, such as an appropriate grain size of bottom sediments. The bottom sediments in the upper reaches of streams in the hilly Khotyn Upland and in the Subcarpathians were fine but at least locally sandy-gravelly with a good amount of rocky debris, thus, they were inhabited by *C. heros*. In contrast, however, the lower reaches of the running waters that we studied below the Khotyn Upland and the Subcarpathians ran through deforested and anthropogenically disturbed areas and predominantly contained highly inappropriate, very fine silt-size bottom sediments, especially loess. *C. heros* was not found there and this kind of substrate appears not to match its ecological requirements.

Considering these habitat requirements, any colonisation of northern Ukraine by *C. heros* seems impossible due to the barrier of the large Podolian Upland (Podil's'ka vysochyna) situated to the north of the Khotyn Upland and the Subcarpathians. A crossing of the Podolian Upland by *C. heros* would be highly improbable due to: a) naturally thin and scattered forest cover in this forest-steppe zone, b) the too flat relief of this region with small local relative elevations, especially in its southern part along the Dniester River, i.e., adjacent to the known *heros*-range, c) a predomination of too fine loess bottom deposits. In the last few centuries, almost total deforestation, together with strong human impact on small flowing waters as a result of agricultural practices, has contributed to the already unfavourable conditions. However, even if *C. heros* had crossed the Podolian Upland occasionally by chance, the colonisation of streams in the northern Ukraine would have been impossible due to their lowland nature and a too severe climate. The Slovak and Czech localities, all situated in warm hilly areas with southern exposure, show how sensitive *C. heros* is to climatic conditions in the northern parts of its range.

It is, therefore, evident that localities in the northern Ukraine are inhabited only by *C. boltonii* (Figs 5, 6). They are clearly situated along the eastern colonisation route of this Atlanto-Mediterranean species. In the postglacial period *C. boltonii* has colonised Eastern Europe proceeding eastwards within a broad but fragmented belt through eastern Poland, the Baltic States, and Belarus to Russia. The northern Ukrainian localities of this largely forest species are generally connected through forest areas to its Polish, Belarussian and Russian localities (Fig. 6). They are also situated in a zone climatically suitable for *C. boltonii* that also offer small lowland forest running waters, i.e., habitats favourable for this species.

As a result, there are two *Cordulegaster* zones in Ukraine divided by the Podolian Upland: the northern *boltonii*-zone and the very local southern *heros*-zone (Figs 5, 6). The range of the latter, however, still remains unclear. Probably, the Khotyn Upland forms the northernmost borderland of the *C. heros* distribution range in Eastern Europe. It is still possible that the species have also colonised some areas west of the Khotyn Upland, i.e., the low northern foothills of the Carpathians. However, the northern foothills are unfavourable for this rather thermophilous species, which prefers southern

exposures in the north. Considering these facts, the locality of '*C. boltonii*' reported from Mykulyczyn in the Ivano-Frankivsk province (Tymochko 2013) and marked by us with a question mark (Fig. 5) may, in fact, refer to *C. heros* or even *C. bidentata*. True *C. boltonii* is least probable there. There are also other reports for '*C. boltonii*' from the Carpathians in the Ivano-Frankivsk province (Tymochko & Kyselyuk 2005; Zamoroka et al. 2005). They are not localised on maps as their details have been unobtainable for us. In our

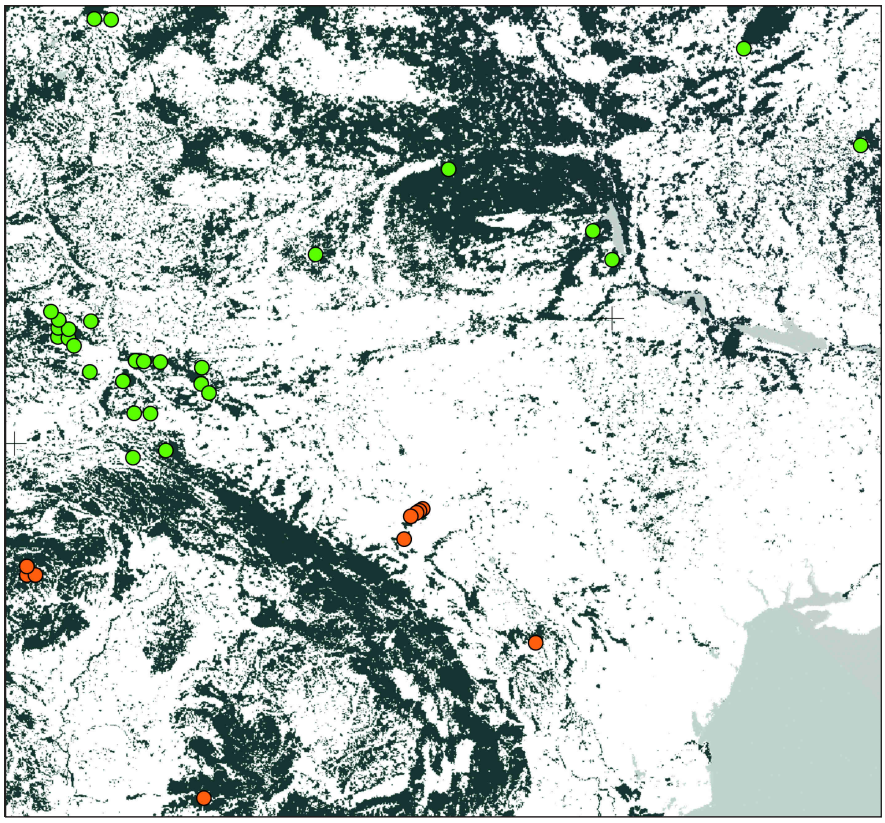


Figure 6. Distribution of *Cordulegaster boltonii* (green) and *Cordulegaster heros* (orange) in relation to the distribution of forest in Ukraine and adjacent lands. Both previously published (see references in the chapter "Study area and methods") and new data are included. The forest background is given according to the Forest Map of Europe 2011 (Päivinen et al. 2001; Schuck et al. 2002; Kempeneers et al. 2011).

opinion, they are highly enigmatic and might refer to *C. bidentata* rather than to *C. boltonii*. In summary, the rare localities of '*C. boltonii*' reported from the Ukrainian Carpathians and Subcarpathians between the Polish localities of this species and the localities of *C. heros* that we found need species verification. It might help to find the true northwestern range limit of *C. heros* and the southeastern extremity of the range of *C. boltonii* in East Europe.

Zoogeography of *Somatochlora meridionalis* in the north of its distribution range

Another Balkan species, *Somatochlora meridionalis*, seems to have a somewhat similar extent of occurrence as *C. heros* (cf. Wildermuth 2006, 2008). This distribution pattern is especially recognisable in the northern part of its range in Central Europe, where the species' fragmented distribution reaches eastern Austria (Raab & Pennerstorfer 2006), the southeastern Czech Republic (Holuša 2007, 2009), and southern Slovakia, with a possibly isolated locality in the northern area of Orava (David 2000, 2011; Janeková & David 2012; Stanislav David, pers. comm.). This part of the range covers: a) the eastern and northern areas of a system of great basins, i.e., of the Pannonian Basin with the Styrian and Vienna Basins, and b) low foothills of the adjacent mountain ranges of the Carpathians and Alps. Although this distribution pattern is fairly similar to that of *C. heros*, it is less focused on hilly areas and also comprises level lowlands in their broad foreground.

The new localities we found in the southwesternmost Ukraine perfectly follow this distribution pattern as they are situated in the extreme northeast of the Pannonian Basin (Great Hungarian Plain) in the direct foreground of the Carpathian foothills. They partly fill the gap in the species range between the known localities in Slovakia (David 2011) and Romania (Manci 2012; Fig. 5). This picture might suggest a central colonisation route that proceeded through Romania's Transsylvanian Basin along the eastern edge of the Great Hungarian Plain. However, Ukrainian localities might have also been colonised through the western route from Hungary and eastern Slovakia. Considering the native occurrence of *S. meridionalis* in running waters, including slow-flowing and quite sizeable rivers (Wildermuth 2008), its dispersal along some river systems is very probable. Therefore, the colonisation of the Ukrainian and eastern Slovakian localities might have proceeded

along the Tisa River and its tributaries, either from the lower reaches of the main river in Hungary, i.e., from southwest, or from the upper Tisa tributaries in Romania, i.e., from southeast. If this is true, some other tributaries of the Tisa River in Romania, Ukraine, Slovakia, and Hungary might presently be inhabited by the species. For example, the situation of the known locality in eastern Slovakia (David 2011) and an analysis of Ukrainian maps lead us to strongly suggest the tributaries of the Latoritsa River as other potential habitats of *S. meridionalis* in southwestern Ukraine.

For *S. meridionalis*, just as for *C. heros*, an eastern 'passage' must have also existed, i.e., the northward colonisation route proceeding along the eastern Subcarpathians and to the east of them. This is recognisable in the east Romanian localities found as far north as Iași in the Moldavian Plateau (Manci 2011, 2012; Fig. 5). Our search for the species farther north, in the Ukrainian Khotyn and Chernivtsi Uplands, did not result in any findings. However, the search was primarily focused on *C. heros* habitats, so there is still a possibility that *S. meridionalis* might be found in this region.

Differences in population sizes show the optimal, acceptable, and marginal habitats of *C. heros*

In our opinion, the Khotyn Upland in the Ukraine is inhabited by one large (meta)population of *Cordulegaster heros*. Although the streams belong to several systems and two river basins, they are situated in relatively close proximity in a compact forest complex. Dispersal of individuals along and between streams and their exchange between neighbouring subpopulations is, therefore, more than probable. The presence of exuviae in a very limited appropriate site beneath the bridge within a generally unsuitable stream (Loc. 3) was evidence of such a female penetrating dispersal.

Holuša & Kudela (2010) and Holuša & Holušova (2012a) describe the species' habitats in the northern limits of the range as shaded streams and streamlets situated in hilly forest areas, both meandering and steep, with: a) clear water, b) a basin width between 20 to 420 cm, c) a water depth of 2–18 cm, d) 15 % of the soil fraction between 5–20 mm, and e) a partial cover of organic detritus. Little is known, however, about the habitat conditions influencing the size of populations. Streams in the small Khotyn Upland offer surprisingly diverse habitat conditions. This diversity is reflected in

the various sizes of local subpopulations allowing us to distinguish between optimal, acceptable, and marginal habitats of *C. heros*. All the inhabited streams were similarly mostly shaded, but they differed in their morphology, inclination, and bottom deposits. Therefore, intense shading with small light gaps was certainly a basic condition for the species occurrence, but not a factor determining its numbers.

The great abundance of larvae and the continuous activity of males at locality 1 were indications of a true stem subpopulation and, hence, pointed to the habitat optimum (Loc. 1; Fig. 1). Such high habitat quality most probably consisted of a combination of: a) the specific stream morphology with its medium size, gentle inclination, meandering nature, and the presence of a small cascade, b) a diverse but generally moderate water flow modified by fallen branches and the cascade, and c) sandy-gravelly bottom deposits, being fine but not too fine and enriched with flat rocky debris. Considering the grain size, bottom sediments were significantly finer than those recorded by Holuša & Holušova (2012a) and Lang et al. (2001). This showed the broader range of the species preference/tolerance towards this factor. At the opposite end of the spectrum was a marginal habitat (Loc. 3). The fast-flowing, straight and quite large stream with a rocky and stony bottom offered quite good conditions for *Onychogomphus forcipatus*, but not for *C. heros*. The occasional occurrence of the latter was limited to single a site beneath the bridge with a greater amount of sandy-gravelly deposits. Between these extremes, some acceptable habitats of moderate quality occurred. This category included a shallow, quite steep trickle with numerous shelves and small cascades (Loc. 2; Fig. 2) and a rather slow-flowing stream (Loc. 4), both of which had only locally appropriate bottom sediments and a large admixture of a very fine silty fraction. These habitats were quite regularly, but not continuously, patrolled by males, while larvae were rare. It must be stressed that all the optimal and acceptable habitats, and thus, all the vital subpopulations (Locs 1, 2, 4) were situated in the upper reaches of streams at elevations between 244 and 375 m a.m.s.l. The lower reaches were simply too large and too deep and almost devoid of suitable microhabitats. The syntopic occurrence of *C. heros* with *C. bidentata* was recorded at three out of five localities. However, the presence of the latter was marginal and was slightly more marked only in the more *bidentata*-type streamlet (Loc. 2).

Ecological and behavioural remarks on *Somatochlora meridionalis*

Morphological differences between »almost identical« or »virtually identical« *S. meridionalis* and *S. metallica* (Vander Linden, 1825) have been commonly described as »very slight« (e.g. Wildermuth 2006, 2008). We would like to point out that, contrarily to these opinions, we recognised *S. meridionalis* as an evidently different species at first glance at all the imagines and exuviae observed and collected in Ukraine. However, this was certainly due to our extensive experience with *S. metallica* in several countries in Central and Eastern Europe and our familiarity with its black-pterostigma-lineage in northeastern Europe and western Siberia. Immediate identification was based not only on a yellow thoracic spot, which is commonly treated as the main difference and the only usable character, but in fact, on a whole complex of features. These include several quite significant, but so far neglected or insufficiently recognised differences in the male cerci and colour of the abdomen. A detailed comparison will be the subject of a separate work.

Of the two Ukrainian localities, the small stream running through meadows at Loc. 7 seemed to be only an occasional site of *S. meridionalis*. Its presence there was most likely only a result of female dispersal from a quite distant main population including Loc. 6. The especially open and sunny nature of that stream was unusual and unfavourable for the species. This was confirmed by the exclusive selection of the totally shaded conditions beneath the bridge for oviposition and larval development. The high affinity of this species to largely shaded flowing water (Utzeri et al. 1998; Wildermuth 2006, 2008) was clearly recognisable in its core habitat in the Mala Borzhava River (Fig. 3). This principal Ukrainian locality was also distinguished by surprisingly slow current and clear 'dark' water as a consequence of dark bottom deposits. In its general appearance, it was quite similar to the species' locality shown in the photograph in the Austrian monograph (Raab & Pennerstorfer 2006). We suggest that rivers that are several metres in breadth, largely shaded and 'dark', also those slow-flowing, and canal-like, may represent important habitats for *S. meridionalis* in the northern part of its range, and that those habitats should be the focus of further searches.

An evident concentration of activity, or at least longer flying periods of particular males within a small area near the culvert, was rather unusual in comparison with the typical male behaviour of *S. meridionalis*, i.e., patrol-

ling 30–50 m long sections of the shore (Wildermuth 2008). Although there was no evidence for territorial activity, the specific conditions of this locality, i.e., a film of water on the detritus bottom near the shore, large stones around the levee, and a current of water concentrated in a broad pipe, must have drawn males to this area, probably offering a greater possibility to meet females. The observed oviposition and collected exuviae seem to confirm this explanation. Both the rapid and seemingly chaotic water-land oviposition manner and the localisation of exuviae under overhanging stones or wood were typical of the species (Utzeri et al. 1998 and Wildermuth 2008, respectively).

Acknowledgements

We are very grateful to Dr. Stanislav David for information on the current distribution of *Somatochlora meridionalis* in Slovakia, to Prof. Marcin Słowik for the analysis of bottom sediments, to the European Forest Institute for the permission to use the Forest Map of Europe 2011, and to reviewers for their comments and suggestions, which helped us to improve the manuscript.

References

Ambrus A., Bánkuti K. & Kovács T. 1992. The Odonata fauna of Kisalföld and the West-Hungarian marginal zone. *A Győr-Moson-Sopron Megyei Múzeumok Kiadványa*, *Tanulmányok* 2: 1-81 [in Hungarian and in English]

Bernard R., Buczyński P., Tończyk G. & Wendzonka J. 2009. A distribution atlas of dragonflies (Odonata) in Poland. Bogucki Wydawnictwo Naukowe, Poznań

Blaškovič T., Bulánková E. & Šíbl J. 2003. First record of *Cordulegaster heros* ssp. *heros* Theischinger, 1979 (Cordulegastridae, Odonata) from Slovakia. *Biologia*, Bratislava 58: 293-294

Brauner A.A. 1910. Zametki o strekozakh Bessarabii [Notes on the dragonflies of Bessarabia]. *Trudy Bessarabskago Obshchestva Estestvoispytatelei i Lyubitelei Estestvoznaniya* [*Travaux de la Société des Naturalistes et des Amateurs des Sciences naturelles de Bessarabie*] 2 (1): 34-36 [in Russian]

Buczyński P., Dawidowicz Ł., Jarska W. & Tończyk G. 2012. On the occurrence of *Cordulegaster boltonii* (Donovan, 1807) (Odonata: Cordulegastridae) in the western part of the Lithuanian Lake District (Poland). *Zoology and Ecology* 22: 198-202

Cîrdei F. & Bulimar F. 1965. Odonata. Fauna Republicii Populare Române, Insecta vol. 7, fasc. 5. Academia Republicii Populare Române, Bucureşti: 1-277 [in Romanian]

David S. 2000. New records of dragonflies (Insecta, Odonata) from Slovakia. *Biologia*, *Bratislava* 55: 444

David S. 2011. Výskyt a ekologická charakteristika *Somatochlora meridionalis* Nielsen, 1935 na Slovensku. 17. Feriancove dni 2011, Prírodovedecká fakulta UK, Bratislava, 24.–25.11.2011, Zborník abstraktov z konferencie: 9 [in Slovak]

de Lattin G. 1967. Grundriß der Zoogeographie. Gustav Fischer, Jena

Dévai G. 1976. A magyarországi szitakötő (Odonata) fauna chorológiai vizsgálata [The chorological research of the dragonfly (Odonata) fauna of Hungary]. *Acta biologica debrecina* 13, Supplement 1: 119-157 [In Hungarian, English summary]

Dévai G., Bodnár G. & Benedek P. 1976. A szitakötők (Odonata) magyarországi előfordulási adatainak elemzése [An analysis of the faunistic records of dragonflies (Odonata) in Hungary]. *Acta biologica debrecina* 13, Supplement 1: 9-92 [in Hungarian, English summary]

Dijkstra K.-D.B. & Koese B. 2001. Dragonflies of Pripyat National Park, Belarus (Odonata). *Opuscula zoologica fluminensia* 192: 1-20

Dolný A. & Holuša O. 2007. Popis druhů [Description of species]. In: Dolný A., Bárta D., Waldhauser M., Holuša O., Hanel L. et al. (Eds), Vážky České Republiky: Ekologie, ochrana a rozšíření [The dragonflies of the Czech Republic: Ecology, conservation and distribution]: 210-658. Český svaz ochránců přírody, Vlašim [in Czech, English summary]

Ermolenko V.M. & Tytar V.M. 2009. Kordulegaster kil'chastyi *Cordulegaster boltoni* (Donovan, 1807). In: Akimov I.A. (ed.), Chervona knyha Ukrainy, Tvarynnyi svit [Red Book of Ukraine, Animals]: 68. Globalkonsaltyng, Kyiv [in Ukrainian]

Gorb S. 1991. The dragonfly *Cordulegaster boltoni* Donovan, 1807 (Odonata, Cordulegastridae) in the Ukraine. *Acta hydroentomologica latvica* 1: 24-27

Gorb S.N., Pavlyuk R.S. & Spuris Z.D. 2000. Babky (Odonata) Ukrainy: faunistychnyi ohlyad [Odonata of Ukraine: a faunistic overview]. *Vestnik Zoologii*, Supplement 15: 1-155. [in Ukrainian, English preface]

Grzędzicka E. 2010. Preferencje siedliskowe ważek na wybranym obszarze Gór Świętokrzyskich i Płaskowyżu Suchedniowskiego oraz możliwości ich ochrony [Habitat preferences of the dragonflies from chosen area of Świętokrzyskie Mountains and Suchedniów Plateau with their conservation abilities]. *Wiadomości Entomologiczne* 29, Supplement: 123-128 [in Polish, English summary]

Grzędzicka E. 2013. Nowe dane o występowaniu *Onychogomphus forcipatus* (Linnaeus, 1758) i *Cordulegaster boltonii* (Donovan, 1807) w Górach Świętokrzyskich (Odonata: Gomphidae, Cordulegastridae) [New data on the occurrence of *Onychogomphus forcipatus* (Linnaeus, 1758) and *Cordulegaster boltonii* (Donovan, 1807) in the Świętokrzyskie Mountains (Odonata: Gomphidae, Cordulegastridae). *Wiadomości Entomologiczne* 32: 298-299 [in Polish, English title]

Holuša O. 2007. Vážka *Somatochlora meridionalis* (Odonata: Corduliidae) zjištěna na území České republiky. In: Bryja J., Zukal J. & Řehák Z. (Eds), Zoologické dny Brno 2007. Sborník abstraktů z konference 8.-9. února 2007: 65-66. Ústav biologie obratlovců AV ČR, Brno [in Czech]

Holuša O. 2009. Notes to the first record of *Somatochlora meridionalis* (Odonata: Corduliidae) in the Czech Republic. *Acta Musei Beskidensis* 1: 89-95

Holuša O. & Holušová K. 2012a. Kolik toho víme o rozšíření největší evropské vážky páskovce velkého *Cordulegaster heros* (Odonata: Cordulegastridae) ve střední Ev-

ropě? Zoologické dny Olomouc 2012, 9.-10. února 2012, Sborník abstraktů z konference: 72-73 [in Czech]

Holuša O. & Holušova K. 2012b. What do we know about the largest European dragonfly *Cordulegaster heros* (Odonata: Cordulegastridae) in the Carpathian Mts.? Forum Carpaticum 2012 – From data to knowledge, from knowledge to action, Stará Lesná, Slovakia, 30 May – 2 June 2012, Conference abstracts: 86-87

Holuša O. & Kúdela M. 2010. New records of *Cordulegaster heros* (Odonata: Cordulegastridae) on its northern area border in Slovakia. *Acta Musei Beskidensis* 2: 75-87

Holuša O., Dalecký V. & Holušova K. 2011. First record of larvae of *Cordulegaster heros* (Odonata: Cordulegastridae) in the Czech Republic. *Acta Musei Beskidensis* 3: 65-69

Janeková K. & David S. 2012. Faunisticko-ekologický výskum vážok dolnej časti inundačného územia rieky Orava [The faunistic-ecological research of Odonata in the lower part of inundation area of the Orava river (NW Slovakia)]. *Folia faunistica slovaca* 17: 117-125 [in Slovak]

Janský V. & David S. 2008. Výskyt vážky *Cordulegaster heros* ssp. *heros* (Odonata: Cordulegastridae) na Slovensku [Occurence of the dragonfly *Cordulegaster heros* ssp. *heros* (Odonata: Cordulegastridae) in Slovakia. *Acta Rerum naturalium Musei nationalis slovaci (Zborník Slovenského Národného Múzea, Prírodné Vedy)* 54: 61-68 [in Slovak, English abstract]

Kempeneers P., Sedano F., Seebach L., Strobl P. & San-Miguel-Ayanz J. 2011. Data fusion of different spatial resolution remote sensing images applied to forest type mapping. *IEEE Transactions on Geoscience and remote sensing* 49: 4977-4986

Kunytsya M. 1994. Khotyns'ka vysochyna [The Khotyn Upland]. In: Maslyak P.O., Shyshchenko P.G. (Eds), Khrestomatiya z geografii Ukrainy: Posibnyk dlia vchitelya [Chrestomathy of geography of Ukraine: a manual for a teacher] Geneza, 1994. [in Ukrainian]

Kutera M. & Woźniak A. 2010. Nowe stanowisko ważki – szklarnika leśnego *Cordulegaster boltonii* (Donovan, 1807) na Przedgórzu Iłżeckim koło Starachowic w obrębie Wyżyny Kieleckiej [New locality of common goldenring *Cordulegaster boltonii* (Donovan, 1807) near Starachowice on the Kielce Upland]. *Chrońmy Przyrodę Ojczystą* 66: 121-124 [in Polish, English summary]

Lang C., Müller H. & Waringer J.A. 2001. Larval habitats and longitudinal distribution patterns of *Cordulegaster heros* Theischinger and *C. bidentata* Sélys in an Austrian forest stream (Anisoptera: Cordulegastridae). *Odonatologica* 30: 395-409

Lehrer A.Z. & Bulimar F. 1979. Sinteze cartografice ale patrimoniului natural al României II. Ordinul Odonata Fabricius, 1792 [Synthèses cartographiques du patrimoine naturel de Roumanie II. Ordre Odonata Fabricius, 1792]. *Nymphaea: Folia Naturae Bihariae* 7: 343-393 [in Romanian, French summary]

Manci C.-O. 2011. The dragonfly (Insecta: Odonata) collection of Iaşi Museum of Natural History (Romania). *Travaux du Muséum national d'Histoire naturelle «Grigore Antipa»* 54: 379-393

Manci C.-O. 2012. Dragonfly fauna (Insecta: Odonata) from Romania. PhD Thesis Abstract. Faculty of Biology and Geology, "Babeş-Bolyai" University, Cluj-Napoca

Miszta A. & Cuber P. 2009. Nowe stanowiska ważek (Odonata) zagrożonych w Polsce

stwierdzone w latach 2006-2008 w województwie śląskim poza obszarami chronionymi [New localities of dragonflies (Odonata) endangered in Poland recorded in the years 2006-2008 in Silesian Province outside of protected areas]. *Odonatrix* 5: 48-54 [in Polish, English summary]

Päivinen R., Lehikoinen M., Schuck A., Häme T., Väätäinen S., Kennedy P. & Folving S. 2001. Combining Earth observation data and forest statistics. EFI Research Report 14. European Forest Institute, Joensuu & Joint Research Centre – European Commission

Raab R. & Pennerstorfer J. 2006. Die Libellenarten Österreichs. In: Raab R., Chovanec A. & Pennerstorfer J. (Eds), Libellen Österreichs: 71-255. Umweltbundesamt, Wien; Springer, Wien, New York

Rozner G., Ferincz Á. & Miókovics E. 2012. Adatok a (*Cordulegaster bidentata* Sélys, 1843) és a kétcsíkos hegyiszitakötő (*Cordulegaster heros* Theischinger, 1979) elterjedéséhez a Bakonyban [Data to the distribution of Golden Ringed Dragonfly (*Cordulegaster bidentata* Sélys, 1843) and Large Golden Ringed Dragonfly (*Cordulegaster heros* Theischinger, 1979) in Bakony Mountains]. *Természetvédelmi Közlemények* 18: 447-455 [in Hungarian, English abstract]

Schuck A., van Brusselen J., Päivinen R., Häme T., Kennedy P. & Folving S. 2002. Compilation of a calibrated European forest map derived from NOAA-AVHRR data. EFI Internal Report 13: 1-44. European Forest Institute, Joensuu

Schweighofer W. 2008. Syntopes Vorkommen von *Cordulegaster boltonii* und *C. heros* an einem Bach im westlichen Niederösterreich (Odonata: Cordulegastridae). *Libellula* 27: 1-32

Sheshurak P.N. & Berest Z.L. 2003. Redkie nasekomye planiruemogo Pridesnyanskogo natsional'nogo prirodnogo parka. [Rare insects from the planned Pridesnyanskyi National Nature Park). In: Materialy konferentsii, prysvyachenoi 80-richchyu Kanivs'kogo pryrodnogo zapovidnyka "Rol' pryrodno-zapovidnykh terytoriy u pidtrymanni bioriznomanittya", Kaniv 9-11 veresnya 2003 [Materials from the conference devoted to the 80 anniversary of the Kaniv National Nature Reserve "Role of protected natural areas in the maintenance of biodiversity", Kaniv 9-11 September 2003]: 308-309 [in Russian]

Sheshurak P.N. & Parkhomenko V.V. 2005. Nakhodka *Cordulegaster annulatus* (Odonata, Cordulegastridae) v Sumskoi oblasti (Ukraina) [Record of *Cordulegaster annulatus* (Odonata, Cordulegastridae) in the Sumy province (Ukraine)]. *Vestnik Zoologii* 39: 48 [in Russian]

Staufer M. & Holuša O. 2010: First record of *Cordulegaster heros* in the Czech Republic, with notes on *Cordulegaster* spp. in southern Moravia (Odonata: Cordulegastridae). *Libellula* 29: 197-204.

Straka V. 1990. Vážky (Odonata) Slovenska [The dragonflies (Odonata) of Slovakia]. *Zborník Slovenského Národného Múzea, Prírodné Vedy (Acta Rerum naturalium Musei nationalis slovaci)* 36: 121-147 [in Slovak, English summary]

Theischinger G. 1979. *Cordulegaster heros* sp. nov. und *Cordulegaster heros pelionensis* ssp. nov., zwei neue Taxa des *Cordulegaster boltoni* (Donovan)-Komplexes aus Europa (Anisoptera: Cordulegasteridae). *Odonatologica* 8: 23-38

Trylis V.V. 1988. Bentofauna reki Tal' kak pokazatel' ee sanitarnogo sostoyaniya [Benthofauna of the Tal' River as an in-

dex of its sanitary conditions]. In: Voprosy gidrobiologii vodoemov Ukrainy, Sbornik nauchnykh trudov [Problems of hydrobiology of Ukrainian water bodies, Collection of scientific papers]: 101-106. Naukova dumka, Kiev [in Russian]

Tymochko V.B. 2013. Suchasnyi stan vyvchenosti ridkisnykh vydiv komakh na terytorii Karpats'kogo NPP [Present state of knowledge of rare species of insects in the territory of Carpathian NNP]. *Naukovi Zapysky Derzhavnogo Pryrodoznavchogo Muzeyu*, *L'viv*, 29: 147-150 [in Ukrainian, English abstract]

Tymochko V.B. & Kyselyuk O.I. 2005. Suchasnyi stan ridkisnykh vydiv komakh na terytorii Karpats'kogo natsional'nogo pryrodnogo parku [Recent status of rare insect species in the Carpathian National Nature Park]. In: Zbirnyk naukovykh prats' za materialamy konferentsii "Ridkisni ta znykayuchi vydy komakh ta kontseptsii Chervonoi Knygy Ukrainy" [Transactions of the conference "Rare and endangered insect species and conceptions of the Red Data Book of Ukraine"]: 108-110 [in Ukrainian, English summary]

Utzeri C., Cordero A., Santolamazza Carbone S., Dell'Anna L. & Mancini L. 1998. *Somatochlora meridionalis* Nielsen, 1935 nel Lazio (Italia centrale), con note di autecologia e comportamento (Odonata: Corduliidae). *Opuscula zoologica fluminensia* 163: 1-16.

van Pelt G.J. 2006. *Cordulegaster* Leach, 1815 – Goldenrings. In: Dijkstra K.-D.B. & Lewington R. (Eds), Field guide to the dragonflies of Britain and Europe including western Turkey and north-western Africa: 210-221. British Wildlife Publishing, Gillingham

Wildermuth H. 2006. *Somatochlora* Selys, 1871 – Striped Emeralds. In: Dijkstra K.-D.B. & Lewington R. (Eds), Field guide to the dragonflies of Britain and Europe including western Turkey and north-western Africa: 224-235. British Wildlife Publishing, Gillingham.

Wildermuth H. 2008. Die Falkenlibellen Europas. Corduliidae. Die Neue Brehm-Bücherei 653. Westarp Wissenschaften, Hohenwarsleben.

Zabłocki P. & Wolny M. 2012. Materiały do poznania niektórych chronionych, rzadkich i interesujących gatunków ważek (Insecta: Odonata) Śląska [Materials to the knowledge of some protected, rare and interesting species of dragonflies (Insecta: Odonata) of Silesia (southwest Poland)]. *Opolski Rocznik Muzealny* 19: 9-48. [in Polish, English abstract]

Zamoroka A.M., Zhyrak P.M. & Pushkar V.S. 2005. Ridkisni ta znykayuchi vydy komakh Ivano-Frankivs'koi oblasti u kolektsiyakh students'kogo naukovogo entomologichnogo tovarystva "Tenax-17" [Rare and declining species of insects from Ivano-Frankivs'k region in the collection of the Students Research Entomological Society "Tenax-17"]. In: Zbirnyk naukovykh prats' za materialamy konferentsii "Ridkisni ta znykayuchi vydy komakh ta kontseptsii Chervonoi Knygy Ukrainy" [Transactions of the conference "Rare and endangered insect species and conceptions of the Red Data Book of Ukraine"]: 34-37 [in Ukrainian, English summary]

1st December 2015

Update of the Odonata fauna of Georgia, southern Caucasus ecoregion

Asmus Schröter[1], Malte Seehausen[2], Bernd Kunz[3], André Günther[4], Thomas Schneider[5] & Reinhard Jödicke[6]

[1] Rasenweg 10, 37130 Gleichen, Germany; <notulae@osmylus.com>

[2] Museum Wiesbaden, Friedrich-Ebert-Allee 2, 65185 Wiesbaden, Germany; <malte.seehausen@museum-wiesbaden.de>

[3] Hauptstraße 111, 74595 Langenburg, Germany; <libellen@berndkunz.de>

[4] Naturschutzinstitut Freiberg, B.-Kellermann-Str. 20, 09599 Freiberg, Germany; <andre.guenther@ioez.tu-freiberg.de>

[5] Arnold-Knoblauch-Ring 76, 14109 Berlin-Wannsee, Germany; <thomas.rs@gmx.de>

[6] Am Liebfrauenbusch 3, 26655 Westerstede, Germany; <reinhard.joedicke@ewetel.net>

Received 20th June 2015; revised and accepted 18th September 2015

Abstract. A total of 63 odonate taxa were recorded in Georgia during nationwide surveys in June–July 2014, and June and July–August 2015, corresponding to at least 85 % of the country's Odonata fauna. For the majority of species information from Georgia is provided in English language for the first time. *Selysiothemis nigra* is a new addition to the country's list. The occurrence of *Chalcolestes parvidens* is confirmed and previous records from Georgia listed as *Lestes viridis* are doubted and believed to pertain to *parvidens*. The second and third records only for *L. macrostigma* are presented. Individuals intermediate between *Enallagma cyathigerum cyathigerum* and *E. c. risi* are reported from Georgia for the first time. As to Georgian *Lestes virens*, the infraspecific taxonomy is critically discussed, with special reference to Central Asian forms described as ssp. *marikovskii*. It is recommended to avoid any further splitting into inadequately defined subspecies, as the variability of eastern forms from Central Europe towards Central Asia can be better described as clinal variation within the ssp. *vestalis*. In consequence, the name *marikovskii* is regarded as a junior synonym of *vestalis*: *Lestes virens vestalis* Rambur, 1842 = *L. virens marikovskii* Belyshev, 1961, syn. nov. The diversity of taxa within the *Calopteryx splendens* complex in the Caucasus region is considered to comprise in fact three subspecies in Georgia: ssp. *intermedia*, spp. *tschaldirica*, and ssp. *mingrelica*. Despite of transition zones and hybridisation each subspecies represents *in toto* a spatially clearly delimited unit. In ssp. *intermedia* androchrome females frequently occurred in the Kakheti region in the east of Georgia. The distinct female colour form '*feminalis*' of *Calopteryx virgo* is illustrated for the first time and the availability of the name *Calopteryx virgo* var. *feminalis* Bartenev, 1910 is critically discussed. For a number of species the

first information from Georgia is provided since their discovery over a century ago, such as *Coenagrion armatum*, *Aeshna serrata*, and *Onychogomphus assimilis*; for *Coenagrion lunulatum* and *C. scitulum* the first data since over 75 years are presented. *Coenagrion ponticum* was recorded throughout the country and at least at two sites found to reproduce syntopically with *C. puella*. New information is provided for the little known *Coenagrion vanbrinkae*, including a formerly unknown pink colour morph of reproductive females. The infraspecific taxonomy of *Ischnura elegans* is critically discussed, with special reference to the taxa *pontica* Schmidt, 1938 and *ebneri* Schmidt, 1938. In addition, new records of *Pyrrhosoma nymphula* and *Coenagrion pulchellum*, both being rare in the Caucasus region, are given. The presence of distinct *Gomphus schneiderii* in Georgia is confirmed as well as the continuous presence of *Gomphus ubadschii* at the Rioni River over 80 years after its description under the homonym »*Gomphus flavipes* var. *lineatus* var. n.«. *Onychogomphus assimilis* and *O. flexuosus* were found to be abundant in the eastern half of the country suggesting that Georgia is an important global stronghold for both threatened species. Males of *Caliaeschna microstigma* exhibited a distinctive tendency for reduced ante-humeral stripes, leaving only a small bluish patch at the posterior part in some males. Vital populations of *Libellula pontica*, endemic to the East Mediterranean, were found and the species is assumed to be well established in the Kakheti region in the East of the country.

Key words. Dragonflies, damselflies, Anisoptera, Zygoptera, new records

Introduction

The Caucasus ecoregion is one of the most biologically diverse and rich areas in the world (Mittermeier et al. 2004). During the Pleistocene glaciations and climatic changes, several parts of the region served as important refugiae resulting in e.g., the highest number of endemic vascular plant species in temperate latitudes of the Northern Hemisphere (Myers et al. 2000). The Caucasus-Anatolian-Hyrcanian Temperate Forests are included in the prestigious "Global 200 list" (Ecoregion 78) of priority ecoregions as the earth's biologically richest habitats (Olsen & Dinerstein 2002). Due to its geographical position and topography Georgia plays a key role in terms of species diversity. Georgia is a small mountainous country situated at the southern slopes of the Greater Caucasus range. The southern part of the country is characterised by the so called Lesser Caucasus as a part of the Anatolian-Iranian fold mountain range. Both the Greater and Lesser Caucasus ranges are running parallel in West–East direction and are divided by the subtropical Transcaucasian depression (Franz 1973). Based on its geographic position at the eastern shore of the Black Sea and a high geomorphological diversity, Georgia offers an amazing variety of different landscapes and microclimates at a small scale (Javakhishvili 1964; Franz 1973) and

is overlapping and bordering area of several biogeographic units. Comprising ca 70 000 km², the territory of Georgia does not even reach the size of Bavaria but includes such contrasting habitats as semi-deserts, lowland and mountain steppes as well as perhumid evergreen broad-leaved temporal rainforest, alternating with glaciated peaks exceeding 5 000 m a.s.l.. Georgia shows a distinct climatic dichotomy formed by the Likhi range (also called Surami range), a bridge ridge in North–South direction, reaching a height of almost 2 000 m a.s.l. and connecting the Greater and Lesser Caucasus. This range is a watershed and functions as an effective climate barrier by forming a topographical triangle which traps moist air masses and cyclones coming from the Black Sea, forcing them to ascend and to release the moisture as rain. It developed during the Tertiary age and divides the Transcaucasian depression, which previously stretched from the Black Sea to the Caspian Sea, into two parts: the perhumid Rioni river basin in the West, which is the so called Colchic lowland with, according to Lydolph (1977), the warmest winters within the territory of the former Soviet Union (*Cfa* in the Köppen's climate classification), and the semihumid continental Kura river basin in the East (*BS* and *BW* in the Köppen's climate classification; cf. Schäfer 2003; Kottek et al. 2006). The gradient of mean annual precipitation of the Transcaucasian depression from West to East within Georgia ranges from locally over 4 000 mm at the western slopes of the Adjarian mountains to lesser than 350 mm at the semi arid southeastern bordering area to Azerbaijan (Berg 1959; Javakhishvili 1964; Franz 1973; Lydolph 1977; Schäfer 2003). According to Berg (1959) the precipitation rate of the Colchic lowland in the Rioni river basin was by far the highest of all humid lowland areas within the borders of the former Soviet Union. This distinctive climate regime with gradually decreasing precipitation from West to East fundamentally influenced the spatial distribution of vegetation in Georgia (Lauer & Rafiqpoor 2002; Nakhutsrishvili 2013) and is also reflected by the distribution pattern of several odonate species as shown in this study.

The first odonate records from the territory of today's Georgia dated back to the times of the Russian Empire (e.g., Kolenati 1846; Hagen 1863; Selys 1869; Eichwald 1873; Selys 1884, 1887; Radde 1899; Bartenev 1909, 1910, 1912a, 1916, 1919) whereas especially the latter author continued odonatological research into the beginnings of the subsequent Soviet age. Most papers

however contained only a small number of odonate species and the majority of Georgian dragonfly records are published as scattered individual data within larger faunistic inventories of the entire Caucasus region. Only few articles dealing entirely or predominantly with the Georgian Odonata fauna have been published during the Soviet period (Bartenev 1925, 1929a, b, 1930a, b; Shengelia 1953, 1964, 1975; Akramowski & Shengelia 1967; Beutler 1987). Recent data from Georgia are especially rare and after gaining political independence in 1991 besides Skvortsov (2010) – of which we recommend a cautious use only (cf. Schröter 2011) – only three short articles dedicated to the Odonata fauna of Georgia have been published at all (Reinhardt 1992; Schröter 2010a; Rodríguez Martínez & Conesa García 2015).

The odonatological exploration of Georgia thus remains on a very low level and the country's dragonfly fauna is less intensively studied than that of several neighbouring countries such as Turkey or Armenia, whose odonate fauna were subject to recent (partly) systematical surveys (Kalkman 2006; Tailly et al. 2004; Ananian & Tailly 2013). This applies to a lesser extent also to Azerbaijan (Dumont 2004; Skvortsov & Snegovaya 2014). Thus, the knowledge on all Georgian dragonfly species remains scanty and of anecdotal nature. Several regions of the country, especially the mountainous areas, such as the territories of the historical provinces of Tusheti and Khevsureti (today part of Mzcheta-Mtianeti and Kakheti provinces, respectively), literally remained *terra incognita* with regards to Odonata and have never been visited by any odonatologist. For a brief summary of the current state of odonatological research in Georgia we refer to Schröter (2010a).

The results presented in the following were obtained during a country-wide survey which was intended as initial study of a planned continuous comprehensive project aiming to restart and trigger odonatological research in Georgia; further objectives of the project are a national distribution atlas and an up-to-date national Red List.

Material and methods

The three weeks' expedition with 17 participants from Georgia, Germany and Switzerland took place from 20-vi till 10-vii-2014. From 05-vi–11-vi-2015 and 27-vii–04-viii-2015 additional data were collected by MS and TS, respectively. At least 3 120 km were covered by minibus. The route

was GPS-tracked and primarily defined by the attempt to cover habitats of all major climate and altitude zones frequented by dragonflies. Sampled localities were additionally recorded by hand-held GPS (Garmin). Initial selection of the destinations was influenced by selected globally threatened species, range restricted species and/or species of special biogeographical or taxonomical interest; several old historical sites were therefore visited in a targeted manner. The chosen time period was considered as ideal compromise in view of varying phenology and different altitudes to cover late flying spring species as well as summer species. Our search strategy was generally focussed on both adults and exuviae, aiming to authenticate all taxa by photographs, exuviae and/or voucher specimens. In the cases of Cordulegastridae and Gomphidae, larvae were selectively sought after. Specimens will be deposited in the collections of the Georgian National Museum (GNM), Senckenberg Museum für Naturkunde Frankfurt, Germany (SMF), Museum Wiesbaden, Germany (MWNH), as well as in private collections of participants. Temperature, conductivity, and pH value were measured *in situ*. For determination of temperature and conductivity a Hanna Conductivity Tester HI98311 was used; for the determination of the pH value universal indicator paper was employed.

List of localities with Odonata records

Indicated are (in that order) the administrative unit on the level of regions, description of the localities with Georgian toponyms, coordinates, altitude in meters above sea level, date(s), and – if available – conductivity [µS/cm], temperature [°C] and pH value of the aquatic habitat.

Loc. 1. Tbilisi (თბილისი), scrubland at the northern slope of Sololaki ridge below Nariqala fortress (ნარიყალა), 41.6883°N, 44.7934°E, 500 m a.s.l., 20-vi-2014; 05-vi-2015, 10-vi-2015, 11-vi-2015

Loc. 2. Tbilisi (თბილისი), gorge of Tsavkisistsqali river (წავკისისწყალი), also called Leghvtakhevi ლეღვთახევი), 41.6828°N, 44.7899°E, 580 m a.s.l., 21-vi-2014, 22-vi-2014, 3-vii-2014, 4-vii-2014, 10-vii-2014, 05-vi-2015, 10-vi-2015, 11-vi-2015; corresponds to loc. 1 in Schröter (2010a)

Loc. 3. Tbilisi (თბილისი), gravelroad to the waterfall along the northern slope of Tsavkisistsqali gorge (წავკისისწყალი), 41.6843°N, 44.7910°E, 600 m a.s.l., 21-vi-2014, 22-vi-2014, 3-vii-2014, 4-vii-2014, 10-vii-2014, 05-vi-2015, 10-vi-2015, 11-vi-2015; corresponds to loc. 1 in Schröter (2010a)

Loc. 4. Tbilisi (თბილისი), Kus lake (კუს ტბა), 41.7004°N, 44.7543°E, 696 m a.s.l., 21-vi--2014

Loc. 5. Tbilisi (თბილისი), Mtatsminda ridge (მთაწმინდა) south of Kus lake (კუს ტბა), 41.6977°N, 44.7524°E, 800 m a.s.l., 21-vi-2014; corresponds to loc. 3 in Schröter (2010)

Loc. 6. Tbilisi (თბილისი), Vere river (ვერე) at the northwestern outskirts of Tbilisi, 41.7171°N, 44.6947°E, 560 m a.s.l., 21-vi-2014

Loc. 7. Tbilisi (თბილისი), southwestern shore of Lisi lake (ლისის ტბა), 41.7431°N, 44.7280°E, 628 m a.s.l., 21-vi-2014, 08-vi-2015; 2 000–2 400 µS/cm

Loc. 8. Kvemo Kartli (ქვემო ქართლი), Vere river (ვერე) west of Betania Monastery (ბეთანიის მონასტერი), 41.6901°N, 44.6022°E, 760 m a.s.l., 22-vi-2014; 810 µS/cm, 19.7°C, pH 7.7

Loc. 9. Kvemo Kartli (ქვემო ქართლი), scrubland and meadows south of Vere river (ვერე), 41.6854°N, 44.6074°E, 980 m a.s.l., 22-vi-2014

Loc. 10. Kvemo Kartli (ქვემო ქართლი), rivulet in the floodplain of Iori river (იორი) 3 km S Ujarma (უჯარმა), 41.7613°N, 45.1607°E, 750 m a.s.l., 23-vi-2014; 1 400 µS/cm, 20.0°C, pH 8.0

Loc. 11. Kakheti (კახეთი), Mukhrovani salty lake (მუხროვანის მლაშე ტბა) ca 2 km south of Ujarma (უჯარმა), 41.7725°N, 45.1486°E, 810 m a.s.l., 23-vi-2014; 4 000 µS/cm, 25.6°C, pH 8.3

Loc. 12. Kakheti (კახეთი), western tributary of Iori river (იორი) ca 1 km north of Ujarma fortress (უჯარმის ციხე), 41.8203°N, 45.1374°E, 865 m a.s.l., 23-vi-2014; 400 µS/cm, 17.0°C, pH 7.6

Loc. 13. Kakheti (კახეთი), ponds in the floodplain of Iori river (იორი) close to the dam bridge road (S 38), 41.8457°N, 45.1375°E, 865 m a.s.l., 23-vi-2014

Loc. 14. Kakheti (კახეთი), small pond and meadows in the floodplain of Iori river (იორი) close to the dam bridge road (S 38), 41.8466°N, 45.1335°E, 875 m a.s.l., 23-vi-2014

Loc. 15. Kakheti (კახეთი), waterfilled tracks on muddy path at the western bank of Iori river (იორი), 41.8441°N, 45.1341°E, 870 m a.s.l., 23-vi-2014

Loc. 16. Kakheti (კახეთი), Gombori river (გომბორი) and ponds in the floodplain east of Sasadilo (სასადილო), 41.8641°N, 45.1473°E, 920 m a.s.l., 23-vi-2014; 1 170 µS/cm, 25.0°C, pH 7.8 (Gombori river)

Loc. 17. Kakheti (კახეთი), scrubland around Ujarma fortress (უჯარმის ციხე), 41. 8113°N, 45.1540°E, 890 m a.s.l., 23-vi-2014

Loc. 18. Kvemo Kartli (ქვემო ქართლი), Khrami river (ხრამი) at the bridge on road S 6 near Nakhiduri (ნახიდური), 41.4714°N, 44.7031°E, 405 m a.s.l., 24-vi-2014; 300 µS/cm, 20.0°C, pH 7.4

Loc. 19. Kvemo Kartli (ქვემო ქართლი), Mashavera river (მაშავერა) east of Rachisubani (რაჭისუბანი) around pedestrial suspension bridge, 41.4429°N, 44.5998°E, 450 m a.s.l., 24--vi-2014; 550 µS/cm, 21.0°C, pH 7.4

Loc. 20. Kvemo Kartli (ქვემო ქართლი), spring and stream along northern bank of Mashavera river (მაშავერა) east of Rachisubani (რაჭისუბანი), 41.4433°N, 44.6013°E, 455 m a.s.l., 24-vi-2014; 1 600 µS/cm, 20.0°C, pH 7.8

Loc. 21. Kvemo Kartli (ქვემო ქართლი), Bolnisistsqali river (ბოლნისისწყალი) at the bridge at Tsughrughasheni Monastery (წუღრუღაშენი ეკლესია), 41.3813°N, 44.5251°E, 575 m a.s.l., 24-vi-2014; 510 µS/cm, 23.0°C, pH 7.8

Loc. 22. Kvemo Kartli (ქვემო ქართლი), Bolnisistsqali river (ბოლნისისწყალი) near Poladauri (ფოლადაური; *Azer*. Çatax), 41.3353°N, 44.5043°E, 670 m a.s.l., 24-vi-2014, 9-vii--2014; 420 µS/cm, 20.0°C, pH 7.6

Loc. 23. Kakheti (კახეთი), stream heavily polluted by household waste water alongside road S 70 N Telavi (თელავი), 41.9765°N, 45.5670°E, 360 m a.s.l., 25-vi-2014; 1 000 µS/cm, 24.6°C, pH 7.3

Loc. 24. Kakheti (კახეთი), pond in the floodplain of Alazani river (ალაზანი) northeast of Telavi (თელავი), 41.9929°N, 45.5778°E, 350 m a.s.l., 25-vi-2014

Loc. 25. Kakheti (კახეთი), rivulet and ditch alongside road S 70 ca 6 km west of Eniseli (ენისელი), 42.0012°N, 45.5991°E, 345 m a.s.l., 25-vi-2014; 600 µS/cm, 25.0°C, pH 7.4

Loc. 26. Kakheti (კახეთი), springs alongside Bursa river (ბურსა) at the bridge of road S 43 south of Kvareli (ყვარელი), 41.9298°N, 45.8254°E, 360 m a.s.l., 25-vi-2014; 150 µS/cm, 25.0°C, pH 7.0

Loc. 27. Kakheti (კახეთი), surroundings of the rivers Lagodekhiskhevi (ლაგოდეხისხევი) and Shromiskhevi (შრომისხევი) within Lagodekhi national park (ლაგოდეხის ნაკრძალი), 41.8600°N, 46.2900°E, 730 m a.s.l., 26-vi-2014

Loc. 28. Kakheti (კახეთი), shrubland in the floodplain of Alazani river (ალაზანი) west of bridge on road S 5, 41.6751°N, 46.0795°E, 205 m a.s.l., 27-vi-2014

Loc. 29. Kakheti (კახეთი), fishponds south Alazani river (ალაზანი) west of bridge on road S 5, 41.6705°N, 46.0767°E, 210 m a.s.l., 27-vi-2014; 2 050 µS/cm, 28.0°C, pH 8.2

Loc. 30. Kakheti (კახეთი), rivulet between Kardenakhi (კარდენახი) and Sabatsminda Church (კარდენახის საბაწმინდა), 41.6703°N, 45.8792°E, 450 m a.s.l., 27-vi-2014; 1 800 µS/cm, 30.0°C, pH 7.9

Loc. 31. Kakheti (კახეთი), slope with shrubland and orchards at Kardenakhi (კარდენახი), 41.6688°N, 45.8841°E, 470 m a.s.l., 27-vi-2014

Loc. 32. Kakheti (კახეთი), rivulet beside road 39 ca 6 km north of Gamarjveba (გამარჯვება), 41.5206°N, 45.9889°E, 585 m a.s.l., 27-vi-2014; 2 460 µS/cm, 29.0°C, pH 8.0

Loc. 33. Kakheti (კახეთი), dam and southeastern shore of Dali reservoir (დალის ტბა/ დალის წყალსაცავი), 41.2829°N, 45.8970°E, 290 m a.s.l., 27-vi-2014; 1 070 µS/cm, 28.0°C, pH 7.8 (Dali reservoir)

Loc. 34. Kakheti (კახეთი), Iori river (იორი) and floodplain south of Dali reservoir (დალის თბა/ დალის წყალსაცავი), 41.2758°N, 45.8931°E, 270 m a.s.l., 27-vi-2014

Loc. 35. Kakheti (კახეთი), western shore of Kochebi lake (კოჭების ტბა) east of Dedoplistsqaro (დედოფლისწყარო), 41.4430°N, 46.1410°E, 782 m a.s.l., 27-vi-2014; >20 000 µS/cm, 25.0°C, pH 8.2

Loc. 36. Kakheti (კახეთი), clay pit beside the road to Davit Gareja monastery (დავითგარეჯის სამონასტრო კომპლექსი) ca 2 km southeast of Sagarejo (საგარეჯო), 41.7061°N, 45.3733°E, 580 m a.s.l., 28-vi-2014; 440 µS/cm, 23.0°C, pH 7.3

Loc. 37. Kakheti (კახეთი), rivulet southeast of the clay pit beside the road to Davit Gareja monastery (დავითგარეჯის სამონასტრო კომპლექსი) ca 2 km southeast of Sagarejo (საგარეჯო), 41.7017°N, 45.3792°E, 570 m a.s.l., 28-vi-2014

Loc. 38. Kakheti (კახეთი), spring ponds in the floodplain of Iori river (იორი) ca 3 km southeast of Sagarejo (საგარეჯო), 41.6762°N, 45.3874°E, 535 m a.s.l., 28-vi-2014; 340 µS/cm, 27.0°C, pH 7.2

Loc. 39. Kakheti (კახეთი), reedy spring brook, inflow of Jikurebi lake (ჯიქურების ტბა), 41.5974°N, 45.3253°E, 778 m a.s.l., 28-vi-2014

Loc. 40. Kakheti (კახეთი), southwestern shore of Sakhare lake (სახარე ტბა), a salty lake of high salinity, 41.5760°N, 45.3188°E, 825 m a.s.l., 28-vi-2014; >20 000 µS/cm

Loc. 41. Kakheti (კახეთი), partly dried out muddy ponds for lifestock watering alongside road to Davit Gareja monastery (დავითგარეჯის სამონასტრო კომპლექსი), 41.4811°N, 45.3243°E, 707 m a.s.l., 28-vi-2014; 1 660 µS/cm, 32.0°C, pH 8.3

Loc. 42. Kakheti (კახეთი), scrubland at Davit Gareja monastery (დავითგარეჯის სამონასტრო კომპლექსი), 41.4486°N, 45.3753°E, 710 m a.s.l., 28-vi-2014

Loc. 43. Kakheti (კახეთი), small brook alongside gravel road in the floodplain of Iori river (იორი) 4 km southeast of Sartichala (სართიჩალა), 41.6949°N, 45.2132°E, 660 m a.s.l., 28--vi-2014; 1 700 µS/cm, 23.0°C, pH 7.9

Loc. 44. Mtskheta-Mtianeti (მცხეთა-მთიანეთი), Jvari lake (ჯვარის თბა) east of Jvari monasteri (ჯვარი, ჯვრის მონასტერი), 41.8386°N, 44.7395°E, 575 m a.s.l., 29-vi-2014

Loc. 45. Mtskheta-Mtianeti (მცხეთა-მთიანეთი), spring mire alongside the Georgian Military Road (საქართველოს სამხედრო გზა) ca 2.5 km north of Pasanauri (ფასანაური), 42.3730°N, 44.6791°E, 1 120 m a.s.l., 29-vi-2014, 07-vi-2015; corresponds to loc. 8. in Beutler (1987)

Loc. 46. Mtskheta-Mtianeti (მცხეთა-მთიანეთი), shrubland alongside the Georgian Military Road (საქართველოს სამხედრო გზა) ca 6 km south of Ananuri castle (ანანური), 42.1421°N, 44.7691°E, 850 m a.s.l., 29-vi-2014

Loc. 47. Mtskheta-Mtianeti (მცხეთა-მთიანეთი), eastern bank of Aragvi river (არაგვი), 42.0072°N, 44.7590°E, 595 m a.s.l., 29-vi-2014

Loc. 48. Shida Kartli (შიდა ქართლი), Prone river (ფრონე) at the bridge on road (E 60), 42.0585°N, 43.8846°E, 650 m a.s.l., 30-vi-2014

Loc. 49. Shida Kartli (შიდა ქართლი), Kura river (მტკვარი) alongside road S 8 between suspension bridge and discharging brook, 41.9607°N, 43.5110°E, 725 m a.s.l., 30-vi-2014, 07-vii-2014

Loc. 50. Samtskhe-Javakheti (სამცხე-ჯავახეთი), brook running through wet and fen-like meadows at the eastern edge of Bakuriani (ბაკურიანი), 41.7542°N, 43.5391°E, 1 675 m a.s.l., 01-vii-2014

Loc. 51. Samtskhe-Javakheti (სამცხე-ჯავახეთი), oxbow lakes of Kura river (მტკვარი) north of Aspindza (ასპინძა), 41.5836°N, 43.2433°E, 1 055 m a.s.l., 02-vii-2014

Loc. 52. Samtskhe-Javakheti (სამცხე-ჯავახეთი), southwestern shore of Madatapa lake (მადათაფას ტბა), 41.1821°N, 43.7582°E, 2 115 m a.s.l., 02-vii-2014, 01-viii-2015

Loc. 53. Samtskhe-Javakheti (სამცხე-ჯავახეთი), discharge of Madatapa lake (მადათაფას ტბა) at Epremovka (ეფრემოვკა), 41.1889°N, 43.7474°E, 2 105 m a.s.l., 02-vii-2014, 01-vii--2015

Loc. 54. Samtskhe-Javakheti (სამცხე-ჯავახეთი), southern shore of Khanchali lake (ხანჩალის ტბა), 41.2425°N, 43.5599°E, 1 930 m a.s.l., 02-vii-2014

Loc. 55. Samtskhe-Javakheti (სამცხე-ჯავახეთი), Kvabliani river (ქვაბლიანი) at confluence with Potskhovi river (ფოცხოვი), 41.6454°N, 42.8541°E, 1 025 m a.s.l., 03-vii-2014

Loc. 56. Adjara (აჭარის ავტონომიური რესპუბლიკა), small pond near Goderdzi pass (გოდერძის უღელტ), 41.6343°N, 42.5087°E, 2 115 m a.s.l., 03-vii-2014

Loc. 57. Adjara (აჭარის ავტონომიური რესპუბლიკა), swampy meadow alongside gravel road, 41.6464°N, 42.4746°E, 1 565 m a.s.l., 03-vii-2014

Loc. 58. Adjara (აჭარის ავტონომიური რესპუბლიკა), floodplain of Chorokhi river (ჭოროხი) at the estuary mouth in the Black Sea, 41.5916°N, 41.5808°E, 3 m a.s.l., 04-vii--2014

Loc. 59. Adjara (აჭარის ავტონომიური რესპუბლიკა), Charnali river (ჭარნალი) south of confluence with Chorokhi river (ჭოროხი), 41.5762°N, 41.6267°E, 20 m a.s.l., 04-vii-2014

Loc. 60. Adjara (აჭარის ავტონომიური რესპუბლიკა), small stream within orchards east Ombolo (ომბოლო), 41.5736°N, 41.6374°E, 25 m a.s.l., 04-vii-2014

Loc. 61. Adjara (აჭარის ავტონომიური რესპუბლიკა), Boloko river (ბოლოქო) south of Zeda-Tkhilnari (ზედა თხილნარი), 41.5415°N, 41.6422°E, 185 m a.s.l., 04-vii-2014

Loc. 62. Adjara (აჭარის ავტონომიური რესპუბლიკა), Western tributary to Boloko river (ბოლოქო) ca 1 km north of Zeda-Tkhilnari (ზედა თხილნარი), 41.5467°N, 41.6423°E, 135 m a.s.l., 04-vii-2014

Loc. 63. Adjara (აჭარის ავტონომიური რესპუბლიკა), tributari to Boloko river (ბოლოქო) north of the school building, 41.5511°N 41.6418°E, 115 m a.s.l., 04-vii-2014

Loc. 64. Adjara (აჭარის ავტონომიური რესპუბლიკა), northern tributary to Kintrishi river (კინტრიში) near Chakhati (ჭახათი), 41.8052°N, 41.9328°E, 215 m a.s.l., 05-vii-2014

Loc. 65. Guria (გურია), channel north of Natanebi river mouth (ნატანები), 41.9125°N, 41.7730°E, 1 m a.s.l., 05-vii-2014

Loc. 66. Guria (გურია), brackish lagoon south of Shekvetili (შეკვეთილი), 41.9136°N, 41.7696°E, 1 m a.s.l., 05-vii-2014

Loc. 67. Adjara (აჭარის ავტონომიური რესპუბლიკა), northern tributary of Chakvistskali river (ჩაქვისწყალი) at Khala (ხალა), 41.7079°N, 41.7884°E, 55 m a.s.l., 05-vii-2014

Loc. 68. Adjara (აჭარის ავტონომიური რესპუბლიკა), Chakvistskali river (ჩაქვისწყალი) at Khala (ხალა), 41.7079°N, 41.7884°E, 55 m a.s.l., 05-vii-2014

Loc. 69. Guria (გურია), Grigoleti lake (გრიგოლეთის თბა) north of the mouth of Supsa river (სუფსა), 42.0284°N, 41.7460°E, 1 m a.s.l., 06-vii-2014

Loc. 70. Guria (გურია), southwestern shore of Paliastomi lake (პალიასტომის ტბა), 42.0810°N, 41.7160°E, 1 m a.s.l., 06-vii-2014

Loc. 71. Guria (გურია), southern shore of Narionali lake (დიდი ნარიონალის ტბა), an oxbow of Rioni river (რიონი), 42.0959°N, 42.2114°E, 15 m a.s.l., 06-vii-2014

Loc. 72. Guria (გურია), Khevistsqali river (ხევისწყალი) north and south of the bridge along road E 692 (S12), 42.0979°N, 42.2545°E, 20 m a.s.l., 06-vii-2014

Loc. 73. Imereti (იმერეთი), southern bank of Rioni river (რიონი) at gravel pit alongside road E 692 (S 12) west of Sajavakho (საჯავახო), 42.1035°N, 42.2806°E, 10 m a.s.l., 06-vii--2014, 07-vii-2014

Loc. 74. Imereti (იმერეთი), banks of Rioni river (რიონი) east and west of bridge on E 692 (S 12) south of Samtredia (სამტრედია), 42.1199°N, 42.3323°E, 10 m a.s.l., 06-vii-2014, 31--vii-2015, 02-vii-2015

Loc. 75. Adjara (აჭარის ავტონომიური რესპუბლიკა), stream and springs ca 1 km east Tsqavroka (წყავროკა), 41.8510°N, 41.8929°E, 65 m a.s.l., 07-vii-2014

Loc. 76. Guria (გურია), Supsa river (სუფსა) at a small bridge ca 13 km north of Ozurgeti (ოზურგეთი), 41.9986°N, 42.0946°E, 55 m a.s.l., 07-vii-2014

Loc. 77. Samtskhe-Javakheti (სამცხე-ჯავახეთი), southwestern tributary of Borjomula river (ბორჯომულა) ca 3 km south of Borjomi (ბორჯომი), 41.8203°N, 43.3975°E, 930 m a.s.l., 08-vii-2014

Loc. 78. Samtskhe-Javakheti (სამცხე-ჯავახეთი), open areas and meadows alongside road 1 km northwest of Sadgeri (სადგერი), 41.8218°N, 43.4031°E, 1 015 m a.s.l., 08-vii-2014

Loc. 79. Samtskhe-Javakheti (სამცხე-ჯავახეთი), Chitakhevi river (ჩითახევი) south of Mtsvane Monastery (მწვანე მონასტერი), 41.8030°N, 43.3183°E, 850 m a.s.l., 08-vii-2014

Loc. 80. Samtskhe-Javakheti (სამცხე-ჯავახეთი), Kvabishkhevi river (ქვაბისხევი) in the village of the same name at the bridge on road S 8, 41.7744°N, 43.2498°E, 880 m a.s.l., 08--vii-2014

Loc. 81. Samtskhe-Javakheti (სამცხე-ჯავახეთი), stretch of Zoreti river (ზორეთი) ca 0.8–2 km north of the Kura river (მტკვარი), 41.7699°N, 43.2358°E, 930 m a.s.l., 08-vii-2014

Loc. 82. Kvemo Kartli (ქვემო ქართლი), Khrami river (ხრამი) west of bridge on road E 001(S 7) ca 10 km south of Marneuli (მარნეული), 41.4056°N, 44.8293°E, 340 m a.s.l., 09-vii-2014

Loc. 83. Tbilisi (თბილისი), northeastern shore of Gldani lake (გლდანის ტბა), 41.8130°N, 44.8408°E, 555 m a.s.l., 04-vii-2014

Loc. 84. Tbilisi (თბილისი), ditch at northeastern shore of Gldani lake (გლდანის ტბა), 41.8136°N, 44.8415°E, 555 m a.s.l., 04-vii-2014

Loc. 85. Kakheti (კახეთი), small side channel of river Lagodekhiskhevi (ლაგოდეხისხევი) within Lagodekhi national park (ლაგოდეხის ნაკრძალი), 41.8483°N, 46.2950°E, 635 m a.s.l., 26-vi-2014

Loc. 86. Tbilisi (თბილისი), fish ponds northwest of Kalajalari (ყარაჯალარი) 41.6373°N, 44.9445°E, 362 m a.s.l., 09-vi-2015; 1 350 µS/cm

Loc. 87. Kvemo Kartli (ქვემო ქართლი), northwestern shore of Jandari reservoir (ჯანდარის ტბა; *Azer.* Candargöl) 41.4453°N, 45.2019°E, 292 m a.s.l., 06-vi-2015; 590 µS/cm

Loc. 88. Kvemo Kartli (ქვემო ქართლი), channel alongside road north of Jandari (ჯანდარი) 41.4810°N, 45.1446°E, 318 m a.s.l., 06-vi-2015

Loc. 89. Tbilisi (თბილისი), small water supply to Lisi lake (ლისის ტბა), 41.7462°N, 44.7248°E, 628 m a.s.l., 08-vi-2015

Loc. 90. Tbilisi (თბილისი), Lochini river (ლოჭინი) at the fish ponds northwest of Kalajalari (ყარაჯალარი), 41.6365°N, 44.9483°E, 368 m a.s.l., 09-vi-2015; 1 350 µS/cm

Loc. 91. Kvemo Kartli (ქვემო ქართლი), Mashavera river (მაშავერა) near Kveshi fortress (ქვეშის ციხე), 41.442917°N, 44.458167°E, 555 m a.s.l., 27-vii-2015

Loc. 92. Kvemo Kartli (ქვემო ქართლი), marshy meadow north of Iakublo reservoir (ფარავანი), 41.382444°N, 44.106194°E, 1 450 m a.s.l., 27-vii-2015

Loc. 93. Samtskhe-Javakheti (სამცხე-ჯავახეთი), meadow near Paravani (ფარავანი), 41.455428°N, 43.847047°E, 2 092 m a.s.l., 27-vii-2015

Loc. 94. Samtskhe-Javakheti (სამცხე-ჯავახეთი), marshy meadows with little ponds southeast of Khanchali lake (ხანჩალის ტბა), 41.241292°N, 43.516914°E, 2 081 m a.s.l.), 03-viii--2015.

Loc. 95. Samtskhe-Javakheti (სამცხე-ჯავახეთი), Paravani river (ფარავანი) east of Khertvisi fortress (ხერთვისის ციხე), 41.490833°N, 43.334833°E, 1 215 m a.s.l, 27-vii-2015

Loc. 96. Imereti (იმერეთი), forest stream west of Khashuri (ხაშური), 42.023861°N, 43.458917°E, 930 m a.s.l., 28-vii-2015

Loc. 97. Adjara (აჭარის ავტონომიური რესპუბლიკა), small lake west of "Green Lake" (მწვანე ტბა), 41.67595°N, 42.496444°E, 2 065 m a.s.l., 29-vii-2015

Loc. 98. Adjara (აჭარის ავტონომიური რესპუბლიკა), stream east of Goderdzi pass, 41.631894°N, 42.568039°E, 1 820 m a.s.l., 29-vii-2015, 30-vii-2015

Loc. 99. Adjara (აჭარის ავტონომიური რესპუბლიკა), stream west of Goderdzi pass, 41.637053°N, 42.379003°E, 906 m a.s.l., 04-viii-2015

Results

Altogether, 63 odonate taxa were recorded at 99 sampling sites (Fig. 1) corresponding to at least 85 % of the Georgian Odonata fauna. *Selysiothemis nigra* is a new species for the country and intermediates between *Enallagma cyathigerum cyathigerum* and *E. c. risi* were reported from Georgia for the first time. Except for *Lindenia tetraphylla* and *Anax ephippiger*, all taxa were authenticated by photographs, voucher specimens and/or exuviae/larve.

List of recorded species and taxa

Roman numerals indicate abundance classes of adults: I = single, II = 2-5, III = 6-10, IV = 11-20, V = 21-50, VI = 51-100, VII = 101-500, VIII = 501-1 000, IX= 1 001-10 000, X= >10 000. Capital letters indicate the following abbreviations: A = individual; C = copula, tandem; L = larvae; indicated only if not collected; O = ovipositing; T = teneral, emergence; U = exuviae, indicated only if not collected.

Zygoptera

Lestidae

1. *Chalcolestes parvidens* (Artobolevskii, 1929)

2014: loc. 65 – AT VI. 2015: loc. 74 – AOT II.
Specimens: 2014: loc. 65 – adults 8♂ 4♀.

2. *Lestes barbarus* (Fabricius, 1798)

2014: loc. 16 – AT II; loc. 41 – A I; loc. 49 – A III; loc. 51 – A II; loc. 54 – AT II.
Specimens: 2014: loc. 16 – exuviae 1♂ 1♀; loc. 51 – adults 1♂.

3. *Lestes dryas* Kirby, 1890

2014: loc. 13 – A II; loc. 49 – A VI; loc. 50 – ATU VI; loc. 51 – A II; loc. 52 – A III; loc. 53 – A I; loc. 54 – AT X. 2015: loc. 52 – A VIII; loc. 92 – A IV; loc. 93 – A VII; loc. 94 – A VI; loc. 97 – A VI.
Specimens: 2014: loc. 13 – adult 1♂; loc. 50 – adult 1♂, exuviae 21♂ 15♀; loc. 51 – adults 2♂ 1♀.

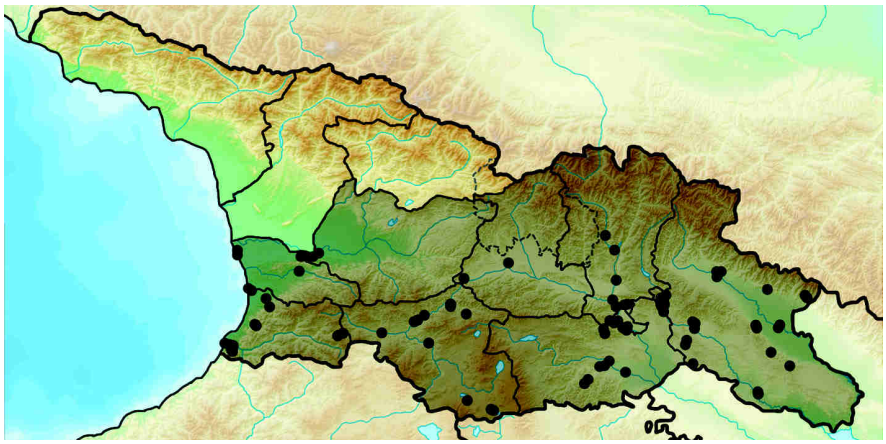


Figure 1. Map of Georgia with the situation of the sampled localities and visited regions (grey shaded areas).

4. *Lestes macrostigma* (Eversmann, 1836)

2015: loc. 7 – A I; loc. 87 – AC III.
Specimens: 2015: loc. 87 – adults 1♂ 1♀.

5. *Lestes sponsa* (Hansemann, 1823)

2014: loc. 52 – AT I; loc. 54 – AT II. 2015: loc. 52 – A VIII; loc. 97 – A VI.
Specimens: 2014: loc. 52 – adult 1♀; loc. 54 – adult 1♂.

6. *Lestes virens vestalis* Rambur, 1842

2014: loc. 51 – A I.
Specimens: 2014: loc. 51 – adult 1♂.

Subspecific assignation acccording to the following diagnosis (RJ) (Fig. 2):

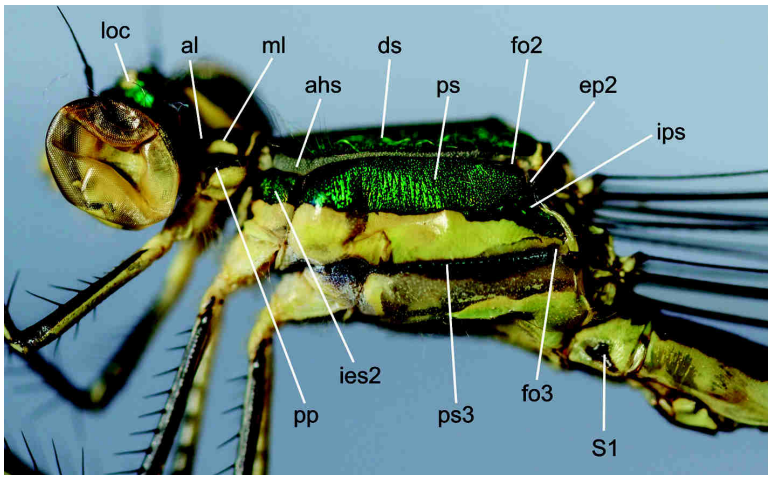


Figure 2. Morphology and diagnostic characters of an immature male of *Lestes virens vestalis*, leg. 02-vii-2014 at loc. 51., Georgia. Head – *loc*: light basis of lateral ocellus. Prothorax – *al*: anterior lobe of pronotum entirely green, except frontal margin; *ml*: middle lobe of pronotum entirely green, except lateral margins; *pp*: propleuron with stripe alongside notopleural suture and downwards on border between proepisternum and proepimeron. Synthorax – *ds*: green dorsal stripe with predominantly blackish middorsal carina; *ahs*: almost open ante-humeral stripe; *fo2*: pigmented humeral fossa, constricting ante-humeral stripe; *ies2*: green spot entirely covering upper half of mesinfraepisternum; *ps*: green pleural stripe not reaching metapleural suture; *ips*: interpleural suture; *ep2*: yellow streak at caudal end of pleural stripe not reaching interpleural suture; *ps3*: blackish stripe alongside metapleural suture; *fo3*: pigmented metapleural fossa, lessening gap between pleural stripe and metapleural suture. Abdomen – *S1*: irregular blackish spot on first segment (photograph by RJ)

An immature male with light yellowish coloration and bright shining green markings, some melanisation but no trace of pruinosity. **Head** — Dorsal parts of head capsule and anteclypeus metallic green, except light bases of antennae and lateral ocelli (*loc*) and two bilateral tiny streaks at occipital rear. **Prothorax** — Pronotum completely green, except outer margins of anterior (*al*) and posterior lobe and lateral margins of middle lobe (*ml*) yellow. Propleuron (*pp*) with an extensive, blackish-green stripe alongside notopleural suture. **Synthorax** — Middorsal carina blackish, except yellow frontal part of ca 1/10 of its total length. Ante-humeral stripe (*ahs*) greyish, wide open only in its frontal section, otherwise narrow; partly interrupted by melanisation of lower half of humeral fossa (*fo2*). Pleural stripe (*ps*) not reaching metapleural suture. Upper half of mesinfraepisternum (*ies2*) entirely green. Metapleural suture (*ps3*) broadly melanised from metinfraepisternum to metapleural fossa (*fo3*), thus forming a blackish band mainly extending to metepimeron. **Abdomen** — S1 with a sublateral, irregular, blackish-green spot; S9+10 with extensive blackish pigmentation of ventral halfs of segments. **Measurements** [mm] — Abdomen length 25.5; Hw length 18.0.

7. *Sympecma fusca* (Vander Linden, 1820)

2014: loc. 8 – A II; loc. 27 – A I; loc. 51 – AT III; loc. 79 – A I.
Specimens: 2014: loc. 51 – adults 2♂.

Calopterygidae

8. *Calopteryx splendens intermedia* Selys, 1890

2014: loc. 2 – AO VII; loc.8 – A I; loc. 10 – A VI; loc. 12 – A III; loc. 18 – ATU V; loc. 19 – A IV; loc. 20 – A V; loc. 21 – A III; loc. 22 – ACL V; loc. 23 – A III; loc. 25 – ACO V; loc. 28 – A III; loc. 34 – ACO VII; loc. 36 – A I; loc. 37 – A III; loc. 37 – A I; Loc. 43 – ACO IX; loc. 47 – A III; loc. 48 – A II; loc. 49 – A I; loc. 74 – A III; loc. 82 – A II. 2015: loc. 2 – AT III; loc. 88 – AT II; loc. 90 – A V, loc. 91 – A IV.
Specimens: 2014: loc. 2 – adults 13♂ 8♀, exuviae 4♂ 4♀; loc. 12 – adults 5♂ 3♀; loc. 18 – exuviae 2♀; loc. 21 – exuvia 1♂; loc. 22 – exuviae 7♂ 6♀, larva 1♂; loc. 25 – adults 7 ♂ 6♀, exuvia 1♀; loc. 36 – adult 1♂; loc. 43 – exuviae 2♂ 9♀; loc. 47 – exuvia 1♀. 2015: loc. 88 – adult 1♂; loc. 90 – adults 2♂.

9. *Calopteryx splendens tschaldirica* Bartenev, 1909

2014: loc. 49 – A V; loc. 51 – A III; loc. 55 – AT IV; loc. 80 – A II. 2015: loc. 95 – A IV.
Specimens: 2014: loc. 49 – adults 12♂ 4♀, exuviae 2♀.

10. *Calopteryx splendens mingrelica* Selys, 1869
2014: loc. 65 – A IV; loc. 73 – A II.
Specimens: 2014: loc. 73 – adult 1♂.

11. *Calopteryx virgo festiva* (Brullé, 1832)
2014: loc. 25 – AO V; loc. 60 – AO V; loc. 67 – A I; loc. 68 – A I; loc. 76 – A I. 2015: loc. 96 – A II.
Specimens: 2014: loc. 25 – adults 5♂ 3♀; loc. 60 – adults 3♂ 3♀; loc. 67 – exuviae 1♂ 4♀.

Euphaeidae

12. *Epallage fatime* (Charpentier, 1840)
2014: loc. 2 – ACOT VI; loc. 6 – A II; loc. 8 – AC IV; loc. 18 – AT V; loc. 20 – A III; loc. 22 – ACO IV; loc. 82 – A II. 2015: loc. 2 – A V; loc. 3 – A I; loc. 91 – A III.
Specimens: 2014: loc. 2 – adults 4♂ 1♀, exuviae 3♂ 2♀; loc. 18 – 1♀; loc. 22 – adults 1♂, exuviae 1♀. 2015: loc. 2 – adult 1♂ 1♀, exuviae 24.

Coenagrionidae

13. *Coenagrion armatum* (Charpentier, 1840)
2014: loc. 52 – ACOTU VII; loc. 53 – A V.
Specimens: 2014: loc. 52 – adults 2♂ 1♀.

14. *Coenagrion lunulatum* (Charpentier, 1840)
2014: loc. 52 – ACOT X; loc. 53 – ACOT VI; loc. 54 – A IV. 2015: loc. 52 – A IV.
Specimens: 2014: loc. 52 – adults 9♂ 4♀, exuviae 3♂ 5♀.

15. *Coenagrion ponticum* (Bartenev, 1929)
2014: loc. 25 – A II; loc. 32 – A II; loc. 53 – A II; loc. 54 – A I; loc. 60 – A II; loc. 65 – A V.
Specimens: 2014: loc. 25 – adults 2♂; loc. 32 – adult 1♂; loc. 53 – adults 2♂; loc. 54 – adult 1♀; loc. 60 – adults 1♂ 1♀; loc. 65 – adults 2♂ 1♀.

16. *Coenagrion puella* (Linnaeus, 1758)
2014: loc. 2 – ACO V; loc. 11 – A II; loc. 13 – ACO VI; loc. 15 – ACO IV; loc. 16 – A III; loc. 19 – A III; loc. 20 – ACO IV; loc. 21 – A II; loc. 22 – ACO V; loc. 26 – A I; loc. 32 – A II; loc. 43 – A III; loc. 45 – ACO V; loc. 48 – AO III; loc. 49 – A I; loc. 50 – A II; loc. 51 – A II; loc. 55 – A I; loc. 60 – A IV; loc. 78 – A II. 2015: loc. 2 – A II; loc. 45 – A III; loc. 89 – A.
Specimens: 2014: loc. 2 – adults 6♂ 1♀; loc. 11 – adults 2♂; loc. 15 – adults 4♂ 1♀; loc. 45 – exuviae 4♂ 1♀; loc. 47 – exuvia 1♀; loc. 48 – adult 1♂; loc. 60 – adults 2♂; loc. 78 – adult 1♂. 2015: loc. 2 – adult 1♂; loc. 45 – adults 2♂ 1♀.

17. *Coenagrion pulchellum* (Vander Linden, 1825)
2014: loc. 53 – A II. 2015: loc. 97 – A V.
Specimens: 2014: loc. 53 – adult 1♀. 2015: loc. 97 – adults 4♂ 1♀.

18. *Coenagrion scitulum* (Rambur, 1842)
2014: loc. 10 – A I; loc. 13 – A II; loc. 36 – ACO V. 2015: loc. 7 – A I.
Specimens: 2014: loc. 10 – adult 1♂; loc. 13 – adults 1♂ 1♀.

19. *Coenagrion vanbrinkae* Lohmann, 1993
2014: loc. 25 – A II; loc. 32 – ACO IV; loc. 45 – ACOT VII. 2015: loc. 45 – A VI.
Specimens: 2014: loc. 25 – adult 1♂; loc. 32 – adults 4♂ 2♀; loc. 45 – adults 14♂ 2♀, exuviae 2♂ 6♀. 2015: loc. 45 – adults 8♂ 2♀, exuvia 1♀.

20. *Enallagma cyathigerum* (Charpentier, 1840)
2014: loc. 11 – A III; loc. 35 – A II; loc. 36 – ACO IV; loc. 41 – A I; loc. 44 – A III; loc. 52 – A V; loc. 53 – A I; loc. 54 – AT III; loc. 58 – A I; loc. 69 – A I; loc. 83 – A II. 2015: loc. 52 – A VIII.
Specimens: 2014: loc. 11 – adults 5♂ 1♀; loc. 35 – adults 2♂; loc. 41 – adult 1♂; loc. 52 – adults 2♂; loc. 53 – adult 1♀.

21. *Erythromma viridulum* (Charpentier, 1840)
2014: loc. 7 – A II; loc. 11 – A II; loc. 29 – ACO IV; loc. 34 – ACO VII; loc. 51 – ACOT V; loc. 69 – A V; loc. 71 – ACO IX. 2015: loc. 7 – A I; loc. 86 – A I; loc. 87 – A IV.
Specimens: 2014: loc. 7 – adult 1♂. 2015: loc. 7 – adult 1♂.

22. *Ischnura elegans* (Vander Linden, 1820)
2014: loc. 4 – A III; loc. 7 – A IV; loc. 11 – ACO V; loc. 13 – ACO V; loc. 19 – AI; loc. 20 – ACO V; loc. 24 – A I; loc. 25 – ACO V; loc. 26 – A I; loc. 29 – ACO V; loc. 32 – A III; loc. 32 – A II; loc. 34 – A III; loc. 36 – AC II; loc. 38 – AC VI; loc. 41 – A II; loc. 43 – A I; loc. 47 – A II; loc. 51 – ACOT VI; loc. 58 – A VII; loc. 65 – A III; loc. 66 – A V; loc. 69 – A II; loc. 70 – A II; loc. 71 – A V; loc. 72 – A II; loc. 82 – A II; loc. 83 – A III. 2015: loc. 7 – A V; loc. 86 – AT V; loc. 87 – A III; loc. 88 – A II; loc. 90 – A III.
Specimens: 2014: loc. 4 – adult 1♂; loc. 19 – adult 1♂; loc. 47 – exuviae 1♂ 1♀; loc. 51 – adults 2♂; loc. 69 – adults 2♂; loc. 71 – adult 1♂. 2015: loc. 87 – adults 1♂ 1♀.

23. *Ischnura pumilio* (Charpentier, 1825)
2014: loc. 15 – A II; loc. 16 – A II; loc. 20 – A III; loc. 25 – AO II; loc. 26 – ACO V; loc. 29 – A IV; loc. 32 – ACO IV; loc. 36 – ACO VI; loc. 38 – AT V; loc. 41 – ACO II; loc. 45 – ACOT V; loc. 47 – A II; loc. 51 – A III; loc. 58 – A II; loc. 72 – AC III; loc. 75 – A II; loc. 83 – A II; loc. 84 – A III. 2015: loc. 7 – A II; loc. 45 – A II.
Specimens: 2014: loc. 15 – adult 1♂; loc. 16 – adult 1♂; loc. 26 – adults 2♂ 1♀; loc. 83 – adults 2♂. 2015: loc. 7 – adults 2♂ 1♀; loc. 45 – adults 1♂ 1♀.

24. *Pyrrhosoma nymphula* (Sulzer, 1776)
2014: loc. 45 – A IV; loc. 50 – A II. 2015: loc. 45 – ACOT VII.
Specimens: 2014: loc. 45 – adult 1♂; loc. 50 – adult 1♂. 2015: loc. 45 – adults 2♂ 2♀, exuviae 5♂ 1♀.

Platycnemididae

25. *Platycnemis dealbata* Selys in Selys & Hagen, 1850

2014: loc. 2 – A III; loc. 10 – A V; loc. 13 – AC IV; loc. 15 – A I; loc. 18 – AC VI; loc. 19 – A III; loc. 20 – ACO VI; loc. 21 – A IV; loc. 22 – A II; loc. 23 – A IV; loc. 25 – ACO VIII; loc. 28 – A V; loc. 29 – ACO VII; loc. 32 – ACO V; loc. 33 – A IV; loc. 34 – ACO IV; loc. 35 – A I; loc. 37 – A II; loc. 38 – A IV; loc. 43 – ACO VIII; loc. 48 – AC II; loc. 49 – A IV; loc. 51 – A I; loc. 82 – ACO V; loc. 84 – A II. 2015: loc. 86 – A V; loc. 88 – A II; loc. 90 – A II; loc. 91 – A III.
Specimens: 2014: loc. 2 – adult 1♂; loc. 13 – adult 1♂; loc. 18 – adults 1♂ 1♀; loc. 2 –exuvia 1♀; loc. 22 – adult 1♂; loc. 25 – adults 4♂ 1♀, exuvia 1♀; loc. 43 – adult 1♀, exuviae 8♂ 14♀; loc. 82 – adults 2♂. 2015: loc. 86 – adults 2♂ 2♀; loc. 90 – exuvia 1 ♀.

26. *Platycnemis pennipes* (Pallas, 1771)

2014: loc. 2 – ACOT V; loc. 10 – A II; loc. 18 – AC V; loc. 19 – A II; loc. 20 – ACO V; loc. 21 – A IV; loc. 48 – A IV; loc. 49 – A VI; loc. 51 – A II; loc. 58 – AT VI; loc. 59 – AC II; loc. 72 – A V; loc. 73 – AC II; loc. 74 – A II; loc. 75 – A IV; loc. 84 – A II.
Specimens: 2014: loc. 72 – exuviae 3♂ 5♀.

Anisoptera

Aeshnidae

27. *Aeshna affinis* Vander Linden, 1820

2014: loc. 5 – A III; loc. 9 – AC II; loc. 29 – A I.

28. *Aeshna cyanea* (Müller, 1764)

2014: loc. 45 – AT II. 2015: 2015: loc. 97 – A II.
Specimens: 2014: loc. 45 – adult 1♀, exuviae 1♂ 3♀. 2015: loc. 97 – adults 2♂.

29. *Aeshna isoceles* (Müller, 1767)

2014: loc. 4 – A II; loc. 13 – A II; loc. 15 – A I; loc. 25 – AO IV; loc. 34 – A II; loc. 36 – A I. 2015: loc. 2 – A I; loc. 7 – A I.
Specimens: 2014: loc. 25 – adult 1♂.

30. *Aeshna juncea* (Linnaeus, 1758)

2014: loc. 45 – T IV; loc. 78 – A I. 2015: loc. 97 – A III.
Specimens: 2014: loc. 45 – adults 1♂ 2♀, exuviae 9♂ 11♀. 2015: loc. 97 – adults 2♂.

31. *Aeshna mixta* Latreille, 1805

2014: loc. 8 – A III; loc. 9 – A III; loc. 16 – AT II; loc. 28 – A II; loc. 29 – A II; loc. 31 – A I; loc. 78 – A II.
Specimens: 2014: loc. 8 – adults 2♂.

32. *Aeshna serrata* Hagen, 1856

2015: loc. 52 – AC VII.
Specimens: 2015: loc. 52 – adults 2♂ 2♀.

33. *Anax ephippiger* (Burmeister, 1839)
2014: loc. 31 – A IV.

34. *Anax imperator* Leach, 1815
2014: loc. 2 – AO II; loc. 4 – A III; loc. 5 – A II; loc. 7 – A I; loc. 9 – A I; loc. 13 – AT II; loc. 14 – A II; loc. 16 – A II; loc. 17 – A I; loc. 25 – AO III; loc. 27 – A I; loc. 28 – AO I; loc. 29 – A II; loc. 36 – AO II; loc. 39 – A I; loc. 51 – A II; loc. 58 – A II; loc. 71 – A III. 2015: loc. 3 – A I; loc. 86 – A II.
Specimens: 2014: loc. 25 – exuviae 1♂ 1♀; loc. 51 – exuvia 1♂; loc. 71 – exuviae 3♂ 7♀.

35. *Anax parthenope* Selys, 1839
2014: loc. 4 – A II; loc. 7 – A II; loc. 9 – A II; loc. 13 – AO II; loc. 25 – AC II; loc. 29 – ACO III; loc. 34 – A II; loc. 36 – A I; loc. 40 – A I; loc. 52 – A III; loc. 53 – A I; loc. 54 – A II; loc. 58 – A II; loc. 83 – A II. 2015: loc. 3 – A I; loc. 86 – A II; loc. 87 – A IV.
Specimens: 2015: loc. 87 – adult 1♂.

36. *Caliaeschna microstigma* (Schneider, 1845)
2014: loc. 2 – ACO III; loc. 8 – A I; loc. 22 – A II; loc. 43 – A III; loc. 61 – A II; loc. 63 – A II. 2015: loc. 2 – A IV; loc. 96 – A II.
Specimens: 2014: loc. 2 – adults 3♂, exuviae 53♂ 48♀; loc. 12 – exuviae 3♂ 2♀; loc. 22 –exuviae 2♀; loc. 43 – exuviae 3♂ 1♀; loc. 47 – exuvia 1♂; loc. 61 – exuviae 1♂ 1♀; loc. 63 – exuviae 1♂ 2♀; loc. 67 – exuviae 2♂. 2015: loc. 2 – adults 2♂, exuviae 11♂ 11♀.

Gomphidae

37. *Gomphus schneiderii* Selys, 1850
2014: loc. 8 – A I; loc. 10 – A II; loc. 22 – A III; loc. 23 – A I; loc. 25 – A II; loc. 37 – A I; loc. 43 – A IV; loc. 48 – A I. 2015: loc. 88 – AT V.
Specimens: 2014: loc. 18 – exuviae 2♂ 1♀; loc. 21 – exuviae 1♂ 1♀; loc. 22 – adult 1♂, exuviae 13♂ 14♀; loc. 43 – exuviae 29♂ 27♀; loc. 47 – exuviae 3♂ 4♀; loc. 48 – exuviae 1♂ 1♀; loc. 49 – exuviae 7♂ 6♀; loc. 55 – exuvia 1♀. 2015: loc. 88 – adults 1♂ 1♀, exuvia 1♀.

38. *Gomphus ubadschii* Schmidt, 1953
2014: loc. 73 – AT V; loc. 74 – AT IV. 2015: loc. 74 – AOT II.
Specimens: 2014: loc. 73 – adult 1♀, exuviae 21♂ 13♀; loc. 74 – adults 1♂ 1♀, exuviae 3 ♂ 3♀. 2015: loc. 74 – adult 1♀, exuviae 3.

39. *Lindenia tetraphylla* (Vander Linden, 1825)
2014: loc. 3 – A I; loc. 5 – A I; loc. 51 – A I; loc. 58 – A II.

40. *Onychogomphus assimilis* (Schneider, 1845)
2014: loc. 8 – A IV; loc.14 – A I; loc. 21 – A I; loc. 22 – ACOT V.
Specimens: 2014: loc. 8 – adult 1♂; loc.14 – adult 1♀, exuviae 7♂ 7♀; loc. 18 – exuviae 7♂ 7♀; loc. 21 – exuviae 88♂ 98♀; loc. 22 – adults 1♂ 1♀, exuviae 251♂ 303♀; loc. 47 – exuviae 1♂ 1♀; loc. 49 – exuviae 1♂ 2♀.

41. *Onychogomphus flexuosus* (Schneider, 1845)

2014: loc. 3 – A V; loc. 5 – A II; loc. 6 – A III; loc. 9 – A I; loc. 17 – A II; loc. 33 – A I; loc. 38 – A I; loc. 40 – A I; loc. 42 – A III; loc. 43 – A I; loc. 46 – A I; loc. 82 – A II.
Specimens: 2014: loc. 3 – adults 4♂ 2♀; loc. 43 – adult 1♀; loc. 82 – adults 1♀.

42. *Onychogomphus forcipatus albotibialis* Schmidt, 1954

2014: loc. 2 – ACOT VI; loc. 3 – A II; loc. 4 – A II; loc. 6 – A I; loc. 8 – A III; loc. 12 – A II; loc. 16 – A III; loc. 18 – AT III; loc. 19 – AT V; loc. 21 – AT VI; loc. 22 – AT III; loc. 25 – A I; loc. 26 – A I; loc. 28 – A I; loc. 32 – A I; loc. 34 – A I; loc. 37 – A I; loc. 38 – A I; loc. 40 – A I; loc. 43 – A III; loc. 47 – AT IV. 2015: loc. 2 – AT III; loc. 3 – A II; loc. 86 – AT I; loc. 90 – AT III; loc. 91 – A II; loc. 96 – A I.
Specimens: 2014: loc. 2 – adults 1♂ 1♀, exuviae 18♂ 11♀; loc. 8 – exuvia 1♂; loc. 12 – adult 1♂; loc. 19 – adult 1♂, exuvia 1♀; loc. 21 – exuviae 10♂ 15♀; loc. 22 – adult 1 ♂, exuviae 6♂ 5♀; loc. 43 – exuvia 1♀; loc. 47 – exuvia 1♂; loc. 48 – exuviae 11♂ 13 ♀; loc. 72 – exuviae 6♂ 2♀; loc. 73 – exuviae 3♂ 1♀; loc. 76 – exuviae 2♂; loc. 82 – exuviae 3♂. 2015: loc. 2 – exuviae 102♂ 117♀; loc. 90 – adults 1♂ 1♀, exuvia 1♀.

Cordulegastridae

43. *Cordulegaster insignis charpentieri* (Kolenati, 1846)

2014: loc. 2 – A II; loc. 9 – A I. 2015: loc. 2 – A I; loc. 3 – AT II.
Specimens: 2014: loc. 2 – exuviae 3♀. 2015: loc. 2 – adult 1♂, exuvia 1♀.

44. *Cordulegaster mzymtae* Bartenev, 1929

2015: loc. 98 – A III; loc. 99 – A III.
Specimens: 2015: loc. 98 – adults 4♂ 2♀; loc. 99 – adults 4♂.

45. *Cordulegaster picta* Selys, 1854

2014: loc. 80 – A I; loc. 81 – A III; loc. 85 – A II. 2015: loc. 96 – A V.
Specimens: 2014: loc. 12 – exuvia 1♀; loc. 22 – exuvia 1♀; loc. 85 – larvae 3♀. 2015: loc. 96 – adults 2♂.

46. *Cordulegaster* spec.

Specimens 2014: loc. 61 – exuviae 2♂ 1♀, 12 larvae; loc. 62 – exuviae 2♂, 3 larvae; loc. 63 – exuvia 1♀; loc. 64 – exuviae 1♀; loc. 67 – exuviae 2♀.

Libellulidae

47. *Libellula depressa* Linnaeus, 1758

2014: loc. 16 – A II Loc. 25 – ACO II; loc. 26 – A I; loc. 27 – AI; loc. 29 – A I; loc. 30 – A I; loc. 32 – AO II; loc. 34 – A I; loc. 36 – A I; loc. 38 – A I; loc. 43 – A I; loc. 50 – A II; loc. 53 – A II; loc. 57 – A I; loc. 78 – A II; loc. 84 – A II. 2015: loc. 2 – AIII; loc. 45 – A III.
2015: loc. 53 – A II; loc. 97 – A V.
Specimens: 2014: loc. 16 – adults 2♂; loc. 25 – exuvia 1♂; loc. 45 – exuviae 1♂ 1♀; 2015: loc. 2 – adult 1♀.

48. *Libellula quadrimaculata* Linnaeus, 1758
2014: loc. 13 – A III; loc. 45 – AU III; loc. 52 – ACO VII; loc. 53 – A III; loc. 54 – A III; loc. 56 – A I. 2015: loc. 45 – AO IV. 2015: loc. 52 – A VI; loc. 94 – A II.
Specimens: 2014: loc. 13 – exuvia 1♀. 2015: loc. 45 – adult 1♂.

49. *Libellula pontica* Selys, 1887
2014: loc. 23 – A I; loc. 25 – ACO V; loc. 43 – A V. 2015: loc. 86 – A II; loc. 90 – A II.
Specimens: 2014: loc. 25 – adults 6♂ 3♀; loc. 43 – adults 3♂, exuviae 2♂ 1 ♀. 2015: loc. 86 – adult 1♀.

On 26-vi-2014, at loc. 25, about 230 eggs were taken from a female caught during copulation. The eggs were incubated in water at ambient temperature. In the morning of 09-vii-2014 the first larva was observed and in the evening a total of 57 larvae were hatched. On 12-vii about 130 larvae were hatched and the last fresh larvae were found on 05-viii-2014. Forty-seven eggs did not hatch, so that the hatchability was amounted to nearly 80 %.

50. *Orthetrum albistylum* (Selys, 1848)
2014: loc. 4 – A II; loc. 7 – AC IV; loc. 11 – A I; loc. 13 – AT III; loc. 19 – T II; loc. 28 – A IV; loc. 29 – AOT V; loc. 34 – AT V; loc. 43 – T I; loc. 58 – ACOT X; loc. 71 – A IX; loc. 72 – A III; loc. 73 – A II; loc. 74 – A II; loc. 82 – O I; loc. 83 – A V; loc. 84 – A II. 2015: loc. 7 – A I; loc. 86 – A IV; loc. 87 – A VI; loc. 88 – A I.
Specimens: 2014: loc. 7 – exuvia 1♂; loc. 13 – adult 1♀; loc. 29 – exuvia 1♂; loc. 58 – exuviae 16♂ 21♀; loc. 83 – adult 1♂. 2015: loc. 86 – adult 1♂.

51. *Orthetrum brunneum* (Fonscolombe, 1837)
2014: loc. 2 – AOLU V; loc. 3 – A II; loc. 6 – A III; loc. 7 – A II; loc. 8 – A II; loc. 10 – A I; loc. 11 – A V; loc. 12 – A II; loc. 13 – A I; loc. 14 – AC II; loc. 16 – AT II; loc. 17 – A I; loc. 19 – AT III; loc. 20 – A III; loc. 21 – AOU III; loc. 22 – A V; loc. 23 – ACO V; loc. 24 – A II; loc. 25 – ACOU IV; loc. 26 – AO III; loc. 27 – A I; loc. 29 – A II; loc. 30 – AT VI; loc. 32 – ACOTU V; loc. 36 – A III; loc. 38 – AT V; loc. 39 – A IV; loc. 41 – A II; loc. 43 – ACOU IV; loc. 44 – A II; loc. 47 – A I; loc. 48 – A II; loc. 51 – AT V; loc. 80 – A I; loc. 81 – A II; loc. 82 – AO II; loc. 83 – A III; loc. 84 – A V. 2015: loc. 2 – AOT IV; loc. 86 – A III; loc. 89 – A I; loc. 90 – A II.
Specimens: 2014: loc. 2 – larvae 10, exuvia 1♀, adults 2♂ 1♀.; loc. 13 – exuvia 1♀; loc. 16 – exuvia 1♀; loc. 21 – exuvia 1♀; loc. 32 – exuviae 3♂ 1♀; loc. 43 – exuviae 3♂ 3♀; loc. 84 – adults 2♂. 2015: loc. 2 – adult 1♂; loc. 86 – adults 2♂ 1♀; loc. 90 – exuvia 1♀.

52. *Orthetrum cancellatum* (Linnaeus, 1758)
2014: loc. 4 – A II; loc. 6 – A II; loc. 7 – A III; loc. 11 – AT V; loc. 21 – A I; loc. 28 – A II; loc. 29 – A II; loc. 34 – A III; loc. 51 – AT III; loc. 52 – A II; loc. 58 – A II; loc. 83 – A II.
2015: loc. 7 – AT II; loc. 86 – A II.
Specimens: 2014: loc. 7 – exuviae 2♂ 1♀.

53. *Orthetrum coerulescens anceps* (Schneider, 1845)

2014: loc. 2 – A III; loc. 3 – A II; loc. 7 – AT III; 11 – AT II; loc. 12 – A III; loc. 13 – A II; loc. 16 – AT II; loc. 17 – A I; loc. 19 – A IV; loc. 20 – A II; loc. 21 – A II; loc. 22 – AT V; loc. 23 – A IV; loc. 25 – ACTUO VI; loc. 26 – A I; loc. 28 – A II; loc. 29 – AT IV; loc. 32 – A IV; loc. 33 – A V; loc. 34 – A VII; loc. 37 – A III; loc. 38 – A II; loc. 41 – A I; loc. 43 – AT III; loc. 45 – ATU VI; loc. 47 – A I; loc. 48 – A II; loc. 51 – ACOTU VII; loc. 60 – A I; loc. 71 – A III; loc. 73 – A II; loc. 75 – ATU III; loc. 82 – A II; loc. 84 – A III. 2015: loc. 3 – A I; loc. 45 – AT II; loc. 86 – AT II; loc. 90 – A II; loc. 95 – A II.
Specimens: 2014: loc. 2 – adults 2♂ 1♀; loc. 25 – adult 1♂, exuvia 1♀; loc. 33 – adults 1♂ 1♀; loc. 45 – exuviae 15♂ 18♀; loc. 51 – exuviae 1♂; loc. 58 – exuviae 2♂ 2♀; loc. 75 – exuviae 3♀. 2015: loc. 45 – exuvia 1♀.

54. *Orthetrum sabina* (Drury, 1773)

2014: loc. 29 – ACO IV.
Specimens: 2014: loc. 29 – adult 1♂.

55. *Selysiothemis nigra* (Vander Linden, 1825)

2014: loc. 33 – A II; loc. 34 – A II. 2015: loc. 87 – A II.
Specimens: 2014: loc. 33 – adult 1♂.

56. *Sympetrum danae* (Sulzer, 1776)

2015: loc. 94 – A II.
Specimens: 2015: loc. 94 – adult ♀.

57. *Sympetrum flaveolum* (Linnaeus, 1758)

2014: loc. 45 – AU VI; loc. 49 – ATU VI; loc. 50 – ATU VI; loc. 54 – T VIII; loc. 55 – A I. 2015: loc. 52 – A VII; loc. 53 – A III; loc. 92 – A V; loc. 93 – A VII; loc. 94 – A V.
Specimens: 2014: loc. 45 – adult 1♂. loc. 50 – exuviae 22♂ 14♀.

58. *Sympetrum fonscolombii* (Selys, 1840)

2014: loc. 9 – A IV; loc. 10 – A I; loc.11 – A II; loc. 14 – A I; loc. 16 – T I; loc. 22 – AU V; loc. 14 – AT III; loc. 33 – A III; loc. 34 – A II; loc. 35 – A III; loc. 36 – ACO V; loc. 38 – ACO V; loc. 39 – ACO IV; loc. 40 – A II; loc. 41– A III; loc. 44 – AT II; loc. 50 – A I; loc. 51 – A III; loc. 54 – A III; loc. 55 – A II; loc. 58 – A II; loc. 69 – A II; loc. 72 – A V; loc. 83 – A II. 2015: loc. 7 – A II; loc. 87 – A II; loc. 88 – A II;
Specimens: 2014: loc. 2 – exuvia 1♂; loc. 13 – exuvia 1♂. 2015: loc. 88 – adult 1♀.

59. *Sympetrum meridionale* (Selys, 1841)

2014: loc. 12 – A I; loc. 27 – A II; loc. 29 – AT V; loc. 43 – A I.
Specimens: 2014: loc. 27 – adult 1♂; loc. 58 – exuvia 1♂.

60. *Sympetrum pedemontanum* (Müller in Allioni, 1766)

2014: loc. 21 – A I; loc. 45 – A I. 2015: loc. 92 – A VII.
Specimens: 2014: loc. 21 – adult 1♂; loc. 45 – adult 1♀.

61. *Sympetrum sanguineum* (Müller, 1764)
2014: loc. 13 – T II; loc. 16 – A II; loc. 19 – A I; loc. 21 – A II; loc. 25 – A II; loc. 45 – TU III; loc. 49 – AT II; loc. 50 – T II; loc. 51 – AT III; loc. 58 – A I; loc. 78 – A I.
Specimens: 2014: loc. 51 – adult 1♂, exuvia 1♂.

62. *Sympetrum striolatum* (Charpentier, 1840)
2014: loc. 5 – A IV; loc. 8 – A II; loc. 9 – A III; loc. 12 – A III; loc. 13 – AT II; loc. 14 – A III; loc. 15 – A I; loc. 16 – A III; loc. 17 – A II; loc. 19 – A III; loc. 20 – T III; loc. 21 – AT III; loc. 22 – A III; loc. 25 – T III; loc. 26 – T II; loc. 27 – A III; loc. 28 – A I; loc. 29 – A II; loc. 31 – A III; loc. 42 – A I; loc. 44 – A I; loc. 48 – T IV; loc. 51 – AT VII; loc. 58 – T V; loc. 62 – A I; loc. 82 – A I. 2015: loc. 1 – AT V; loc. 2 – AT II; loc. 3 – AT III.
Specimens: 2014: loc. 20 – exuviae 3♂ 1♀; loc. 25 – adult 1♀; loc. 51 – exuviae 4♂ 2♀.
2015: loc. 2 – adult 1♂.

63. *Sympetrum vulgatum decoloratum* (Selys, 1884)
2014: loc. 51 – AT V. 2015: loc. 94 – A I; loc. 97 – A I.
Specimens: 2014: loc. 51 – adults 1♂ 2♀, exuviae 3♀; loc. 53 – adult 1♂.

Discussion

Notes on selected species

Chalcolestes parvidens

All specimens (8♂ 4♀) of *Chalcolestes* clearly belonged to *parvidens* as well as several further individuals which could be clearly identified based on photographs. This species is also known from Azerbaijan (Dumont 2004; Skvortsov & Snegovaya 2014) and northeastern Turkey, where it is scarce (Kalkman 2006; Miroğlu & Kartal 2008; Schneider & Schneider 2013). Yet it hasn't been found in Armenia (Tailly et al. 2004; Ananian & Tailly 2013).

Beutler (1987) reported a single male of *Chalcolestes* from Pizunda (Abkhazia), situated at the Black Sea coast about 180 km north of our locality, which he assigned to the nominate taxon of *Chalcolestes viridis* (»*Lestes v. viridis*«) without any further indication. This record is doubtful as Georgia is most likely not situated within the sympatric zone of both species (Jödicke 1997; Olias et al. 2007). We therefore assume that all Georgian *Chalcolestes* in fact pertain to *parvidens*. The same goes for old records listed under *Lestes viridis* without further taxonomic indication (Bartenev 1930a).

According to present knowledge *C. parvidens* seems to be uncommon in Georgia. However it appears that the majority of available records of *Chalcolestes* cf. *parvidens* are located close to the Black Sea coast, suggesting that the species might become increasingly scarce in the inland. The same pattern can be observed in Azerbaijan with regard to the Caspian Sea, suggesting that in the Transcaucasus *C. parvidens* prefers maritime climate, which might explain its absence in landlocked Armenia (Tailly et al. 2004).

Lestes macrostigma

Our two data represent only the second and third Georgian records of *Lestes macrostigma* since its discovery near Veli in Abkhazia (Shengelia 1953). One of our two new sites was a shallow reedy lake with brackish water (loc. 7) typically for the species (Jödicke 1997; Boudot et al. 2009) whereas the second site (loc. 87) referred to a large reservoir lake with fresh water. Other data of *L. macrostigma* available from the Transcaucasus are limited and mainly old. Besides a historical record from the Russian city Tuapse, not far from today's Georgian border (Bartenev 1930a) and two old Armenian records (Akramowski 1948, 1964), only one site each is currently known from Armenia and Azerbaijan (Dumont 2004; Ananian & Tailly 2013). In Turkey this species is only known from the western part of the country and has never been found at the eastern Black Sea coast and the provinces bordering Georgia (Boudot et al. 2009). However, these poor data do most likely not reflect real frequency and abundance of species in the region. Georgia offers numerous habitats which potentially meet the ecological requirements of *L. macrostigma*, especially in Tbilisi and Kakheti regions. It can therefore be assumed that this inconspicuous spring species has rather been overlooked due to its phenology than being actually rare.

***Lestes virens* in Georgia: taxonomical status with reference to ssp. *marikovskii* Belyshev, 1961**

Lestes virens is apparently rare and localized in Georgia and only a handful of records are available (Bartenev 1925, 1929b, 1930a). It seems to be rare or scattered as well in the neighbouring countries Armenia (Ananian & Tailly 2013), Turkey (Kalkman 2006) and Azerbaijan (Jödicke 1997: 85; Skvortsov & Snegovaya 2014). The status of Western and Central Asian

populations of *L. virens* as well as the nature of several other European and Maghrebian populations and taxa allied to this species remains unclear (Jödicke 1997: 85 ff.; Samraoui et al. 2003; Dijkstra 2006; Schröter 2010b).

The following assessment on the taxonomical status of the Georgian male collected on 02-vii-2014 at loc. 51 with reference to material of *Lestes virens* from adjacent Eastern Turkey and Central Asia was provided by RJ. All comments on *L. virens* specimens of other proveniences than the Georgian locality refer to the coll. Jödicke and coll. Schröter, respectively, to be deposited in SMF, unless otherwise indicated.

A taxonomical assignment of the Georgian specimen is as difficult as it is with all Asian *virens* forms. The *virens* complex is considered to be polytypic, consisting of different taxa on species and subspecies level (e.g., Dijkstra 2006). The complex-specific phenomenon of successive melanisation, colour change from bright to coppery green or copper red, and, in males, development of pruinosity during maturation and ageing is not discussed in this context, as the Georgian male is in an immature state.

Typical *L. virens virens* (Charpentier, 1825) is a West European insect with a bicoloured Pt – the distal third is whitish in the Portuguese holotype – and reduced green markings (Hartung 1993), which strongly resembles *L. barbarus*. The whitish sector becomes smaller to the East: In Catalonia it is reduced to ⅕ of Pt length and to ⅐ in southwestern France or Sicily. Another phenotype from southern France, Corsica, Sardinia, and the Maghreb has reduced green markings as well but no trace of a whitish Pt section. This form has traditionally been subsumed under the name *L. virens virens*. Samraoui et al. (2003) discovered that this latter form consists, at least in North Africa, of two different species, which are phenotypically undiscernible, but different regards genetics and adult life cycle: one starts reproduction without prereproductive diapause, the other is late reproducing due to a long estivation before maturation. However, Samraoui et al. (2003) have introduced the new species name *numidicus* for the late form, although typical ssp. *virens* was known for its long flying season until mid November (e.g., Ferreras Romero & Puchol Caballero 1984). In fact, the early reproducing form from Algeria was actually unknown so far and thus in need of a new name, while the given name *numidicus* to denote the late form must

be judged to enter into synonymy of *virens* (Jödicke 2003). The existence of two different phenological cycles have not been reported from Europe so far, but might explain extreme early and late oviposition dates in Sardinia (BK unpubl.).

Schmidt (1939) pooled all darker *virens* forms from Central Europe and Asia Minor as a distinct subspecies and and saved the [oldest] available name *vestalis* Rambur, 1842 for its denomination. The transition zone of ssp. *virens* and ssp. *vestalis* is only roughly known and runs from the Tyrrhenean Sea over the mouth of the Rhône River to the Gironde (Jödicke 1997: 85); there is no information about a possible overlap or a clear separation of characters in that zone. In typical *L. virens vestalis* all green markings are significantly more extended. This applies to all characters mentioned in the description above but most significant are: (1) a bridge between dorsal and pleural stripes, which shortens the ante-humeral stripe in its caudal section; (2) the pleural stripe reaches the metapleural suture; (3) a coppery-blackish stripe alongside the upper edge of propleuron; (4) in males: melanisation mainly along the metapleural suture, on the prothorax and on S1 (sides of tergum only) and S9+10 (complete) as basis for an extensive pruinosity. However, these characters don't apply to all Central and Eastern European populations, as the extension of metallic green tends to decrease successively to the South. For instance, series from the Peloponnes, Greece, are heterogeneous, with some specimens showing all true *vestalis* characters, others being much paler and thus resembling the western nominotypical subspecies, and also intermediate specimens. This is why the uttermost southeast of Europe was not included to the range of typical ssp. *vestalis* (Jödicke 1997: 79 f., 82).

The same dilemma is typical of series from Asia. The easternmost records of *L. virens* stem from the Altai Mts., Russia (Belyshev 1964, 1973: 516). Its eastern range also includes the Kazakh desert southeast of Lake Balkhash (Belyshev 1961; Borisov & Haritonov 2007), the mountains of Tajikistan and Kyrgyzstan (Borisov & Haritonov 2007; Schröter 2010b) and northeastern Afghanistan (Schmidt 1961). Most Asian populations are paler than typical *vestalis*; even a northerly population in West Siberia (Inya River 100 km east of Novosibirsk) shows a distinct tendency to a gap between the pleural stripe and the metapleural suture and a slight tendency to

completely open ante-humeral stripes. However, specimens from southern Ural resemble the darkest *vestalis* phenotype known from northwestern Europe, e.g., Lower Saxony. The palest coloration is known from arid southern Kazakhstan. A series from several localities in this region around the Ili and Karatal River has been described as *L. virens marikovskii* (Belyshev 1961); the author gave no detailed description but pointed out their small dimensions. One syntype female attained to coll. Jödicke: with an abdomen length of 25.5 mm and a Hw length of 19.0 mm it is not small. With its significantly reduced metallic green it is even paler than the palest individuals in southeastern Europe and thus strongly resembles ssp. *virens*. Only the distinctive stripe over the propleuron, the darker head dorsum, the narrower ante-humeral stripe and the more extensive patch on mesinfraepisternum differ from the western taxa. In one respect, the metallic green is even more reduced in the Kazakh female than in ssp. *virens*, i.e., the yellow streak at the caudal end of the pleural stripe (Fig. 2: *ep2*) runs down from the humeral fossa to the interpleural suture. This is a unique character seen in the *virens* complex so far and is only shared with a series collected in about 500 km distance in adjacent Kyrgyzstan (Schröter 2010b).

The Georgian male (Fig. 2) is placed in between the dark and pale extremes known from Asia. With its maximum extent of green on head dorsum, pronotum, propleuron, and mesinfraepisternum it resembles ssp. *vestalis*. Its anterior lobe of the pronotum is even darker than in typical *vestalis*, where the green is reduced to a broad median and two slimmer lateral stripes. On the other hand, its ante-humeral stripe is almost open, and its pleural stripe does not extend to the metapleural suture, which points at *marikovskii*. A comparison between the Georgian male and 12 specimens from southeastern Anatolia, Turkey, which have been collected only ca 400 km south of the Georgian locality and are deposited in ZSM (Zoologische Staatssammlung München, Germany), demonstrates a great similarity. Within the Turkish series there is some variability in the pigmentation of the ante-humeral stripe in its distal end and in the extension of the pleural stripe towards the humeral suture, also a slight tendency to smaller spots on the mesinfraepisternum. Unfortunately, there are no notes on the pigmentation of the anterior lobe of pronotum but a photo of one male shows a complete green pigmentation like the Georgian male. The only significant difference is that

all 11 Turkish males, although being in a slightly advanced state of maturity, have only traces of black pimentation alongside the metapleural suture. Such a pigmentation type is unusual in *vestalis* and easterly populations; the most extensive black band on the metepimeron has been seen in a male from Lesbos, Greece. A Kyrgyz series (see Schröter 2010b) is paler than the male from Georgia and the specimens from southeastern Turkey. They don't have any green bridge across the ante-humeral stripe and their pleural stripe does not reach the metapleural suture. Their metallic green is also more reduced at occipital ridge, anterior lobe of pronotum, propleuron (stripe split into two parts), and mesinfraepisternum. Kyrgyz specimens therefore look more alike the *marikovskii* syntype but are smaller on an average.

The name *marikovskii* remained almost unused after Belyshev (1973) but has been picked up again by Samraoui et al. (2003) for »all populations between central Asia and central Europe«, by Chaplina et al. (2007) for the population of Kazakhstan and by Schröter (2010b) to preliminarily denote the »distinct Central Asian populations by pragmatic reasons«. However, we have neither a differential diagnosis, nor a geographic definition of a possible ssp. *marikovskii* so far. This failure makes a usage of this name so unsatisfying, even for the populations in Central Asia. It would make no sense to define ssp. *marikovskii* as the southeasternmost subspecies and accept a huge transition zone between Central Europe and Central Asia with undefinable *virens* forms as ever. Having seen so many *virens* phenotypes we are convinced that any splitting in subspecies will not be a constructive solution for a better understanding of all eastern forms. The tendency of ssp. *vestalis* to become generally paler from North to South in Europe also applies to the range in Asia: Here our preliminary analysis of all *virens* specimens kept in coll. Jödicke strongly suggests a clinal variation of all characters separating the darkest and palest phenotypes. This cline would run from Northwest with an Atlantic climate (mild winter, moderate summer) to Southeast with a continental climate (severe winter, hot summer). Such a hypothesis is supported by the observation that specimens collected in high altitude are generally darker than those from moderate altitude. A further support comes from the fact that most characters may show a vivid variation within a syntopic series. This especially applies to the most widely used *vestalis* characters in identification keys: the green bridge across the

ante-humeral stripe to connect the dorsal and pleural stripes and the extent of the pleural stripe as far as the pleural suture. We therefore suggest to maintain the original definition of ssp. *vestalis* by Schmidt (1939) and to understand the variability within this subspecies as a consequence of clinal variation. In this tenor, the Georgian male and all other Asiatic forms belong to ssp. *vestalis*. The name *marikovskii* consequently drops into synonymy of *vestalis*. It would be appreciated to test the cline by means of genetic analyses across the Eurasian region.

***Calopteryx splendens* taxa complex**

The intriguing and bewildering number of regional forms of *Calopteryx splendens* (Harris, 1780) in the Caucasus region and both validity and scientific content of many related infraspecific taxa has been, and still is, subject of discussion (Bartenev 1930b; Dumont et al. 1987; Sadeghi et al. 2009; Sadeghi & Dumont 2014). At least five taxa have been established to accommodate the variety of *C. splendens* forms occurring in Georgia (Bartenev 1912b, 1930b; Shengelia 1953, 1975). In this study three taxa are distinguished for Georgia and treated on a subspecific level in the species list. Besides the comparatively distinctive ssp. *intermedia* Selys, 1887, these are ssp. *mingrelica* Selys, 1868 and ssp. *tschaldirica* Bartenev, 1909. *Calopteryx s. intermedia* has by far the largest range of all taxa of the *C. splendens* complex and, according to genetic studies, is one of the three "core subspecies" (besides *C. s. waterstoni* Schneider, 1984 and *C. s. xanthostoma* [Charpentier, 1825]), which radiated independently in separated phylogeographic glacial refugia (Sadeghi 2008).

According to Dumont et al. (1987), populations of ssp. *mingrelica* and ssp. *tschaldirica* might in fact be the result of a genetic flow between ssp. *waterstoni* Schneider, 1984, with entirely hyaline wings, from the northeastern corner of adjacent Turkey, and the darkest regional form ssp. *amasina*. On this account all individuals presented in our study assigned to ssp. *mingrelica* or ssp. *tschaldirica* might alternatively be considered as hybrids with wing spots of all kind of variation, extending between the two extreme types *waterstoni* (entirely uncoloured hyaline wings) and *intermedia* (wings fully coloured except bases). They could therefore be subsummed formally under *Calopteryx splendens* ssp. [trans *intermedia* ad *waterstoni*].

However, even though the members of this complex are connected by clines of different steepness, Dumont et al. (1987) give support to treat ssp. *mingrelica* and ssp. *tschaldirica* as regional subspecies. Here, we follow this line of arguments despite ongoing hybridisation in the contact zones. According to our experience, on Georgian territory the three taxa form recognizable entities that can sufficiently be defined on the base of phenotype and regional range.

Two other taxa were described as occurring in Georgia, ssp. *cartvelica* Bartenev, 1930 and ssp. *cecilia* Bartenev, 1912 (sub *C. intermedia cecilia*). According to Bartenev the small range of the exclusively Georgian ssp. *cartvelica* was centred in the historical region of Kartli (central-to-eastern Georgia, including the capital area) and replaced to the East by ssp. *cecilia*. However

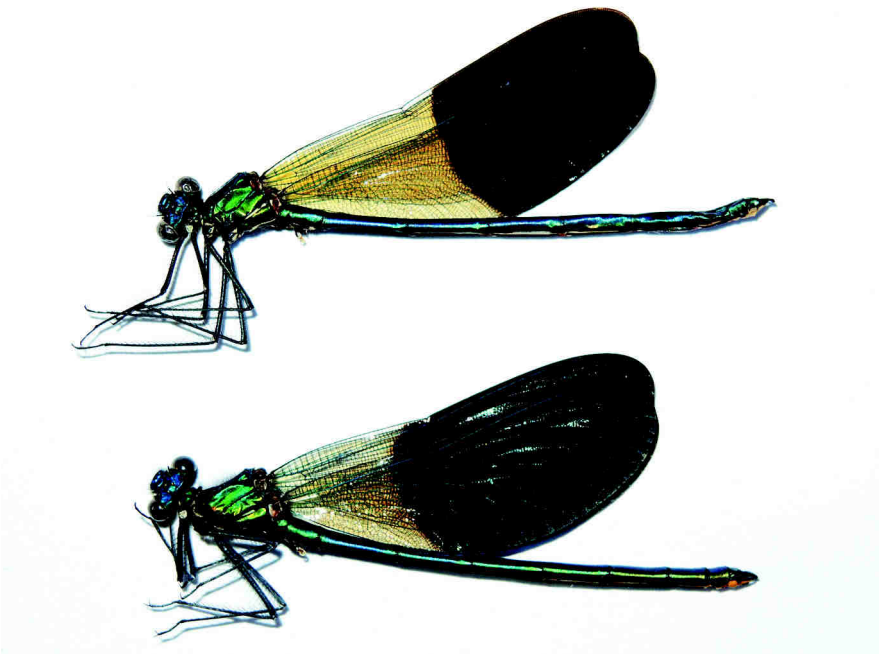


Figure 3. Two males of *Calopteryx splendens intermedia* from Georgia. The extension of the dark wing spot decreases gradually from east to west: The upper individual originated from Sajavakho in the west, the lower from the capital area in the eastern half of the country (15-vii-2014; photograph by MS)

according to Bartenev's description and our data obtained in this area, both taxa clearly belong to the Selysian *intermedia* with large dark wings spots covering the apices in males. The wing spots seem to differ marginally only, if at all, in their extension, exceeding the nodus rather clearly (ssp. *cecilia*) or ending at or before it (ssp. *cartvelica*). In Georgia, as a rule the extension of the wing spots towards the base in ssp. *intermedia* gradually seemed to reduce slightly from the East towards the West, besides some variation on an individual level within populations. Specimens from beyond the Likhi range at the upper parts of the Colchic depression might even be transition types of *mingrelica* (Fig. 3).

In her compilation of Georgian odonate data Shengelia (1975) synonymised *C. intermedia cecilia* with *C. splendens cartvelica*. On account of our data we go one step further and in turn synonymise ssp. *cartvelica* with ssp. *intermedia* and thus consider all Georgian populations of *C. splendens* showing invariably entirely coloured wing apices as pertaining to this taxon. This conclusion was (at least implicitly) also drawn by Kalkman (2006: 5), who did not consider ssp. *cartvelica* in the list of the *splendens* taxa occurring in the Caucasus region.

Bartenev (1912c) interestingly reported ssp. *cecilia* from the capital area from where later also the type series of ssp. *cartvelica* was collected, indicating that the author's trust in his own concept of these two taxa was rather limited. The same applies to a later study of the same author, in which he tried to give an up-to-date review on the issue but in the bottom line raised more new questions than providing answers and objective facts (Bartenev 1930b).

Calopteryx splendens intermedia

This most widespread and abundant subspecies of *C. splendens* in Georgia appears to be the only member of the *C. splendens* complex over large parts of the lower regions of the eastern half of the country. Males have shiny coloured dark blue to almost blackish wing spots covering the wing apices. The basal border is always clear cut but the extension varies on both an individual level and between populations. *In toto* they did not differ from populations in southern Turkey usually ascribed to ssp. *intermedia* (AS unpubl.). We understand all populations with large wing spots constantly cov-

ering the entire wing apices as ssp. *intermedia*. The character »wing spot in the FW starts more than 10 cells before the nodus« (Kalkman 2006) can therefore no longer be maintained.

At two sites in the Alazani valley, in the Kakheti region in the East of the country, we found androchrome females of *C. s. intermedia* that have never been reported before from Georgia. Besides one single individual at loc. 23, we encountered such females more frequently at loc. 25, where an estimated 2 % of all females were androchrome. In all other parts of Georgia only females with more or less clear wings were observed and collected. Single females showed a light greenish or brownish tinting of whole wings but never an androchrome colouration. These results are rather unexpected since e.g., in southern Turkey androchrome females are very common. Along Turkey's southeastern coast locally all females are androchrome, e.g., near Adana (Dumont 2006) or between Alanya and Anamur (AG unpubl.).

Calopteryx splendens mingrelica

Males of *C. splendens* at the Black Sea coast showed deep blue wing spots not entirely covering the wing apices, leaving at least a small part hyaline. In 1868, based upon 2♂ from Mingrelia, a historical province in the subtropical Colchic depression of western Georgia situated just a few kilometers north to the site from where our data were obtained, Selys described the taxon *mingrelica*. The wing spots of both males did not exceeded the nodi but, indicatively, were heterogeneous in view of the apices, with narrow hyaline outer edges in one male: »la partie terminale opaque des ailes ne commence qu'un peu après le nodus (chez un exemplaire le bout des ailes est légèrement hyaline)« (Selys 1868: 106) [The opaque terminal wing part begins shortly after the nodus (in one specimen the wing tip is slightly transparent)].

Other data on ssp. *mingrelica* from the Georgian territory are scarce and historical only (Selys 1868; Bartenev 1930b). To current knowledge, ssp. *mingrelica* is confined to the western half of the Transcaucasian depression and most probably does not cross the Likhi range (Bartenev 1912b, 1930b; Dumont et al. 1987). However as long as the nature of alleged ssp. *intermedia* populations with individuals showing clearly reduced wing spots (in this study preliminarily assigned to ssp. *intermedia*, see above) at the eastern border of the Colchic depression towards the western foothills of the Likhi

range remains unclear, also the course of the eastern limit of ssp. *mingrelica* has to be left open.

Calopteryx splendens tschaldirica

At the middle and upper course of the Kura river and its tributaries within the region of Samtkhe-Javakheti and bordering areas to the Shida-Kartli region, we encountered a distinctly small and dainty form of *C. splendens* with comparatively narrow wings. Males had broadly hyaline wing apices and small rather diffuse blue spots not reaching the wing hind margin (Fig. 4). While the wing spots faded out distally, their proximate border was distinctively clear cut and straight. The matt blue wing spots strongly varied in size and markedness and several males appeared to have almost entirely hyaline wings with traces of a blue tinge only. The length of the male's abdomen was roughly a centimetre shorter than in average males of *ssp. intermedia* from the adjacent capital area (31 mm; n = 8, vs 40 mm in ssp. *intermedia*, n = 11). These males perfectly matched both the description and the distribution of ssp. *tschaldirica* Bartenev, 1909, described from specimens collected in 1909 within the former Kars Oblast (Карсская область) of the Russian Empire, on today's Turkish territory (Ardahan and Kars provinces) at the source of

Figure 4. Male of *Calopteryx splendens tschaldirica*. Kura river southwest Khashuri, Georgia (29-vi-2014; photograph by Stefan Kohl)

the Kura river around Tschildir lake ("Чилдыр"; Turk. Çıldır Gölü) (Bartenev 1909). We therefore assign this form to ssp. *tschaldirica*, which is in perfect accordance with descriptions and illustrations given by Dumont et al. (1987), who revealed the true nature and status of this taxon that had been unclear for decades. This was probably due to individual unjustified changes of its taxonomical status by Bartenev himself, who in 1912 treated it as a ssp. of the Selysian *taurica* (Bartenev 1912: 80; cf. Selys 1853).

As stated by Dumont et al. (1987), available data suggest that ssp. *tschaldirica* is an altitudinal form centred on the volcanic plateau of the Armenian highland from where it penetrates into the lower regions towards the East along the course of the Kura, being replaced by ssp. *intermedia* roughly west of Mzcheta. The western limit of its Georgian range remains rather unclear; however, ssp. *tschaldirica* obviously does not enter deeply into Adjaria and the Colchic lowland, where it is largely replaced by ssp. *mingrelica*. What regards alleged ssp. *tschaldirica* reported from northeast of Batumi by Bartenev (1930a), see Dumont et al. (1987).

Calopteryx virgo festiva: on the availability of the name _Calopteryx virgo_ var. _feminalis_ Bartenev, 1910

Calopteryx virgo has been first mentioned from today's Georgian territory by Eichwald (1837) in a report on his expedition across the Colchic lowland. He described the species as being abundant at brooks in forests of Mingrelia (sub *Agrion colchicum*). Only a short time later *C. virgo* was repeatedly reported from Mingrelia by Selys (1868), who stated that it corresponded to Brullé's taxon *festiva*. According to our data, Georgian *C. virgo* indeed generally correspond to ssp. *festiva* in all characters described by Brullé (1832), with all blackish wings in males and conspicuously dark winged females (Bartenev 1912b). The species appeared to be scarce and localised in Georgia and to be strictly confined to the lowlands in smaller abundances only. In adjacent Azerbaijan it seems to be very rare (Skvortsov & Snegovaya 2014) and it has never been recorded in Armenia so far (Tailly et al. 2004; Ananian & Tailly 2013).

At loc. 60 we discovered a small population of *C. virgo festiva* with conspicuously different looking females, which had brightened, entirely translucent fore wings and two third translucent hind wings with contrasting

dark tips and white pseudopterostigmata (Fig. 5). In single females the contrast of this colour pattern was even more pronounced than shown on the photo and the basal borders of the dark tips were sharper delimited. These females were comparatively large (up to 54 mm total length) and, they strikingly resembled females of *C. haemorrhoidalis*, a western Mediterranean endemic. However, we also observed single typical coloured females flying syntopically with this form at loc. 60.

In his publication on dragonflies of the former Kuban oblast, Bartenev (1910: 35) introduced the name »var. ♀ *feminalis* nov.« based on females collected at Goryachy Klyuch (Горячий Ключ) on the nortwestern foothills of the Caucasus range, north of Sochi, Russia. We here give the original quotation of the Latin description: »alae anteriores pelucentes concolores, posteriores triente apicali fasciâ introrsum rectilineatim atque argute terminatâ adumbratae« [forewings unicolour translucent, the outer third of the hind wings with a straight-lined and clearly confined tinted band]. Bartenev's description thus perfectly matched our *haemorrhoidalis*-like Georgian females. Moreover, in the introduction Bartenev decidedly stated the similarity of his newly described female colour form of *C. virgo* to *C. haemorrhoidalis* females. We are therefore sure that our females correspond to Bartenev's *feminalis* type females he collected some 300 km north of our site, within the same climatic and natural unit along the humid subtropical eastern shore of the Black Sea.

The nomenclatural status of *feminalis* can be derived from the fact that Bartenev introduced the name in combination with the term »var. ♀ nov..«. He therefore clearly intended to denote a new, female-linked variety defined upon the female only. Such third variety name in binominal taxa should be regarded as subspecific if published before 1961 unless it is unambiguously clear that it was proposed for an infrasubspecific entity (Code Art. 45.6.4. ICZN; International Commission on Zoological Nomenclature 1999). This infrasubspecific rank in our opinion became unambiguous in 1930, when the author used the heading »*Calopteryx virgo festiva* var. *feminalis* Bart« in his compilation of the Odonata of the Western Caucasus (Bartenev 1930a). This agrees with the etymological aspect of the *feminalis* name. The latter implicitly means 'relating to females only' as *feminalis* is an adjective, newly created by Bartnenev, and composed according to the modular prin-

ciple: femina – 'woman/female' and -(a)lis – 'referring to' (linguistic expertise and translation kindly provided by H. Fliedner). Thus we can accept that the infrasubspecific rank of "*feminalis*" was implicit although not explicited already in the original (1910) paper and therefore has no nomenclatural status, making this name unavailable.

To our knowledge this female colour form has never been illustrated before and our data represent the first detailed information on it since over a century. The males of the population with *feminalis*-type females did not deviate in any character from other Georgian populations of *C. virgo festiva*. It is very likely that *feminalis*-types occur also along the adjacent Turkish Black Sea coast. However, obviously this phenomenon occurs also outside Caucasus region and in the cases of erratic records of alleged single females of *C. haemorrhoidalis* as, e.g., the Bulgarian specimen presented by Beschovski (1994: 62) almost certainly this female colour form of *C. virgo festiva* was involved.

The only other reference in English language in which the name *feminalis* was mentioned is the key to Turkish Odonata by Kalkman (2006: 10, 17). Based on unpublished data by H.J. Dumont the author assumed that male specimens with a whitish underside of S10 and a black one of S9 (instead of S9–10 red as in typical *C. virgo festiva*) from Rize and Trabzon, deposited in the RMNH, pertain to »subspecies *feminalis*« and, putting things into perspective, the author added: »information on the distribution of this subspecies is scarce«. In the key *feminalis* is listed as a subspecies of *C. virgo* and set apart from *C. virgo festiva* based on the male characters of the ventral abdomen tip. This assumption was incorrect as the description (Bartenev 1910) strictly refers to the female and does not mention characters for males, using the name *feminalis* for an infrasubspecific variety of females exclusively. However, nature and status of the Turkish males of *C. virgo* mentioned by Kalkman (2006) have yet to be left open. According to Miroğlu et al. (2011) males of *C. virgo* with both characters syntopically occur widely in the region, disproving the existence of a second subspecies along the northeastern Black Sea coast of Turkey.

The similarity of these *feminalis*-type females to females of *C. haemorrhoidalis* (Fig. 5) raises the question whether this phenomenon is due to pure evolutionary coincidence or a causal connection might be involved here.

According to genetic analysis *C. haemorrhoidalis* and *C. virgo* are sister taxa (Misof et al. 2000). This suggests that females of the *feminalis* type from the Colchis at the eastern shore of the Black Sea might represent an atavistic ancestral female type with alleles inherited from the last common ancestor of *C. virgo* and the Western Mediterranean *C. haemorrhoidalis*. According to Grand & Boudot (2006: 206) in southern France single females of *C. virgo meridionalis* can also look similar to *C. haemorrhoidalis* females.

Our records of the *feminalis* type of *C. virgo festiva* thus seem to be the only ones on Georgian territory so far. However, in his compilation of odonate data of the Western Caucasus Bartenev (1930a) combined all hitherto known records of *C. virgo festiva* under the heading "*Calopteryx virgo festiva* var. *feminalis* Bart", including records from Kobuleti on Georgian territory and – particularly questionable – from Mingrelia reported by Selys (1887). Especially Selys' Mingrelian specimens have hardly been at Bartenev's disposal, which is why this statement can be rejected.

Figure 5. Female of *Calopteryx virgo festiva* of the colour form '*feminalis*' resembling female *C. haemorrhoidalis*. This is the first photograph capturing a living individual of this colour form. Near Ombolo south of Batumi, Georgia (04-vii-2014; photograph by Stefan Kohl)

Figure 6. Pair of *Coenagrion armatum* in tandem linkage. Madatapa lake, Javakheti volcanic plateau, Georgia (29-vi-2014; photograph by Stefan Kohl)

Figure 7. Stands of common spikerush *Eleocharis palustris* agg. at the southwestern shore of Madatapa lake as habitat of a huge population of *Coenagrion armatum*. Javakheti volcanic plateau, Georgia (02-vii-2014; photograph by Stefan Kohl)

Coenagrion armatum

Our records of this species are one of the most significant results of the expedition (Fig. 6). Our data represent the first confirmation of *C. armatum* on Georgian territory for over a century since this isolated regional population in the mountain steppe of the Javakheti volcanic plateau in the Armenian highland has been discovered by Bartenev (1909). He reported the species from three of the shallow lakes of the plateau: Akhmaz lake (1♂ on 20-vi-1907), Madatapa lake (1♂ on 21-vi-1907), and Khanshali lake (9♂ 6♀ on 19-vi-1907). The two latter localities correspond to loc. 52 and 54 in our list. We could find the species only at the Madatapa lake, yet in the range of hundreds of individuals, a high abundance as compared to Bartenev's single male. Individuals found at the discharge (loc. 53) of Madatapa lake were considered part of the lake population.

Located above 2 000 m a.s.l. and with a surface of over 880 ha, Madatapa lake had clear water. The sampled section at the southwestern edge of the lake (loc. 52; cf. Fig. 7) was almost completely overgrown with both submerged and emerged vegetation, namely *Potamogeton natans*, *P. gramineus, P. lucens, Myriophyllum spicatum,* and *Poligonum amphibium*. A dense belt of *Carex acuta* and *C. vesicaria* stretched 20–50 m from the embankment into the shallow water. With increasing distance to the shore this broad belt of tall sedges was interrupted and merged into large patches of *Eleocharis palustris* agg. in at least knee-deep water, interspersed with *Sagittaria sagittifolia, Utricularia vulgaris,* and *Lemna trisulca.*

Helophytic vegetation of specific structure and density has previously been reported to be a key factor for *C. armatum* in many sites of this species (e.g., Bouwman & Ketelaar 2008; Winkler et al. 2009), which can be confirmed here. Whilst *C. lunulatum* also frequented the *Eleocharis*-patches, *C. armatum* appeared to be separated from the tall sedge belt by an invisible fence and obviously only *Eleocharis* fulfilled its microhabitat requirements of vegetation structure. Regarding this and in view of altitude, vegetation structure and the surrounding landscape character of an open mountain steppe, the conditions resembled the second known southern disjunct mountain population of *C. armatum* which was found in 2009 in the Kyrgyz Tian Shan at a synclinal high valley (Schröter 2010b). Both the Georgian and Kyrgyz populations are geographically isolated from the

main range of this transpalaearctic boreal species by vast deserts and semi-deserts. From this we can assume that, apart from microhabitat vegetation structure, treeless mountain steppe with continental climate above 2 000 m a.s.l. might be the common denominator for the existence of southern relict populations of *C. armatum*. The area examined by us and defined as loc. 52 covered only a small fraction of the extensive riparian vegetation along the embankment of the large Madatapa lake. It can be assumed that the overall local population of *C. armatum* in fact moves in the range of thousands or tens of thousands. In view of the background of records recently reported from the adjacent Armenia at about only 20 km distance (Ananian & Tailly 2013; Durand & Rigaux 2015), the Georgian population possibly functions as source population for a network of smaller populations stretching into Armenia and – quite likely – Eastern Turkey, where the species has been anticipated to occur by Kalkman (2006).

Coenagrion lunulatum

Coenagrion lunulatum was discovered in Georgia on the Javakheti volcanic plateau of the Armenian highland by Bartenev (1909). Over a century later we confirm the occurrence of this species at two lakes already mentioned by Bartenev (1909), where it turned out to be the most abundant odonate species. Only four days later, on 06-vii-2014, the same species was also encountered at nearby Tabatskuri lake by Rodríguez Martínez & Conesa García (2015). Bartenev (1912c) mentioned two other males collected by K.A. Satunin on 23-viii-1906 on the Black Sea coast at Kobuleti, which, in view of the phenology and geographical position, is more than doubtful. In the Mediterranean, this Eurosiberian species is strictly confined to mountainous areas (Boudot et al. 2009), why a late August record of *C. lunulatum* from the subtropical Black Sea coast of the Colchic depression is erroneous with absolute certitude. All other few records available referred to lakes of the Javakheti volcanic plateau or its slopes (Bartenev 1909, 1913). Thus we assume that in Georgia, like *C. pulchellum*, also *C. lunulatum* is generally confined to higher altitudes of Samtskhe-Javakheti region and Georgian sites are part of a larger regional population including the adjacent Armenian and Turkish parts of the high plateau (Kalkman & van Pelt 2006; Ananian & Tailly 2013).

Coenagrion ponticum

We encountered *Coenagrion ponticum* throughout the country, from sea level to over 2 000 m a.s.l, in the eastern Kakheti region as well as in the south-central part and at the Black Sea coast in the very West. At two of the six sites the species bred syntopically with *C. puella*. This is in contrast to previous assumption that *C. ponticum* should be restricted to coastal areas of the Black Sea, being separated ecologically from *C. puella* by altitude (Battin 1993). According to our current knowledge no clear pattern of ecological separation of the two species could be recognized in Georgia. The same seems to apply to adjacent Turkey (Miroğlu 2011). Whilst in Armenia only *C. puella* has been found yet (Tailly et al. 2004; Ananian & Tailly 2013), *C. ponticum* has also been reported from middle altitudes in Azerbaijan (Dumont 2004). Together with our Georgian records, this confirms the earlier suggestion of Lohmann (1993) that the species is definitively not confined to the Black Sea region. Thus distribution pattern and ecological differentiation of *C. ponticum* relative to its regional congeners *C. puella* and *C. australocaspicum* (for the latter see Dumont 2004) remain puzzling. The same applies to taxonomical and phylogenetical relationship of *C. ponticum*, about which a wide range of opinions and concepts exist. Battin (1993) in his thorough morphological analysis considered *C. ponticum* to be a member of the *puella* group that includes *C. puella*, *C. intermedia*, and *C. syriacum*. Lohmann (1993) called this *puella* group, established by Battin (1993), into question and doubted its monophyletic status. In addition, Schneider (1986) had already doubted the close relationship to *C. puella* due to shape and position of the dorsal branches of the male's upper appendages and considered *C. ponticum* to be closer to *C. pulchellum* or at least emphasized a possible close relationship (cf. Beutler 1987, sub *C. syriacum*).

We have the impression that, besides the male appendages, Georgian *C. ponticum* phenotypically appear to be rather close to *C. pulchellum*. Males of *C. ponticum* showed extended black colour pattern on thorax (narrowed blue ante-humeral stripes with distinctive necking at the distal half) and abdomen (especially tergites 4–6), leading to a dark overall appearance rather resembling more to the average colour type of *C. pulchellum* in Central and Northern Europe than to *C. puella* (cf. Fig. 8). This was especial-

ly obvious at sites where *C. ponticum* and *C. puella* occurred syntopically; males of *C. ponticum* were quite easily distinguished from males of its congener even in the field. Both species, *C. ponticum* and *C. pulchellum*, apparently meet locally on the Javakheti volcanic plateau of the Armenian highland, although in very low abundances only. The overall similar appearance of *C. ponticum* and *C. pulchellum* has been already outlined by Bartenev (1929a) in his tabular comparison of the two species and in the last passage of his paper. Therein he withdrew his own records from the Black Sea coast, previously assigned to *C. pulchellum*, and stated that all older records of *C. pulchellum* (and *C. puella*) from there most likely referred to *C. ponticum*. Therefore, alleged *C. pulchellum* with distinctively uninterrupted antehumeral stripes reported from Mingrelia by Selys (1869) appear in a new light. On page 106, »*Agrion pulchellum*, Vander Linden« is annotated with the comment: »Les dix exemplaires reçus appartiennent à la variété chez laquelle la raie antéhumérale bleue (♂) ou verdàtre (♀) est entière comme chez l'*Agrion puella*, L. et non interrompue en point d'exclamation. Cette variété est au contraire peu fréquente en Europe«. This description clearly

Figure 8. Male of *Coenagrion ponticum*. Natanebi river mouth north of Kobuleti, Georgia (05-vii-2014; photograph by Jörg Adelmann)

points to *C. ponticum*, which was still unknown at that time and which in Georgia invariably showed uninterrupted but clearly necked ante-humeral stripes, sometimes reduced to a thin streak at the necking area at the distal half, which came close to the 'exclamation mark' pattern mentioned by Selys (Fig. 8 and above comment). Also Shengelia (1975) made the general remark that western Georgian *C. pulchellum* might possibly be mistaken for *C. ponticum* (sub »*C. puella syriaca* Mort.«).

Coenagrion pulchellum

Apparently *Coenagrion pulchellum* is rare in Georgia and hitherto only one reliable record was available (Bartenev 1925), taken near the town of Bakuriani at about 1 600 m a.s.l. at the northern slopes of the Javakheti volcanic plateau. Data compiled by Shengelia (1975) referring to *C. pulchellum* are partly misleading due to redundancy and circular reference. As reference for the site "Bakuriani" Akramowski (1948) is referred to who in turn specified this site as "Sakochavi" with reference to Bartenev (1925) whereas Akramowski's specified information "Sakochavi" is subsequently quoted as alleged second site by Shengelia. In fact both sites are the same single one as the small lake near Bakuriani from where Bartenev (1925) obtained his data on *C. pulchellum* is called "Sakochavi" (სკოჭავი). A further record given by Shengelia (1975) from Kumisi lake, a reservoir lake at 477 m a.s.l. in hot semi-arid open landscape northwest of Rustavi intensively used for fishing by the local population (AS unpubl.), referred to larvae collected by T. Kakauridze. Due to lack of knowledge of discriminating traits a proper identification of larvae of the genus *Coenagrion* has to be considered as impossible at that time. Even recent larval data in this area would appear highly problematic from a today's perspective as larvae of at least two of the members of the *C. puella* species group potentially present in Georgia are yet undescribed. This record therefore should be left unconsidered.

Older records of alleged *C. pulchellum* from the Black Sea coast near Kobuleti published by Bartenev have later on been withdrawn by the author himself (Bartenev 1929a, cf. 1930a). The already discussed *C. pulchellum* specimens with uninterrupted ante-humeral stripes from Mingrelia reported by Selys (1868: 106) with the outermost probability belonged to *C. ponticum* as well. Thus, in Georgia *C. pulchellum* seems to be confined to higher

altitudes of the Samtskhe-Javakheti region and mountain ranges of adjacent Autonomous Republic of Adjara. Moreover it seems to be rare throughout the Caucasus region and is apparently absent in Azerbaijan and rare in Turkey (Kalkman 2006; Boudot et al. 2009; Miroğlu et al. 2011) and Armenia. There it was recorded near Arpi lake at only about 20 km distance to our loc. 53 on the Armenian highland plateau where, like in Georgia, it is usually found in low abundances only (Ananian & Tailly 2013).

Coenagrion scitulum

Coenagrion scitulum is fairly common in the western part of Turkey but becomes increasingly rare towards the East and is one of the least recorded odonates in the Caucasus region (Schröter & Borisov 2012). From Armenia only one population is currently known (Ananian & Tailly 2013). The only two Georgian records were obtained in the 1920s by Bartenev (1929b). The *C. scitulum* data provided by Shengelia (1975) are misleading due to redundancy and circular reference. Of the three mentioned sites, "Tbilisi", "Lisi lake" and "Cherepashye lake", the reference "Tbilisi" is cited after Akramowski (1948), who in turn referred to Bartenev's (1929b) "Lisi lake" (loc. 7 in our study) and "Cherepashye lake" (loc. 4 in our study), both situated in the outskirts of Tbilisi. Thus, *C. scitulum* has actually been found before at two sites only, the Lisi and the Cherepashye lakes by Bartenev, summed up under "Tbilisi" by Akramowski.

The three sites we add here were discovered more or less randomly besides the road suggesting that this rather inconspicuous *Coenagrion* species has probably been overlooked and at least in the eastern half of Georgia might be less rare than expected.

Coenagrion vanbrinkae

This little known species is said to replace the closely related *Coenagrion ornatum* (Selys, 1850) in the eastern part of Turkey, Armenia, Azerbaijan, Georgia, Iran, Syria, and Lebanon (Lohmann 1993, Tailly et al. 2004; Kalkman 2006; Sadhegi & Mohammadalizadeh 2009; Skvortsov & Snegovaya 2014; Schneider & Dumont 2015; this study). Based on our examination of 12 ♂ and 5 ♀, Georgian populations of what has previously been assigned to *C. ornatum* in fact correspond to *C. vanbrinkae* sensu

Lohmann (1993). Compared to *C. ornatum* specimens from Germany and Greece, size and shape of male upper appendages differed, showing a different position and direction of the spine which caused a different shape of the female pronota as well. These differences were rather subtle but consistent. Recently examined specimens from Armenia and Azerbaijan agreed as well to *C. vanbrinkae* (Tailly et al. 2004; Skvortsov & Snegovaya 2014). As these morphological differences are minor only, the taxonomic status of *C. vanbrinkae* is debated (Boudot & Kalkman 2014). Due to lack of genetic data, limited reference material and limited knowledge about the morphological variation within *C. ornatum* s. str., which might be stronger than the quite uniform series from Germany and Greece suggested, we can't assess whether these differences justify full species rank. For pragmatic reasons however we list it under *C. vanbrinkae*.

Figure 9. Female of *Coenagrion vanbrinkae* of the pink colour form. North of Pasanauri (29-vi-2014; photograph by Stefan Kohl)

We found *C. vanbrinkae* at three localities whereas loc. 45 corresponds to the only previously known Georgian site or its immediate environments (Bartenev 1912a; Beutler 1987; both sub *C. ornatum*).

At loc. 45 several females showed a distinctive pink colour form, including several sexually active individuals (Fig. 9), which has not been reported yet for *C. ornatum*. However, such a pink colour form of obviously mature females has also been observed in Moroccan *C. mercuriale* (J.-P. Boudot and S. Ferreira pers. comm.).

Enallagma cyathigerum

At least two males collected at loc. 35, a lake with high salinity (conductivity >20 000 µS]), show characteristics of the taxon *risi* Schmidt, 1961, which is reported from Georgia for the first time. According to O. Kosterin (pers. comm.) our Georgian specimens represent the »intermediate between *E. c. cyathigerum* and *E. c. risi* Schmidt, 1961«, possibly as result of introgression with the nominate taxon (cf. Kosterin & Zaika 2010). *Enallagma c. risi* is found in the arid zones of Asia from the Caspian Sea in the West across Central Asia to northeastern China in the East, where it typically occurs in saline water bodies, whereas the nominate taxon prefers lakes at higher altitudes in more humid climate (Kosterin 2004). In the transition zones of rather humid mountain climate and forest-steppe, gene flow between the two taxa widely occurs. This might well also be the case in the Caucasus region and in Georgia in particular, which due to high geomorphological diversity is characterised by a tight intermeshing of vegetation and climate zones.

In this regard it appears to be noteworthy that Bartenev (1929a) described »*Enallagma cyathigerum* var. *rotundatum* var. nov.« based on specimens collected in the West Caucasus (Russia). According to Bartenev, *rotundatum* should clearly differ from nominotypical *cyathigerum* from other localities in the Transcaucasus, e.g., along the Georgian Military road. Although Bartenev's description of *rotundatum* is rather poor it might well be a senior synonym of Schmidt's *risi* and in consequence *rotundatum* would be the valid name of the taxon (cf. Kosterin 2004). The *locus typicus* of Bartenev's *rotundatum* was a group of subalpine mire lakes not immediately brought in accordance with the favourable habitat of *E. c.risi* elsewhere. According to

O. Kosterin (pers. comm.) this issue is currently worked on and a *rotundatum* topotype is under investigation.

Ischnura elegans

According to the distribution of infraspecific taxa of *Ischnura elegans* as outlined by Schmidt (1967), the areal of ssp. *pontica* Schmidt, 1938 should include Georgia. Both the description of ssp. *pontica* and Schmidt's (1967) elaborations in German language are unclear, confused, and partly contradictory. With regard to Georgian specimens of *I. elegans* his definition of spp. *pontica* remained incomprehensible to us. He personally reduced his taxon *pontica ad absurdum* by stating that males of ssp. *pontica* are indistinguishable from ssp. *tuberculata*, which in turn was said to be distributed from Finland to Bavaria (p. 211). According to the author, females of all infraspecific taxa of *I. elegans* generally do not differ structurally (p. 194). Several specimens of *I. elegans*, which had been assigned to ssp. *pontica* by Schmidt (1954) were now considered as pertaining to ssp. *ebneri* Schmidt, 1938 (p. 207 f.) whereas in the introduction Schmidt explicitly downgraded ssp. *ebneri* to a »Forma atavistica« (p. 189), which should be found in disjunct populations from Hokkaido (Japan) over Crete (Greece), southern Italy to Bonn (Germany) (p. 208). Moreover, on the same page he stated that the definition of infraspecific taxa of *I. elegans* have been made primarily for the purpose to support the 'Reinig'sche Eliminationshypothese' (Reinig 1938, 1939) he believed in at that time (Schmidt 1954). This hypothesis however is not applicable to Odonata and other insects and has later on been thoroughly refuted (Mayr 1967). Thus Schmidt's infraspecific taxa of *I. elegans* have to be considered just as a means to an end and not grounded on a scientific base. We therefore are arguing to neglect them at all. For similar reasons, with regard to Azeiri *I. elegans* Skvortsov & Snegovaya (2014) refrained from infraspecific subdivision (see also Kalkman 2006: 11; Boudot et al. 2009: 64). As the infraspecific taxonomy situation is far from clear, a major revision is needed.

Pyrrhosoma nymphula

Besides our two findings presented here – loc. 45 corresponded to the site mentioned in Beutler (1987) or at least to its immediate environments – only one record from the historical Black Sea province Mingrelia (Selys

1869: 106, sub *Agrion minium*, Harris) and one recent record from south of Borjomi are available (Reinhardt 1992). This record was taken close to our loc. 50. Thus *P. nymphula* is obviously not only one of the rarest odonate species of the country but its Georgian populations are apparently geographically isolated as the species is neither known from Azerbaijan nor from Armenia (Dumont 2004; Tailly et al. 2004; Ananian & Tailly 2013). In Turkey *P. nymphula* is scarce as well and confined to the western half of the country (Kalkman 2006; Boudot et al. 2009).

Aeshna isoceles

Georgian *A. isoceles* showed extended yellow lateral thorax stripes and well developed ante-humeral stripes, corresponding to ssp. *antehumeralis* (Schmidt, 1950). However several other *Aeshna* species are known to show extended yellow colouration with decreasing latitude (Selys 1887; Asahina 1966; Schröter 2010b, 2012). This tendency is thus probably just due to warmer climate and therefore could hardly warrant a taxonomic status unless genetic differences would appear (Kalkman 2006).

Aeshna serrata

The first confirmation of *A. serrata* on Georgian territory for over a century since its discovery by Bartenev (1909) at the same site, Madatapa lake (loc. 52). Our reconfirmation of a thriving population of this aeshnid appears to be one of the most interesting results of the project. The main range of *A. serrata* is situated along the belt of steppes, forest steppes and open landscape of temperate Asia (Peters 1985, 1987; Kosterin & Zaika 2010) and, with several isolated outposts and disjunct populations, appears to be highly fragmented especially at its western edge (Bernard & Daraż 2009). Besides single records from Armenia (Akramowski 1948, 1964) and an old record from Van area in Turkey (Morton 1914) no data are available from adjacent countries of the southern Caucasus ecoregion. However, a female reported from the Iranian West Azerbaijan province (Rastegar et al. 2013) may indicate that this species might in fact be more widespread in the region. Targeted research at further lakes of the Javakheti volcanic plateau of southern Georgia and adjacent areas of Armenia and Turkey might well reveal further populations.

In view of size and morphology, Georgian specimens were virtually identical to those from around the Baltic Sea. Compared to this European population, however, the apparent absence of androchrome females at Madatapa lake site is noteworthy (Karjalainen 2010: 123; Wildermuth & Martens 2014: 325).

Caliaeschna microstigma

Single males of *C. microstigma* from the same population demonstrate a considerable tendency to reduced ante-humeral stripes. Several males had only a small bluish patch left at the posterior parts of the stripes. Morphologically neither adults nor exuviae however deviated from Turkish or Greek individuals (AS unpubl.).

Gomphus schneiderii

The first record for Georgia dates back to Selys (1887), who mentioned this species from Mingrelia. In accordance with Reinhardt (1992) we confirm the presence of true *Gomphus schneiderii* for Georgia. All individuals collected and photographed in view of morphology and colouration were typical *G. schneiderii* and showed no signs of transition towards the closely related *G. vulgatissimus* (cf. De Knijf et al. 2013). They were virtually identical to specimens from southern Turkey (AS unpubl.). The same applied for all collected exuviae. We therefore assume that in Georgia only *G. schneiderii* occurs. The same seems to apply for adjacent Armenia, where only *G. schneiderii* is known so far (Tailly et al. 2004). However especially with regard to several older records the overall picture on the status of both species in the region remains puzzling. Bartenev (1930a) considered a male from Maikop at the foothills of the Russian West Caucasus as »*Gomphus vulgatissimus* trans ad *Schneideri* Selys«. In this assignment he also included records from Mingrelia reported by Selys (1887), which seems to be fairly curious as Bartenev hardly had these Mingrelian specimens at his disposal. On the other hand, a male and female collected 1911 near Sighnaghi in the Kakheti region of eastern Georgia were claimed to pertain to *G. vulgatissimus* (Bartenev 1912a). Moreover a single male of *G. vulgatissimus* was recently reported from Azerbaijan where also *G. schneiderii* is known to occur (Skvortsov & Snegovaya 2014). Reasons for this rather inconsistent picture may be manifold. Restricted general knowledge about discriminat-

ing characters and the true nature of *G. schneiderii* at that time may have played a role (Kalkman 2006: 51). Given correct determination, also single migrants of *Gomphus vulgatissimus* may have been involved here and it appears to be possible that at least the contact zone of both species might run through the eastern part of the Transcaucasian depression.

Gomphus ubadschii

This rare and little known gomphid (Data Deficient according to IUCN Red List criteria; cf. Boudot & Kalkman 2014) was rediscovered at Rioni river (loc. 73, 74), which drains the Colchic depression and flows into the Black Sea near Poti, over 80 years after a female of this species had been collected there by Bartenev (1929a: »Poti, 22.VI.1928«, sub »*Gomphus flavipes* var. *lineatus* var. n.«). Two measured exuviae turned out to be rather large compared to reference material of *G. ubadschii* from Asia Minor. With abdomen lengths of 32 mm (♂) and 34 mm (♀) two adult specimens from loc. 74 (dried in acetone) were however rather in the lower range according to data provided by Suhling & Müller (1996: range for ♂ 31–37 mm, ♀ 32–40 mm).

Due to high relief intensity of the Caucasus range and the high denudation rate the major rivers of Georgia transport huge loads of sediment. The Rioni river is only 327 km long but transports annually about 8.3 million tons of sediment that are accumulated along its course and raised to massive sandy embankments (Franz 1973). At loc. 73 and 74 we found *G. ubadschii* emerging at such embankments. *Gomphus ubadschii* could most likely be found at several further stretches of the lower course of the Rioni river between Kutaisi and the river delta at the Black Sea coast near Poti.

This Georgian population of *G. ubadschii* at the Rioni river is remarkable in several aspects. It is the northernmost occurrence of the species in the Western Palaearctic and geographically isolated as the species has neither been recorded in Armenia nor in Azerbaijan. The scattered Turkish records are situated in the western half of the country (Kalkman & van Pelt 2006; Boudot et al. 2009). Moreover the Rioni river basin has perhumid subtropical climate, which is in contrast to further populations elsewhere between Turkey, Iran, Iraq, Syria, and the deserts of Central Asia. Therefore it appears to be curious that in Georgia *G. ubadschii* has not yet been found outside the perhumid subtropical Rioni basin; long stretches of several oth-

er rivers of the continental semi-arid Kura basin structurally resemble the Rioni river and are rich in fine sand, e.g., parts of the lower courses of the Iori river and the Alazani river north of the town of Znori.

Onychogomphus assimilis

This globally threatened gomphid (Boudot & Kalkman 2014) is confined to a rather small area ranging from western Turkmenistan in the East across Iran and the Transcaucasus to Western Turkey. Our data confirm the presence of *O. assimilis* in Georgia after the species had been discovered there over a century ago by Bartenev (sub *O. fulvipennis*; Bartenev 1912a). Altogether, we observed dozens of adults and collected hundreds of exuviae, which is why we assume that in Georgia *O. assimilis* is rather widespread and probably occurs at forested middle courses of all river systems below 1 500 m a.s.l. east of the Likhi range draining both the Caucasus main range as well as the Armenian Highland. Especially some rivers draining the densely forested Trialety and Javakheti ranges at the bordering area to Armenia harboured strong populations, e.g., Mashavera, Bolnisi and Khrami rivers (Fig. 10). These results are remarkable as the Javakheti range stretches

Figure 10. Male of *Onychogomphus assimilis*. Bolnisistsqali river near Poladauri, Georgia (photograph by BK)

into the Lori province of Armenia where *O. assimilis* is rare and localised and currently only four sites are known (Ananian 2012; Ananian & Tailly 2013). Our records suggest that the species has been overlooked in northern Armenia and a targeted search at rivers draining the Javakheti and Bazum ranges appears to be most promising. With its numerous still unspoilt upper and middle river courses Georgia is expected to be of global importance for this range-limited Southwest Asian species.

Onychogomphus flexuosus

There is probably no second country in the world where this globally threatened species (Boudot & Kalkman 2014) can be encountered so easily as in Georgia. In late June, adults can be expected virtually everywhere in terrestrial habitats in open dry landscape of the colline zone of the Kura river basin (Fig. 11). Even within the capital Tbilisi it can be found by the dozen hunting on wasteland and perching alongside paths and walks (Schröter 2010a; this study). This is even more astonishing under consideration of the general scarcity of this primarily Central Asian species. It is considered as »rare throughout its range« by Boudot et al. (2009), which applies also to Turkey (Kalkman 2006) and the comparatively well explored Armenia, where it was considered as very rare by Tailly et al. (2004) with only a few recent records (Ananian & Tailly 2013). In Azerbaijan *O. flexuosus* seems to be even rarer and the only three records that could reliably be located on the Azeiri territory date back to the first half of the 19th century (Selys 1854; cf. Bartenev 1912c; Akramowski 1948; Dumont 2004). All this suggests that Georgia is a stronghold of international importance for this species. Especially the high frequency of occurrence in the capital region where it is steadily present now for more than a century is exceptional (Bartenev 1925, 1929b; Beutler 1987; Schröter 2010a, 2013; this study).

Despite the considerable number of adults we encountered it remains a mystery for us where the species actually reproduces. All our data refer to individuals observed in terrestrial habitats and despite systematic search for exuviae we didn't manage to find even one. Whilst Schröter (2010a) reported at least five pairs *in copulae* we neither noticed a single mating pair nor any other signs of reproduction. This is an obvious contrast to its also scarce congener *O. assimilis*. We therefore assume phenological and life-

cycle differences for these opposed results. However, available phenological data of both species are scanty and hardly sufficient to be interpreted in a meaningful way. Histograms of flight periods of both species from adjacent Turkey could be interpreted as indicating that *O. flexuosus* might reach its peak two weeks earlier than *O. assimilis* (Kalkman & van Pelt 2006: 114). Even if this was true, the phenological differences are negligible and can't explain our failure to find *O. flexuosus* exuviae. At the Vakhsh river at the "Tigrovaya Balka" reserve in southern Tajikistan, exuviae have even been collected as late as August (Dumont et al. 1992). Thus rather place than time might be the reason for the different results we obtained. Indeed, our data of *O. flexuosus* are spatially concentrated to the Kura river valley. Loc. 3 for instance, where around 50 individuals were observed, was only 2 km away from the Kura river. However, of all larger rivers visited the Kura was only very sketchily examined for exuviae. We therefore assume that the numerous individuals of *O. flexuosus* present in the capital region actually originated from the Kura river.

The knowledge on the ecology of *O. flexuosus* seems to be limited and with regard to the larval habitat virtually nothing is known (Dumont et al 1992; Suhling & Müller 1996: 201; Kalkman 2006; Borisov & Haritonov 2008). Adults of *O. flexuosus* apparently wander around widely and our data suggest that rendezvous sites are situated away from the water whereas embankments and immediate surroundings of rivers are only used for foraging and maturation (Schröter 2010a), as it was the case with a single female at loc. 38 of the Iori river (Fig. 12). Similar observations on gravelly floodplains of large rivers without reproduction activity are also known from Kyrgyzstan (AS unpubl.; cf. Schröter 2010b). Individuals recently observed in adjacent Armenia were also found perching on rocky slopes and alongside roads (Ananian & Tailly 2013), which corresponds to our idea of the species occurrence in Georgia.

Onychogomphus forcipatus albotibialis

The most abundant and widespread Georgian species of Gomphidae. The majority of exuviae we collected shows well developed lateral spines on four abdominal segments including S6, which is usually considered a discriminating character for ssp. *forcipatus* (Juliand & Juliand 1994; Seiden-

Figure 11. Male of *Onychogomphus flexuosus*. Davit Gareja monastery, Georgia (28-vi-2014; photograph by BK)

Figure 12. Female of *Onychogomphus flexuosus*. Iori river southeast of Sagarejo, Georgia (28-vi-2014; photograph by Stefan Kohl)

busch 1995; Suhling & Müller 1996). On the other hand, all adults collected showed discriminating morphological traits provided by Boudot et al. (1990) and Suhling & Müller (1996; 2006) for typical ssp. *albotibialis*. Based on the examination of adults Reinhardt (1992) stated that Georgian *O. forcipatus* pertained to ssp. *albotibialis*. Suhling & Müller (1996) subsequently analysed a series of exuviae collected by Reinhardt (1992) at the Vere river (identical to the river of our loc. 6, 8) which turned out to be heterogeneous regards the presence of lateral spines on abdominal segment 6 and therefore assumed that Georgia might be part of an intergradation zone of ssp. *albotibialis* and ssp. *forcipatus*. However, the fact that all adults reported from Georgia yet were typical ssp. *albotibialis* without exception (Schröter 2010a; this study) may cast a different light on the apparent discrepancy of infraspecific affiliation between adults and exuviae. As in the case of Transcaucasian *Cordulegaster* species (see below) it has to be noted that all measurement data and descriptions of larvae and exuviae of ssp. *albotibialis* provided in literature were based on exuviae from Western Turkey only (Seidenbusch 1995; Suhling & Müller 1996). It is quite likely that exuviae of ssp. *albotibialis* from areas of Eastern Turkey may feature the same combinations of characters than our exuviae collected in adjacent Georgia. The same could be assumed of exuviae from adjacent Armenia and Azerbaijan, where based on diagnosis of adults, *O. forcipatus* has recently been recognised as clearly pertaining to ssp. *albotibialis* (Dumont 2004; Ananian & Tailly 2013). Therefore it may be well possible that the range of morphological variation of larvae of ssp. *albotibialis* is broader than expected. The function of the spines of dragonfly larvae is not entirely understood and their efficiency as taxonomically valid discriminator is questionable. In *Leucorrhinia dubia* (Vander Linden, 1825) spines were developed depending on the presence of fish predators (Johannson & Samuelsson 1994; Flenner et al. 2009). However, this does not apply to burrowing gomphid larvae (Corbet 1999: 155; Suhling & Müller 1996: 84), suggesting that yet unknown environmental factors are involved (F. Suhling pers. comm.).

***Cordulegaster* sp.**

Exuviae and larvae collected at several sites in Adjaria in the Colchic lowland showed an extraordinary combination of features, which did not fit

to any set of characters known yet from western Palaearctic *Cordulegaster* species (C. Brochard pers. comm.). Besides peculiar hairy outer edges of the prementa these larvae and exuviae showed traits of both the '*boltonii* group' and the '*bidentata* group' *sensu* Verschuren (1989; see also Boudot 2001). Thus this basic dichotomy as backbone of available identification keys of larvae of western Palaearctic *Cordulegaster* species is not applicable on larvae from western Georgia, raising the question whether a yet unknown taxon could be involved. On the other hand, virtually all measurement data and descriptions of larvae of the eastern subgroup of the '*boltonii* group'

Figure 13. *Cordulegaster mzymtae* male. East of Goderdzi pass, Georgia (30-vii-2015; photograph by Elias Schneider)

Figure 14. Male of *Cordulegaster insignis charpentieri*. Tbilisi, Georgia (11-vi-2015; photograph by MS)

and the '*bidentata* group' are based on material from Greece and Turkey only (Verschuren 1989). Against this background it is likely that the variation range of Georgian representatives of both species groups – i.e., *Cordulegaster picta*, *C. mzymtae* (Fig. 13) and *C. insignis charpentieri* (Fig. 14) – could just be broader than expected.

Libellula pontica

The first Georgian records of *L. pontica* date back to Hagen (1863), Selys (1887) and Bartenev (1912a, 1916, sub *Leptetrum rubrum*). Since that not even a handful of records are known and whilst Selys' records are from Mingrelia, the majority of our data (just as Hagen's and Bartenev's) were obtained in the Alazani river valley in the East of the country. We found strong populations next to the road with dozens of individuals (Fig. 15), suggest-

Figure 15. Immature male of *Libellula pontica*. Alazani river valley west of Eniseli, Georgia (25-vi-2014; photograph by BK)

ing that the species might be rather widespread in the Kakheti region. In contrast it is apparently very rare in Azerbaijan and Armenia, where hitherto only single individuals came to known (Ananian 2012; Ananian & Tailly 2013; Skvortsov & Snegovaya 2014). The vital populations in eastern Georgia are therefore of international importance for this generally rare species.

The duration of the embryonic development of *L. pontica* was hitherto unknown. We determined a minimum of 13 days under changing expedition conditions where temperatures were more or less similar to natural conditions in the waterbodies. This corresponds to the data of Münchberg (1931) for *Libellula fulva* with 12 days found at a temperature of 23°C. Therefore a minimum duration of the embryonic development in the field can be considered of about two weeks.

Selysiothemis nigra

New to the fauna of Georgia. Due to hydro-ingeneering and increasing number of artificial water bodies in arid regions, *S. nigra* recently showed positive trends in many countries (Boudot et al. 2009; Uboni et al. 2015) why the first record for Georgia was long overdue. The habitat where we found the species, large dam lakes in the arid Iori table land, could therefore be considered as typical. From Armenia and Azerbaijan also just a handful of records are known so far (Dumont 2004; Ananian & Tailly 2013) which might reflect a low level of odonatological exploration of the arid areas rather than real rareness. In the case of Georgia we assume further populations of *S. nigra* to be found in the steppes and semi deserts in the southeastern corner of the country.

Acknowledgements

We are grateful to all participants who contributed to the outcome of the tour: Jörg Adelmann, Jörg Arlt, Natia Berdzenishvili, Burkhard Grebe, Petra Grebe, Stefan Kohl, Martin Lemke, Badri Meparishvili, Michael Post, Hanns-Jürgen Roland, Jürgen Ruddek, and Silke Tesch. We owe special thanks to Zurab Shevardnadze for his friendship and continuous support and Natia Berdzenishvili and Badri Meparishvili for excellent guidance and patently taking care of the exalted needs of dragonfly hunters in Georgia.

We are greatly obliged to Oleg Kosterin for providing an expert assessment on *Enallagma cyathigerum risi* and to Jean-Pierre Boudot for intensive exchange and great readiness to help during various stages of the writing process. Heinrich Fliedner kindly gave etymological and linguistic advice, Angelika Borkenstein gave phototechnical support, and Stefan Kohl, Jörg Adelmann, and Elias Schneider kindly provided outstanding photographs of Georgian dragonflies. Silke Tesch provided hydrochemical data, Christophe Brochard and Richard Seidenbusch shared with us their comprehensive knowledge on exuviae and Vincent Kalkman, Henri Dumont, Frank Suhling, Hansruedi Wildermuth, Matti Hämäläinen, and Milen Marinov gave many valuable comments which greatly improved the manuscript. The FAN(B)-foundation gave financial support and Martin Schorr helped with literature. Natia Berdzenishvili and Levan Mumladze kindly checked the spelling of the Georgian toponyms. We are indebted to them all.

References

Akramowski N.N. 1948. [The Dragonfly fauna of the Soviet Armenia]. *Zoologicheskii Sbornik, Akademya Nauk Armyanskoi SSR* 5: 117-188 [In Russian]

Akramowski N.N. 1964. [Additions to the dragonfly fauna of eastern Transcaucasus (Insecta: Odonata). *Izvestiya Akademii Nauk Armyanskoj SSR* 17: 99-101 [In Russian]

Akramowski N.N. & Shengelia E.S. 1967. Neue Angaben über *Cordulegaster mzymtae* Barteneff, 1930. *Deutsche entomologische Zeitschrift* 14: 313-321

Ananian V. 2012. New finds of 'critical' species of Odonata in Armenia – *Onychogomphus assimilis* and *Libellula pontica*. *Brachytron* 15: 36-42

Ananian V. & Tailly M. 2013. Additions to the dragonfly (Odonata) fauna of Armenia, with new records of rare or uncommon species. *Russian entomological Journal* 22: 249-254

Asahina S. 1966. The Afghan Odonata taken by Dr. Josii in 1960. *Publications of Kyoto University* 3: 159-163

Bartenev A.N. 1909. [Odonata of the Kars excursion]. *Trudy Studencheskogo Kruzhka dlya issledovaniy russkoy prirody pri Moskovskom universitete* 4: 63-75 [In Russian]

Bartenev A.N. 1910. [On the Odonata fauna of the Kuban Oblast]. *Revue russe d'Entomologie* 10: 27-38 [In Russian]

Bartenev A.N. 1912a. [On a collection of dragonflies from the Transcaucasus of the summer 1911]. *Raboty laboratorii Zoologicheskago kabineta Imperatorskago Varshavskago Universiteta* (1912): 132-161 [In Russian, English subheadings]

Bartenev A.N. 1912b. [The Palaearctic and East Asian species and subspecies of the genus Calopteryx Leach (Odonata, Calopterygidae)]. *Raboty laboratorii Zoologicheskago kabineta Imperatorskago*

Varshavskago Universiteta [1911]: 63-257 [In Russian]

Bartenev A.N. 1912c. Über eine Kollektion von Odonaten des Kaukasischen Museums von Tiflis. [*Proceedings of the Caucasian Museum*] 7: 107-116 [In Russian, German title]

Bartenev A.N. 1916. Notices sur les Odonates des environs de la ville Signach, gouvernement de Tiflis. *Revue russe d'Entomologie* 16: 343-345 [In Russian, French title]

Bartenev A.N. 1919. [Notes on the Odonata of the Transcaucasus]. [*Proceedings of the Caucasian Museum*] 12: 196-199 [In Russian]

Bartenev A.N. 1925. [On the odonate fauna of the Caucasus]. *Bulletin du Musée de Géorgie* 2: 28-86 [In Russian]

Bartenev A.N. 1929a. Neue Arten und Varietäten der Odonaten aus dem West-Kaukasus. *Zoologischer Anzeiger* 85: 54-68

Bartenev A.N. 1929b [Odonata from Tbilisi and other regions of Georgia]. *Bulletin du Musée de Géorgie* 5: 65-86 [In Russian]

Bartenev A.N. 1930a. [Materials to the knowledge of the Odonata fauna of the Western Caucasus]. *Trudy Severo-Kavkazskoy assotsiatsii nauchno-issledovatel'skikh institutov* 72: 1-138 [In Russian]

Bartenev A.N. 1930b. Über *Calopteryx splendens* und ihre Biotypen, besonders die westasiatischen. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 58: 521-540

Battin T.J. 1993. Revision of the *puella* group of the genus *Coenagrion* Kirby, 1890 (Odonata, Zygoptera), with emphasis on morphologies contributing to reproductive isolation. *Hydrobiologia* 262: 13-29

Belyshev B.F. 1961. Notes on the fauna of Odonata of Eastern Kazakhstan. *Fragmenta faunistica* 9: 27-42 [In Russian, English title and abstract]

Belyshev B.F. 1964. [Odonata fauna of the Upper Ob' river basin]. Strekozy Sibiri. Trudy Vostochno-Sibirskogo filiala Akademii Nauk SSSR. Seriya biologicheskaya. [Dragonflies of Siberia. Proceedings of the East Siberian Branch of the Academy of Sciences of the USSR] 40: 4-70 [In Russian]

Belyshev B.F. 1973. The dragonflies of Siberia (Odonata). Nauka, Novosibirsk. Vol. 2: 333-620 [In Russian, English title]

Berg L.S. 1959. Die geographischen Zonen der Sowjetunion. Band 2. B.G. Teubner Verlagsgesellschaft, Leipzig

Bernard R. & Daraż B. 2010. Relict occurrence of East Palaearctic dragonflies in Northern European Russia, with first records of *Coenagrion glaciale* in Europe (Odonata: Coenagrionidae). *International Journal of Odonatology* 13: 39-62

Beschovski V.L. 1994. Insecta, Odonata. Fauna bulgarica 23. Aedibus Academiae Scietarum Bulgaricae, Sofia.

Beutler H. 1987. Odonaten aus dem Kaukasus und Transkaukasien (Georgische SSR, UdSSR). *Notulae odonatologicae* 2: 137-139

Borisov S.N. & Haritonov A.Y. 2007. The Dragonflies (Odonata) of Middle Asia. Part 1 (Caloptera, Zygoptera). *Euroasian entomological Journal* 6: 343-360 [In Russian, English abstract]

Borisov S.N. & Haritonov A.Y. 2008. The Dragonflies (Odonata) of Middle Asia. Part 2 (Anisoptera). *Euroasian entomological Journal* 7: 97-123 [In Russian, English abstract]

Boudot J.-P. 2001. Les *Cordulegaster* du Paléarctique occidental: identification et répartition (Odonata, Anisoptera, Cordulegastridae). *Martinia* 17: 1-34

Boudot J.-P., Jacquemin G. & Dumont H.J. 1990. Revision of the subspecies of *Onychogomphus forcipatus* (Linnaeus, 1758) in Europa and Asia Minor, and the distribution of *Onychogomphus forcipatus unguiculatus* (Vander Linden, 1823) (Odonata: Gomphidae). *Bulletin et Annales de la Société royale Belge d'Entomologie* 126: 95-111

Boudot J.-P., Kalkman V.J., Azpilicueta Amorín M., Bogdanović T., Cordero Rivera A., Degabriele G., Dommanget J.L., Ferreira S., Garrigós B., Jović M., Kotarac M., Lopau W., Marinov M., Mihoković N., Riservato E., Samraoui B. & Schneider W. 2009. Atlas of the Odonata of the Mediterranean and North Africa. *Libellula Supplement* 9: 1-256

Boudot J.-P. & Kalkman V.J. 2014. Chapter 5. Odonata (dragonflies and damselflies). In: Smith K.G., Barrios V., Darwall W.R.T. & Numa C. (Eds), The Status and Distribution of Freshwater Biodiversity in the Eastern Mediterranean. Cambridge, UK, Malaga, Spain and Gland, Switzerland: IUCN

Bouwman J.H. & Ketelaar R. 2008. New records of *Coenagrion armatum* in Schleswig-Holstein (Odonata: Coenagrionidae). *Libellula* 27: 185-190

Brullé G.A. 1832. Expédition scientifique de Morée. Section des sciences physiques. Vol. 3(1), Zoologie. Deuxième section. – Des animaux articulés. Dictyoptères: 98-106. Levrault, Paris

Chaplina I.A., Dumont H.J., Haritonov A.Y. & Popova O.N. 2007. A review of the Odonata of Kazakhstan. *Odonatologica* 36: 349-364

Corbet P.S. 1999. Dragonflies. Behavior and ecology of Odonata. Cornell University Press, Ithaca

De Knijf G., Vannappelghem C. & Demolder H. 2013. Odonata from Montenegro, with notes on taxonomy, regional diversity and conservation. *Odonatologica* 41: 1-29

Dijkstra K.-D.B. 2006. *Lestes*, Leach 1815 – Spreadwings. In: Dijkstra K.-D.B. & Lewington R. (Eds), Field guide to the dragonflies of Britain and Europe: 81. British Wildlife Publishing, Gillingham

Dumont H.J. 2004. Dragonflies from Azerbaijan. *Zoology in the Middle East* 31: 87-92

Dumont H.J. 2006. *Calopteryx*, Leach 1815 – Demoiselles. In: Dijkstra K.-D.B. & R. Lewington (Eds), Field guide to the dragonflies of Britain and Europe: 66. British Wildlife Publishing, Gillingham

Dumont H.J., Demirsoy A. & Verschuren D. 1987. Breaking the *Calopteryx*-bottleneck: taxonomy and range of *Calopteryx splendens waterstoni* Schneider, 1984 and of *C. splendens tschaldirica* Bartenef, 1909 (Zygoptera: Calopterygidae). *Odonatologica* 16: 239-247

Dumont H.J., Haritonov A.Y. & Borisov N. 1992. Larval morphology and range of three West Asiatic species of the genus *Onychogomphus* Selys, 1854 (Insecta: Odonata). *Hydrobiologia* 245: 169-177

Durand E. & Rigaux J. 2015. Further additions to the knowledge of the odonate fauna of Armenia, with first record of *Pantala flavescens* (Odonata: Libellulidae). *Notulae odonatologicae* 8: 184-190

Eichwald K.E. 1837. Reise auf dem Kaspischen Meere und in den Kaukasus. Band 1. Cotta, Stuttgart

Ferreras Romero M. & Puchol Caballero V. 1984. Los insectos Odonatos en Andalu-

cía. Bases para su estudio faunístico. Servicio de Publicaciones de la Universidad de Córdoba, Textos e Instrumentos 9, Córdoba

Flenner I., Olne K., Suhling F. & Sahlén G. 2009. Predator-induced spine length and exocuticle thickness in *Leucorrhinia dubia* (Insecta: Odonata): a simple physiological trade-off? *Ecological Entomology* 34: 735-740

Franz H.-J. 1973. Physische Geographie der Sowjetunion. Hermann Haack, Gotha

Grand D. & Boudot J.-P. 2006. Les libellules de France, Belgique et Luxembourg. Biotope, Mèze (Collection Parthénope)

Hagen H.A. 1863. Die Odonaten- und Neuropteren-Fauna Syriens und Klein-Asiens. *Wiener entomologische Monatsschrift* 7: 193-199

Hartung M. 1993. What is the true *Lestes virens virens* (Charpentier, 1825)? Book of abstracts of the XII International Symposium of Odonatology in Osaka: 11-12

International Commission on Zoological Nomenclature 1999. International code of zoological nomenclature. Fourth edition. The International Trust for Zoological Nomenclature, London

Javakhishvili A.N. (Ed.). 1964. [Atlas of the Georgian Soviet Socialist Republic]. Glavnoe Upravlenie Geodezii i Kartografii Gosudarstvennogo Geologičeskogo Komiteta SSSR. Tbilisi [In Russian]

Jödicke R. 1997. Die Binsenjungfern und Winterlibellen Europas. Lestidae. Die Neue-Brehm-Bücherei 631. Westarp, Magdeburg

Jödicke R. 2003. Mid-winter occurrence of dragonflies in southern Tunisia (Insecta: Odonata). *Kaupia* 12: 119-128

Johansson F. & Samuelsson L. 1994. Fish-induced variation in abdominal spine length of *Leucorrhinia dubia* (Odonata) larvae? *Oecologia* 100: 74-79

Juliand P. & Juliand C. 1994. Sur l'identification des exuvies d'*Onychogomphus forcipatus forcipatus* (L., 1758) et *Onychogomphus forcipatus unguiculatus* (Vander Linden, 1820). *Martinia* 10: 3-5

Kalkman V.J. 2006. Key to the dragonflies of Turkey, including species known from Greece, Bulgaria, Lebanon, Syria, the Trans-Caucasus and Iran. *Brachytron* 10: 3-82

Kalkman V.J. & van Pelt G.J. 2006. The distribution and flight period of the dragonflies of Turkey. *Brachytron* 10: 83-153

Kolenati F.A. 1846. Insecta Caucasi. Coleoptera, Dermaptera, Lepidoptera, Neuroptera, Mutillidae, Aphaniptera, Anoplura. *Meletemata entomologica* 5: 113-115

Kosterin, O. E. 2004. Odonata of the Daurskiy State Nature Reserve area, Transbaikalia, Russia. *Odonatologica* 33: 41-71

Kosterin O.E & Zaika V.V. 2010. Odonata of Tuva. *International Journal of Odonatology* 13: 277-328

Lauer W. & Rafiqpoor M.D. 2002. Die Klimate der Erde – Eine Klassifikation auf der Grundlage der ökophysiologischen Merkmale der realen Vegetation. Erdwissenschaftliche Forschung Vol. 40. Franz Steiner, Stuttgart

Lohmann H. 1993. *Coenagrion vanbrinki* spec. nov. und *C. persicum* spec. nov. aus Vorderasien (Zygoptera: Coenagrionidae). *Odonatologica* 22: 203-211

Lydolph P.E. 1977. Climates of the Soviet Union – World Survey of Climatology Volume 7. Elsevier, Amsterdam, Oxford, New York

Mayr E. 1967. Artbegriff und Evolution. Parey, Hamburg

Miroğlu A. & Kartal V. 2008. Additional notes on the Odonata fauna of Kurupelit (Samsun, Turkey). *Turkish Journal of Zoology* 32: 33-41

Miroğlu A., Kartal V. & Salur A. 2011. Odonata of the eastern Black Sea region of Turkey, with some taxonomic notes. *Odonatologica* 40: 105-122

Misof B., Anderson C.L. & Hadrys H. 2000. A phylogeny of the damselfly genus *Calopteryx* (Odonata) using mitochondrial 16S rDNA markers. *Molecular Phylogenetics and Evolution* 15: 5-14

Mittermeier R.A., Gil P.R., Hoffmann M., Pilgrim J., Brooks T., Mittermeier C.G., Lamoreaux J. & Da Fonseca G.A.B. 2004. Hotspots Revisited. Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, Mexico City

Morton K.J. 1914. Notes on a collection of Odonata from Van, Turkey in Asia. *The Entomologist's monthly Magazine* 50: 56-59

Münchberg P. 1931. Beiträge zur Kenntnis der Biologie der Odonatengenera *Libellula* L., *Orthetrum* Newm. und *Leucorrhinia* Britt. in Nordostdeutschland. *Abhandlungen und Berichte der naturwissenschaftlichen Abteilung der Grenzmärkischen Gesellschaft zur Erforschung und Pflege der Heimat* 6: 128-145

Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-845

Nakhutsrishvili G. 2013. The Vegetation of Georgia (South Caucasus). Springer, Berlin, Heidelberg

Olias M., Weihrauch F., Bedjanič M., Hacet N., Marinov M. & Šalamun A. 2007. *Lestes parvidens* and *L. viridis* in southeastern Europe: a chorological analysis (Odonata: Lestidae). *Libellula* 26: 243-272

Olson D.M. & Dinerstein E. 2002. The Global 200: Priority ecoregions for conservation. *Annals of the Missouri Botanical Garden* 89: 199-224

Peters G. 1985. Die Libellenfauna der westlichen und nördlichen Mongolei und einige Phänomene ihrer intrakontinentalen Isolation. *Mitteilungen des Zoologischen Museums Berlin* 61: 11- 42

Peters G. 1987. Die Edellibellen Europas: Aeshnidae. Die Neue Brehm Bücherei 585. Ziemsen, Wittenberg

Radde G. 1899. Die Sammlungen des Kaukasischen Museums, Band 1. Verlag des Kaukasischen Museums Tiflis

Rastegar J., Havaskary M., Khodaparast S. & Rafeii A. 2013. A contribution to the knowledge of Odonata (Insecta) from West Azerbaijan province, northwestern Iran. *Entomofauna* 34: 369-375

Reinhardt K. 1992. Beobachtungen von Libellen an Fließgewässern in Georgien (Odonata). *Entomologische Nachrichten und Berichte* 36: 243-248

Reinig W.F. 1938. Elimination und Selektion. Eine Untersuchung über Merkmalsprogressionen bei Tieren und Pflanzen auf genetisch- und historisch-chorologischer Grundlage. Gustav Fischer, Jena

Reinig W.F. 1939. Die genetisch-chorologischen Grundlagen der gerichteten geographischen Variabilität. *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 76: 260-308

Rodríguez Martínez D. & Conesa García M.A. 2015. *Coenagrion lunulatum* (Charpentier, 1840) & *Sympetrum flaveolum* (L., 1758) in Lake Tabatskuri, Georgia (Caucasus). *Boletín de la Asociación odonatológica de Andalucía* 3: 18-24

Sadeghi S. 2008. Aspects of infraspecific phylogeography of *Calopteryx splendens*. (Calopterygidae, Odonata). PhD Thesis, Gent University

Sadeghi S. & Mohammadalizadeh J. 2009. Additions to the Odonata fauna of Iran. *Iranian Journal of Science and Technology* 33: 355-359

Sadeghi S. & Dumont H.J. 2014. Variation in the shape of the wings and taxonomy of Eurasian populations of the *Calopteryx splendens* complex (Odonata: Calopterygidae). *European Journal of Entomology* 111: 575-583

Sadeghi S., Adriaens D. & Dumont H.J. 2009. Geometric morphometric analysis of wing shape variation in ten European populations of *Calopteryx splendens* Harris (1782) (Zygoptera: Odonata). *Odonatologica* 38: 343-360

Samraoui B., Weekers P.H.H. & Dumont H.J. 2003. Two taxa within the North African *Lestes virens* complex (Zygoptera: Lestidae). *Odonatologica* 32: 131-142

Schäfer M.C. 2003. Klimazonierung von Georgien – Dokumentation und Kritik bestehender Klimaklassifikationen anhand von langjährigen Klimadaten und mittels eines Geographischen Informationssystems. Staatsexamensarbeit Universität Gießen

Schmidt E. 1939. Odonaten aus Syrien und Palästina. *Sitzungsberichte der Akademie der Wissenschaften Wien, mathematisch-naturwissenschaftliche Klasse, Abteilung I* 147: 135-150

Schmidt E. 1954. Die Libellen Irans. *Sitzungsberichte der Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Klasse, Abteilung I*, 163: 223-260, 1 pl.

Schmidt E. 1961. Ergebnisse der Deutschen Afghanistan-Expedition 1956 der Landessammlung für Naturkunde Karlsruhe sowie der Expedition J. Klapperich, Bonn 1952–53 und Dr. K. Lindberg, Lund (Schweden) 1957–60. Libellen (Odonata). *Beiträge zur naturkundlichen Forschung in Südwestdeutschland* 19: 399-435

Schmidt E. 1967. Versuch einer Analyse der *Ischnura elegans*-Gruppe (Odonata, Zygoptera). *Entomologisk Tidskrift* 88: 188-225

Schneider W. 1986. Systematik und Zoogeographie der Odonata der Levante unter besonderer Berücksichtigung der Zygoptera. Dissertation, Universität Mainz

Schneider T. & Dumont H.J. 2015. Odonata records from southern Iran. *Notulae odonatologicae* 8: 137-156

Schneider T. & Schneider E. 2013. Beobachtungen zur Gefährdung der Fließgewässer und ihrer Libellen in der türkischen Schwarzmeerregion (Odonata). *Libellula* 32: 75-90

Schröter A. 2010a. On a collection of dragonflies from eastern Georgia, with the first record of *Sympetrum arenicolor* (Odonata: Libellulidae). *Libellula* 29: 209-222

Schröter A. 2010b. The Odonata of Kyrgyzstan, part I – Critical national checklist, annotated list of records and collected data of the summer half-years 2008 and 2009. *International Dragonfly Fund Report* 28: 1-72

Schröter A. 2011. Book review: Skvortsov, V.E. 2010. The dragonflies of Eastern Europe and Caucasus: An illustrated guide. KMK Scientific Press Ltd. Moscow. In: Reinhardt K., Schorr M. & Marinov M. (Eds), Odonatological Abstract Service published by the International Dragonfly Fund (IDF) in cooperation with the Worldwide Dragonfly Association (WDA) 30: 57-69

Schröter A. 2012. Obere vertikale Verbreitungsgrenze und Habitatspektrum von *Aeshna juncea* im kirgisischen Tian Shan (Odonata: Aeshnidae). *Libellula Supplement* 12: 49-76

Schröter A. 2013. Sammel- und Fotoreise nach Georgien. *Libellennachrichten* 29: 13-15

Schröter A. & Borisov S.N. 2012. *Coenagrion scitulum* in Central Asia: a biogeographical analysis and rectification (Odonata: Coenagrionidae). *Libellula* 31: 267-283

Seidenbusch R. 1995. Comparison of the last instar larvae of *Onychgomphus flexuosus* Schneider, 1845 and *Onychogomphus forcipatus albotibialis* Schmidt, 1954. Sulzbach-Rosenberger Libellenrundbriefe 2. Selbstverlag, Sulzbach-Rosenberg

Selys Longchamps de E. 1853. Synopsis des Calopterygines. *Bulletins de l'Académie royale des Sciences, des Lettres et des Beaux-arts de Belgique* 20: 1-73

Selys Longchamps de E. 1869. Note sur les névroptères odonates recueillis en Mingrélie en 1868 par M. Théophile Deyrolle. *Annales de la Société entomologique de Belgique* 12: 105-106

Selys Longchamps de E. 1884. Révision des Diplax paléarctiques. *Annales de la Société entomologique de Belgique* 28: 29-45

Selys Longchamps de E. 1887. Odonates de l'Asie Mineure et révision de ceux des autres parties de la faune dite Européenne. *Annales de la Société entomologique de Belgique* 31: 1-85

Shengelia E.S. 1953. [The dragonflies (Odonata) of Georgia]. *Trudy Instituta Zoologii* 11: 147-165 [In Georgian, Russian summary]

Shengelia E.S. 1964. [Dragonflies (Odonata) in the alpine fauna of the High Caucasus within the limits of Georgia]. In: Fauna vysokogorya Bolshogo Kavkaza v predelakh Gruzii. Meznierebа, Tbilisi [In Russian]

Shengelia E.S. 1975. [The dragonflies (Odonata) of Georgia]. *Materialy k Faune Gruzii* 5: 61-81 [In Russian]

Skvortsov V.E. 2010. The dragonflies of Eastern Europe and Caucasus: An illustrated guide. KMK Scientific Press, Moscow

Skvortsov V.E. & Snegovaya N.Y. 2014. Additions to the knowledge of the Odonata fauna of Azerbaijan, with six new records. *Notulae odonatologicae* 8: 67-76

Suhling F. & Müller O. 1996. Die Flußjungfern Europas. Gomphidae. Die Neue Brehm-Bücherei 628. Westarp Wissenschaften, Heidelberg

Tailly M., Ananian V. & Dumont H.J. 2004. Recent dragonfly observations in Armenia, with an updated checklist. *Zoology in the Middle East* 31: 93-102

Uboni C., Nadalon G. & Schröter A. 2015. Evidence of breeding of *Selysiothemis nigra* in the regions of Friuli Venezia Giulia and Veneto, northeastern Italy (Odonata: Libellulidae). *Notulae odonatologicae* 8: 128-136

Verschuren D. 1989. Revision of the larvae of West-Palaearctic *Cordulegaster* Leach, 1815 (Odonata, Cordulegastridae), with a key to the considered taxa and a discussion on their affinity. *Bulletin et Annales de la Société royale entomologique de Belgique* 125: 5-35

Wildermuth H. & Martens A. 2014. Taschenlexikon der Libellen Europas. Quelle & Meyer, Wiebelsheim

Winkler C., Neumann H. & Drews A. 2009. Verbreitung und Ökologie von *Coenagrion armatum* am südwestlichen Arealrand in Schleswig-Holstein (Odonata, Coenagrionidae). *Libellula* 28: 1-24

1st December 2015

Abdomen or wings? Comparing two body places for marking in *Mesamphiagrion laterale* (Odonata: Coenagrionidae)

Catalina Álvarez-Covelli[1], María Alejandra Álvarez-Covelli[1] & Fredy Palacino-Rodríguez[1,2]

[1] Grupo de Investigación en Odonatos de Colombia (GINOCO), Grupo de Investigación en Biología (GRIB), Departamento de Biología Universidad El Bosque, Avenida carrera 9 No. 131 A-02, Bogotá D.C., Colombia; <catalinaalvarezcovelli@gmail.com>

[2] Laboratorio de Artrópodos, Centro Internacional de Física, Universidad Nacional de Colombia, Carrera 45 No. 26-85, Bogotá D.C., Colombia; <odonata17@hotmail.com>

Received 5th January 2015; revised and accepted 5th October 2015

Abstract. To assess a marking technique that avoids alteration of wing aspect and thereby reduces the effect of marking on the organisms' behavior, adult individuals of *Mesamphiagrion laterale* (Selys, 1876) were marked on two body regions and their probability of resighting (PR) was estimated. Marks were placed as irregular spots of turquois, magenta, lime, and orange color. The PR of wing-marked individuals and abdomen-marked individuals was compared. A total PR of 80 % was detected. PR was higher when the marks were placed on the abdomen (PR = 0.72) than on the wings (PR = 0.62), but no significance was found between these recapture rates (χ^2 = 0.413). This exercise should be implemented in other odonate species to see the widespread nature of our results.

Key words. Dragonfly, damselfly, Zygoptera, South America, Colombia

Introduction

Mark–recapture techniques have been widely used to study demographic aspects in macroinvertebrates (Garmendia & Samo 2005), particularly insects such as odonates (reviewed by Cordero & Stoks 2008). In odonates, some of these techniques include the use of different colors and body locations to write the marks (e.g. Borror 1934) being the number codes on wings the more widespread (e.g. Watanabe et al. 2004; Cordero & Stoks 2008). To a minor extent, dots on the dorsal regions of the thorax (Sher-

ratt et al. 2010) and on the abdomen (Knopf 1974; Anderson et al. 2011) have been used. Marks are usually placed with permanent ink using fine point markers (Sherratt et al. 2010), but other less conventional materials such as fluorescent pigments mixed with vaseline (Knopf 1974), rubidium dissolved in water (Payne & Dunley 2002) and fluorescent or ultraviolet light inks (Röske & Hunger 2003) have been also used.
Despite the widespread use of wing-marking in odonates, it affects fitness (e.g. Banks & Thompson 1985; Fincke 1986). Because of this, some authors (e.g. Hagler & Jackson 2001) have called for a prior assessment of the marking technique. However, few researchers have evaluated the alternatives for marking odonates (Bennett & Mill 1995; Anderson et al. 2011; Palacino-Rodríguez & Contreras-Sánchez 2014). Anderson et al. (2011), for example, compared the effect of placing 3–6 color dots on the abdomen vs color marks on wing in two calopterygid species. These authors found higher resighting rates for abdomen-marked adults than wing-marked adults, so that they suggested that abdominal marking should be used rather than wing marking.

In our study we evaluated the alternative proposed by Anderson et al. (2011) with the objective to compare the effectiveness of wing marks vs abdomen marks, based on the recapture rates of individuals.

Materials and methods

Study species

Mesamphiagrion laterale (Selys, 1876) is an endemic coenagrionid of the Eastern Cordillera of Colombia and the Cordillera de Mérida in northwestern Venezuela. It occurs between 750 and 2 850 m a.s.l. in locations associated with lentic water bodies such as impoundments, small lakes and swamps, with grasses and bushes that they use as shelter (Bota-Sierra & Wolff 2013). Except for the wings, the body of adult males is black with blue spots over most of 7–9 abdominal segments. Teneral individuals are reddish in S1–3. Females exhibit great color plasticity, presenting or not the two blue color spots over S8 (Bota-Sierra & Wolff 2013).

Study area

The study was conducted in an area of 1 843 m² in the Tominé impoundment, Municipality of Guatavita, Department of Cundinamarca, Colombia (04°56'N, 73°50'W), at 2 600 m a.s.l. Predominant vegetation in the zone was *Acacia* sp. (Fabaceae), *Commelina* sp. (Commelinaceae), *Eichornia crassipes* (Pontederiaceae), and *Brachiaria* sp. (Poaceae) (cf. Palacino-Rodríguez & Contreras-Sánchez 2014).

Collecting and marking

Our study comprised a total of 70 h of fieldwork conducted on 16- and 23-ii, 02-, 09-, 16-, 23-, and 30-iii, and 06-, 13-, and 20-iv-2014, from 09:00 to 16:00 h COT (= UTC-5). The sampling days covered the rainy and dry season in this region. On the given dates, individuals were marked and, at the same time, we checked to see which marked odonates were still alive.

Altogether 392 individuals were marked, 285 on abdomen and 107 on wing (Table 1). Adults were collected with an aerial net and gently marked over the dorsal region of abdominal segments 2–4 or on the postnodal region of one of the hind wings, using fine point makers Sharpie® in turquoise, magenta, lime, and orange colors. The colors were randomly selected from the range offered by the brand (www.sharpie.com). Marking took less than a minute per individual. After marking, individuals were released in the same place where they had been collected.

Statistical analyses

A chi-square test was used to compare the probability of resighting (PR) of wing-marked individuals vs abdomen-marked individuals. Analysis was done with the software Past 2.17c (Hammer et al. 2001).

Results

Abdomen vs wing marks

The recapture rate was higher when marks were placed on the abdomen (PR = 0.72) than on the wing (PR = 0.62), but no significant difference was found between these recapture rates ($\chi^2 = 0.413$; Table 1).

Table 1. Resighting probabilities of *Mesamphiagrion laterale* according to alternatives of marking. N – total of individuals marked by body region; RC – number of individuals resighted; PR – probability of resighting. *P*-value is from χ^2-contingency tests.

Marking on	N	RC	PR	χ^2
Abdomen	285	182	0.72	
Wing	107	67	0.62	$P = 0.413$

Discussion

In the study by Anderson et al. (2011) on marking effects in the family Calopterygidae, a lower PR for wing-marked individuals as compared to those with abdomen marking (55.0 % vs 73.8 %) was interpreted in a way that wing marking may affect the occupation of a territory or fighting ability of territorial males. Anderson et al. (2011) used *Hetaerina titia* (Drury, 1773) and *Calopteryx haemorrhoidalis* (Vander Linden, 1825) as study species and adult males of these species naturally bear wing pigmentation patches that communicate territory defense (e.g. González-Santoyo et al. 2014). Wing marking in these species may thus interfere with the males' ability to defend their territory. On the other hand, Anderson et al. (2011) found that in *H. titia* males the agonistic rate from territory holders towards intruding males with abdomen marks did not show a significant difference compared to the aggression rate towards unmarked intruders. Thus, although a marking effect might be a consequence of marking in any body region, it seems that marks on the abdomen do not substantially affect the organisms' performance. However, as recommended by Anderson et al. (2011), the marks we placed on the thin abdomen of *Mesamphiagrion laterale* individuals were little spots to avoid adding weight to the abdomen and thereby affecting the damselflies' efficacy of flight.

Because the PR showed no difference between the alternatives tested in our study, we infer that abdomen marking does not significantly affect aspects such as survival or behavior of individuals. Although the marks are larger on the wings than on the abdomen, the males of *M. laterale* do not exhibit territoriality, and they do not have spots that can be used in inter- or

intrasexual aspects. We therefore assume that any of the two body regions may be used to mark *M. laterale* individuals. What's more, the markings on the abdomen do not seem to affect the ability of abdominal signalization exhibited by individuals of *M. laterale*, which has been reported for *Mesamphiagrion tamaense* (De Marmels, 1988) as another species of the genus (Bota-Sierra & wolff 2013). However, the marking effect of any of these alternatives on the fitness of coenagrionids will be studied in more detail in the future, and according experiments should be conducted with other odonate species to assess whether our results can probably be generalised.

Acknowledgements

We are grateful to Santiago Yagama and Juan Villota Burbano for providing valuable field assistance. We thank Dr. Adolfo Cordero-Rivera and M. Sc. Alexander Sabogal for scientific support in the preparation of this paper. We thank the Grupo de Investigación en Odonatos de Colombia (GINOCO), Laboratorio de Artrópodos – Universidad Nacional de Colombia, and Grupo de Investigación en Biología, Departamento de Biología, Facultad de Ciencias, Universidad El Bosque (Bogotá, Colombia) for the scientific support.

References

Anderson C.N., Córdoba-Aguilar A., Drury J.P. & Grether G.F. 2011. An assessment of marking techniques for odonates in the family Calopterygidae. *Entomologia experimentalis et applicata* 141: 258-261

Banks M.J. & Thompson D.J. 1985. Lifetime mating success in the damselfly *Coenagrion puella*. *Animal Behaviour* 33: 1175-1183

Bennett S. & Mill P.J. 1995. Pre-maturation and post-maturation survival in adults of the damselfly *Pyrrhosoma nymphula* (Zygoptera, Coenagrionidae). *Journal of Zoology* 235: 559-575

Borror D.J. 1934. Ecological Studies of *Argia moesta* Hagen (Odonata: Coenagrionidae) by means of marking. *Ohio Journal of Science* 34: 97-108

Bota-Sierra C.A. & Wolff M.I. 2013. Taxonomic revision of *Mesamphiagrion* Kennedy, 1920 from Colombia (Odonata: Coenagrionidae), with the description of four new species. *Zootaxa* 3718: 401-440

Cordero-Rivera A. & Stoks R. 2008. Mark–recapture studies and demography. In: A. Córdoba-Aguilar (Ed.), Dragonflies and damselflies: Model organisms for ecological and evolutionary research: 7-20. Oxford University Press, Oxford

Fincke O.M. 1986. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata, Coenagrionidae). *Evolution* 40: 791-803

Garmendia A. & Samo J.A. 2005. Prácticas de Ecología. Editorial de la Universidad Politécnica de Valencia

González-Santoyo I., González-Tokman D.M., Munguía-Steyer R. & Córdoba-Aguilar A. 2014. A mismatch between the perceived fighting signal and fighting ability reveals survival and physiological costs for bearers. *PLoS One* 9: e84571

Hagler J.R. & Jackson C.G. 2001. Methods for marking insects: current techniques and future prospects. *Annual Review of Entomology* 46: 511-543

Hammer Ø., Harper D.A.T. & Ryan P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia electronica* 4: 1-9

Knopf K.W. 1974. A new marking technique for studying the mating behavior of Odonata. *Florida agricultural Experiment Stations Journal Series* 57: 149-150

Palacino-Rodríguez F. & Contreras-Sánchez N.A. 2014. Does experimental marking of wings influence resighting success in *Mesamphiagrion laterale* and *Erythrodiplax umbrata*? (Odonata: Coenagrionidae, Libellulidae). *Odonatologica* 43: 237-246

Payne J.C. & Dunley J.E. 2002. Use of an elemental marker, rubidium, to study dispersal of aquatic insects. *Journal of the North American Benthological Society* 21: 715-727

Röske W. & Hunger H. 2001. Short-range dispersal of the Southern Damselfly (*Coenagrion mercuriale*, Odonata) defined experimentally using UV fluorescent ink. *Zeitschrift für Ökologie und Naturschutz* 9: 181-187

Sherratt T.N., Laird R.A., Hassall C., Lowe C.D., Harvey I.F., Watts P.C., Thompson D.J. & Cordero-Rivera A. 2010. Empirical evidence of senescence in adult damselflies. *Journal of Animal Ecology* 79: 1034-1044

Watanabe M., Matsuoka H. & Taguchi M. 2004. Habitat selection and population parameters of *Sympetrum infuscatum* (Selys) during sexually mature stages in a cool temperate zone of Japan (Anisoptera: Libellulidae). *Odonatologica* 33: 169-179

1st December 2015

Contrasting life-history patterns between vernal pond specialists and hydroperiod generalists in *Lestes* damselflies (Odonata: Lestidae)

Franz-Josef Schiel[1] & Rainer Buchwald[2]

[1] Institut für Naturschutz und Landschaftsanalyse – INULA, Turenneweg 9, 77880 Sasbach, Germany; <franz-josef.schiel@inula.de>

[2] Institut für Biologie und Umweltwissenschaften, Carl von Ossietzky Universität, IBU-A1, 26111 Oldenburg, Germany; <rainer.buchwald@uni-oldenburg.de>

Received 28th April 2015; revised and accepted 28th September 2015

Abstract. The aim of our study was to identify life-history mechanisms enabling typical inhabitants of vernal ponds to complete their larval development under the time constrained conditions of their temporary larval habitats. For that reason we compared both hatching phenology and larval development of vernal pond specialists *Lestes barbarus*, *L. dryas*, and *L. macrostigma* with those of the closely related hydroperiod generalists *L. sponsa*, *L. virens*, and *L. viridis* under seminatural conditions. As hypothesized, we found vernal pond specialists of the genus *Lestes* to cope with the short water coverage of their typical larval habitats by the following developmental traits: a) an early hatching date in *L. dryas* and *L. barbarus*, b) large second-stadium larvae, which have to grow less and with fewer larval stadia than the hydroperiod generalists *L. dryas* and *L. macrostigma*, c) a short larval development time in *L. macrostigma* and d) higher growth rates in *L. dryas* and *L. barbarus* than in the other species. Degree day sums in vernal pond specialists were significantly lower than in their less specialized counterparts. This means, that they would have grown faster than hydroperiod generalists, if thermal conditions during larval development were identical in all species. Due to these developmental adaptations, larvae of *L. dryas* and *L. barbarus* emerged significantly earlier in the course of year than both *L. macrostigma* and the three hydroperiod generalists. Unexpectedly, none of the three studied vernal pond specialists has evolved all of these particular adaptations. This may be because of the close ecological relationship within the genus *Lestes*, and the studied species being generally characterized by univoltine life cycles and fast larval development, which enables all of the European species to reproduce in temporary ponds.

Key words. Dragonfly, damselfly, Zygoptera, hatching phenology, larval development, number of larval stadia

Introduction

Lentic freshwater habitats in temperate regions can be placed along a gradient ranging from small, highly ephemeral puddles to large lakes that have been present for several thousand years (Wellborn et al. 1996).

Along this axis of permanence, temporary ponds »may be defined as bodies of water that experience a recurrent dry phase of varying length that is sometimes predictable in its time of onset and duration« (Williams 1997).

A distinctive type of temporary water are vernal ponds that contain water from late autumn or winter to early summer. Typically, vernal ponds are filled by winter rainfall and/or melt water and desiccate during the summer by evapotranspiration (Williams 2007). According to Williams (1996, 1997), species inhabiting temporary ponds have evolved adaptations permitting their survival. These adaptations can be classified into three types: physiological tolerance, including some form of diapause in the stage surviving the drought, life history modification, and migration. Linked with the loss of water are »the decrease in habitat volume, increase in insolation with subsequent links to water temperature, dissolved oxygen level, primary productivity, pH, and water chemistry« (Williams 1997). As a further consequence of these periodic alterations of water coverage, vernal ponds are usually not inhabited by fish and/or other larger predators (e.g., larvae of semivoltine Odonata species), because the short period during which they contain water does not allow these taxa to complete their life cycles (Williams 1996).

The usability of temporary waters for reproduction is restricted by abiotic conditions, primarily the duration of water coverage. In contrast the distribution of organisms in permanent water is limited largely by biotic factors, especially predation and competition (Wellborn et al. 1996; Williams 1996). It has been demonstrated by Stoks & McPeek (2003a) that both the duration of water cover and the presence or absence of large dragonfly larvae or fish as predators influence the composition of *Lestes* species assemblages in North America.

Within Europe, there are seven *Lestes* Leach, 1815 species (Dijkstra & Lewington 2006), although some authors place *L. parvidens* Artobolevskii, 1929 and *L. viridis* (Vander Linden, 1825) in subgenus *Chalcolestes* Kennedy, 1920 (e.g., Sternberg 1999a; Wildermuth & Martens 2014). Because

our study focuses on life history and developmental aspects of these species, we consider them all *Lestes* for simplicity. All European species of the genus *Lestes*, including *Chalcolestes*, reproduce in shallow water-bodies or shallow parts of larger waters with reed vegetation (reviewed in Jödicke 1997). All of them have a rapid univoltine development with nine to 13 larval stadia (Jödicke 1997; cf. Table 5), have an egg diapause and overwinter in the egg stage (reviewed in Jödicke 1997). Therefore, they can all develop successfully in vernal ponds. However, three of them, *Lestes barbarus* (Fabricius, 1798), *L. dryas* Kirby, 1890, and *L. macrostigma* (Eversmann, 1836), are specialized for this unique type of water body (reviewed in Jödicke 1997). Subsequently, we term the specialized species "vernal pond specialists" and the less specialized species "hydroperiod generalists".

To the best of our knowledge no comparative studies on developmental differences between the three vernal pond *Lestes* species and the four hydroperiod generalists have been published hitherto. We hypothesise that in order to face the special demands of their summer-dry larval habitats, the vernal pond specialists *L. barbarus*, *L. dryas*, and *L. macrostigma* hatch earlier in the course of the year. Their second-stadium larvae are expected to be larger, and their larvae should develop faster and with a lower number of larval stadia than the four less specialized congeners *L. parvidens*, *L. sponsa* (Hansemann, 1823), *L. virens* (Charpentier, 1825), and *L. viridis*.

Material and methods

Study sites and egg collection

In 2010, eggs of *L. barbarus*, *L. dryas*, *L. sponsa*, *L. virens*, and *L. viridis* were collected from their oviposition plant tissues in situ (cf. Corbet 1956a; Sawchyn & Church 1973) at different sites in southwestern Germany, in a range of 47°50'N to 49°11'N (Table 1). Stems of *Bolboschoenus maritimus* containing eggs of *L. macrostigma*, collected in 2009 and 2010 in eastern Austria (Table 1), were provided by courtesy of Theodor Benken. The eggs were kept in the oviposition tissues and placed in plastic boxes with a wet piece of cotton to prevent desiccation. The boxes were stored outside under semi-natural conditions. Rain water was used to prevent accumulation of

Table 1. Sampling sites in southwestern Germany and dates for the collection of eggs of *Lestes* species from their oviposition plant tissues *in situ* for this study. As an exception, *L. macrostigma* eggs were collected by T. Benken in eastern Austria.

Species	Sampling date	Sampling site	Latitude	Longitude	Type of hydroperiod
L. barbarus	06-vii-2010/ 19-ix-2010	pond W of Baden-Baden	48°47'23''N	08°10'51''E	vernal
L. dryas	19-vii-2010	gravel pit SE of Löffingen	47°50'60''N	08°22'33''E	vernal
	05-viii-2010	pond I Freudenstadt	48°27'35''N	08°26'47''E	vernal
L. macro-stigma	01-vii-2009 06-viii-2010	Sechsmahd-lacke, Illmitz	47°47'03''N	16°52'52''E	vernal
L. sponsa	05-viii-2010	pond II Freudenstadt	48°27'24''N	08°26'34''E	permanent
	28-viii-2010	pond W of Achern	48°37'19''N	07°57'18''E	permanent
L. virens	12-ix-2010	gravel pit S of Karlsruhe	48°54'48''N	08°19'53''E	(semi-) permanent
L. viridis	05-xii-2010	gravel pit S of Karlsruhe	48°54'48''N	08°19'53''E	(semi-) permanent

soluble salts. Data on daily average air temperatures were obtained from the nearby weather station of the German Weather Service (DWD) in Rheinau-Memprechtshofen (48°40'N, 07°59'E), which was located about 9 km west of the site where larvae were reared in Sasbach, Baden-Württemberg, Germany (Table 2).

Temperatures and, in consequence, both hatching dates and duration of larval development in natural habitats differ slightly from the semi-natural situation. According to our own occasional measurements, temperatures in the semi-natural conditions were one to two degrees higher than at a pond situated in the open.

Larvae were reared in an unheated room. In this "rearing room", temperatures were more stable, with higher nocturnal lows and lower diurnal highs compared to field conditions. Therefore, the DWD weather station temperature data have to be interpreted with care.

Table 2. Mean air temperatures [°C] during the study period from the DWD weather station at Rheinau-Memprechtshofen (48°40'N, 07°59'E), located close to the study site in southwestern Germany.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2010	-0.9	2.5	5.9	11.0	12.6	18.6	21.2	18.1	13.8	9.0	6.8	-0.9
2011	2.7	3.9	7.7	13.3	16.2	18.4	17.5	19.5	16.8	10.1	5.5	5.8

Comparison of hatching phenology

On 30-xi-2010, we transferred plant stems containing eggs of *Lestes barbarus*, *L. dryas*, *L. macrostigma*, *L. sponsa*, and *L. virens* in uncovered plastic boxes filled with 400 ml rain water. Twigs with eggs of *L. viridis* were placed in an open bucket with water-covered bottom; the eggs of this species did not get in contact with water. All eggs were kept at outdoor temperature and natural light conditions on an easterly exposed balcony (48°38'N, 08°05'E). The egg containers were kept together in open cardboard boxes placed on the floor. The eggs received no direct sunlight. There was no artificial source of light such as streetlamps disturbing natural photoperiod. However, a possible disturbance of natural photoperiod may have been caused by recording hatching events in the late evening.

The number of freshly hatched larvae was monitored daily, usually in the late evening. During periods with high hatching activity, additional monitoring was carried out in the early morning. The hatchlings were removed from their containers to prevent double counts. In this way, we were able to determine the hatching date of each larva to a precision of one day.

Larval development

Larvae were reared in plastic boxes of volumes ranging between 0.1 and 0.5 l and filled with rain water. The rearing boxes contained pieces of filter paper serving as perching sites. They were placed in an unheated room (48°38'N, 08°05'E) under natural light conditions, provided through windows in the room. Larvae were fed daily *ad libitum* during their complete development. Small larvae were fed with freshly hatched nauplia of *Artemia salina* and later on with *Daphnia* spp. Larger larvae were fed with larvae of Culicidae, Chironomidae, and Chaoboridae.

Table 3. Numbers of hatching events and numbers of larvae of six *Lestes* species analysed concerning various aspects of development. Vernal pond specialists are shaded.

Species	Number of larvae involved in analysis of				
	Hatching events	Number of larval stadia	Duration of larval development	Second stadium larvae measured	F-0 larvae measured
L. barbarus	406	249	271	50	50
L. dryas	242	174	147	50	50
L. macrostigma	12	9	9	12	9
L. sponsa	154	25	24	25	22
L. virens	695	43	43	50	30
L. viridis	10 357	40	40	25	25

We documented the number of larval stadia of each larva and the duration of the complete larval development time (Table 3). Concerning the number of larval stadia we refer to Corbet's (1999: 71) definition, which includes the non-feeding prolarva as the first larval stadium. The prolarva differs morphologically from all following stadia and – although the first larval moult can be postponed for up to 14 hours under unsuitable conditions (reviewed in Corbet 1999: 71) – the prolarval stadium lasts less than one minute in most cases (Corbet 1999: 71). Therefore, we term larvae of the second larval stadium, which succeed the prolarval stadium immediately in our study species, as "second-stadium larvae" (Corbet 2002). The final larval stadium prior to emergence we term F-0 larva *sensu* Corbet (1999, 2002). Data about larval sizes in the following refer either to the second-stadium larvae or to F-0 larvae.

Larvae of each species were kept together in hatching and moult cohorts of a one day precision. Duration between each two moults varied between individuals of an age cohort. Therefore, larvae had to be singularised successively in their containers in order to document the number of larval stadia and development time.

Head width (distance between the outer margins of the eyes) and total length without caudal lamellae of larvae of each stadium were measured one day after each moult using a measuring eyepiece for small larvae and a slide gauge for large larvae. In *Lestes barbarus*, *L. dryas*, and *L. virens* we measured 50 larvae of each stadium, in *L. sponsa* and *L. viridis* 25 larvae of each stadium were measured. We measured all larvae of larger larval stadia when fewer individuals were available. In *L. macrostigma* only 12 larvae were available. Three of them died during development. All individuals were measured (Table 3).

To find out whether there are differences in the development rate of vernal pond specialists *Lestes barbarus*, *L. dryas*, and *L. macrostigma* and the hydroperiod generalists *L. sponsa*, *L. virens*, and *L. viridis*, we compared head width and total length of second-stadium larvae and of F-0 larvae. The quotient of head width of F-0 larvae and head width of second-stadium larvae yielded a "growth coefficient". This expresses how many times the second larval stadia had to multiply their head width until completion of larval development. We also compared growth rates calculated by: (ln[final head width]-ln[initial head width])/(time from hatching until moult in F-0). We determined both growth coefficient and growth rate only for head width, because it is less variable than total length and hence the most reliable measure of overall size in larvae of Odonata (Benke 1970).

Furthermore, we determined the number of larval stadia, the complete duration of larval development from hatching to emergence and the degree day sum per larva. We calculated degree days by summing daily average air temperatures from the DWD weather station (for monthly average temperatures see Table 2) for each larva from hatching to emergence date. The degree day sums calculated with the data of the weather station and those experienced by the larvae in the unheated rearing room differed. Nevertheless, as the temperature conditions in the room changed proportionally to those outside, we consider these data as suitable approximation to compare the degree day sums of the studied species.

Statistical analyses

The software xlstat2014 (Addinsoft 2014) was used for all statistical tests. Since most of the data were not normally distributed, the significance of

all comparisons was tested with non-parametrical two sided Kruskal-Wallis tests, followed by a pairwise comparison using the two sided Mann-Whitney U test with Bonferroni correction. We report original *p*-values.

Results

The hatching phenology of all six *Lestes* species differed significantly (Kruskal-Wallis test among species, p <0.0001). Larvae of the vernal pond specialists, *L. barbarus* and *L. dryas*, hatched significantly earlier (Mann-Whitney U test, *p* <0.0001) than those of the hydroperiod generalists (Fig. 1, Table 4). The third vernal pond specialist, *L. macrostigma*, hatched later than hydroperiod generalist *L. sponsa*, but earlier than *L. virens* and *L. viridis*.

Both head width and total length of second-stadium larvae and of F-0 larvae differed significantly (Kruskal-Wallis test, *p* <0.0001) (Figs 2, 3). Head widths of second-stadium larvae of the vernal pond specialists, *Lestes dryas* and *L. macrostigma*, were significantly larger than those of the other species studied (Mann-Whitney U-test, *p* <0.0001) (Fig. 2). Total length of *L. dryas*

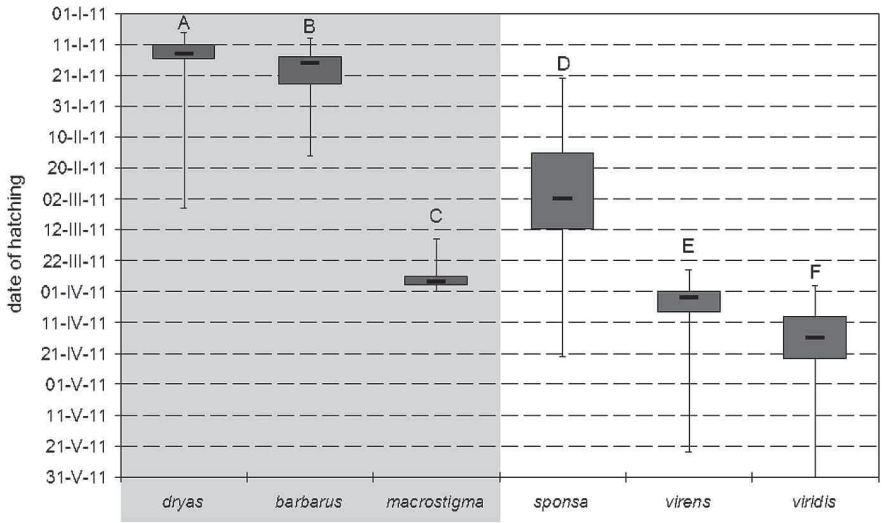


Figure 1. Hatching phenology of all six *Lestes* species in 2011. Boxplots showing maximum and minimum hatching date, quartile 1, 3, and median hatching date. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

second-stadium-larvae was significantly larger than that of all other species (Mann-Whitney U-test, p <0.0001). Total length of *L. macrostigma* second-stadium larvae did not differ significantly from that of *L. sponsa*, but was significantly larger than that of *L. barbarus*, *L. virens*, and *L. viridis* (Fig. 2). Second-stadium larvae of the vernal pond specialist *L. barbarus* did not differ significantly from the hydroperiod generalists either in head width or in total length (Fig. 2).

In F-0 larvae, head width of the vernal pond specialist *L. dryas* was significantly larger, and head width of the hydroperiod generalist *L. virens* significantly smaller than that of all other species (Mann-Whitney U-test, p <0.0001) (Fig. 3).

In a pairwise comparison, total length of F-0 larvae of the vernal pond specialist *L. dryas* was significantly larger than total length of all other species except for *L. sponsa*, from which it did not differ significantly. Total length of F-0 larvae of the hydroperiod generalist *L. virens* was significantly smaller than total length of all other species (Mann-Whitney U-test,

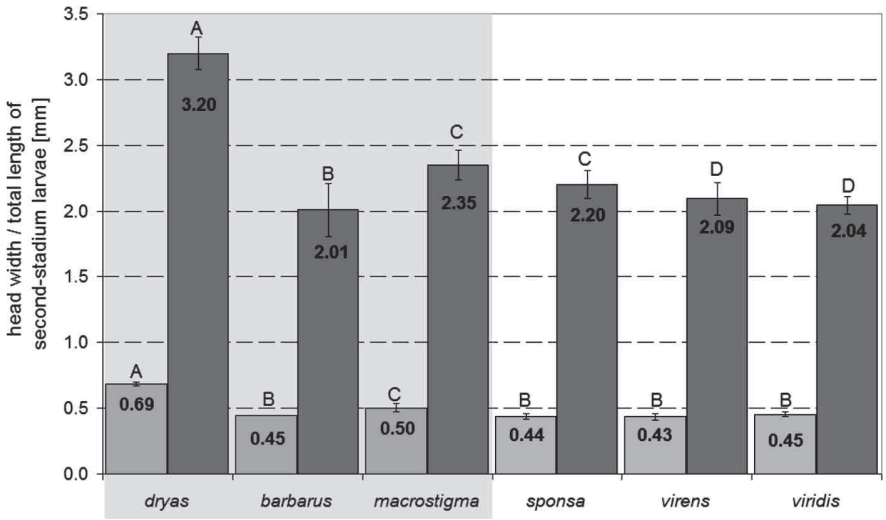


Figure 2. Head width / total length of second-stadium larvae of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

p <0.0001) (Fig. 3). Total length of F-0 larvae of *L. barbarus* was significantly larger than total length of *L. viridis*, but smaller than that of *L. sponsa*. Total length of F-0 larvae of *L. macrostigma* did not differ significantly from that of *L. viridis* (Mann-Whitney U-test, *p* <0.0001) (Fig. 3).

Second-stadium larvae and F-0 larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* grew less than the other species. Second-stadium larvae of *L. dryas* increased their head width on average 6.1 times, those of *L. macrostigma* 7.7 times. Growth coefficients of the three hydroperiod generalists and of the third vernal pond specialist *L. barbarus* ranged between 8.3 and 9.1 (Fig. 4). Growth coefficients of the vernal pond specialists *L. dryas* and *L. macrostigma* differed significantly from each other and from all other species studied (Mann-Whitney U-test, *p* <0.0001). Furthermore, the growth coefficient of *L. virens* larvae differed significantly from all other species. Growth coefficient of the vernal pond specialist *L. barbarus* was higher than in all other species; it did not differ significantly from growth coefficients of *L. sponsa* and *L. viridis* (Mann-Whitney U-test, *p* <0.0001) (Fig. 4).

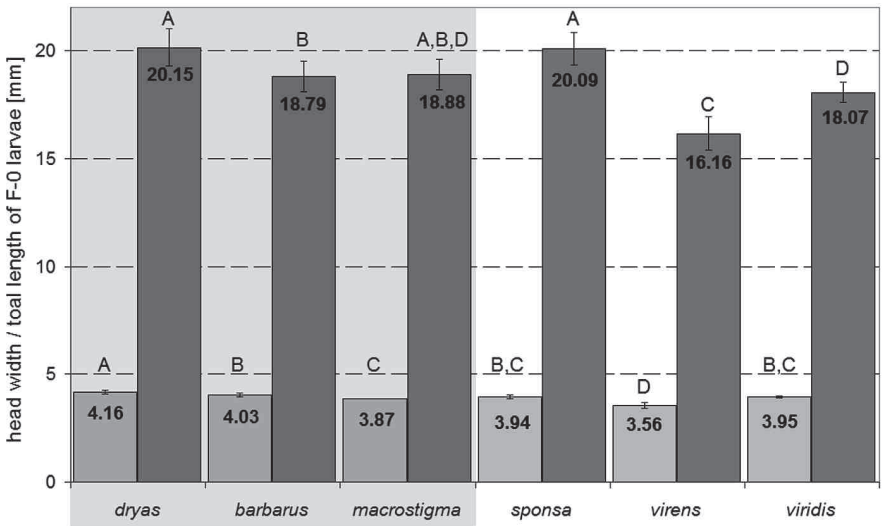


Figure 3. Head width / total length of F-0 larvae of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

To complete their larval development, the six studied *Lestes* species needed between eight and 12 larval stadia including the prolarva. In our study the number of stadia varied within each species except for *L. viridis*, in which all individuals needed ten stadia to complete larval development. The median number of larval stadia differed significantly among species (Kruskal-Wallis test, p <0.0001). Larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* needed significantly less stadia than the other species and also differed significantly from each other (Mann-Whitney U-test, p <0.0001). Vernal pond specialist *L. barbarus* needed significantly less stadia than *L. sponsa* and *L. virens*, but did not differ significantly from the hydroperiod generalist *L. viridis* (Mann-Whitney U-test, p <0.0001) (Fig. 5).

Complete larval development took between 40 days in one individual of hydroperiod generalist *L. virens* and 105 days in one individual of the vernal pond specialist *L. barbarus*. Medians ranged between 51 days in *L. macrostigma* and 83 days in *L. barbarus* (Fig. 6, Table 6). Median duration of larval development of the six species differed significantly (Kruskal-Wallis test, p <0.0001; Fig. 6). Larvae of vernal pond specialist *L. macrostigma*

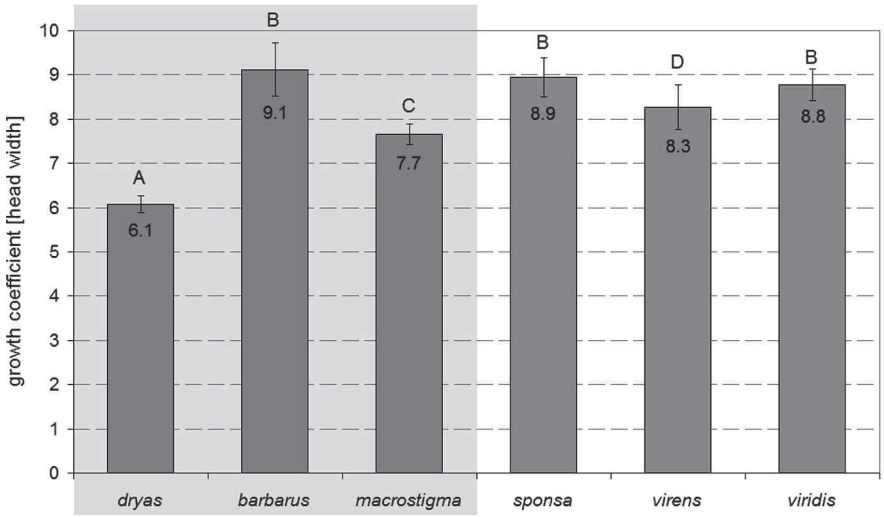


Figure 4. Growth coefficients of six *Lestes* species, calculated by dividing head width of F-0 larvae by that of second-stadium larvae. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

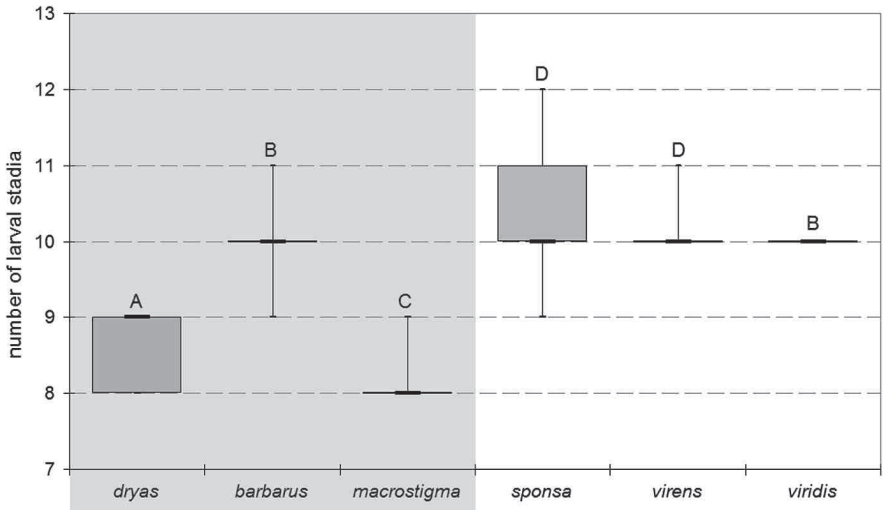


Figure 5. Number of larval stadia of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

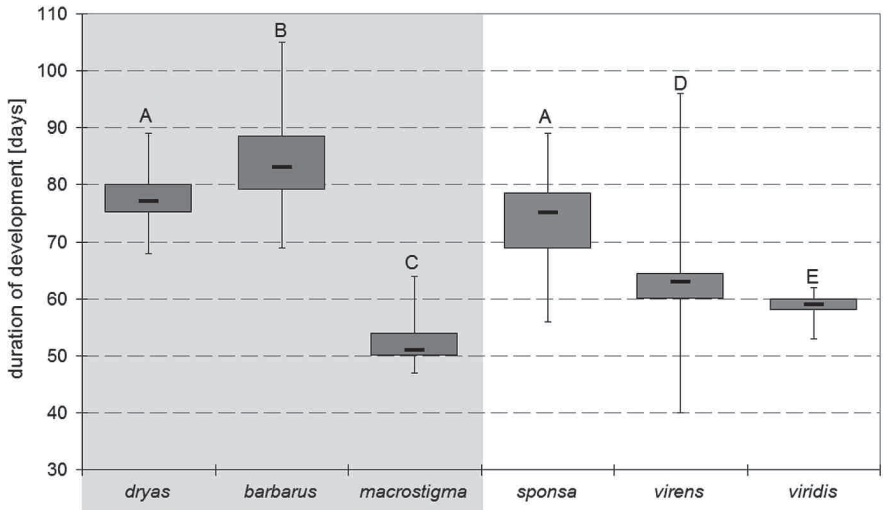


Figure 6. Duration of larval development of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

developed significantly faster than those of all other species (Mann-Whitney U-test, p <0.005; Fig. 6). They are followed, in order of development time, by the three hydroperiod generalists *L. viridis*, *L. virens*, and *L. sponsa*. Larvae of vernal pond specialists *L. dryas* and *L. barbarus* had the longest development time. In a pairwise comparison the differences in larval development time among all species were significant except for the difference between median development time of *L. dryas* and *L. sponsa* larvae (Mann-Whitney U-test, p <0.005).

Growth rate differed significantly between species (Kruskal-Wallis test, p <0.0001). Growth rate of vernal pond specialist *L. dryas* was significantly higher, and that of hydroperiod generalist *L. virens* was significantly lower than those of all other species (Mann-Whitney U-test, p <0.0001) (Fig. 7). *Lestes barbarus* had the second highest growth rate followed by that of *L. viridis*, *L. sponsa*, *L. macrostigma*, and *L. virens* (Fig. 7). In a pairwise comparison the growth rates of *L. barbarus* and *L. viridis* and those of *L. viridis*, *L. sponsa*, and *L. macrostigma* did not differ significantly (Mann-Whitney U-test, p >0.005).

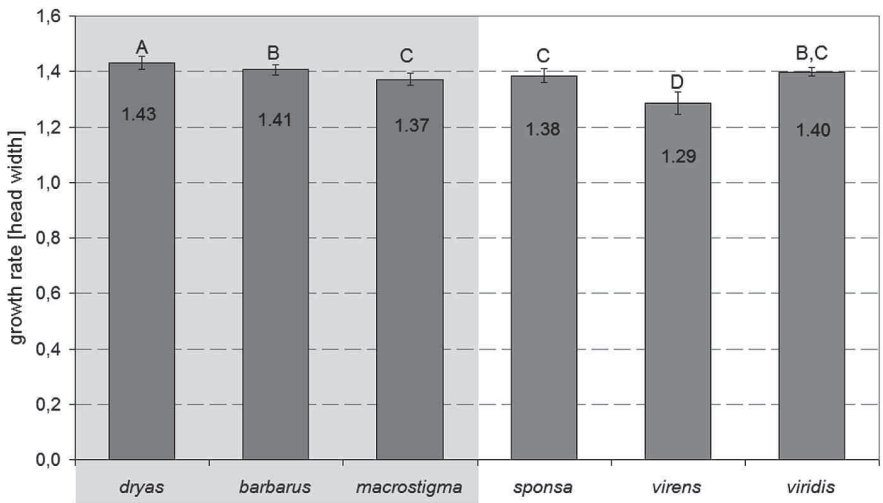


Figure 7. Growth rates of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

To take temperatures during larval development into account, we expressed development in degree day sums per larva. This resulted in a different order among the species. Median degree day sums ranged between 411.5 in *L. dryas* and 915.6 in *L. virens* (Fig. 8). Median degree day sums of the six species differed significantly (Kruskal-Wallis test, $p < 0.0001$; Fig. 8). Larvae of the vernal pond specialists *L. dryas* and *L. barbarus* had significant lower degree day sums than all other species and also differed significantly from each other (Mann-Whitney U-test, $p < 0.005$; Fig. 8). They are followed, in order of degree day sums, by the vernal pond specialist *L. macrostigma* and the three hydroperiod generalists *L. sponsa, L. viridis*, and *L. virens*.

Vernal pond specialists *L. dryas* and *L. barbarus* completed larval development first followed by – in order of emergence – hydroperiod generalist *L. sponsa*, vernal pond specialist *L. macrostigma*, and hydroperiod generalists *L. virens* and *L. viridis* (Fig. 9). The differences in median emergence date of the six species were significant (Kruskal-Wallis test, $p < 0.0001$). In a pairwise comparison all differences except that between *L. macrostigma* and *L. sponsa* were significant (Mann-Whitney U-test, $p < 0.005$).

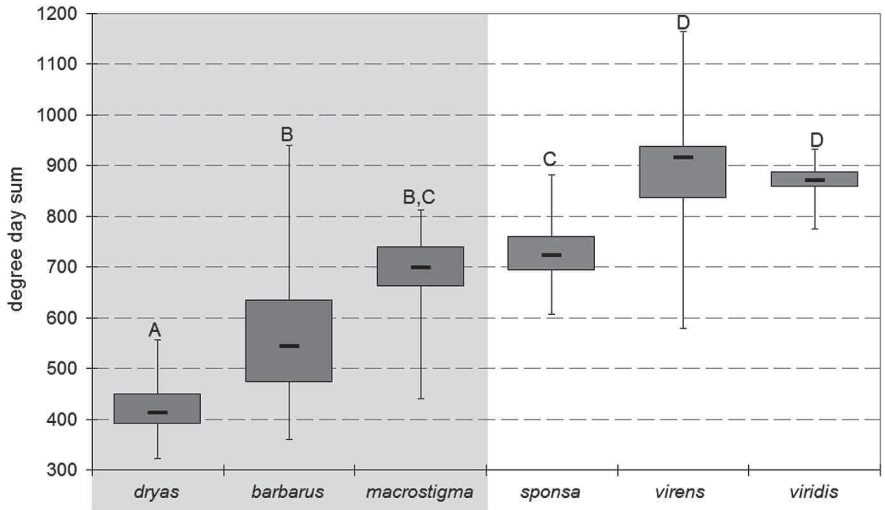


Figure 8. Degree day sums of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

Discussion

In our study we aimed to find out if there are developmental differences between larvae of Odonata species ecologically specialized in vernal ponds and less specialized congeners reproducing both in temporary and permanent water bodies.

Vernal ponds are a distinctive type of temporary wetland typically filled by winter rains and/or melt water and drying out in the course of summer; therefore vernal ponds are usually free of large predators such as fish or larger dragonfly larvae (Stoks & McPeek 2003a; Wellborn et al. 1996;

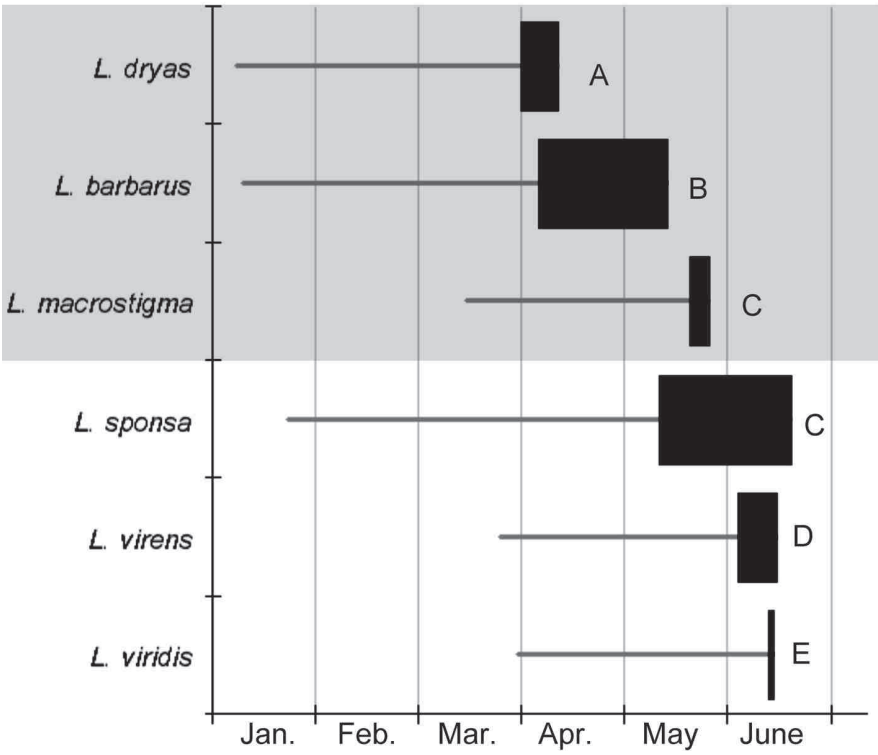


Figure 9. Emergence phenology of all six *Lestes* species in 2011 by combining hatching phenology with larval development time. The lines represent the larval development time from hatching to start of emergence, the bars the complete emergence period. Data identified with different letters differ significantly. Vernal pond specialists are shaded.

Williams 2007). Therefore, reproduction in vernal ponds may be a strategy to avoid competition with and predation by congeners and other predators developing in semi-permanent or permanent waters (Wellborn et al. 1996; Stoks & McPeek 2003a; Williams 2007). In vernal pond specialists, the avoidance or at least reduction of predation and competition by other species apparently outweighs the great disadvantage that duration of water coverage is restricted. Next to behavioural adaptations like a fast and open life style (Johansson & Suhling 2004) and physiological traits like a higher digestive efficiency (Stoks & McPeek 2003b) this specialization has implications for life history (Wellborn et al. 1996; Stoks & McPeek 2003a; Williams 2007). To cope with the risk of early drying-up of the larval habitats, specialized species should be adapted by both early hatching and shortened larval development.

Concerning early hatching, our results support the hypothesis for vernal pond specialists *L. barbarus* and *L. dryas*, whereas *L. macrostigma* hatched at an intermediate period significantly earlier than hydroperiod generalists *L. virens* and *L. viridis*, but significantly later than the two other vernal pond specialists and than hydroperiod generalist *L. sponsa* (Table 4). Early hatching has already been demonstrated to be a strategy in temporary pond populations of *L. viridis* (De Block & Stoks 2004, 2005a; De Block et al. 2005). It has also been shown in a comparative study on 15 European species including typical vernal pond specialists *Aeshna affinis* Vander Linden, 1820 and *Sympetrum flaveolum* (Linnaeus, 1758) (Schiel & Buchwald 2015). In a pond in Latium, Italy, *L. barbarus* hatched two months earlier than coexisting *L. virens* (Carchini & Nicolai 1984). In Canadian populations of *L. dryas*, early hatching in comparison with populations of *L. unguiculatus* Hagen, 1861 and *L. disjunctus* Selys, 1862 was suspected by Sawchyn & Gillott (1974a).

To protect the supposed cold-sensitive early larval stadia of univoltine *Lestes* species (Corbet 1999) from unfavourable low winter temperatures and to survive drought phases in the larval habitats (Williams 1996) many of these species exhibit delayed development with egg diapause, which is regarded as a special type of physiological adaptation (Williams 1996, 1997); egg diapause can be terminated by water contact (e.g., Sawchyn & Gillot 1974b, for *Lestes congener*) and controlled by temperature (e.g., Münch-

Table 4. Overview of published hatching dates of the investigated *Lestes* species, compared with the data of this study. Based on Table 24 in Jödicke (1997). In the columns "Data from this study" and "Literature", months without brackets represent the hatching span between quartile 1 and 3, months in brackets represent minimum and maximum hatching data observed, which may be not typical or artefact. Vernal pond specialists are shaded.

Species	Data from this study	Literature	Sources
L. barbarus	January (to February)	(October to December), (January) February to April	Loibl (1958); Aguesse (1961); Carchini & Nicolai (1984); Rota & Carchini (1988)
L. dryas	January (to March)	(November) March / April	Needham (1903); Wesenberg-Lund (1913); Gardner (1952); Sawchyn & Church (1973)
L. macrostigma	March	no data available	Jödicke (1997)
L. sponsa	February / March (January to April)	(September, October to December), April to June	Wesenberg-Lund (1913); Münchberg (1933); Corbet (1956b); Loibl (1958); Śniegula & Johansson (2010)
L. virens	(March) first decade of April to May	(October) April to End of May	Münchberg (1933); Carchini & Nikolai (1984); Rota & Carchini (1988)
L. viridis	(March) mid-April to May	Beginning of April to mid-June	Münchberg (1933); Loibl (1958); Sternberg (1999a); De Block et al. (2005a)

berg 1933; Corbet 1956a, for *L. sponsa*), and photoperiod (e.g., Sawchyn & Church 1973, for *L. disjunctus* and *L. unguiculatus;* Śniegula & Johansson 2010, for *L. sponsa*). The influence of day length in triggering hatching has already been shown for *L. disjunctus*, *L. unguiculatus*, and *L. dryas* in Canada (Sawchyn & Church 1973) and for *L. sponsa* in Europe (Śniegula & Johansson 2010). The latter species hatched earlier in longer photoperiods, which is typical for higher latitudes (Śniegula & Johansson 2010).

In addition to early hatching, fast larval development should be an appropriate adaptation facing drought in immature water insects. Fast larval development includes physiological, behavioural, and morphological aspects (Williams 1996, 1997). In our study we focussed on size and development

time. Among other traits, fast development may be optimised by large larval size at hatching and a comparatively small size difference between second-stadium larvae and F-0 larvae. This would enable development with fewer larval stadia and within a shorter time span.

Indeed, head widths of second-stadium larvae of vernal pond specialists *Lestes dryas* and *L. macrostigma* were significantly larger than those of other species studied, and both size differences between second-stadium larvae and F-0 larvae and number of larval stadia were smaller in these two species than in hydroperiod generalists and in the third vernal pond specialist, *L. barbarus*.

According to our data, *L. sponsa* needed up to one, *L. barbarus* up to two, and *L. dryas* between two and five stadia less than has been documented in previous studies (for references see Table 5). *Lestes viridis* was the only species in which the number of larval stadia was within the range of former studies (Table 5). To the best of our knowledge, the number of larval stadia of *L. macrostigma* and of *L. virens* was unknown hitherto (Jödicke 1997, Table 5). With eight to nine larval stadia, *L. macrostigma* is at the lower end and *L. virens*, with 10–11 larval stadia, in the center of the known span of larval stadia in *Lestes* (Fig. 5, Table 5).

Growth rate and larval development time are influenced by environmental factors like photoperiod (e.g., Norling 1984a, 1984b; De Block & Stoks 2004, 2005b; Śniegula & Johansson 2010; Śniegula et al. 2012, 2014), temperature (e.g., Pickup & Thompson 1984; Krishnaraj & Pritchard 1995; De Block & Stoks 2003), food availability (e.g., Fischer 1972; Pickup & Thompson 1984; Johansson et al. 2001), and larval densities (De Block & Stoks 2005a). Differences in these variables may have contributed to the different results concerning number of larval stadia (Table 5) and duration of larval development (Table 6). This demonstrates high developmental plasticity in all species (reviewed in Stoks et al. 2008). In our study only photoperiod and temperature changed according to natural conditions. Larvae that hatch later experience inherently longer photoperiods and higher water temperatures.

Larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* needed only eight to nine larval stadia. This was a significantly lower number of larval stadia than in all other species including the third vernal pond

Table 5. Overview on published data about the number of larval stadia (counting the prolarva as stadium 1) of the investigated *Lestes* species, compared with the data from this study. Vernal pond specialists are shaded.

Species	Number of larval stadia	Sources	Data from this study
L. barbarus	11–12	Loibl (1958)	9–11 (12)
	12	Aguesse (1961)	
L. dryas	11	Gardner (1952)	8–9
	12–13	Fischer (1964)	
L. macrostigma	unknown		8–9
L. sponsa	10–12	Loibl (1958)	9–12
	13	Münchberg (1933); Fischer (1959)	
L. virens	unknown		10–11
L. viridis	9–10	Loibl (1958)	10
	10	Prenn (1927); Robert (1959)	
	10–11	Geijskes (1928)	
	13	Münchberg (1933)	

specialist *L. barbarus*, which needed nine to eleven stadia in our study. The latter needed significantly less stadia than *L. sponsa* and *L. virens*, but did not differ significantly from the hydroperiod generalist *L. viridis* (Fig. 5).

According to an analysis comprising 85 Odonata species from 47 genera and 11 families, the number of larval stadia, including the prolarva, ranges generally from 8 to 17 with a median of twelve stadia (Corbet 1999: 208). Of the analysed species, 63 % needed 11 to 13, 86 % 10 to 14, and 96 % nine to 15 stadia (Corbet 1999: 208). The number of larval stadia in European *Lestes* species generally ranges between nine and 13 stadia (reviewed in Jödicke 1997). Therefore, number of larval stadia in the genus *Lestes* is towards the lower end of the range needed to complete larval development. In *L. dryas* and *L. macrostigma* the number of larval stadia even falls outside the widest range.

In our rearing study *L. macrostigma* was the only vernal pond specialist, which developed significantly faster than its less specialized congeners.

Unexpectedly, the vernal pond specialists *L. barbarus* and *L. dryas* had the longest development time among all studied *Lestes* species and developed significantly slower than hydroperiod generalists *L. virens* and *L. viridis*. This paradox may be explained by differences of temperature and photoperiod. From experiments conducted by Krishnaraj & Pritchard (1995) on *Coenagrion resolutum* (Hagen *in* Selys, 1876) and *L. disjunctus* it can be assumed that obligatory univoltine *Lestes* species have a higher thermal coefficient than non-obligatory univoltine summer species like *C. resolutum*. In our study the late-hatching hydroperiod generalists may have reacted to the higher temperatures at this later time of year by accelerating their growth rate and developing faster than their vernal pond congeners, which had hatched earlier in the course of the year when temperatures were lower. This explanation is supported by our analysis of degree day sums (Fig. 8). Furthermore it has been demonstrated in several studies (e.g., Strobbe & Stoks 2004; De Block & Stoks 2004, 2005a, b) that late-hatching larvae are capable of growing and developing faster under photoperiodically regulated time constraints than larvae of the same species that hatched earlier in the course of the year. According to Stoks et al. (2008), without time constraints damselfly larvae may not make use of their growth and development potential to reduce their risk of starvation (De Block & Stoks 2004) or predation (Stoks et al. 2005).

This regulation may also have resulted in the unexpected faster development of hydroperiod generalist species compared to the vernal pond specialists *L. barbarus* and *L. dryas*. Nevertheless, the vernal pond specialists *L. barbarus* and *L. dryas* completed larval development significantly earlier than all other species in our study due to their early hatching date. In fact, in our study both *L. barbarus* and *L. dryas* emerged more than one month earlier than under natural conditions in these latitudes (Hunger et al. 2006). This may have been caused primarily by the very early hatching dates, because larval development time span tended to be longer in our study than in other studies (Table 6).

According to Corbet (1962, 2003) there are three different types of life cycles in Odonata in temperate latitudes. Species of the genus *Lestes* belong to a small subset of summer species that overwinter in (usually) obligate egg diapause and are obligatorily univoltine and develop in 2–3 months in

Table 6. Selection of exemplary studies about total development time of the investigated *Lestes* species, compared with data from this study. Vernal pond specialists are shaded.

Species	Minimum time span of larval development [d]	Sources	Median development time span in this study [d] (total time span)
L. barbarus	~ 30 (?)	Schmidt (1990)	83 (69–105)
	~ 46–60	Aguesse (1961)	
	~ 90	Carchini & Nicolai (1984)	
L. dryas	43–46	De Block et al. (2007, 2008)	77 (68–89)
	45	Robert (1959)	
	~ 60–74	Schiemenz (1953)	
	195	Gardner (1952)	
L. macrostigma	~ 56–70	Wildermuth & Martens (2014)	51 (47–64)
L. sponsa	37	Schmidt (1993)	75 (56–89)
	42	Wesenberg-Lund (1913); Clausnitzer (1974)	
	42–60	Loibl (1958)	
	50–64	Śniegula & Johannson (2010)	
	71	Corbet (1956b)	
	68–83	Pickup et al. (1984)	
	~ 100	Johansson et al. (2001)	
L. virens	~ 60–90	Carchini & Nicolai (1984)	61 (40–96)
L. viridis	48–62	Loibl (1958)	59 (53–62)
	61	Rolff et al. (2004)	
	62	De Block & Stoks (2005a, b)	
	62–67	Prenn (1927)	
	65–70	Münchberg (1933)	
	106	Robert (1959)	

spring and early summer. Their obligatory univoltine life cycle (Corbet et al. 2005), with fast larval development and egg diapause, may serve to protect temperature sensitive early larval stadia from winter cold (Corbet

1999), but is a good pre-adaptation to colonize vernal ponds, where the genus is well represented (reviewed by Jödicke 1997). In fact, De Block et al. (2007) concluded that vernal pond inhabitants of the genus *Lestes,* such as *L. dryas,* have evolved from ancestral species, which reproduced in temporary waters. Compared with *L. barbarus* and *L. macrostigma*, *L. dryas* shows more developmental adaptations for successful reproduction in vernal ponds. This might be correlated with its high latitudinal range (reviewed by Jödicke 1997). In comparison with both of its more southerly distributed vernal pond congeners (reviewed by Jödicke 1997) some populations of *L. dryas* are not only time-constrained by drying up of larval habitats, but may also experience lower temperature sums in their larval habitats due to harsher climate conditions in higher latitudes.

As hypothesized, the following developmental traits are put into effect in typical vernal pond specialists of the genus *Lestes*: a) an early hatching date in *L. barbarus* and *L. dryas*, b) large second-stadium larvae in *L. dryas* and *L. macrostigma*, which have to grow less and with fewer larval stadia than permanent pond congeners, c) a very short larval development time in *L. macrostigma,* and d) highest growth rates in *L. dryas* and *L. barbarus*. Degree day sums in vernal pond specialists were significantly lower than in their less specialized counterparts. Unexpectedly, none of the three studied vernal pond specialists has evolved all of these particular adaptations. This may be caused by the close ecological relationship within the genus *Lestes*, with all studied species being characterized by univoltine life cycles and fast larval development, which enables all of the European species to reproduce in vernal ponds (e.g., Jödicke 1997; Röhn et al. 1999; Sternberg 1999a, b; Sternberg & Röske 1999; Wildermuth & Martens 2014).

Acknowledgements

We are indebted to Hansruedi Wildermuth for his advice, Martin Schorr, Klaus Sternberg, and Melanie Willen for help with literature, Theodor Benken for help with statistics and collecting *L. macrostigma* eggs, Holger Hunger for English language support, and Lioba Schiel for her help with the documentation of hatching events and the food supply of the continuously hungry larvae.

References

Addinsoft 2014. XLSTAT-Pro, Version 2014.4.04. Addinsoft SARL, Paris

Aguesse P. 1961. Contribution à l'étude écologique des zygoptères de Camargue. Dissertation, Université de Paris. Centre régional de documentation pédagogique, Aix-en-Provence

Benke A.C. 1970. A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology* 51: 328-331

Carchini G. & P. Nikolai 1984. Food and time resource partitioning in two coexisting *Lestes* species (Zygoptera: Lestidae). *Odonatologica* 13: 461-466

Clausnitzer H.-J. 1974. Die ökologischen Bedingungen für Libellen (Odonaten) an intensiv bewirtschafteten Fischteichen. *Beiträge zur Naturkunde Niedersachsens* 27: 78-90

Corbet P.S. 1956a. The influence of temperature on diapause development in the dragonfly *Lestes sponsa* (Hansemann) (Odonata: Lestidae). *Proceedings of the Royal Entomological Society of London* (A) 31: 45-48

Corbet P.S. 1956b. The life histories of *Lestes sponsa* (Hansemann) and *Sympetrum striolatum* (Charpentier) (Odonata). *Tijdschrift voor Entomologie* 99: 217-229

Corbet P.S. 1962. A biology of dragonflies. Quadrangle Books, Chicago

Corbet P.S. 1999. Dragonflies. Behaviour and ecology of Odonata. Harley Books, Colchester

Corbet P.S. 2002. Stadia and growth ratios of Odonata: a review. *International Journal of Odonatology* 5: 45-73

Corbet P.S. 2003. A positive correlation between photoperiod and development rate in summer species of Odonata could help to make emergence date appropriate to latitude: a testable hypothesis. *Journal of the Entomological Society of British Columbia* 100: 3-16

Corbet P.S., Suhling F. & Soendgerath D. 2005. Voltinism of Odonata: a review. *International Journal of Odonatology* 9: 1-44

De Block M. & Stoks R. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of evolutionary Biology* 16: 986-995

De Block M. & Stoks R. 2004. Life-history variation in relation to time constraints in a damselfly. *Oecologia* 140: 68-75

De Block M. & Stoks R. 2005a. Pond drying and hatching date shape the trade-off between age and size at emergence in a damselfly. *Oikos* 180: 485-494

De Block M. & Stoks R. 2005b. Fitness effects from egg to reproduction: Bridging the life history transition. *Ecology* 86: 185-197

De Block M., Stoks R. & De Bruyn L. 2005. Egg hatching patterns within and among populations of a damselfly occupying permanent and temporary ponds. *Archiv für Hydrobiologie* 163: 195-209

De Block M., McPeek M.A. & Stoks R. 2007. Life-history evolution when Lestes damselflies invaded vernal ponds. *Evolution* 62: 485-493. doi: 10.1111/j.1558-5646.2007.00283.x

De Block M., McPeek M.A. & Stoks R. 2008. Life history plasticity to combined time and biotic constraints in *Lestes* damselflies from vernal and temporary ponds. *Oikos* 117: 908-916

Dijkstra K.-D.B. & Lewington R. 2006. Field guide to the dragonflies of Britain and Europe. British Wildlife Publishing, Gillingham

Fischer Z. 1959. Odonata in small pools situated in the environs of Mikolajki. *Polskie Archiwum Hydrobiologii* 5: 183-201 [In Polish, English summary and captions]

Fischer Z. 1964. Cycle vital de certaines espèces de libellules du genre *Lestes* dans les petits bassins astatiques. *Polskie Archiwum Hydrobiologii* 12: 349-382

Fischer Z. 1972. The energy budget of *Lestes sponsa* (Hans.) during its larval development. *Polskie Archiwum Hydrobiologii* 19: 215-222

Gardner A.E. 1952. The life-history of *Lestes dryas* Kirby (Odonata). *Entomologist's Gazette* 3: 4-26

Geijskes D.C. 1928. De levenswijze en ontwikkeling van *Lestes viridis* Vanderl. *De levende Natuur* 33: 17-24, 48-52, 85-90

Hunger H., Schiel F.-J. & Kunz B. 2006. Verbreitung und Phänologie der Libellen Baden-Württembergs. *Libellula Supplement* 7: 15-188

Jödicke R. 1997. Die Binsenjungfern und Winterlibellen Europas. Westarp Wissenschaften, Magdeburg

Johansson F., Stoks R., Rowe L. & de Block M. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. *Ecology* 82: 1857-1869

Johansson F. & Suhling F. 2004. Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. *Ecological Entomology* 29: 196-202

Krishnaraj R. & Pritchard G. 1995. The influence of larval size, temperature, and the components of the functional response to prey density on growth rates of the dragonflies *Lestes disjunctus* and *Coenagrion resolutum* (Insecta: Odonata). *Canadian Journal of Zoology* 73: 1672-1680

Loibl E. 1958. Zur Ethologie und Biologie der deutschen Lestiden (Odonata). *Zeitschrift für Tierpsychologie* 15: 54-81

Münchberg P. 1933. Beiträge zur Kenntnis der Biologie der Lestinae Calv. (Odonata). *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 28: 141-171

Needham J.G. 1903. Aquatic insects in New York State. Part 3. Life histories of Odonata, suborder Zygoptera. *New York State Museum Bulletin* 68: 204-217

Norling U. 1984a. The life cycle and larval photoperiodic responses of *Coenagrion hastulatum* (Charpentier) in two climatically different areas (Zygoptera: Coenagrionidae). *Odonatologica* 13: 429-449

Norling U. 1984b. Photoperiodic control of larval development in *Leucorrhinia dubia* (Vander Linden): a comparison between populations from northern and southern Sweden (Anisoptera: Libellulidae). *Odonatologica* 13: 529-550

Pickup J. & Thompson D.J. 1984. The effects of prey density and temperature on the development of the larvae of the damselfly *Lestes sponsa* (Hans.) (Zygoptera: Lestidae). *Advances in Odonatology* 2: 169-167

Pickup J., Thompson D.J. & Lawton J.H. 1984. The life history of *Lestes sponsa* (Hansemann): Larval growth (Zygoptera: Lestidae). *Odonatologica* 13: 451-459

Prenn F. 1927. Aus der Nordtiroler Libellenfauna. 1. Zur Biologie von *Lestes viridis* (Vanderl.). *Verhandlungen der zoologisch-botanischen Gesellschaft in Wien* 76: 26-33

Robert P.-A. 1959. Die Libellen (Odonaten). Kümmerly & Frey, Bern

Röhn C., Sternberg K. & Kuhn J. 1999. *Lestes dryas* (Kirby, 1890). In: Sternberg K. & Buchwald R. (Eds), Die Libellen Baden-Württembergs, Vol. 1: 398-408. Ulmer, Stuttgart

Rolff J., van de Meutter F. & Stoks R. 2004. Time constraints decouple age and size at maturity and physiological traits. *The American Naturalist* 164: 559-565

Rota E. & Carchini G. 1988. Considerations on an autumn record of *Lestes* larvae in Italy (Zygoptera: Lestidae). *Notulae odonatologicae* 3: 9-13

Sawchyn W.W. & Church N.S. 1973. The effects of temperature and photoperiod on diapause development in the eggs of four species of *Lestes* (Odonata: Zygoptera). *Canadian Journal of Zoology* 51: 1257-1265

Sawchyn W.W. & Gillott C. 1974a. The life histories of three species of *Lestes* (Odonata: Zygoptera) in Saskatchewan. *Canadian Journal of Entomology* 106: 1283-1293

Sawchyn W.W. & Gillott C. 1974b. The life history of *Lestes congener* (Odonata: Zygoptera) on the Canadian Prairies. *The Canadian Entomologist* 106: 367-376

Schiel F.-J. & Buchwald R. 2015. Hatching phenology of Odonata species inhabiting temporary and permanent water bodies (Odonata: Lestidae, Aeshnidae, Libellulidae). *International Journal of Odonatology* 18: 105-123

Schiemenz H. 1953. Die Libellen unserer Heimat. Urania, Jena

Schmidt B. 1990. Faunistisch-ökologische Untersuchungen zur Libellenfauna (Odonata) der Streuwiesen im NSG Wollmatinger Ried bei Konstanz. Auswirkung und Bedeutung der Streuwiesenmahd und Überschwemmungen auf die Libellenbesiedlung. *Naturschutzforum* 3/4: 39-80

Schmidt E.G. 1993. Die ökologische Nische von *Sympetrum depressiusculum* (Selys) im Münsterland (Naturschutzgebiet Heubachwiesen). *Libellula* 12: 175-189

Śniegula S. & Johansson F. 2010. Photoperiod affects compensating developmental rate across latitudes in the damselfly *Lestes sponsa*. *Ecological Entomology* 35: 149-157

Śniegula S., Johansson F. & Nilsson-Örtman V. 2012. Differentiation in developmental rate across geographic regions: a photoperiod driven latitude compensating mechanism? *Oikos* 121: 1073-1082. doi:10.1111/j.1600-0706.2011.20015.x

Śniegula S., Drobniak S.M., Gołąb M.J. & Johansson F. 2014. Photoperiod and variation in life history traits in core and peripheral populations in the damselfly *Lestes sponsa*. *Ecological Entomology* 39: 137-148

Sternberg K. 1999a. *Chalcolestes viridis* (Vander Linden, 1825). In: Sternberg K. & Buchwald R. (Eds), Die Libellen Baden-Württembergs, Vol. 1: 379-388. Ulmer, Stuttgart

Sternberg K. 1999b. *Lestes sponsa* (Hansemann, 1823). In: Sternberg K. & Buchwald R. (Eds), Die Libellen Baden-Württembergs, Vol. 1: 409-418. Ulmer, Stuttgart

Sternberg K. & Röske W. 1999. *Lestes barbarus* (Fabricius, 1798). In: Sternberg K. & Buchwald R. (Eds), Die Libellen Baden-Württembergs, Vol. 1: 388-398. Ulmer, Stuttgart

Stoks R. & McPeek M.A. 2003a. Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. *Ecology* 84: 1576-1587

Stoks R. & McPeek M.A. 2003b. Antipredator behavior and physiology determine *Lestes* species turnover along the pond-permanence gradient. *Ecology* 84: 3327-3338

Stoks R., de Block M., van de Meutter F. & Johansson F. 2005. Predation cost of rapid growth: behavioural coupling and physiological decoupling. *Journal of Animal Ecology* 74: 708-715. doi: 10.1111/j.1365-2656.2005.00969.x

Stoks R., Johansson F. & de Block M. 2008. Life-history plasticity under time stress in damselfly larvae. Dragonflies & Damselflies. In: Córdoba-Aguilar A. (Ed.), Model Organisms for ecological and evolutionary research: 39-50. Oxford University Press, Oxford

Strobbe F. & Stoks R. 2004. Life history reaction norms to time constraints in a damselfly: differential effects in size and mass. *Biological Journal of the Linnean Society* 83: 187-196

Wellborn G.A., Skelly D.K. & Werner E.E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27: 337-363

Wesenberg-Lund C. 1913. Odonaten-Studien. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 6: 155-228, 373-422

Wildermuth H. & Martens A. 2014. Taschenlexikon der Libellen Europas. Quelle & Meyer, Wiebelsheim

Williams D.D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society* 15: 634-650

Williams D.D. 1997. Temporary ponds and their invertebrate communities. *Aquatic conservation: Marine and Freshwater Ecosystems* 7: 105-117

Williams D.D. 2007. The biology of temporary waters. Oxford University Press, Oxford

1st December 2015

The daily food intake of *Pantala flavescens* females from foraging swarms estimated by the faeces excreted (Odonata: Libellulidae)

Yuta Ichikawa & Mamoru Watanabe[1]

Graduate School of Life and Environmental Science, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

[1] corresponding author, <watanabe@kankyo.envr.tsukuba.ac.jp>

Received 30th March 2015; revised and accepted 19th June 2015

Abstract. *Pantala flavescens* migrates to Japan every spring, where the population rapidly increases until autumn. Adults often form swarms above open grasslands for foraging. Little has been reported on the daily food intake in *P. flavescens*, probably due to the difficulty of observing foraging behaviour. We captured females from foraging swarms and kept them alive in the laboratory, and the faeces excreted were collected each 24-hour-period after capture. Faeces excreted within 24 hours after capture were typically dark brown, formed in oval pellets, including a lot of fragments of cuticle, which must have been derived from the prey. The total dry weight of faeces was 8.00 mg on average. The size of the subsequent faeces decreased, and the colour changed to reddish brown and detectable cuticle fragments were no longer present, suggesting that most of the indigestible parts had been excreted within 24 hours after feeding. When a female was handfed a single sheep blowfly, 4.51 mg of faeces were excreted within 24 hours after feeding, while a starved female excreted 2.23 mg. The daily food intake of a female was estimated to be about 14 mg, corresponding to about 185 small prey insects. Therefore, the mass flight of *P. flavescens* might affect populations of small insects in the open landscape in Japan.

Key words. Dragonfly, Anisoptera, feeding activity, flier, foraging flight, hand-feeding method, metabolism, percher, swarming

Introduction

In Odonata the phenologies of prey species have critical consequences for life history strategies including longevity and reproductive output (Anholt et al. 1991). Stored reserves accumulated during the larval stage and food ingested in the adult stage provide some resources for egg production (Bennettova & Fraenkel 1981). However since odonate adults have little fat in their bodies immediately after emergence, they must gain added nutrition

for somatic maintenance and, in females, oogenesis. It is known that nutritional factors increase longevity and raise reproductive output (Plaistow & Siva-Jothy 1999). Throughout the adult stages, odonates are predators, feeding on small insects including Diptera, Hymenoptera, Lepidoptera, and so on, reviewed by Corbet (1999: 339). Marden (1989) pointed out that feeding during the pre-reproductive stage of adults mainly helps to develop their flight muscles. Hardening of the exoskeleton (Neville 1983) and the increase in the number of mature eggs developing in the ovaries (Ichikawa & Watanabe 2014) have also been reported during this period. After maturation, foraging activity continues to increase the quantity of fat bodies, but the nutritional uptake is mainly allocated to body maintenance and reproductive activities (Baird & May 1997). Therefore, as shown in *Ischnura verticalis* (Say, 1839), the amount of food ingested is a more important determinant of the number of eggs laid rather than adult body size (Richardson & Baker 1997).

Studies on the feeding activity of adult dragonflies have focused on territorial males or "perchers" (Oehme 1999; May & Baird 2002), probably due to the ease of observation, given their habit of staying in the same spot. Kato & Watanabe (2011) revealed that the frequency of foraging flights in *Sympetrum infuscatum* (Selys, 1883) increased at around noon in forest gaps, which are the main habitat of adults for feeding and resting during both the pre-reproductive and reproductive stages. Previous studies have described the feeding site in relation to prey density in *Pachydiplax longipennis* (Burmeister, 1839) (Baird & May 1997), the diversity of prey species in *Sympetrum frequens* (Selys, 1883) (Higashi 1978), and the diurnal rhythm of prey activity in *S. infuscatum* (Iwasaki et al. 2009). The relation of gut contents to the amount of food intake was reported in *Enallagma boreale* (Selys, 1875) (Anholt 1992). Although the behaviour of feeding fliers has been described in several species, e.g., by H. Kaiser in *Aeshna cyanea* (Müller 1764) (cf. Corbet 1999: 348), however, there have been few studies on the feeding habits of fliers compared to the perchers, probably due to the short observation period available for each individual, and to their rapid foraging on the wing, often high above the ground.

Pantala flavescens (Fabricius, 1798) is one of the best known fliers dwelling in tropical and subtropical regions (Dumont & Verschuren 1991)

and migrates to Japan every spring. Then the population rapidly increases, with frequent swarms of adults (Arai 2007: 90). Hirake (2012) pointed out that *P. flavescens* in foraging swarms often attacks swarming insects such as Ephemeroptera over baseball grounds or natural grasslands in late summer. Samways & Caldwell (1989) also observed mass feeding swarms of *P. flavescens* attacking swarms of small Diptera. Chowdhury & Barman (1986) mention some examples in which fliers seemed to significantly reduce the number of small insects, since in swarm feeding they could consume large numbers of prey items in a short period. Therefore, *P. flavescens* might reduce the number of prey insects especially in summer and autumn in Japan.

The daily food intake of adults is a function of the diurnal rhythm of foraging flights, the foraging success in each foraging flight, and the mass of the prey, all of which can be observed directly at the feeding site of perchers (Higashi 1973, 1978; Kato & Watanabe 2011). After feeding, adults eject faeces, the mass of which could be partly related to the amount of prey insects as well as the absorption efficiency of the dragonfly. Thus, the weight of faeces in addition to the gut contents could be a useful tool for evaluating the daily food intake of adult dragonflies (Watanabe 2015: 93). Fried & May (1983) estimated the daily food intake of *Pachydiplax longipennis* males in relation to energy expenditure, by using the weight of faeces excreted. Mayhew (1994) examined the gut contents of *Calopteryx splendens* (Harris, 1780) and *Erythromma najas* (Hansemann, 1823) after feeding and pointed out that the guts would be emptied a few hours after feeding, due to absorption and excretion. Watanabe et al. (2011) reported that *S. infuscatum* adults kept in the laboratory and using hand-feeding, excreted their indigestible food remnants within 24 hours after feeding. Corbet (1999: 363) points out that quantitative information about gut contents of migrating dragonflies, which travel long distances by flying toward high altitude and by crossing the sea, would help clarify the foraging activities of such species during migration. In addition, Corbet (1984) observed a considerable amount of undigested foods in the guts of Anisopteran species when they landed overnight on bushes during migration, and mentions that they probably fed on prey taken at altitude during migration. On the other hand, Tyagi (1995) found 25 isopteran individuals in the gut of *P. flavescens* in India. The guts of *P. flavescens* adults flying in the early morning were empty, as

reported by Warren (cf. Corbet (1999: 374). The mid-guts of adults of *Anax junius* (Drury, 1773), *P. flavescens*, and *Tramea virginia* (Rambur, 1842) captured on a ship in the southern Sea of Japan were also empty (Hashimoto & Asahina 1969).

The ultimate goal of our study was to reveal details about the life history strategy of *P. flavescens*. Banks & Thompson (1987) pointed out that the number of eggs actually laid by females throughout their life-span was one of the most important factors ensuring the increasing population. Ichikawa & Watanabe (2014) showed that the number of eggs in the ovaries of *P. flavescens* females in the field changed with their age. Despite the fact that daily egg production of females must be affected by daily food intake, a method for estimating the food intake of fliers has not been developed yet. In the present study, as a first step, we tried to estimate the daily food intake of *P. flavescens* females by capturing mature individuals from foraging swarms, and measuring the weight of faeces subsequently excreted by each female in the laboratory. The hand-feeding technique described by Watanabe et al. (2011) was applied to establish the relationships between the food intake and the weight of faeces excreted.

Material and methods

From August to mid-September 2014 swarms of foraging *Pantala flavescens* flew at a low altitude above the grassland in Tsukuba City, Ibaraki Prefecture, central Japan. Females were opportunistically sampled as allowed by the length of the net handle (about 2 m) for a total of 14 sunny and windless days in 2014. The sampling was carried out for the females on the wing before the onset of foraging [07:00–09:00 h JST (UTC+9), 07:20–09:20 h solar time], during active flight (09:00–15:00 h), and after foraging (15:00–17:00 h). Females sampled were in reproductive stage M, just after sexual maturation and with partly brownish wings without visible damage, identified by their worn wing condition (Ichikawa & Watanabe 2014); pre-reproductive females and older, worn individuals were released when captured. We encountered 37 foraging swarms during 14 days, and 13 out of 37 swarms seemed to consist of pre-reproductive stages. Then, in total, 50 females of reproductive stage M were captured from 24 foraging swarms during our study period.

Immediately after the capture, the hind wing length of each female was measured with electronic callipers (accuracy, 0.01 mm). Then, each female was kept individually in envelopes at laboratory conditions of 26°C and a photoperiod regime of 14L:10D. We used envelopes instead of plastic cups for holding the insects because mortalities from injury can occur with the high activity even in small cups. They were fed with a single drop of water (about 50 µl) by syringe in the morning, noon, and afternoon every day. After the females had died, they were put into an oven at 80°C for eight hours and the dry weight was measured using an electronic balance (accuracy, 0.01 mg).

Since the faeces excreted by females in the envelope consisted of rather dry granular pellets, these were easily collected from the envelope using a brush. For five days after capture, the faeces excreted by females that were captured from 07:00–09:00 h in the field were collected at 24-hour-intervals (24, 48, 72, 96, and 120 hours after capture). Then, the faeces were dried in an oven at 80°C for eight hours and their dry weight was measured.

We used the hand-feeding technique for individual females, described in detail by Watanabe et al. (2011). In the present study, the diet for the adults in the laboratory was the sheep blowfly, *Phaenicia cuprina* (Wiedemann, 1830), from stock culture in our laboratory. The dry weight of the fly was 5.42 ± 0.55 mg (SD, n = 17). When the live fly was pressed against the female's mouth using forceps, each female started to chew and completely consumed the whole body within five minutes without leaving any residue. Females which had been held in the envelope for 24 hours were used for the experiment and fed with a single fly. Then, the faeces excreted in the subsequent 24-hour-period were collected and weighed after drying.

All statistical analysis was carried out using R 3.1.1. Dunnett's test was used to compare the dry weight of faeces within 24 hours after capture excreted by females collected from 07:00 to 09:00 with those of females captured from 09:00 to 11:00, 11:00 to 13:00, 13:00 to 15:00 and 15:00 to 17:00. Dunnett's test was also applied to compare the dry weight of faeces excreted by females captured from 07:00 to 09:00 within the first 24 hours after capture with the second, the third, the fourth and the fifth day after capture. A regression analysis was used to investigate the relationships between the longevity of females fed only with water and their dry body mass when they died.

Results

Small foraging swarms of *Pantala flavescens* were observed above the grassland before 09:00. Most swarms including both sexes formed loose aggregations on the wing. At this time they were rather inactive and foraging behaviour had not yet begun. Active flight behaviour in swarms was observed after 09:00 and the swarms increased in size around noon, when most adults were foraging. The flight altitude of the adults was relatively high (about 2–5 m above the ground). In the afternoon, the swarm size gradually decreased and the adults began to leave the grasslands, probably to rest in the bushes near the grasslands. In total, we captured 10 reproductive stage (M) females before the onset of foraging (07:00–09:00), 27 females during the active foraging periods (12 females 09:00–11:00, 5 females 11:00–13:00, 10 females 13:00–15:00) and 13 females after the daily foraging period (15:00–17:00). The hind wing length of the females collected showed little variation: 40.26 ± 1.02 mm (SD, n = 50).

As shown in Figure 1a, faeces from the 24-hour-period after capture were excreted as oval pellets, with a typical length and width of about 3.0 mm and 0.7 mm, respectively. They were dark brown and included many cuticle fragments, probably remnants of the prey insects consumed on the previous day. During the second day after capture, the faecal pellet size decreased, the colour changed to reddish brown, and there were no detectable cuticle fragments (Fig. 1b), suggesting that most of the indigestible food in the gut was excreted within 24 hours of feeding. Although the faeces excreted on the third day after capture remained reddish brown without any cuticle fragments, the shape changed further, to powdery pellets (Fig. 1c). Thereafter, the shape and colour of faecal pellets were similar to those of faecal pellets excreted on the third day after capture.

The dry weight of faeces excreted by females during the first 24 hours after collection from 07:00 to 09:00 was 8.00 ± 1.06 mg (SE, n = 10) and included about 30 pellets. As shown in Figure 2, the dry weight of faeces excreted during the first 24 hours after capture by females collected from 09:00 to 11:00 was 9.65 ± 0.69 mg, which was not significantly different from that of females collected from 07:00 to 09:00. However, females captured from 11:00 to 13:00 and from 13:00 to 15:00 excreted significantly more faeces during the first 24 hours after capture than those collected from 07:00 to

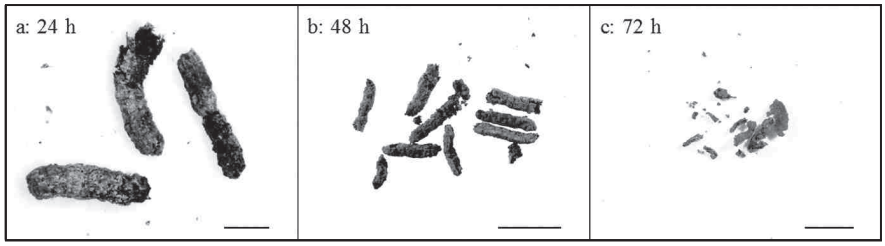


Figure 1. Faeces excreted by *Pantala flavescens* females during three 24-hour-periods after capture; a – first day after capture: dark brown oval pellets with many cuticle fragments, obviously from consumed small insects; b – second day: reddish-brown faeces without cuticle fragments; c – third day: reddish-brown, powdery pellets without cuticle fragments. Each bar represents 1 mm.

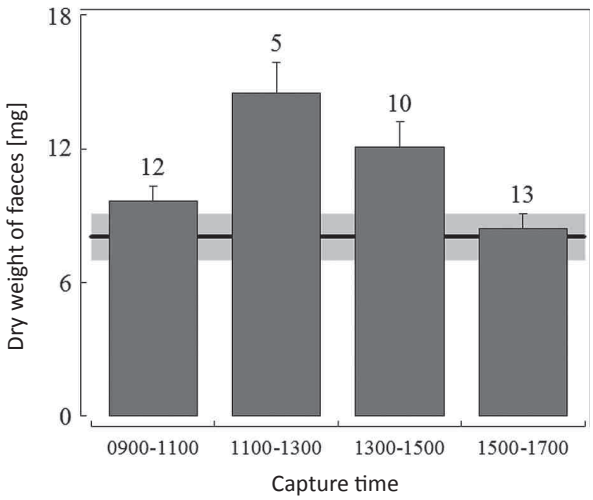


Figure 2. Dry weight of faeces excreted by *Pantala flavescens* females within the first 24 h after capture from 09:00–17:00 (+SE). The line behind the bars with shaded area represents dry weight of faeces excreted during the first 24 h after capture from 07:00–09:00 ± SE (n = 10). This weight was significantly less than for females captured from 11:00–13:00 (Dunnett's test, $\tau = 4.02$, $p < 0.001$) and from 13:00–15:00 ($\tau = 3.03$, $p < 0.05$) but not for those captured from 09:00–11:00 ($\tau = 1.30$, $p = 0.51$) or 15:00–17:00 ($\tau = 0.33$, $p = 0.99$). Numerals above the bars represent sample size.

09:00, i.e. 14.55 ± 1.36 mg and 12.02 ± 1.21 mg, respectively. The faeces excreted by females during the first 24 hours collected from 15:00 to 17:00 weighed 8.41 ± 0.64 mg which was not significantly different from that of females captured from 07:00 to 09:00.

Figure 3 shows the changes in the dry weight of faeces excreted by the females captured from 07:00 to 09:00, each 24-hour-period for five days after capture. The total dry weight of faecal pellets excreted during the second 24-hour-period after capture significantly decreased compared with the total dry weight of faecal pellets excreted in the first 24 hours after capture (Dunnett's τ-test, $\tau = 6.19$, $p < 0.001$). Thereafter the dry weights of faeces excreted on the third, fourth and fifth day after capture were 1.46 ± 0.25 mg, 0.78 ± 0.20 mg and 0.97 ± 0.12 mg, respectively (SE); each was significantly less than that of the faeces excreted during the first 24 hours after capture. The dry weight of faeces excreted in the first 24-hour-period by females captured from 07:00 to 09:00, must reflect the quantity of food intake in the previous day, because most females captured from 07:00 to 09:00 had not yet fed on the day of collection.

The females kept with water only in the laboratory died about three days after capture. The average weight of the females was 96.31 ± 1.67 mg (SE, n = 44), though the dry weight of females depended on the holding period ($y = -2.0 + 102.8\,x$, $r^2 = 0.11$, $p < 0.05$), probably due to females continuously excreting faeces until they died.

The dry weight of faeces excreted by females within 24 hours after being fed with a sheep blowfly was 4.51 ± 0.38 mg (SE, n = 6). Many cuticle fragments, which must have originated from the prey were observed in the faeces excreted by females within 24 hours after feeding.

Discussion

In the present study, because females excreted most of the indigestible food within 24 hours after feeding, the reddish brown faeces excreted on the second, third, fourth and fifth day after capture must be mainly the waste derived from the females metabolising reserves in the fat body. The weight of faeces excreted on the second day by females captured from 07:00 to 09:00 (2.23 mg) must be the dry weight of faeces excreted by starved females with empty guts over a 24-hour-period, i.e., the majority of the waste was de-

rived from the females metabolising reserves (Fig. 4). The faeces excreted by females within 24 hours after being fed with a sheep blowfly must include predicted wastes derived from background metabolism during the 24-hour-period (2.23 mg). Therefore, the dry weight of faeces derived from a fly was 2.28 mg (4.51–2.23 mg). As the weight of a sheep blowfly was 5.42 mg, females absorbed 3.14 mg (5.42–2.28 mg) from the blowfly. On the other hand, the weight of faeces excreted by females captured from 07:00–09:00 in the field, during 24 hours after capture was 8.00 mg; thus, the dry weight of faeces derived from the small insect prey fed on the previous day was 5.77 mg (8.00–2.23 mg). Because each blowfly yielded 2.28 mg undigested material, the faeces corresponded to 2.53 sheep blowflies (5.77 mg/2.28 mg). Thus, mature females can be estimated to feed on about 13.71 mg dry weight (2.53 sheep blowflies × 5.42 mg) per day. Consequently, in the present study, the assimilatory quotient of *P. flavescens* females was 57.9 %. Fried & May

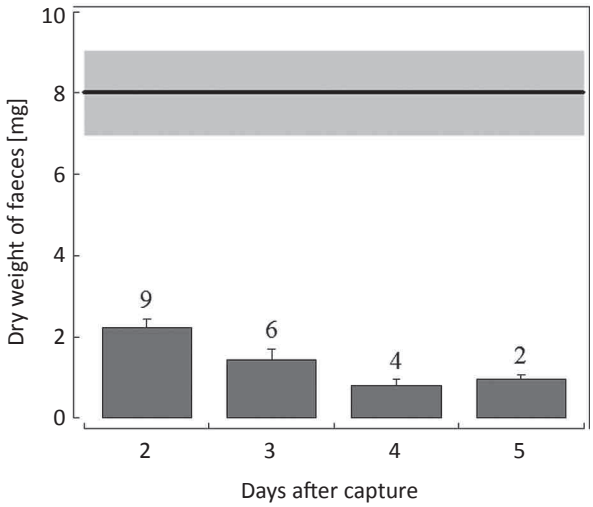


Figure 3. Daily changes in dry weight of faeces excreted by *Pantala flavescens* females. The line with shaded area represents dry weight of faeces ± SE (n = 10) within 24 h after capture, excreted by females captured in the morning from 07:00–09:00. From the second day onwards, dry weight of faeces is significantly lower (Dunnett's test, p <0.001; day 2, τ = 6.19; day 3, τ = 6.24; day 4, τ = 6.01; day 5, τ = 4.47). Numerals above the bars represent sample size.

(1983) examined the energy expenditure and food intake of territorial male *Pachydiplax longipennis*, and calculated that the assimilatory quotient was 78 %. Higashi (1973) reported that the assimilatory quotient of *Sympetrum frequens* adult in the fields was 75 %. Therefore, the assimilatory quotient of *P. flavescens* females might be rather small comparing with other libellulid species, due to the feeding technique. The individual blowfly must be considerably larger than the common prey insect for *P. flavescens* females. In addition, Arrese & Soulages (2010) pointed out that the lipid metabolism in insects is essential for growth and reproduction, though the mechanism of energy storage and release was changed on the duration of non-feeding periods.

The daily food intake of *Pantala flavescens* females in the field was estimated by comparing the weight of faeces excreted by females fed with a sheep blowfly using the hand-feeding technique with that of starved females. Reproductive-stage *P. flavescens* females consumed about 13.7 mg food (dry weight) daily, corresponding to about 14.1 % of their body weight.

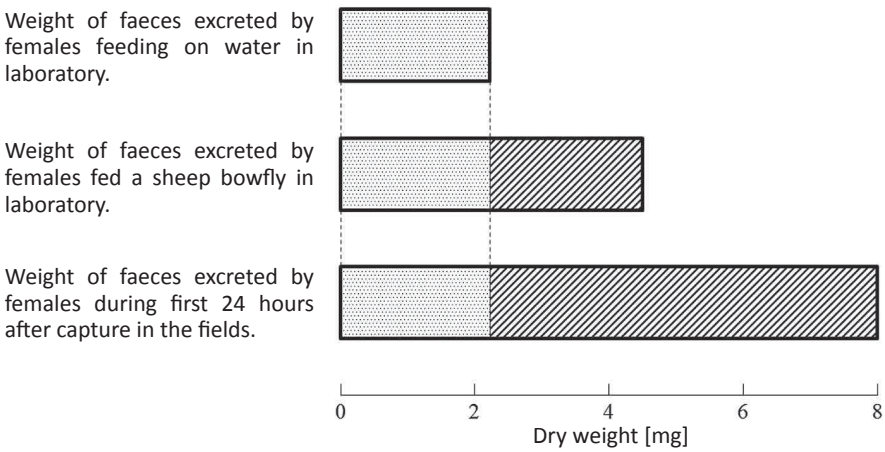


Figure 4. Dry weight of faeces excreted by *Pantala flavescens* females during 24 h after having been fed in the laboratory on water only (top), a sheep blowfly (middle) and after capture in the field between 07:00 and 09:00 (bottom). The dotted area and the striped area correspond to the dry weight of wastes derived from metabolism of reserves and the dry weight of faeces derived from the prey, respectively.

In perchers, adults of *Calopteryx cornelia* (Selys, 1853) and *Sympetrum frequens* ate about 6.3 mg and 11.8–12.3 mg in a day, respectively, corresponding to about 11–15 % of their body weight in both cases (Higashi 1973). *Pachydiplax longipennis* males ingested 8.2–9.9 mg a day, corresponding to 14–15 % of their body weight (Fried & May 1983). Watanabe et al. (2011) reported that the mature females of *Sympetrum infuscatum* fed on 17.7 mg a day, corresponding to 14.3 % of their dry body weight. Thus, the physiology and the metabolism of digestive organs of dragonflies of similar size might be similar among the species including both perchers and fliers. However, May (1979) pointed out that the basal metabolism of fliers was higher than that of perchers, because fliers spend all their time in the air when foraging, while perchers rest on plants or on the ground (May 1984). Baird & May (1997) reported that in *P. longipennis* the level of energy consumption on the wing was 85 times greater than on the perch. In the present study, *P. flavescens* females were reared in envelopes and were not allowed to fly, thus they consumed very little energy. Consequently, the amount of faeces excreted derived from metabolism is expected to be lower than that in the field.

Baird & May (1997) investigated the abundance of small insects at the foraging sites of dragonflies by using sticky traps, and reported that most insects captured by the traps were small Diptera and their number became greatest from late morning to mid-afternoon. Kato & Watanabe (2011) reported that *S. infuscatum* females consumed about 102 small insects per day and Oehme (1999) recorded 16.14 successful foraging flights per hour in the same male *S. striolatum* (Charpentier, 1840). Iwasaki et al. (2009) also used a sticky trap to investigate the species composition and the abundance of prey insects flying in the forest gaps, identified as feeding sites of adult dragonflies, and then reported that the dry weight of each prey insect was about 0.17 mg. Higashi (1978) estimated the dry weight of prey insects of dragonflies for calculating the daily food intake in the deforested area, where a large number of *P. flavescens* adults were aggregated in early autumn, and estimated the dry weight of each potential prey insect at about 0.074 mg. In the present study, we captured *P. flavescens* females in the open grassland, with similar prey composition as in Higashi (1978); i.e., small insects including especially Diptera and Hymenoptera. Thus, we

used his estimated dry weight for single potential prey insects, 0.074 mg. Because the daily food intake of *P. flavescens* was about 13.71 mg, each female would have to consume about 185 small insects (13.71 mg/0.074 mg) in a day.

Corbet (1999: 360) points out that dragonflies tend to forage at sites where prey insects are abundant. In the central valley of California, swarms of male mosquitoes, *Anopheles freeborni* (Aitken, 1939), appearing in the evenings from July to late September were attacked by large numbers of libellulid dragonflies (Yuval et al. 1993). Gibo (1981) reported that fliers could forage sites, where large numbers of small insects aggregated by thermal air currents. Baird & May (1997) revealed that the frequency and success of foraging by each *P. longipennis* adult increased with the swarm size of small insects, though the degree of interference among conspecifics increased. Adults of *P. flavescens* often aggregate and forage on swarms of small insects in the field (Moore 1993; Arai 2007: 33). Therefore, *P. flavescens* in Japan might search for foraging sites, where prey insects are abundant including swarm sites, and as a result, affect the population dynamics of the prey insects.

Pantala flavescens is well known for its opportunistic reproductive strategies, with females laying eggs in small ponds (Hawking & Ingram 1994), rice paddy fields (Arai 2012), swimming pools (Watanabe 1999) and puddles (Hirake 2012). In addition, the eggs and larvae of *P. flavescens* develop very rapidly, completing development within 50 days (Suhling et al. 2004; Iwata et al. 2009). Since the species is considered to be a typical *r*-strategist (Corbet 1999: 10), females must lay a large number of eggs throughout their life span. Ichikawa & Watanabe (2014) reported that *P. flavescens* females of stage M, i.e., just after sexual maturation, had about 1 100 ovarioles each containing about four submature eggs (oval eggs without chorion), indicating that they might have the ability to develop a large number of mature eggs in a short time. Koch & Suhling (2005) reported that *P. flavescens* females laid about 981 eggs in a single oviposition bout. A detailed study on the relationships between daily food intake and the egg production process in reproductive females of *P. flavescens* is needed to reveal their life history strategies focusing on their migration to Japan every spring and the rapid increase in their population towards early autumn.

Acknowledgements

We would like to thank Dr T. Yokoi for critical reading of the manuscript. Dr F. Weihrauch, Dr H. Wildermuth, and Dr A. Martens also provided useful comments on the manuscript.

References

Anholt B.R. 1992. Sex and habitat differences in feeding by an adult damselfly. *Oikos* 65: 428-432

Anholt B.R., Marden J.H. & Jenkins D.M. 1991. Patterns of mass gain and sexual dimorphism in adult dragonflies (Insecta: Odonata). *Canadian Journal of Zoology* 69: 1156-1163

Arai Y. 2007. [The mystery of red dragonflies]. Doubutsu-sha, Tokyo [In Japanese]

Arai Y. 2012. Some ecological observations of *Pantala flavescens* (Fabricius) in Kanto District. *Gracile* 72: 32-39 [In Japanese, English summary]

Arrese E.L. & Soulages J.L. 2010. Insect fat body: energy, metabolism, and regulation. *Annual Review of Entomology* 55: 207-225

Baird J.M. & May M.L. 1997. Foraging behavior of *Pachydiplax longipennis* (Odonata: Libellulidae). *Journal of Insect Behavior* 5: 655-678

Banks M.J. & Thompson D.J. 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *Journal of Animal Ecology* 56: 815-832

Bennettova B. & Fraenkel G. 1981. What determines the number of ovarioles in a fly ovary? *Journal of Insect Physiology* 27: 403-410

Chowdhury S.H. & Barman A. 1986. Food habits of a libellulid dragonfly *Pantala flavescens* (Fabricius). *Annals of the Entomological Society of America* 4: 1-6

Corbet P.S. 1984. Orientation and reproductive condition of migrating dragonflies (Anisoptera). *Odonatologica* 13: 81-88

Corbet P.S. 1999. Dragonflies: Behavior and ecology of Odonata. Cornell University Press, Ithaca, New York

Dumont H.J. & Verschuren D. 1991. Atypical ecology of *Pantala flavescens* (Fabr.) on Easter Island (Anisoptera: Libellulidae). *Odonatologica* 20: 45-51

Fried C. & May M.L. 1983. Energy expenditure and food intake of territorial male *Pachydiplax longipennis* (Odonata: Libellulidae). *Ecological Entomology* 8: 283-292

Gibo D.L. 1981. Some observation on slope soaring in *Pantala flavescens* (Odonata: Libellulidae). *Journal of the New York Entomological Society* 89: 184-187

Hashimoto H. & Asahina S. 1969. [Records of the insects visited a weather-ship located at the Ocean Weather Station "Tango" on the Pacific: IV Observations on the dragonflies]. *Kontyu* 37: 305-319 [In Japanese]

Hawking J.H. & Ingram B.A. 1994. Rate of larval development of *Pantala flavescens* (Fabricius) at its southern limit of range in Australia (Anisoptera: Libellulidae). *Odonatologica* 23: 63-68

Higashi K. 1973. Estimation of the consumption for some species dragonflies. 1. Estimation by observation for the frequency of feeding flights of dragonflies. *Reports from the Ebino Biological Laboratory*,

Kyushu University 1: 119-129 [In Japanese, English summary]

Higashi K. 1978. Daily food consumption of *Sympetrum frequens* Selys (Odonata: Libellulidae). *J.I.B.P. Synthesis* (*Japanese Committee for the International Biological Program*, *Tokyo*) 18: 199-207

Hirake T. 2012. Marking and flight observation of *Pantala flavescens*. *Gracile* 72: 42-47 [In Japanese, English summary]

Ichikawa Y. & Watanabe M. 2014. Changes in the number of eggs loaded in *Pantala flavescens* females with age from mass flights (Odonata: Libellulidae). *Zoological Science* 31: 721-724

Iwasaki H., Suda D. & Watanabe M. 2009. Foraging activity of *Sympetrum infuscatum* (Selys) adults living in satoyama forest gaps. *Japanese Journal of applied Entomology and Zoology* 53: 165-171 [In Japanese, English summary]

Iwata N., Akieda N., Hirai N. & Ishii M. 2009. Seasonal prevalence of the migratory dragonfly, *Pantala flavescens* (Anisoptera, Libellulidae), in Sakai City, Osaka Prefecture, central Japan. *Tombo* 51: 29-37 [In Japanese, English summary]

Kato K. & Watanabe M. 2011. Foraging flights of *Sympetrum infuscatum* (Selys) adults inhabiting cedar forest gaps of satoyama (Odonata: Libellulidae). *Japanese Journal of Entomology* (NS) 14: 177-186 [In Japanese, English summary]

Koch K. & Suhling F. 2005. Do behavioural and life-history traits vary with mate-guarding intensity in libellulid odonates? *Canadian Journal of Zoology* 83: 1631-1637

Marden J.H. 1989. Body building dragonflies: costs and benefits of maximizing flight muscle. *Physiological Zoology* 62: 505-521

May M.L. 1979. Energy metabolism of dragonflies (Odonata: Anisoptera) at rest and during endothermic warm-up. *Journal of experimental Biology* 83: 79-94

May M.L. 1984. Energetics of adult Anisoptera, with special reference to feeding and reproductive behavior. *Advances in Odonatology* 2: 95-116

May M.L. & Baird J.M. 2002. A comparison of foraging behavior in tow "percher" dragonflies, *Pachydiplax longipennis* and *Erythemis simplicicollis* (Odonata: Libellulidae). *Journal of Insect Behavior* 15: 765-778

Mayhew P.J. 1994. Food intake and adult feeding behaviour in *Calopteryx pterygidae* (Harris) and *Erythromma najas* (Hansemann) (Zygoptera: Calopterygidae, Coenagrionidae). *Odonatologica* 23: 112-124

Moore N.W. 1993. Behaviour of imaginal *Pantala flavescens* (Fabr.) on Easter Island (Anisoptera: Libellulidae). *Odonatologica* 22: 71-76

Neville A.C. 1983. Daily cuticular growth layers and the teneral stage in adult insects: a review. *Journal of Insect Physiology* 29: 211-219

Oehme H. 1999. Jagderfolg und Jagdtaktik bei *Sympetrum striolatum* (Charpentier) (Anisoptera: Libellulidae). *Libellula* 18: 79-87

Plaistow S. & Siva-Jothy M.T. 1999. The ontogenetic switch between odonate life history stages: effects on fitness when time and food are limited. *Animal Behaviour* 58: 659-667

Richardson J.M.L. & Baker R.L. 1997. Effect of body size and feeding on fecundity in the damselfly *Ischnura verticalis* (Odonata: Coenagrionidae). *Oikos* 79: 477-483

Samways M.J. & Caldwell P. 1989. Flight behaviour and mass feeding swarms of *Pantala flavescens* (Fabricius) (Odonata:

Anisoptera: Libellulidae). *Journal of the Entomological Society of Southern Africa* 52: 326-327

Suhling F., Schenk K., Padeffke T. & Martens A. 2004. A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata). *Hydrobiology* 528: 75-85

Tyagi B.K. 1995. A note on termite consumption by *Pantala flavescens* (Fabr.) (Anisoptera: Libellulidae) *Notulae odonatologicae* 4: 92

Watanabe M. 1999. Basic research on the Odonata larvae as a teaching material from the swimming pool of elementary and junior high schools. *Japanese Journal of biological Education* 39: 65-76 [In Japanese, English summary]

Watanabe M. 2015. [Ecology of Odonata]. University of Tokyo Press [In Japanese]

Watanabe M., Suda D. & Iwasaki H. 2011. The number of eggs developed in the ovaries of the dragonfly *Sympetrum infuscatum* (Selys) in relation to daily food intake in forest gaps (Anisoptera: Libellulidae). *Odonatologica* 40: 317-325

Yuval B., Wekesa W. & Washino R.K. (1993) Effects of body size on swarming behavior and mating success of male *Anopheles freeborni* (Diptera: Culicidae). *Journal of Insect Behavior* 6: 333-342

1st December 2015

Heteragrion thais sp. nov. from the Atlantic Forest of Brazil (Odonata: Heteragrionidae)

Angelo B.M. Machado

Departamento de Zoologia, Instituto de Ciências Biológicas,
Universidade Federal de Minas Gerais, Caixa Postal 486,
31270-901 Belo Horizonte, Minas Gerais, Brazil; <angelo@icb.ufmg.br>

Received 13th April 2015; revised and accepted 30th September 2015

Abstract. A new *Heteragrion* damselfly species, *Heteragrion thais* sp. nov. (Holotype deposited in ABMM) from Brazil, Minas Gerais State, Municipality of Barroso, is described and illustrated. This species is most similar to *H. beschkii*, *H. gracile*, and *H. luizfelipei*, from which it can be distinguished by the shape of the cercus and the colour of the posterior lobe of the prothorax.

Key words. Dragonfly, damselfly, new species, Zygoptera

Introduction

Heteragrion Rambur, 1842 is a Neotropical genus of Zygoptera that comprises 53 species and one subspecies (Garrison et al. 2010; Lencioni 2013; Machado & Souza 2014). The genus, together with *Oxystigma* Selys, 1862, has recently been raised to the rank of a family, Heteragrionidae (Dijkstra et al. 2014). It has been divided into two groups by Lencioni (2013). In Group A, which corresponds to groups 1 and 2 of Selys (1886), the males lack an elongated paraproct and females have several rows of teeth on the ventral surface of genital valves. In Group B, which corresponds to Selys' group 3, the males have an elongated paraproct and females possess a single row of teeth on the ventral surface of genital valves. Group A comprises the majority of Brazilian species, and its taxonomy has been long hampered by the lack of a modern comprehensive review and difficulties in identifying some poorly described species, most of them by Selys (1862, 1886). This problem has been, in great part, solved by the important and richly illustrated review of the genus by Lencioni (2013). However, the identification of three species – *H. obsoletum* Selys, 1886, *H. ochraceum* Hagen *in* Selys

1862, and *H. ovatum* Selys, 1862 – remains uncertain. I describe herewith a new species of Group A from Brazil, thus, elevating the number of *Heteragrion* species to 54. It was collected at Mata do Baú (Baú Forest) in the municipality of Barroso, southeastern Minas Gerais State, where 57 species of odonates have been recorded (Souza et al. 2014), five of which are from the genus *Heteragrion*.

Heteragrion thais **sp. nov.**
(Figs 1–5)

Material studied
Holotype ♂. Brazil, Minas Gerais State, Municipality of Barroso (21°11'13"S, 43°58'34"W), Mata do Baú (Baú Forest), elevation 1 100 m a.s.l., 28-i-2011, M.M. de Souza leg.
Paratypes (all from the same site as holotype, M.M. de Souza leg.). 1♂, 20--xi-2010; 1♂, 05-ii-2011.
Type material was deposited in A.B.M. Machado collection (coll. ABMM) of the Department of Zoology at the Federal University of Minas Gerais, Belo Horizonte, Brazil.

Etymology
Named for Thaís Fernanda Costa e Silva Magalhães de Souza (name in apposition), wife of Professor Marcos Magalhães de Souza, who collected this species.

Male (holotype)
Head (Fig. 2) – Labrum reddish-orange, anteclypeus, base of mandibles, genae and antefrons orange; postclypeus black, laterally orange. Upper part of head with black and orange markings as shown in Figure 2.

Figure 1. Holotype male of *Heteragrion thais* sp. nov., thorax in lateral view.

Thorax (Figs 1, 3) – anterior lobe of prothorax black, median lobe orange, posterior lobe orange, with a small black spot laterally and a large rounded median black spot (Fig. 3). Pterothorax (Fig. 1): mesepisternum orange, middorsal carina and a narrow line adjacent to it black; ante-alar sinus orange, mesepimeron orange with a subrectangular black stripe not reaching the dorsal and ventral limits of the sclerite (Fig. 1). Metepisternum orange, with some irregular translucent areas. Metepimeron orange red. Wings hyaline, slightly suffused with yellow, pterostigma dark brown, legs yellowish brown. Venation: Px in Fw 22, in Hw 19, RP2 arising near Px 10 in Fw, Px 8 in Hw. IR1 arising near Px 12 in Fw, Px 10 in Hw: Petiolation arising distal to CuP by a distance 3x the length of CuP in Fw, 4x in Hw.

Abdomen – S1 orange; S2 laterally orange, dorsally black; S3–7 black with a proximal orange ring and a distolateral yellow streak not reaching the distal black area. S8 orange except for a dorsal black area occupying its proximal half; S9–10 orange, the latter with a short, dark middorsal marking. Cercus black, with ventral expansion orange.

Structural characters – Hind prothoracic lobe (Fig. 3) smoothly rounded with no well-defined lateral portions. Mesostigmal plates as in Figure 3. Cercus in lateral view (Fig. 4) with dorsobasal expansion well-developed, ventrobasal expansion occupying half of cercus length. In mediodorsal view (Fig. 5) medial and distal portions subequal, basal portion slightly longer. Apex of medial process of cercus in mediodorsal view rounded (Fig. 5).

Measurements [mm] – Fore wing 26.0, hind wing 27.0, abdomen 39.2.

Variability in paratypes

In one teneral paratype, the wings are totally hyaline and the mesepisternum is grayish orange.

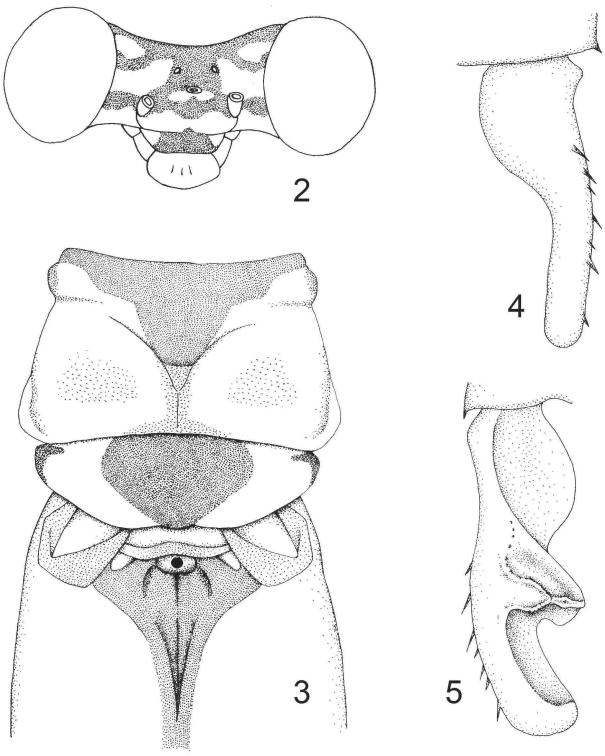
Measurements [mm] – Fore wing 26.0-27.0, hind wing 27.0-28.0, abdomen 39.0-39.3.

Female

Unknown.

Remarks

As it lacks paraprocts, *Heteragrion thais* sp. nov. belongs to the species group A of Lencioni (2013). Within this group it shares with *H. beschkii* Hagen *in* Selys, 1862, *H. gracile* Machado, 2006, and *H. luizfelipei* Machado, 2006 the orange mesepisternum and metepimeron, the first with a short black stripe not reaching the dorsal and ventral limits of the sclerite. It differs from *H. luizfelipei* mainly by having the medial process of cercus rounded and not forming two triangles and from *H. gracile* and *H. beschkii* by the hind prothoracic lobe with a black spot (pale in both species). Table 1 shows the characters separating males of *H. thais* sp. nov. from those of *H. beschkii, H. luizfelipei*, and *H. gracile*.



Figures 2–5. Holotype male of *Heteragrion thais* sp. nov.; 2 – head in dorsal view; 3 – thorax in dorsal view; 4–5 – cercus in lateral (4) and mediodorsal (5) view.

Table 1. Characters separating males of *Heteragrion thais* sp. nov. from *H. beschkii*, *H. gracile*, and *H. luizfelipei*.

	H. thais sp. nov.	*H. beschkii*	*H. gracile*	*H. luizfelipei*
Hind prothoracic lobe black spot	Present	Absent	Absent	Present
Apex of medial process of cercus in mediodorsal view	Rounded	Truncate	With a small and a large triangle	With a small and a large triangle
Ventrobasal expansion of cercus in lateral view	Occupying *ca* ½ of cercus length	Occupying *ca* ¼ of cercus length	Occupying ⅓ of cercus length	Occupying *ca* ⅓ of cercus length
Relationship of portions of cercus in mediodorsal view	Medial and distal portion subequal. Proximal portion slightly longer.	Proximal and medial portions subequal. Distal portion shorter.	Proximal and median portions subequal. Distal portion small.	Proximal and distal portions subequal. Median portion longer.
Hw size [mm]	27–28	25	30.4	26.1
Abdomen size [mm]	39.0	39	42.3	38.8
Anteclypeus	Orange	Grayish orange	Grayish orange	Brown

Acknowledgements

I thank FAPEMIG for the financial support for this project (Programa Biota Minas, Edital 14/2009), which resulted in the finding of *H. thais*, and Professor Marcos Magalhães Souza for having collected the type material. I also thank Myrian Morato Duarte for the drawings illustrating this paper and the biologist Lucio Bedê for critically revising this manuscript.

References

Dijkstra K.-D.B., Kalkman V.J., Dow R.A., Stokvis F.R. & van Tol J. 2013. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology* 39: 68-96

Garrison R.W., von Ellenrieder N. & Louton J.A. 2010. Damselfly genera of the New World: An illustrated and annotated key to the Zygoptera. John Hopkins University Press, Baltimore

Lencioni F.A.A. 2013. Diagnoses and discussion of the group 1 and 2 Brazilian species of *Heteragrion*, with descriptions of four new species (Odonata: Megapodagrionidae). *Zootaxa* 3685 (1): 1-80

Machado A.B.M. & Souza M.M. 2014. A remarkable new species of *Heteragrion* from Brazil (Odonata: Megapodagrionidae). *International Journal of Odonatology* 17: 95-99

Selys Longchamps de M.E. 1862. Synopsis des Agrionines, troisième légion: *Podagrion*. *Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique* (II) 14: 5-44

Selys Longchamps de M.E. 1886. Révision du synopsis des Agrionines, Première partie comprenant les légions *Pseudostigma-Podagrion-Platycnemis et Protoneura. Mémoires couronnés et autres Mémoires de l'Académie royale des Sciences, des Lettres et des Beaux-arts de Belgique* 38 (4): i-iv, 2-233

Souza M.M., Souza B., Pereira M.C.S.A. & Machado A.B.M. 2014. List of Odonates from Mata do Baú, Barroso, Minas Gerais, Brazil. *Check List* 9: 1367-1370

1st December 2015

Four new species of *Calvertagrion* St. Quentin from South America (Odonata: Coenagrionidae)

Kenneth J. Tennessen

P.O. Box 585, Wautoma, WI 54982, USA; <ktennessen@centurytel.net>

Received 12th February 2015; revised and accepted 21st May 2015

Abstract. Four new species of *Calvertagrion* are described from the upper Amazon region of South America east of the Andes foothills, namely *C. albatum* sp. nov. (holotype male, Madre de Dios Department, Peru), *C. charis* sp. nov. (holotype male, Loreto Department, Peru), *C. declivatum* sp. nov. (holotype male, Santa Cruz Department, Bolivia), and *C. mauffrayi* sp. nov. (holotype male, Orellana Province, Ecuador). These additions bring the total number of species in the genus to five. Differences in thoracic and abdominal color pattern, morphology of the pronotum and male appendages are presented as characters in a key separating the known species. The male genital ligula is remarkably uniform within the genus, which is unusual within coenagrionid genera with multiple species.

Key words. Dragonfly, damselfly, Zygoptera, new species, Amazon Basin, Bolivia, Ecuador, Peru

Introduction

Damselflies in the genus *Calvertagrion* St. Quentin are among the smallest Zygoptera, total length within 19 to 25 mm, comparable to *Ischnura capreolus* (Hagen, 1861), one of the smallest species in the New World (Westfall & May 2006). Only one species of *Calvertagrion* has been described to date, *C. minutissimum* (Selys, 1876), known only from Brazil (Garrison & Costa 2002). Garrison et al. (2010) based the characterization of the genus *Calvertagrion* on that species alone.

St. Quentin (1960) established the genus *Calvertagrion* for a species he thought was undescribed that did not fit in any established genus. He named the species *Calvertagrion dicellularis*, based on three specimens from Taperinha near Santarém, in western Pará State, Brazil, collected 21–31-vii-1927 by Hans Zerny, and deposited in the Natural History Museum, Vienna, Austria (NMW, Naturhistorisches Museum Wien). Garrison & Costa (2002)

examined the holotype female of *Agrion? minutissimum* Selys, 1876, a name which had been long forgotten, and discovered that it and *C. dicellularis* belonged to the same species. They compared wing venation with St. Quentin's holotype and allotype, and provided illustrations of the prothorax of the females to prove the synonymy; therefore, the correct name for this species is *Calvertagrion minutissimum* (Selys).

I collected two species that are very similar to *C. minutissimum*, one in Ecuador and one in Bolivia, but differing in male appendages, prothoracic structure and color pattern to warrant describing them as distinct species. Two additional undescribed species from Peru, based on specimens sent to me by Sidney W. Dunkle, Rosser W. Garrison, and Dennis R. Paulson, are also described, making a total of five species for the genus. A key to the known species is presented and character states of all five species are combined to diagnose the genus *Calvertagrion*.

Material and methods

Illustrations were made with aid of camera lucida and digital camera attached to a Wild stereomicroscope. Wing nomenclature follows Riek & Kukalovà-Peck (1984). Measurements were made with an ocular micrometer. Total length and abdomen length include male anal appendages and female ovipositor; pterostigma length was measured along the costa and includes the widths of the enclosing proximal and apical cross-veins. Lat/long coordinates are in decimal degrees, taken either in the field with a handheld GPS device or approximated using GoogleEarth.

Abbreviations: L (length), W (width), Fw (fore wing), Hw (hind wing), Px (postnodal cross-veins), S (abdominal segment); FSCA (Florida State Collection of Arthropods, Gainesville, Florida, USA), USNM (United States National Museum), UMMZ (University of Michigan Museum of Zoology), CEUA (Colección de entomología de la Universidad de Antioquia, Colombia), JJD (Jerrell J. Daigle), SWD (Sidney W. Dunkle), RWG (Rosser W. Garrison), JTJ (Jim T. Johnson), WFM (Bill Mauffray), DRP (Dennis R. Paulson), KJT (Kenneth J. Tennessen). All primary types have been designated to be deposited in the FSCA.

***Calvertagrion albatum* sp. nov.**
(Figs 1, 2, 5a–12a, 16a)

Specimens studied
Holotype ♂. Peru, Madre de Dios Department, Tambopata Nature Reserve, 30 km SW Puerto Maldonado (general vicinity of -12.837°, -69.294°), in grass on sandy bank of Rio La Torre, 19-ii-1982, D.L. Pearson leg.
Allotype ♀. Peru, Madre de Dios Department, same general locality as holotype but »marsh behind willow bar«, 01-iii-1989, P. Donahue leg.
Paratypes (4♂). 1♂, same data as holotype; 1♂, same general loc., except »clearing«, 12-iii-1983, M. Frisbie leg; 1♂, Tambopata-Candamo Reserved Zone, Camp 5, »rio Tambopata east bank, marsh« (-12.838°, -69.2997°), 05--xii-1992, Martin Butt leg; 1♂, same loc., 10-xii-1992, Martin Butt leg.

The holotype and allotype are currently housed in the collection of DRP, but are to be deposited in the FSCA, Gainesville, Florida. Paratypes are in the collections of DRP and RWG.

Etymology
Derived from the Latin adjective *albus* meaning "clothed in white" for the thick, white pruinosity on the thorax.

Male (holotype)
Head – Labium light tan; labrum and base of mandible dark green to brown; anteclypeus and genae brown; postclypeus and frons black; occiput black with pair of blue post-ocular spots 0.6 mm wide (Fig. 1); rear of head black (posterior surface of occiput) dorsally and medially around occipital foramen, blue laterally and ventrally; antennae brown.

Thorax – Pronotum black; medial projection of hind lobe directed dorsally, apex situated above level of middle lobe, projection entire but in lateral view with posterior margin angulate (Fig. 5a); propleuron tan, covered with pruinosity. Pterothorax covered with white pruinosity, thick dorsally, very thin on venter. Mesepisternum black except for a small, posterior, triangular green spot; mesinfraepisternum black on upper ¾, lower ¼ tan; mesepimeron mostly brown to gray-green or blue, with black spot anteri-

orly and posteriorly; metepisternum and metepimeron grayish-blue; metinfraepisternum with blackish-brown spot antero-medially, otherwise light brown; legs mostly yellowish tan except coxae darker brown and femora with brown dorsal stripe, spines black, apex of 3rd tarsomere black, claws with apex black and well-developed black supplementary tooth. Anterior vein of Fw quadrangle twice length of proximal vein, half length of posterior vein; 6 Px in right Fw, 5 in left Fw, 5 in right Hw (left Hw missing); pterostigma black, surmounting less than half cell below it (Fig. 2).

Abdomen – Dorsum mostly black; S1 with apical fifth blue, sides blue, lightly pruinose; S2–6 with longitudinal black stripe, constricted by blue basally and in posterior fourth, sides blue above, tan below; S7 mostly black dorsally except blue in anterior 1/20, sides tan; S8 mostly blue but with black dorsal stripe narrow in anterior 2/3, widened in posterior third; S9 mostly black, sides blue; S10 black, tan latero-ventrally (Fig. 6a). Cercus 0.34 mm long, brown, in lateral view triangular with sharply acuminate tips (Fig. 7a), in dorsal view appearing blade-like with a long, shallow curved depression from near medial angle to tip; in dorsal view outer margins of cerci parallel (Fig. 8a). Paraprocts in lateral view broadly triangular, elongate, directed posteriorly but slightly dorsally inclined (Fig. 7a), length about 80 % length of cercus, tips black, rounded. Genital ligula with three small pale setae on each side of basal segment, without terminal fold but with a small, triangular membranous inner fold distal to flexure of second segment, terminal segment with margins produced into a sclerotized, mid-lateral right angle; apex pale, in lateral view elongate with apex triangular, in ectal view wide with apical margin slightly concave and lateral extremities acutely tapered (Fig. 9a).

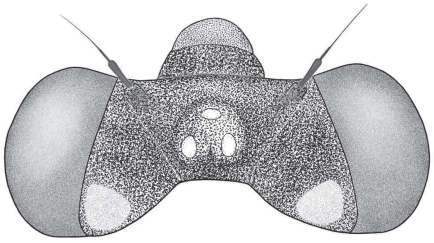


Figure 1. *Calvertagrion albatum* sp. nov., holotype male head, dorsal view.

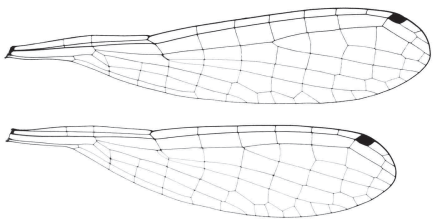


Figure 2. *Calvertagrion albatum* sp. nov. wings, male.

Measurements [mm] - Total length 24.2, abdomen length 19.7, Hw length 11.1.

Female (allotype)
Similar to holotype except as follows:
Head – Most of head light brown with thin, dark brown lines dorsally, no post-ocular spots apparent; rear of head completely tan.

Thorax – Pronotum brown; medial projection of hind lobe similar to that of male (Fig. 10a). Pterothorax mostly medium brown with orange cast, no pruinosity apparent; mesostigmal plates with low medial ridge, distinct anterior and posterior ridges, transverse depression, pale rounded corners (Fig. 11a); 8 Px in Fw, 7 in right Hw, 6 in left Hw; pterostigma brown, surmounting *ca* 50 % or more of cell below.

Abdomen – Mostly shades of brown; S1 and S2 tan; S3 mostly tan with an isolated dorsal brown spot in posterior ⅕ ; S3–5 with dorsal dark brown stripe narrow in anterior ¾, widened posteriorly except constricted in posterior ⅕ ; S6–7 similar but with dorsal dark brown stripe wider; S8–10 more uniform, medium brown on dorsum and sides pale brown (Fig. 12a). Ovipositor light brown, curved upward, ventral margin setose, serrate in posterior half; stylus dark brown, 0.31 mm long. Cercus brown, triangular, 0.20 mm long; paraproct rounded, pale brown.

Measurements [mm] – Total length 23.4, abdomen length 18.5, Hw length 12.5, ovipositor length 1.43.

Variation in paratype males
Px ranged from 6–7 in Fw, 5–6 in Hw; pterostigma usually surmounting about ⅖ of cell below; range in measurements [mm]: total length 22.3–24.2, abdomen length 17.9–19.7, Hw length 10.2–11.1, cercus length 0.33–0.37.

Diagnosis
Calvertagrion albatum sp. nov. males share with *C. charis* sp. nov. and *C. minutissimum* a comparatively long paraproct, at least 70 % length of cer-

cus (vs less than 50 % in *C. declivatum* sp. nov. and *C. mauffrayi* sp. nov.). Males of *C. albatum* are distinct from *C. charis* mainly by color pattern, with black markings on the dorsum of the head, thorax and abdomen (vs orange-brown and blue) and from *C. minutissimum* by the medial process on the pronotal hind lobe being conical (Fig. 5a) (vs transversely flattened and slightly bifid) and cercus longer than wide (Fig. 8a) (vs wider than long). The anterior lobe of the prothorax is completely to largely black in mature *C. albatum* males, similar to *C. declivatum*, whereas it is mostly blue in the other three species. Females of *C. albatum* share a medial pronotal process that is raised above the level of the middle lobe of the pronotum with *C. charis* and *C. minutissimum* but they are distinct from *C. charis* by the dark brown color pattern (vs orange and blue) and from *C. minutissimum* by the medial pronotal process protruding above the base of the process and being angulate on its posterior margin (Fig. 10a) (vs lower than rounded base and without a posterior angulation, Fig. 10e).

Remarks

The *C. albatum* sp. nov. type specimens appear to have been air-dried, at least the acetone method was not used; in such specimens, because post-mortem deterioration can alter pigments, I am uncertain of some of the paler colors of the thorax and abdomen. The allotype is not shriveled and appears to be relatively mature, although the body is mostly ocher to brown in color, indicative of a pre-reproductive state in the other species. Notes on the specimen cards for the *Calvertagrion albatum* series state that they were collected in various microhabitats such as »in grass on sandy bank of Rio La Torre«, »marsh behind willow bar« and in a »clearing«. These notes indicate that the species is active at least in partial to perhaps nearly full sunshine.

***Calvertagrion charis* sp. nov.**

(Figs 3, 5b–12b)

Specimens studied

Holotype ♂. Peru, Loreto Department, Explorama Lodge, about 50 km NE Iquitos on Amazon River at junction with Yanamono River (-3.44°, -72.85°), 31-viii-1989, S.W. Dunkle leg.

Allotype ♀. Same data as holotype.

Paratypes (24♂, 28♀). 17♂, 20♀, Peru, Loreto Department, same locality as holotype, 15–31-viii-1989, S.W. Dunkle leg; 2♂, 2♀, Loreto Department, Explorama Inn, 25 km NE of Iquitos (-3.51°, -73.06°), 19–21-viii-1989, S.W. Dunkle leg; 1♀, same locality, 17–21-viii-1989, G.B. Edwards leg; 5♂ 5♀, Loreto Department, Yarinococha, forest trail at La Cabaña (-8.33°, -74.60°), 12-vii-1977, D.R. Paulson leg.

Additional specimens: 1♂ 1♀, Colombia, Amazonas Department, Puerto Nariño, road to San Francisco, small stream in cleared forest (3.7696°S -70.3842°W), 22-vii-2011, S. Bota & C.A. Bota-Sierra leg (CEUA).

1♂, Brazil, Amazonas State, Esperanza, 09-viii-1920, coll. unknown, stored in the FSCA. I could not find »Esperanza« on any map of Amazonas State – maybe just a misspelling of the Portuguese "Esperança"; also, the collector was not provided on the label. Therefore the exact locality where this specimen was collected is dubious and I did not include it on the distribution map (Fig. 13).

The holotype, allotype, and 34 paratypes are deposited in the FSCA in Gainesville, Florida. Paratypes have been deposited also in the UMMZ and the collections of KJT, JJD, RWG, and DRP.

Etymology

Based on the Greek *charieis*, a noun in apposition, meaning graceful, beautiful, elegant.

Male (holotype)

Head – Labium light tan; labrum medium blue; base of mandibles and genae light blue; anteclypeus dark blue and black; postclypeus black with small, brown, oval, sub-lateral spot on each side of median; frons and occiput dark gray to brown, blue post-ocular spots 0.30 mm wide; rear of head light brown medially, light tan-blue laterally and ventrally; antennae brown (Fig. 3).

Thorax – Anterior lobe of pronotum blue, middle and hind lobes brown; propleuron blue; medial projection of hind lobe directed dorsally, apex situated above level of middle lobe, projection entire but in lateral view pos-

terior margin angulate (Fig. 5b). Mesepisternum orange-brown with narrow blue ante-humeral stripe constricted to less than 0.1 mm wide at mid-length; upper 60 % of mesinfraepisternum orange-brown, lower 40 % pale blue; mesepimeron orange-brown below humeral suture, light blue; metepisternum orange-brown; metepimeron tan-blue; metinfraepisternum light brown; legs yellowish tan, spines black, claws brown, tips dark, well-developed supplementary tooth present. Anterior vein of Fw quadrangle equal to length of proximal vein, less than half (42 %) length of posterior vein; 7 Px in right Fw, 6 in left, 5 in each Hw; pterostigma black, surmounting in both Fw and Hw about ¼, more or less, of cell below.

Abdomen – Dorsum orange-brown and light blue; S1 and S2 orange-brown dorsally, pale blue laterally; S3–8 orange-brown dorsally, darker in apical ⅕, with small basal blue spot; S9 and S10 orange-brown. Cercus 0.34 mm long, brown, in lateral view triangular with sharply acuminate tips (Fig. 7b), in

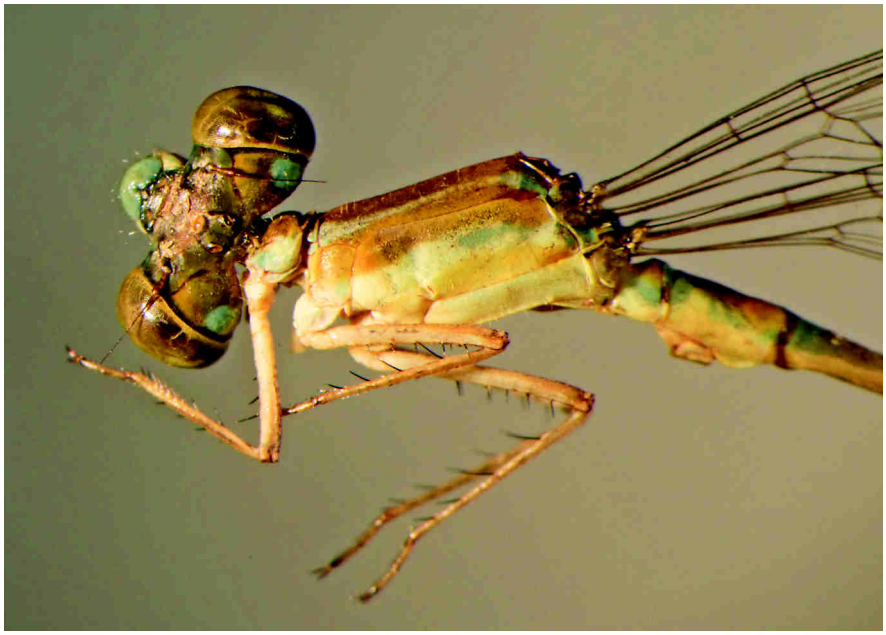


Figure 3. *Calvertagrion charis* sp. nov. male, head and thorax.

dorsal view appearing blade-like with a long, shallow curved depression from near medial angle to tip; in dorsal view outer margins of cerci slightly convergent, probably due to lateral pressure during drying in preservation (Fig. 8b). Paraprocts in lateral view triangular, elongate, directed posteriorly although apex slightly dorsally inclined, length about 0.85 length of cercus (Fig. 7b), lighter brown than cercus, tips black. Genital ligula (Figs 9b) with 3 small, golden yellow setae on each side of basal segment, otherwise similar to *C. albatum*.

Measurements [mm] – Total length 26.0, abdomen length 21.3, Hw length 10.8.

Female (allotype)
Similar to holotype except as follows:
Head –Anteclypeus dark gray-black; postclypeus gray-blue; frons and occiput mostly gray-blue, small light brown area anterior to median ocellus, occipital lobes brown, no post-ocular spots evident; rear of head tan.

Thorax – Anterior lobe of pronotum faded blue; medial projection of hind lobe (Fig. 10b) higher than level of middle pronotal lobe, directed dorsally but slightly posteriorly. Mesostigmal plates similar to *C. albatum* except mostly orange-brown, extremities pale blue (Fig. 11b); upper half of mesinfraepisternum light orange-brown, lower half pale blue; metepisternum and metepimeron pale blue; metinfraepisternum pale blue-tan. Anterior vein for Fw quadrangle about ⅓ length of posterior vein; 7 Px in right Fw, 8 in right, 7 in each Hw; pterostigma brown, surmounting slightly less than 50 % of cell below.

Abdomen –S1 orange-brown dorsally, sides pale blue; S2–7 with dorsal brown stripe constricted basally and at 60 % of length by lateral blue marking, the longer anterior portion of the stripe gray-brown, the shorter posterior portion orange-brown; S8–10 orange-brown on dorsum, sides pale blue and tan, apical margin of S8 and S9 with small black denticles (Fig. 12b), S8 without vulvar spine, posterior part of S10 mid-dorsum compressed into a narrow, longitudinal ridge. Ovipositor 1.45 mm long, outer valves tan and

blue, curved upward, ventral margin with light setae along entire length, posterior third serrate; stylus dark brown, 0.29 mm long. Cercus brown, triangular, 0.22 mm long; paraproct rounded, pale tan.

Measurements [mm] – Total length 26.7, abdomen length 21.5, Hw length 12.8.

Variation in paratypes

Males – In a few males, the narrow blue ante-humeral stripe is interrupted at ⅔ its length by the orange dorsal stripe. There was minor variation in the shape of the medial process of the pronotal lobe, mainly in being stouter than in the holotype. Px in Fw ranged from 6–8, in Hw 5–6. Measurements [mm]: total length 23.5–26.7, abdomen length 19.1–21.8, Hw length 9.9–11.6, cercus length 0.31–0.37. In females, Fw Px ranged from 7–9, Hw 6–8; ovipositor ranged from 1.39–1.53 mm long.

Diagnosis

Calvertagrion charis sp. nov. is distinct from all congeners in color pattern, both males and females mostly orange-brown on the dorsum with pale blue stripes on the thorax and anterior abdominal segments (Fig. 3) and with the apical abdominal segments orange to red-orange. A color photograph of a male *C. charis* from Yarinacocha, Loreto Department, was presented by Garrison et al. (2010: pl. 15), and a male and female were shown by Bota-Sierra (2012). The majority of specimens I studied (n = 54) were not teneral, although I cannot be certain that they were reproductively mature. It is possible that in July and August – a period of slightly less rainfall than in subsequent months in northern Peru – these damselflies were in a pre-reproductive state. The other four species, when mature, have black markings on the head, thorax and abdomen. Also, if the *C. charis* specimens were reproductively mature, it indicates that they do not become pruinose with age whereas the other species do. Structurally, *C. charis* males differ from *C. minutissimum* in the medial process on the pronotal hind lobe being conical and pointed (Fig. 5b) instead of flattened and slightly bifid (Fig. 5e) and from *C. albatum* sp. nov. in the tip of the paraproct being truncate (Fig. 16b) instead of rounded (Fig. 16a). Females

of *C. charis* are unique in the extreme compression of the posterior third of S10 dorsum forming a ridge only *ca* 0.05 mm wide in dorsal view (vs *ca* 0.10 or more mm wide).

Remarks

Calvertagrion charis males and females were found in dense grass and under shrubs in shade at the edge of a trail. Zygoptera taken in the same habitat along the trails were *Aeolagrion dorsale* (Burmeister, 1839), *A. inca* (Selys, 1876), *Mesoleptobasis* sp., *Metaleptobasis leniloba* von Ellenrieder, 2013, *Phoenicagrion flammeum* (Selys, 1876), and *Telebasis dunklei* Bick & Bick, 1995. Bota-Sierra (2012) observed this species flying in forest clearings crossed by little streams in the Amazon region of Colombia.

***Calvertagrion declivatum* sp. nov.**

(Figs 4, 5c–12c)

Specimens studied (all from Bolivia)

Holotype ♂. Bolivia, Santa Cruz Department, Ñuflo de Chavez Province, small tributary of Rio San Julian, 5 km S of San Ramon (-16.642°, -62.5076°), 14-xi-1998, KJT leg.

Allotype ♀. Bolivia, Cochabamba Department, Chapare Province, pond about 25 km N of Villa Tunari (-16.847°, -65.485°), 18-xi-1999, KJT leg.

Paratypes (16♂, 19♀). 1♂, Cochabamba Dept., Tiraque Province, pond 0.7 km S of hwy, E of Shinahota (-17.001°, -65.220°), 05-xi-2001, KJT leg; 1♂, Tiraque Province, pond 4.5 km N of Ibuelo (-16.968°, -65.299°), 09-xi--2001, KJT leg; 1♂, 6♀, Santa Cruz Department, Guarayos Province, grassy wetlands, Hwy 9, 49 km N of Ascension de Guarayos (-15.661°, -63.518°), 23-viii-2003, KJT leg; 3♂, 4♀, same locality and date, JTJ leg; 2♀, Guarayos Province, wetlands *ca* 23 km NW of Ascension de Guarayos, Hwy 9 (-15.827°, -63.381°), WFM leg; 1♂, Guarayos Province, duckweed/Heliconia pond, 3.2 km N of Hwy 9, road from Santa Maria to Yaguaru (-15.703°, -63.438°), 26-viii-2003, KJT leg; 5♂, 2♀, Ichilo Province, Lagunas Curichi, 3.5 km S of Buena Vista, 04-ii-2000, JJD leg; 3♂, 5♀, Ichilo Province, Rio Palacito, 3 km S of Buena Vista (-17.484°, -63.654°), 11-ii-2001, KJT leg; 1♂, Ñuflo de Chavez Province, small stream 18 km E of San Ramon (-16.6317°, -62.385°), elev. 460 m, 15-xi-1998, WFM leg.

All specimens acetoned. The holotype and allotype are deposited in FSCA. Paratypes are deposited in FSCA, UMMZ, USNM and the collections of KJT, JJD and JTJ.

Etymology
The name *declivatum* is derived from the Latin adjective *declivis* (sloping or shelving downwards), referring to the sloping or bent-down dorsal margin of the male cercus in lateral view.

Male (holotype)
Head – Labium light tan; labrum, base of mandibles, anteclypeus, and genae yellowish green; postclypeus and frons black; occiput black with pair of large blue post-ocular spots (0.45 mm wide); rear of head black dorsally and medially, blue laterally and ventrally.

Thorax – Anterior lobe of prothorax blue, middle and hind lobes black dorsally, blue laterally; hind lobe with a medial projection directed posteriorly *ca* at level of middle lobe (Fig. 5d). Mesepisternum black except for an antero-lateral blue oblong spot and a postero-lateral triangular blue spot; pruinose over black area above humeral suture; mesinfraepisternum black dorsally, blue ventrally; mesepimeron mostly blue, pruinose, and with large black anterior and posterior spots; metepisternum and metepimeron blue; metinfraepisternum yellow; legs yellowish tan except femora with black markings distally, spines black, distal part of last tarsal segment black. Arculus distal to 2nd antenodal cross-vein; anterior vein of quadrangle in Fw *ca* 1.2 times as long as proximal vein, *ca* ⅖ as long as posterior vein; anal vein arising proximal to anal crossing, about 4 cells long. Fw Px: 7 in right, 8 in left, Hw Px 6 in both wings; pterostigma black, without posterior cross-vein under apical margin, surmounting ⅓ of a cell.

Abdomen – Dorsum of segments mostly black; S1 with apical fourth and sides blue; black stripe on dorsum of S2–7 with narrow basal constriction, black on S3–6 slightly constricted at 75 % length of segment, black on dorsum of S8–10 less constricted basally to wholly black (Fig. 6c), sides of S2–10 blue and/or yellow to yellow-tan. Cercus 0.37 mm long, brown, in

lateral view triangular with dorsal margin convex basally beyond which it is strongly declined, ventral margin slightly concave with a small tooth projecting ventrally near mid-length of cercus (Fig. 7c), in dorsal view blade-like with a baso-medial right angle and a long, outwardly curved arm with a low ridge and adjacent depression beginning medially and ending slightly before apex of cercus (Fig. 8c); the outer margins of the two cerci are slightly divergent. Paraproct short, about 30 % length of cercus, tips black and directed dorso-apically in lateral view (Fig. 7a). Genital ligula (Fig. 9c) as described for *C. albatum*.

Measurements [mm] – Total length 25.8, abdomen length 21.1, Hw length 11.6.

Female (allotype)
Similar to holotype except as follows:
Head – Labrum, anteclypeus and occiput blackened, post-ocular spots not evident; dorsal and medial brown marking on rear of head not as dark as in holotype.

Thorax – Prothorax pruinose, middle and hind lobes partly brown; hind lobe tripartite with a median triangular, pointed process (Fig. 10c), lateral lobes rounded (Fig. 11c). Mesostigmal plate dark medially, medial ridge low, anterior ridge distinct, sinuous, posterior ridge distinct, a transverse depression between the anterior and posterior ridges, lateral extremity blue, prominent

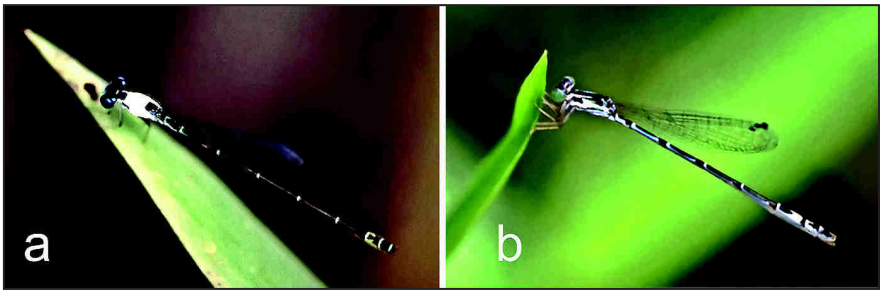


Figure 4. *Calvertagrion declivatum* sp. nov.; a – male; b – female; near Buena Vista, Santa Cruz Department, Bolivia (11-ii-2001); photos by KJT.

and lobe-like (Fig. 11c); mesepisternum with blue ante-humeral stripe in basal 70 % extending ventrally to humeral suture and with small blue apical spot; mesinfraepisternum black-brown on upper ¼, blue on lower ¾; mesepimeron mostly blue; metepisternum and metepimeron tan-blue; upper margin of metinfraepisternum blue; legs somewhat paler than in holotype. Fw with 8 Px, Hw with 6; pterostigma brown, surmounting 55 % of cell below.

Abdomen – S3–6 black dorsal stripes constricted at extreme base and at *ca* 80 % of segment length, blue basally and laterally, shading to yellow on ventro-lateral surfaces; dorsal black stripe on S7 with an apical point at mid-length of segment, black interrupted dorsally near middle of segment by pale blue, posterior ⅕ black with a small anterior point, dorsal black on S8–10 not constricted (Fig. 12c), sides blue shading to tan ventro-laterally. Ovipositor tan-blue, 1.55 mm long, tip surpassing apical margin of paraprocts by *ca* 0.25 mm, ventral margin of outer gonapophyses setose, serrate in distal 0.33 (Fig. 12c); stylus black, 0.30 mm long. Cercus blackish brown, in dorsal view about as wide at base as long, in lateral view 0.20 mm long.

Measurements [mm] – Total length 23.7, abdomen length 19.3, Hw length 12.4.

Living eye color of males very dark red-brown dorsally, bright green ventrally, females dark green dorsally, light gray-tan ventrally.

Variation in paratypes

In several males, the dorsum of S8 is grayish green in basal ⅔. S7 with very narrow mid-dorsal black line connecting anterior and posterior dorsal black markings; black on dorsum of S8 in some females with a small rounded extension at mid-length of segment, but it is not directed anteriorly. Px in Fw ranged from 6–8, in Hw 5–6. Measurements (mm): total 22.5–26.8, abdomen 18.4–22.1, Hw 10.0–11.9. In several females, the labrum and anteclypeus was dark blue, S8 and S9 dorsum varied from all black to black with a very small blue mark at base; in old females, the proximal 30–50 % is covered with pruinescence (Fig. 4b).

Measurements [mm]: total length 23.2–27.5, abdomen length 18.8–22.3, Hw length 11.5–14.0.

Diagnosis

Males of *C. declivatum* sp. nov. share with *C. mauffrayi* sp. nov. longer cerci (0.37–0.43 mm) than *C. albatum* sp. nov., *C. charis* sp. nov., and *C. minutissimum* (0.30–0.37 mm). *Calvertagrion declivatum* males are unique in the shape of the cercus in lateral view – the dorsal margin of each cercus is convex basally but the apical portion is oriented postero-ventrally, making the appendage appear decumbent (Fig. 7c). Females share with *C. mauffrayi* the low ridge on the apical portion of S10 dorsum but are separable by the trilobed shape of the hind lobe of the pronotum (Fig. 11c), and the mesostigmal plates with a sinuous anterior margin (Fig. 11c), compared to a straight margin in *C. mauffrayi*. In addition, the L:W ratio of one mesostigmal plate of *C. declivatum* is <1.0 compared to >1.0 in *C. mauffrayi*, and the black on dorsum of S8 is without an anteriorly-directed black lobe (Fig. 12c). Mature females of *C. declivatum* have a gray-brown to almost black occiput compared to the gray-blue of *C. mauffrayi*. Wings of females that are not yet mature have a slight amber cast.

Remarks

I found *C. declivatum* sp. nov. along small, shallow, vegetated streams and also ponds in central Bolivia. The first male I saw prompted me to exclaim to my field companion, Bill Mauffray, »here's a flying white dot«; I was not sure it was a damselfly until I got a close look. Both sexes of *C. declivatum* perched and flew low in grass and other vegetation. Other species of Zygoptera collected in these habitats were *Acanthagrion chararum* Calvert, 1909, several unidentified *Acanthagrion*, *Aeolagrion philipi* Tennessen, 2009, *Argentagrion ambiguum* (Ris, 1904), several species of *Argia*, *Ischnura capreolus*, *Oxyagrion chapadense* Costa, 1978, *Telebasis willinki* Fraser, 1948, *Telebasis* sp., and *Neoneura sylvatica* Hagen, in Selys, 1886. Reproductively immature individuals are orange to ocher, areas that are black in mature individuals becoming darker brown with age.

Calvertagrion mauffrayi sp. nov.
(Figs 5d–12d)

Specimens studied (all from Ecuador)
Holotype ♂. Ecuador, Orellana Province, Parque Nacional Yasuni, ditch near Rio Savaleto, Yasuni Rd km marker 31 (-0.47°, -76.585°), 12-vi-1995, KJT leg.
Allotype ♀. Same locality as holotype, 17-vi-1996, KJT leg.
Paratypes (35♂, 65♀). 1♂, 2♀, same data as holotype, KJT leg; 2♂, 2♀, same data, SWD leg; 2♂, 3♀, same data, WFM leg; 5♂, 4♀, same locality, 17-vii-1996, KJT leg; 3♂, 8♀, same data, SWD leg; 7♂, 20♀, same data, WFM leg; 1♂, same locality, 17-xi-1997, KJT leg; 4♂, 3♀, Orellana Province, Pompeya, 0.5 km N of Rio Napo ferry (-0.445°, -76.629°), 19-vii-1996, KJT leg; 2♂, 6♀, same data, SWD leg; 4♂, 3♀, same data, WFM leg; 1♂, 1♀, same data, JJD leg; 1♀, Orellana Province, pools/marshes near Payamino, Loreto Rd, 1.7 km W of Coca Rd (-0.436°, -77.004°), 19-vii-1996, WFM leg; 1♀, same data, SWD leg; 1♀, Napo Province, pond along Rio Sinde, 5.3 km E of Puerto Napo (-1.051°, -77.751°), 13-vii-1996, KJT leg; 1♂, same data, JJD leg; 1♀, Napo Province, oxbow pool along Rio Chinchipino, 27.7 km E of Puerto Napo (-1.06°, -77.59°), 13-xi--1997, KJT leg; 1♂, 1♀, same data, SWD leg; 1♀, Napo Province, slough along Rio Napo, 3.2 km E of Tena Rd (-1.045°, -77.763°), 23-vii-1996, SWD leg; 4♀, Sucumbios Province, stream 39 km NE of Chaco (0.08°, -77.59°), 18-viii--1980, SWD leg; 1♂, Sucumbios Province, ponds 53 km NE of Chaco (0.004°, -77.416°), 18-viii-1980, SWD leg; 1♀, Sucumbios Province, swamp 17 km S of Lago Agrio (Nueva Loja) (0.096°, -76.868°), 19-viii-1980, SWD leg; 1♀, Sucumbios Province, stream 26 km S of Lago Agrio (Nueva Loja) (0.14°, -76.85°), 19-viii-1980, SWD leg; 1♀, Sucumbios Province, La Selva, Heron Lake (-0.498°, -76.374°), 13-iv-1992, E.M. Smith leg.

All specimens acetoned. The holotype and allotype are deposited in the FSCA, Gainesville, Florida, USA. Paratypes are deposited in the FSCA, UMMZ, USNM and in the collections of KJT, RWG, JJD, and DRP.

Etymology
Named for my colleague and friend, William F. Mauffray, who was the first to detect this small, low-flying, inconspicuous species on our initial visit to Yasuni National Park in 1995.

Male (holotype)
Head – Labium light tan; labrum, base of mandibles, anteclypeus and genae yellowish green; postclypeus and frons black; occiput black with pair of large blue post-ocular spots (0.45 mm wide); rear of head black dorsally and medially, blue laterally and ventrally.

Thorax – Anterior lobe of prothorax blue, middle and hind lobes black dorsally, blue laterally; hind lobe with a medial projection directed posteriorly but not raised above level of lobe (Fig. 5d). Mesepisternum black except for an antero-lateral blue oblong spot and a postero-lateral triangular blue spot; pruinose over black area above mesopleural (humeral) suture; mesinfraepisternum black dorsally, blue ventrally; mesepimeron mostly blue, pruinose, and with large black anterior and posterior spots; metepisternum and metepimeron blue; metinfraepisternum yellow; legs yellowish tan except femora with black markings distally, spines black, and distal part of last tarsal segment black. Arculus distal to 2nd antenodal cross-vein; anterior vein of quadrangle in Fw *ca* 1.4–1.7 times length of proximal vein, *ca* half the length of posterior vein; anal vein arising proximal to anal crossing, about 4 cells long; Px of first series: 7 in right Fw, 8 in left Fw, 6 in Hw; pterostigma black, surmounting only *ca* ⅓ of cell below in right Fw and both Hw but ½ in left Fw.

Abdomen – Dorsum of S1 with basal ⁴⁄₅ black, apical ¹⁄₅ and sides blue; dorsum of S2 with black marking entire length of segment, widened posteriorly, sides yellowish green; S3–6 black dorsally except for narrow basal green ring; S7 also with narrow basal green ring, but with black dorsal marking extending only ⅔ length of segment, posterior ⅓ green and rusty brown; S8 green dorsally except slightly golden yellow on apical ⅓; S9 with small basal green marking, mostly golden yellow dorsally, at mid-length with a pair of latero-dorsal dark spots and a postero-lateral green mark; sides of S3–9 yellow; dorsum of S10 dark except for posterior rim, sides dull yellow. Cerci 0.44 mm long, brown, blade-like, in lateral view elongate triangular (Fig. 7d), in dorsal view with a long shallow depression from base to tip (Fig. 8d), and with a basal medial flattened area. Paraprocts short, about ¼ length of cerci, tips black and directed dorsally in lateral view (Fig. 7d). Genital ligula as described for *C. albatum*.

Based on notes taken by S.W. Dunkle on 12-vi-1995, the eyes of living males are black dorsally and pale green ventrally.

Measurements [mm] – Total length 25.8, abdomen length 21.1, Hw length 11.6.

Female (allotype)
Similar to holotype except as follows:
Head – Labrum, base of mandibles and genae blue, anteclypeus dark blue; postclypeus, frons and occiput blue-gray, no blue post-ocular spots; slender dark marking at junction of postclypeus and antefrons, frontal suture and a narrow sinuate line from compound eye to rear of head; top of occiput brown; rear of head nearly entirely pale blue.

Thorax – Prothorax mostly blue, middle and hind lobes with pair of dorsal, dark brown, crescent-shaped marks; hind lobe with a small, brown, medial projection directed dorsally, *circa* level with dorsal margin of middle lobe (Fig. 10d). Pterothorax with brown markings instead of black, mesepisternum less pruinose. Mesostigmal plate dark medially, medial ridge low, anterior ridge and ridges distinct between which lies a transverse depression, lateral extremity blue, prominent and lobe-like (Fig. 11d); femora with intricate pattern of grayish blue markings and without dark distal markings. Pterostigma brown, surmounting *ca* ½ of cell below; Px in right Fw 9, 8 in left Fw, 7 Px in Hw.

Abdomen – Dorso-lateral pale markings blue, ventro-lateral areas yellow; dorsal black stripe on S7 with an apical point at mid-length of segment, black interrupted dorsally near middle of segment by pale blue, posterior ⅕ black; S8–10 black dorsally, S8 black with a lateral, anteriorly-directed extension near mid-length of segment (Fig. 12d), intersegmental membranes blue. Ovipositor yellowish tan, 1.55 mm long, setose along ventral margin, serrate in distal third, tips of gonapophyses surpassing apex of paraproct by *ca* 0.15 mm; stylus dark brown, 0.30 mm long (Fig. 12d). Cercus dark brown, in dorsal view elongate triangular, basal width equal to length, in lateral view 0.23 mm long.

Measurements [mm] – Total length 26.9, abdomen length 22.3, Hw length 13.9.

Variation in paratypes

The paratypes reveal color pattern differences undoubtedly related to differences in maturity. In immature individuals, dark markings are not yet developed and orange-ocher is the predominant pale color. In particular, the labrum and anteclypeus are orange and the occiput ranges from orange to a mottled brown and black pattern; the mesepisternum in immature males is brown without pruinescence, and in females it is completely orange; S1–3 may be completely orange or have dorsal brown markings. Blue post-ocular spots are evident in immature males but not immature females. The medial process of the pronotal hind lobe showed minor variation in males, being slightly narrower than shown for the holotype (Fig. 5d – insets). In males, Fw Px ranged from 6–8, Hw 5–7; in females, Fw Px ranged from 7–10, Hw 6–8. Male cercus length ranged from 0.37–0.43 mm, female ovipositor length 1.40–1.58 mm. Measurements [mm]: males total length 23.8–27.1, abdomen length 19.5–22.3, Hw length 10.7–11.9; females total length 23.9–27.8, abdomen length 19.2–22.3, Hw length 12.6–14.4.

Diagnosis

Calvertagrion mauffrayi sp. nov. males share with *C. declivatum* sp. nov. a short paraproct, less than half the length of the cercus (Fig. 7d). Males are distinguished from that species by the cercus being oriented straight to rearward in lateral view (Fig. 7d) compared to the decumbent cercus of *C. declivatum* (Fig. 7c). Also in *C. mauffrayi*, the angular medial process of the cercus is usually directed posteriorly so that it is not visible in lateral view (Fig. 7d), whereas in *C. declivatum* it is usually bent ventrally to a varying degree so that it is often evident in lateral view (Fig. 7c). In *C. mauffrayi* males, the dorsum of S8 is orange and/or green and S9 and S10 are orange to partly brown, whereas in *C. declivatum* the dorsum of S8–10 is largely black dorsally. Females share with *C. declivatum* a medial process on the pronotal hind lobe not exceeding the level of the dorsal margin of the pronotal middle lobe (Fig. 10d) and S10 with the posterior third barely raised as a low, wide ridge (Fig. 12d). In female *C. mauffrayi* the hind lobe of the prothorax,

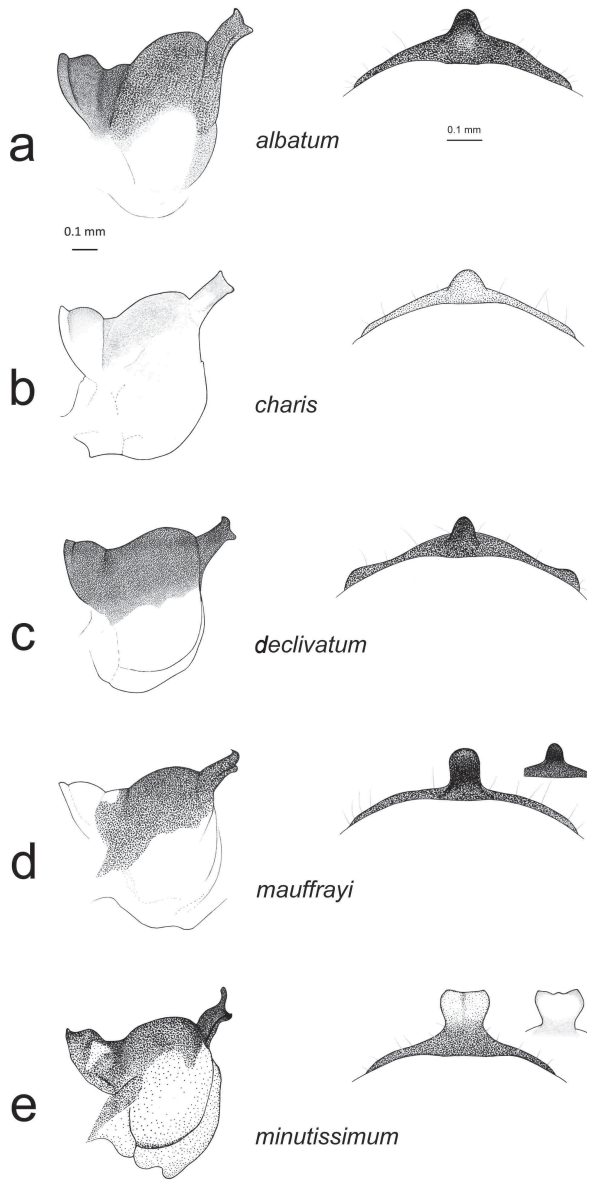


Figure 5. Prothorax of *Calvertagrion* males, lateral view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

in dorsal view, continues in a virtually straight line from the medial process to the lowly rounded corners (Fig. 11d) whereas the hind lobe appears trilobed in *C. declivatum* (Fig. 11c).

Remarks

Calvertagrion mauffrayi sp. nov. was collected in a variety of shallow ponds and ditches filled with water in the upper Amazon basin of Ecuador, perch-

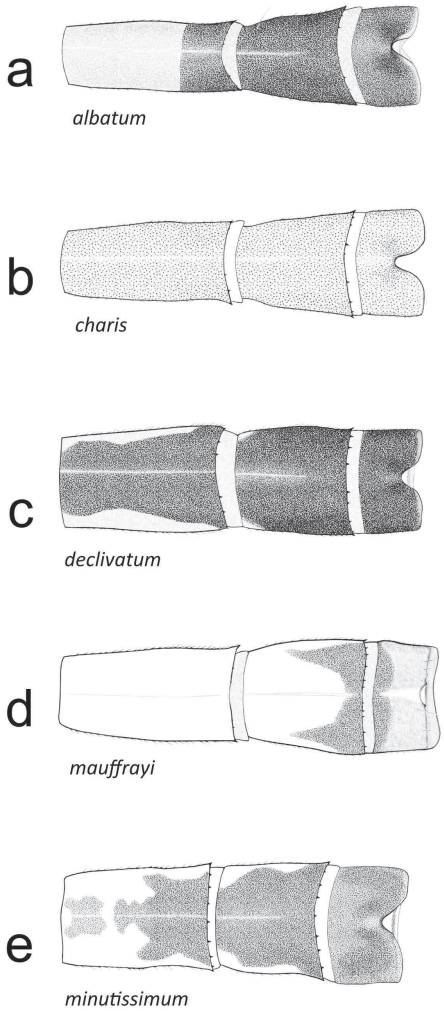
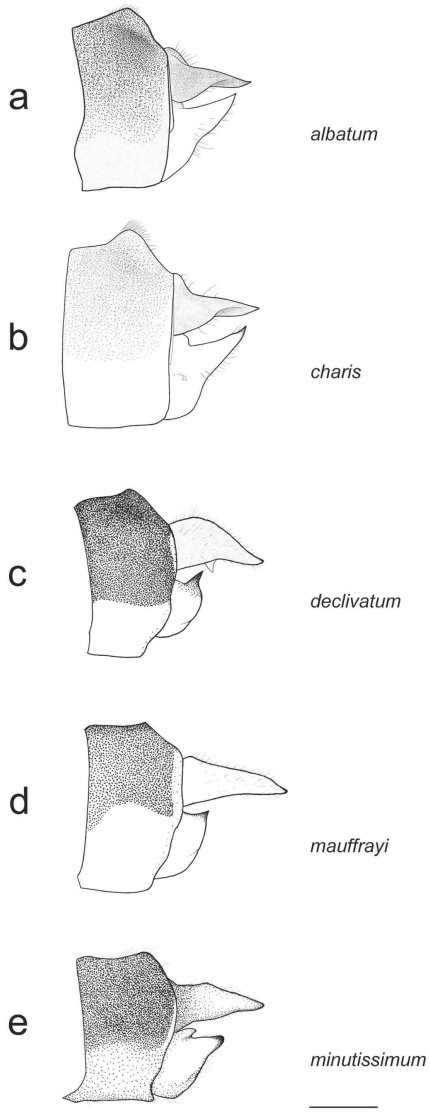


Figure 6. S8–10 pattern of *Calvertagrion* males, dorsal view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.



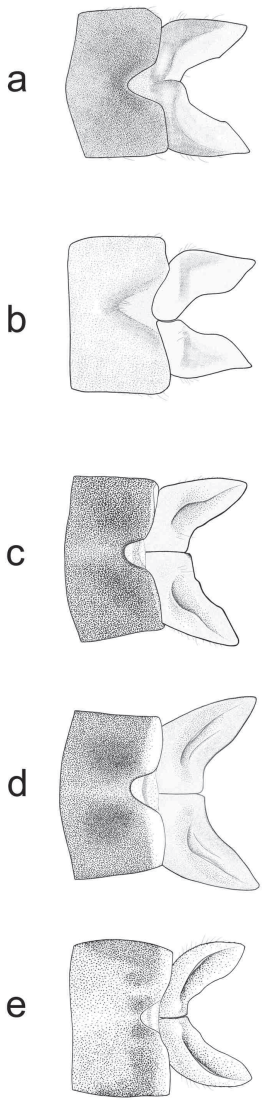


Figure 7. S10 + appendages of *Calvertagrion* males, lateral view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

Figure 8. S10 + appendages of *Calvertagrion* males, dorsal view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

ing on and/or flying low amidst grasses and other partly shady vegetation. They did not occur in nearby deeply shaded rainforest. Other Zygoptera collected in these habitats included *Acanthagrion apicale* Selys 1876, *A. ascendens* Calvert, 1909, *A. obsoletum* (Förster, 1914), *A. phallicorne* Leonard,

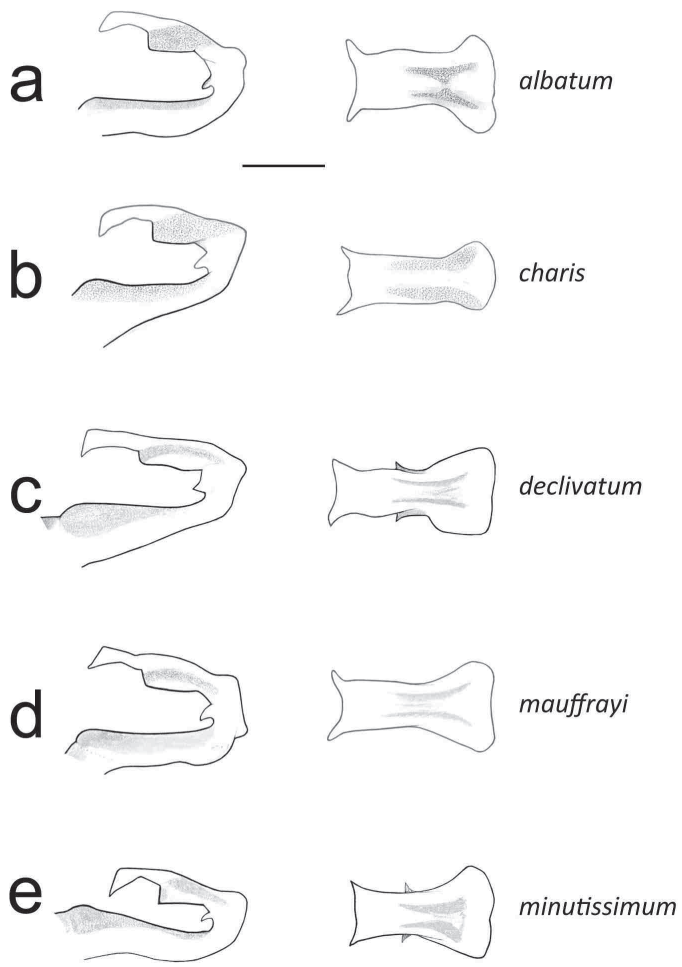


Figure 9. Genital ligula of *Calvertagrion* males, lateral view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

1977, *Aeolagrion axine* Dunkle, 1991, *A. dorsale*, *Telebasis griffinii* (Martin, 1896), *T. livida* Kennedy, 1936, and *Lestes jerrelli* Tennessen, 1997.

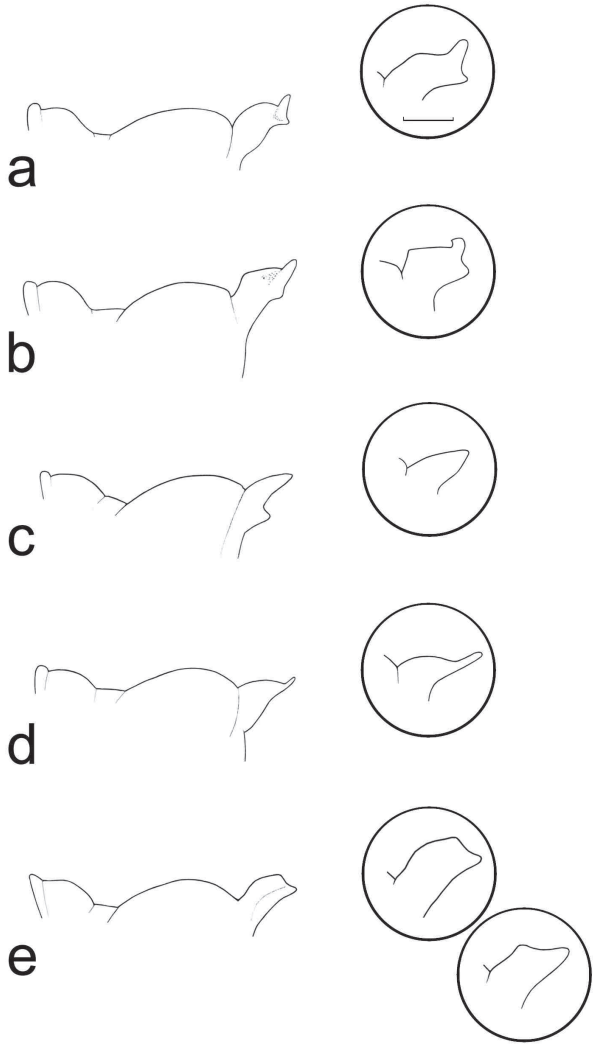


Figure 10. Pronotum dorsal profiles of *Calvertagrion* females: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

***Calvertagrion minutissimum* (Selys, 1876)**
(Figs 5e–12e)

Agrion? minutissimum Selys, 1876: 1250–1251, holotype ♀ description.
Calvertagrion dicellularis St. Quentin, 1960.
Calvertagrion minutissimum: Garrison & Costa (2002: 396 ff.; illustrations of male appendages, hind lobe of prothorax, head; synonymy of *C. dicellularis*); Lencioni (2006: 113; illustrations of male appendages, prothorax, body, wings); Garrison et al. (2010: 225 ff.; description, illustrations of body pattern, hind lobe of prothorax, tarsal claws, wings, genital ligula, male appendages, female S8–S10+ovipositor).

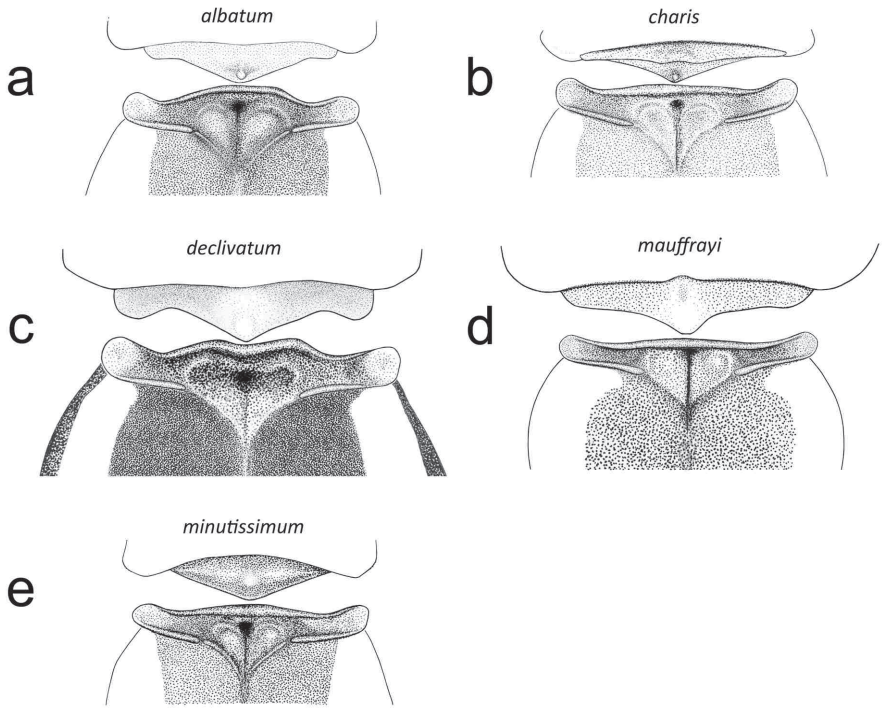


Figure 11. Prothoracic hind lobe and mesostigmal plates of *Calvertagrion* females, lateral view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

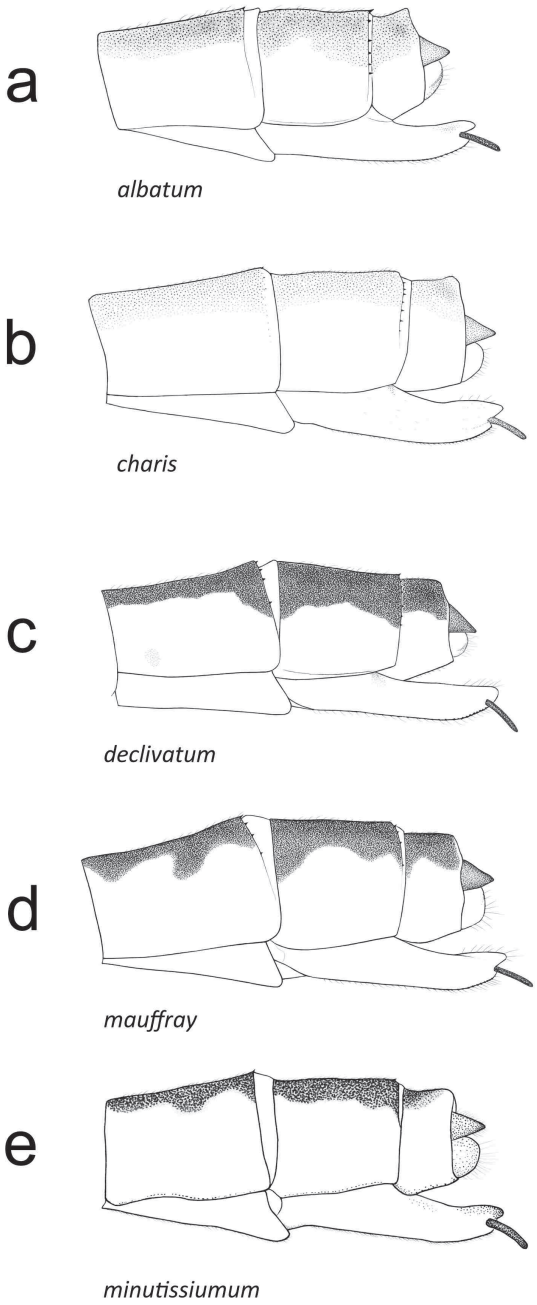


Figure 12. S8–10 of *Calvertagrion* females, lateral view: a – *C. albatum* sp. nov.; b – *C. charis* sp. nov.; c – *C. declivatum* sp. nov.; d – *C. mauffrayi* sp. nov.; e – *C. minutissimum*.

Diagnosis

Both sexes of *Calvertagrion minutissimum* are unique in the genus in the shape of the medial process of the pronotal hind lobe. In males this process is flange-like and the dorsal margin is slightly bifid to almost straight (Fig. 5e) compared to the basic conical shape in the other species. The only other species which approaches *C. minutissimum* in this condition is *C. mauffrayi* sp. nov. in which the medial process in males is flattened but convex on the dorsal margin (Figs 5d). In females of *C. minutissimum* the process is not flange-like, rather there is a low, rounded swelling anterior to a simple, distal point (Fig. 10e). Another distinguishing feature of male *C. minutissimum* is that the ratio of cercus L:W is ≤1.0 vs >1.0 in the other four species. The thorax of *C. minutissimum* becomes pruinose with age, as in *C. albatum* sp. nov., *C. declivatum* sp. nov., and *C. mauffrayi* sp. nov.. Females of *C. minutissimum* are most likely to be confused with *C. albatum*; an additional distinguishing character is that the base of the stylus of the ovipositor is positioned at the same level as the tip of the cercus (Fig. 12e) versus posterad of the cercus tip in *C. albatum* (Fig. 12a).

Selys (1876) gave only »Amazone« for the locality of the single female sent to him by Henry Bates, who collected in Brazil from 1848 to 1859 (Wasscher & Dumont 2013). No further locality information is available. I have been unable to find any notes on the habitat or biology of this species.

Distribution of *Calvertagrion* species

The genus *Calvertagrion* is restricted to South America, being distributed east of the Andes from the foothills eastward to the Amazon lowlands. The five species are allopatric, as presently known (Fig. 13). Two centers of origin for the genus can be postulated: Firstly, the preponderance of species occurring in the upper Amazon indicates that the genus probably arose in this region; and secondly, the progenitor of the genus arose in the lower Amazon and underwent species radiation in the upper Amazon and eastern foothills of the Andes. As large areas of the Amazon basin have been under-collected, future survey work will undoubtedly yield many new localities for *Calvertagrion*, quite possibly including more undescribed species.

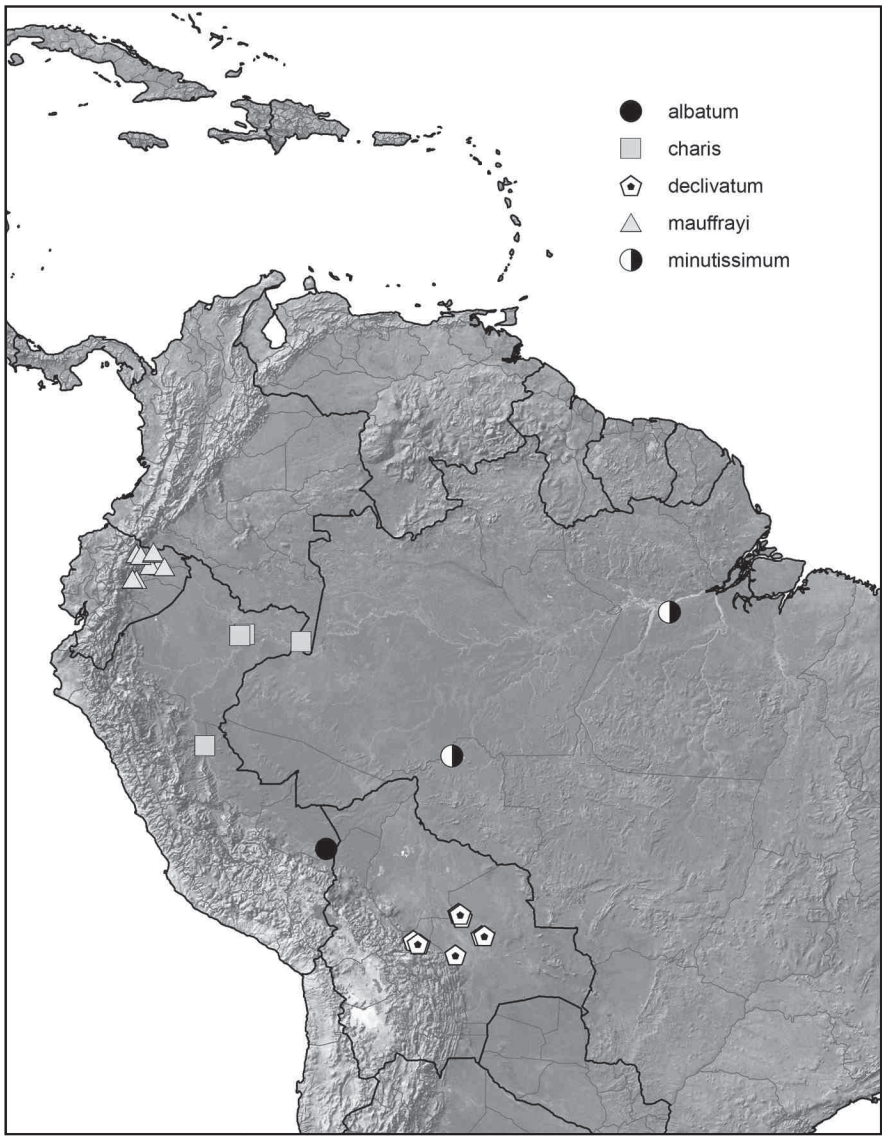


Figure 13. Distribution of *Calvertagrion albatum* sp. nov., *C. charis* sp. nov., *C. declivatum* sp. nov., *C. mauffrayi* sp. nov., and *C. minutissimum* in South America.

Keys

The following keys to males and females of *Calvertagrion* pertain only to mature individuals. Adults that are not yet reproductively mature can be recognized by an overall rather uniform ocher body coloration, lacking blue, green and yellow markings and in most species black markings and pruinosity; in attempts to identify such specimens, color characters in the following key should be avoided and only structural key characters should be used. Male cercus L and W were measured as in Figure 14. Female mesostigmal plate L and W were measured as in Figure 15.

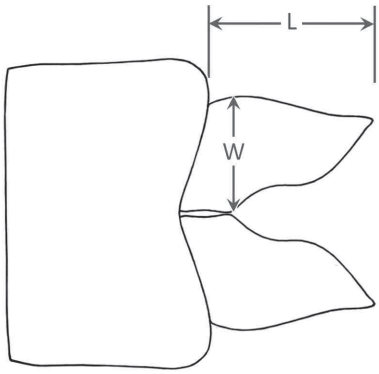


Figure 14. Dimensions of *Calvertagrion* male cercus, dorsal view.

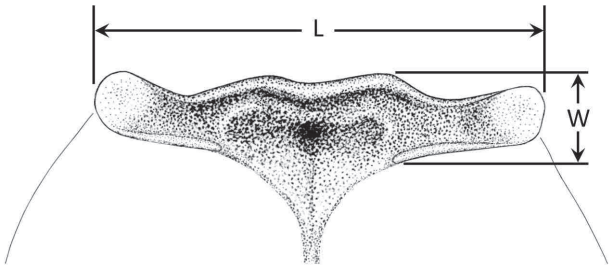


Figure 15. Dimensions of *Calvertagrion* female mesostigmal plates, dorsal view.

Key to *Calvertagrion* mature males

1a – Paraproct in lateral view less than 0.5 length of cercus, apex directed dorsally and often hidden by base of cercus (Figs 7c, d); cercus L 0.37–0.43 mm **2**

1b – Paraproct in lateral view at least 0.7 length of cercus, apex directed posteriorly to slightly dorso-posteriorly and clearly visible (Figs 7a, b, e); cercus L 0.30–0.37 mm **3**

2a – Cercus appearing decumbent in lateral view, dorsal margin markedly convex and angled postero-ventrally (Fig. 7c); S8–10 mostly black dorsally (Fig. 6c), S8 blue anteriorly in some specimens; mesepimeron of mature individuals completely black above humeral suture ..... ***declivatum*** sp. nov.

2b – Cercus straight in lateral view (Fig. 7d); S8 orange and/or green, S9 and S10 orange to partly brown (Fig. 6d); mesepimeron of mature individuals black anteriorly and posteriorly, intermediate area blue above humeral suture ..... ***mauffrayi*** sp. nov.

3a – Hind lobe of pronotum with medial protuberance flattened and slightly bifid (Fig. 5e); cercus, in dorsal view, with a L:W ratio < 1.0 (Fig. 8e) .....***minutissimum***

3b – Hind lobe of pronotum with medial protuberance entire (Figs 5a, b); cercus, in dorsal view, with a L:W ratio > 1.0 (Figs 8a, b) **4**

4a – Pterothorax heavily pruinose, dorsum beneath pruinosity mostly black; S8 black posteriorly, S9–10 mostly black; tip of paraproct viewed ventrally rounded, narrow (Fig. 16a) ..... ***albatum*** sp. nov.

4b – Pterothorax without pruinosity, dorsum orange-brown with a narrow, pale blue antehumeral stripe; S8–10 mostly reddish-orange; tip of paraproct truncate, wider (Fig. 16b) ..... ***charis*** sp. nov.

I examined the genital ligula of the five *Calvertagrion* species under the highest magnification on my stereomicroscope (60x) and could not find any significant differences of diagnostic value. The uniformity in this structure in *Calvertagrion* (Figs 9a–e) is unusual for coenagrionid genera with multiple species.

Key to *Calvertagrion* mature females

1a – Dorso-medial projection of prothoracic hind lobe not protruding above general outline of pronotum, posterior margin straight (Figs 10c, d – insets); posterior third of S10 dorsum not or barely raised above margin of segment (Figs 12c, d) **2**

1b – Dorso-medial projection of prothoracic hind lobe protruding above general outline of pronotum, posterior margin angulate (Figs 10a, b, e – insets); posterior third of S10 dorsum distinctly raised above margin of segment (Figs 12a, b, e) **3**

2a – Hind lobe of prothorax with corners well-developed, appearing trilobed (Fig. 11c); anterior rim of mesostigmal plates sinuous (Fig. 11c); dark mark on dorsum of S8 with ventro-lateral margin rather straight, without antero-ventrally directed extension (Fig. 12c) ..... ***declivatum*** sp. nov.

2b – Hind lobe of prothorax with corners rounded but not appearing trilobed (Fig. 11d); anterior rim of mesostigmal plates straight (Fig. 11d); dark mark on dorsum of S8 with an antero-ventrally directed lobe (Fig. 12d) ..... ***mauffrayi*** sp. nov.

3a – Dorsum of abdomen with small blue and larger rusty orange markings; anterior rim of mesostigmal plate nearly straight, not produced forward (Fig. 11b); posterior third of S10 dorsum markedly compressed laterally, ridge *ca* 0.05 mm wide . ***charis*** sp. nov.

3b – Dorsum of abdomen with mostly dark markings; anterior rim of mesostigmal plate convex, produced forward (Figs 11a, e); posterior third of S10 dorsum moderately compressed laterally, ridge *ca* 0.10 mm wide **4**

4a – Distal point of dorso-medial projection of prothoracic hind lobe protruding above anterior rounded portion (Fig. 10a); base of stylus of ovipositor posterior to level of apex of cercus (Fig. 12a) ..... ***albatum*** sp. nov.

4b – Distal point of dorso-medial projection of prothoracic hind lobe below anterior rounded portion (Fig. 10e); base of stylus of ovipositor anterior to or at level of apex of cercus (Fig. 12e) . ***minutissimum***

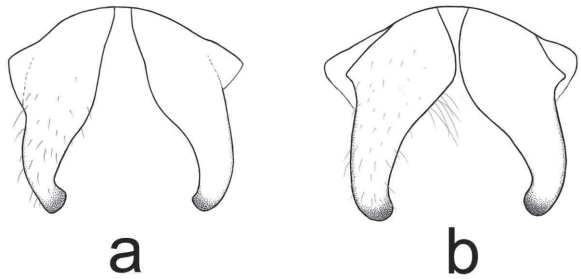


Figure 16. Male paraprocts, ventral view: a – *Calvertagrion albatum* sp. nov.; b – *C. charis* sp. nov.

Discussion

The generic description of *Calvertagrion* by Garrison et al. (2010), based solely on *C. minutissimum*, applies in general also to the four new species added here. However, several characteristics must now be amended. Although pale post-ocular spots were present in all males available to me, including those apparently reproductively immature, they were absent in all females I examined. The dorso-medial process of the pronotal hind lobe varies in males from a conical, tapered process with or without a posterior angle to a flattened process on which its dorsal margin can be convex, straight, or slightly bifid. The thorax does not always have a dark mid-dorsal stripe, exemplified by *C. charis* sp. nov. with an orange-brown and blue-striped mesepisternum, and unless *C. charis* becomes pruinose with age (see description and diagnosis under that species), only four of the known species have pruinescence. Male cerci, while slightly wider than long in *C. minutissimum*, are slightly longer than wide in the other four species. The distally projecting arm on male paraprocts varies from nearly as long as the cerci to about only one third as long, their apices usually hidden beneath the bases of the cerci in two species. In females, the apical margin of S8, in addition to S9, usually bears small black denticles, and the tip of the ovipositor varies from level with the tips of the cerci to extending beyond. In all five species, female S8 lacks a vulvar spine.

Despite these alterations to the generic description, every one of the five species will key correctly to *Calvertagrion* in the male and female keys to

the genera of Coenagrionidae in Garrison et al. (2010). Additional characters that help distinguish *Calvertagrion* are the pterostigma that surmounts less than half of the cell below it in the great majority of specimens (e.g. Fig. 2), and the shape of the male cerci, being dorso-ventrally flattened and blade-like with the medial margin curved and sharp-edged, is without parallel among the New World members of this family.

Maturational changes in color pattern in *Calvertagrion*, especially as related to reproductive activity, have yet to be studied in detail. *Calvertagrion* has been placed in Ischnurinae (Dijkstra et al. 2013), and pronounced color changes with age have been revealed within this subfamily. Calvert (1901) and Paulson (2009) described and illustrated age-related changes in *Hesperagrion*, a New World genus that appears to belong in Ischnurinae, and Dunkle (1990) described changes in *Ischnura*, another genus presumably related to *Calvertagrion*. Reproductively immature adults of *Calvertagrion* are mostly light orange to ocher, but what environmental cues trigger changes to mature coloration is unknown. Why four of the five species of *Calvertagrion* develop pruinescence is an intriguing question. They appear to be partial shade, partial sun dwellers, and perhaps pruinosity functions in a thermoregulatory sense, acting as a shield to avoid overheating from UV radiation, or it might help prevent dehydration in these small damselflies. *Calvertagrion charis* sp. nov. appears to dwell more in shade than the other species; no individuals of this species were pruinose. Larval stages of *Calvertagrion* species have yet to be discovered.

Acknowledgments

I thank Rosser W. Garrison for advice on several matters, a loan of specimens, and for creating the distribution map. I thank Jerrell J. Daigle, Sidney Dunkle, Bill Mauffray, and Dennis Paulson for allowing me to examine specimens of *Calvertagrion* in their collections. Dennis Paulson also provided notes on the habitat and habits of *C. charis*. Wolfgang Schneider and Natalia von Ellenrieder helped translate several papers from German and Spanish to English. Dr. Heinrich Fliedner (Bremen, Germany) suggested the name *C. charis* for the Peru species from Loreto Province.

References

Bota-Sierra C.A. 2012. Rediscovery of *Proneura prolongata* (Zygoptera: Protoneuridae) and other new Odonata records from Colombian Amazon. *Agrion* 16: 34-41

Calvert P.P. 1901. Fam. Odonata. In: Godman F.D. & Salvin O. (Eds), Biologia Centrali-Americana. Insecta Neuroptera: 17-410, plates 2-10. R.H. Porter and Dulau Co., London

Dijkstra K.-D.B., Kalkman V.J., Dow R.A., Stoks F.R. & van Tol J. 2013. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology* 39: 68-96

Dunkle S.W. 1990. Damselflies of Florida, Bermuda and the Bahamas. Scientific Publishers, Gainesville, Florida

Garrison R.W. & Costa J.M. 2002. The identity of *Agrion? minutissimum* Selys, 1876 and *Leptobasis rosea* Selys, 1877 (Zygoptera: Coenagrionidae). *Odonatologica* 31: 395-401

Garrison R.W., von Ellenrieder N. & Louton J.A. 2010. Damselfly genera of the New World. An illustrated and annotated key to the Zygoptera. The John Hopkins University Press, Baltimore

Lencioni F.A.A. 2006. Damselflies of Brazil. An illustrated identification guide. 2 – Coenagrionidae. All Print Editora, São Paulo

Paulson D.R. 2009. Dragonflies and damselflies of the West. Princeton University Press, Princeton, New Jersey

Riek E.F. & Kukalová-Peck J. 1984. A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Canadian Journal of Zoology* 62: 1150-1166

Selys Longchamps de M.E. 1876. Synopsis des Agrionines, cinquième légion: Agrion (suite). Le genre Agrion. *Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique* (II) 41: 247-322, 496-539, 1233-1309

St. Quentin D. 1960. Zur Kenntnis der Agrioninae (Coenagrioninae) Südamerikas (Odonata). *Beiträge zur neotropischen Fauna* 2: 45-64

Wasscher M.Th. & Dumont H.J. 2013. Life and work of Michel Edmond de Selys Longchamps (1813-1900), the founder of odonatology. *Odonatologica* 42: 369-402

Westfall M.J. & May M.L. 2006. Damselflies of North America. Revised Edition. Scientific Publishers, Gainesville

1st December 2015

New species of damselflies from the Hindenburg Wall region of western Papua New Guinea (Odonata: Coenagrionidae, Platycnemididae)

Günther Theischinger[1] & Stephen J. Richards[2]

[1] NSW Department of Planning and Environment, Office of Environment and Heritage, Water Science, PO Box 29, Lidcombe, NSW 1825, Australia; <gunther.theischinger@environment.nsw.gov.au>

[2] Herpetology Department, South Australian Museum, North Terrace, Adelaide, SA 5000, Australia; and Wildlife Conservation Society, Goroka, Papua New Guinea; <steve.richards@samuseum.sa.gov.au>

Received 9th September 2015; revised and accepted 5th October 2015

Abstract. Two new species of *Teinobasis* and one new species of *Nososticta* from the Hindenburg Wall region of western Papua New Guinea are described and illustrated. They are *Teinobasis cuneata* sp. nov. (Holotype SAMA 07-001421), *Teinobasis flavolineata* sp. nov. (Holotype SAMA07-001422), and *Nososticta oculata* sp. nov. (Holotype SAMA 07-001424). The new *Teinobasis* species are both moderately large, slender species with predominantly yellow/orange faces and black abdomens and they are most similar to *T. angusticlavia* Ris from the Aru Islands and *T. albula* Ris from the Lorentz River. The new *Nososticta* species is most similar to *N. finisterrae* Förster, a species that is widespread in south-eastern New Guinea, but differs from it in having the blue inter-ocular bar that is typical of *finisterrae* reduced to two widely separated pale blue spots on the anterior frons.

Key words. Dragonfly, damselfly, Zygoptera, new species, *Nososticta*, *Teinobasis*

Introduction

New Guinea has proven to be a hotspot of odonate diversity, with numerous new species described from the island in recent years. Among these have been several damselflies of the coenagrionid genus *Teinobasis* Kirby, 1890, with recent treatments of the genus increasing to 33 the number of species currently known from the region (Theischinger & Richards 2007, 2013; Michalski 2012; Kalkman & Orr 2013; Theischinger & Kalkman 2014). Another group that has proven to be far more diverse than pre-

viously recognized is the platycnemidid damselfly genus *Nososticta* Hagen in Selys. *Nososticta* is a group of predominantly stream-dwelling species that reaches its greatest diversity in the lowland and foothill forests of mainland New Guinea. The genus was treated most recently by Theischinger & Richards (2015) who described ten new taxa from New Guinea and noted that it is likely »several dozens« of species remain to be discovered in previously unexplored regions there.

A rapid biodiversity assessment of the rugged Hindenburg Wall region of western Papua New Guinea in 2013 documented a large number of odonatological novelties from the southern slopes of the Hindenburg Range (Richards & Theischinger 2015). Several of these have subsequently been described (Orr et al. 2014; Theischinger & Richards 2014; Theischinger et al. 2015) and we here describe two new species of *Teinobasis* and one new species of *Nososticta* discovered during that expedition, bringing to 35 and 51 respectively the number of species group taxa known from New Guinea in these two speciose genera.

Material and methods

The descriptive terminology largely follows Chao (1953) and Watson & O'Farrell (1991). Colouration is given as detectable from the preserved material and supported by live photographs. All illustrations were done with the aid of a camera lucida and are not to scale. Voucher material is deposited in the collection of the South Australian Museum, Adelaide, Australia (SAMA).

Teinobasis cuneata sp. nov.

(Figs 1–10)

Material studied

Holotype ♂. Papua New Guinea, Western Province, Umansim Stream, at intersection with Kiunga-Tabubil Road south of Tabubil Town (5.3328°S, 141.2780°E; 365 m a.s.l.), 10-ii-2013, S.J. Richards leg. (SAMA 07-001421).

Etymology

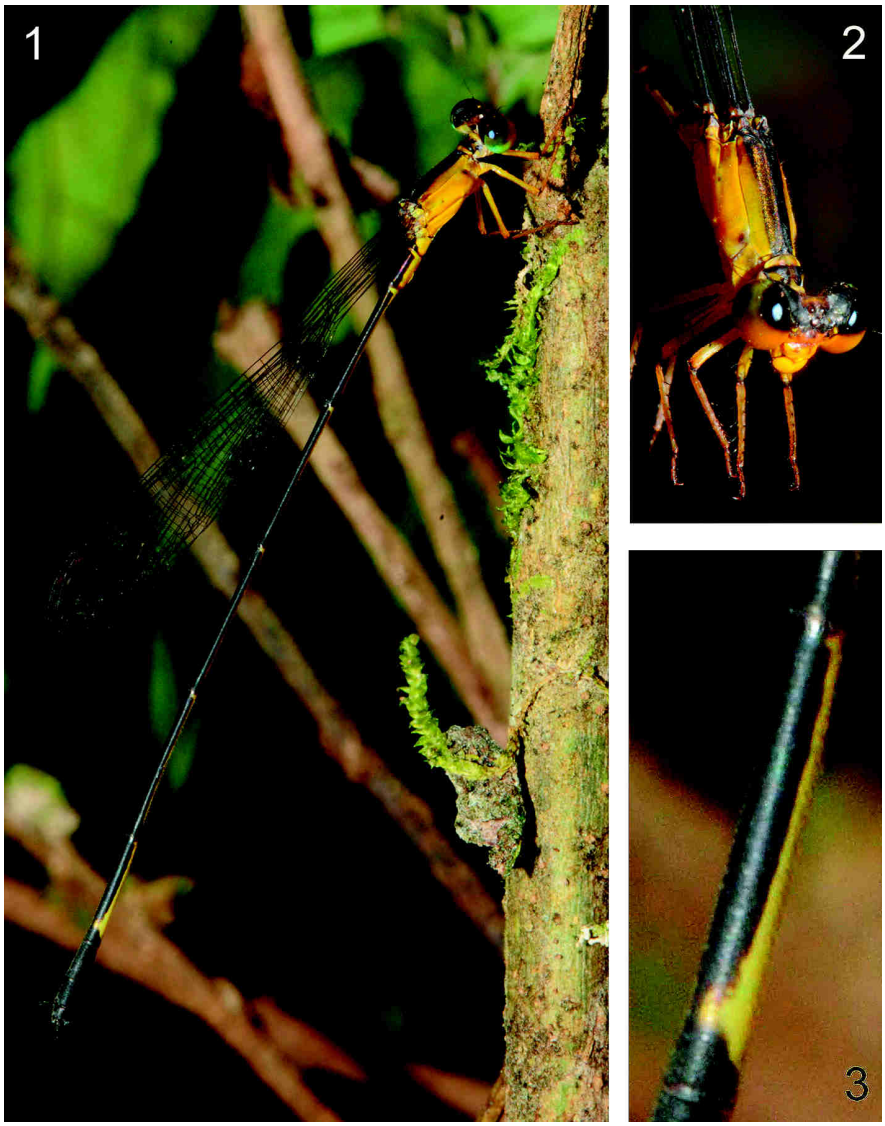
The specific name *cuneatus*, *-a*, *-um*, a Latin adjective meaning wedge-shaped, refers to the black wedge-shaped dorsal mark on S1 of the male.

Male (holotype)
Head – Labium pale brownish yellow; labrum, base of mandibles, genae, clypeus, and anterior frons largely orange; a black spot each side at the base of labrum and some ill-defined patches close to and along epistomal suture and in front of median ocellus; tips of mandibles brownish black; top of frons, vertex, antennae, post-ocular lobes, top, and a spot each side near centre of postgenae largely black, only face and apex of scape, a short narrow line between antennal base and lateral ocellus and an ill-defined stripe along occipital margin dull orange.

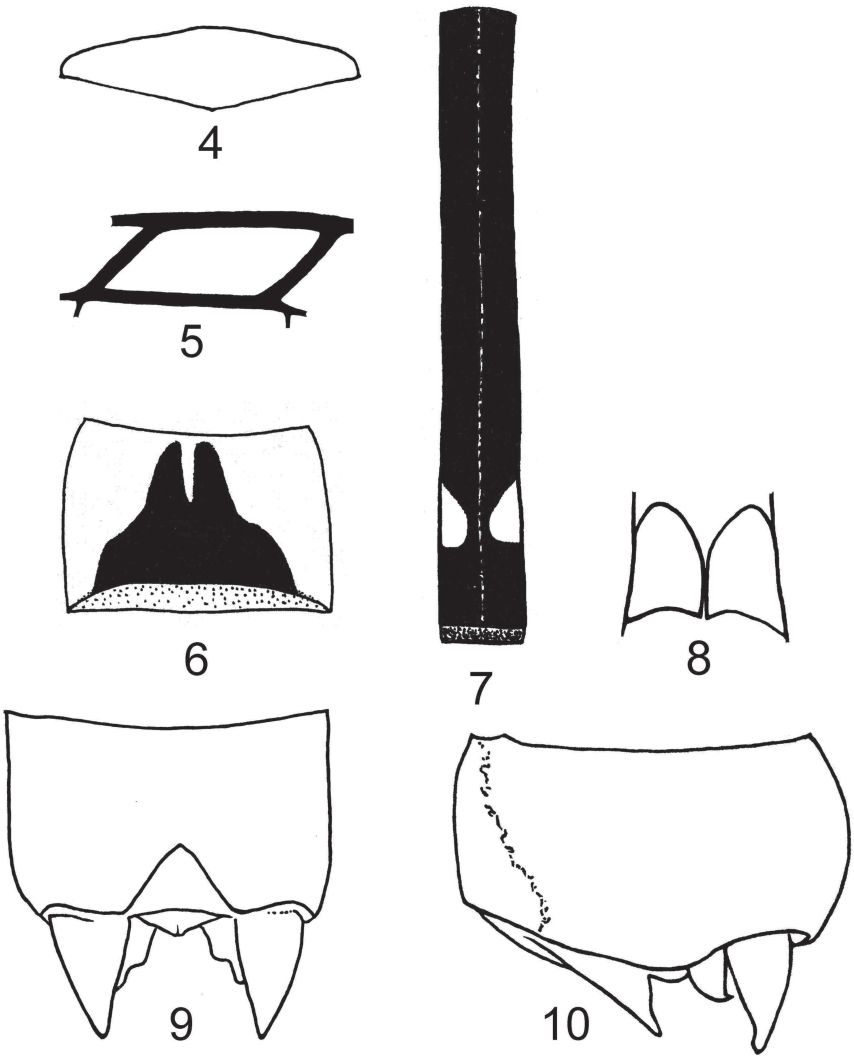
Thorax – Prothorax: Anterior and posterior lobe (Fig. 4) of notum yellow; median lobe largely black, orange along black dorsal margin of the largely yellow pleura. Synthorax: Largely pale orange. Mid-dorsal carina, inner half of mesanepisternum, most of spiracular dorsum and the extreme dorsal edge of metapostepimeron black; small black spots on mesepimeron just dorsal to suture between mesanepisternum and katepisternum, dorsal to mesepimeron adjacent to ante-alar and subalar ridge, and dorsal to metepimeron adjacent to subalar ridge; a small brown patch each at dorsal end of mesopleural and of metapleural suture. Thoracic terga and sclerites at wing base yellow. Postcoxae and poststernum pale orange. Legs yellow with only the spines black.

Wings – Membrane hyaline, venation blackish brown; pterostigma (Fig. 5) greyish brown with yellowish margin, *ca* twice as long as wide, strongly slanting; antenodals 14–15/14.

Abdomen – Largely black. S1 yellow with black wedge-shaped dorsal mark (Fig. 6); much of sides of S2, ventral edge of S3–7 and a connected wedge-shaped subapical patch, extending almost to mid-dorsum, in S7, yellow (Fig. 7); S8–10 yellow ventrally; inner corner of valvae not produced (Fig. 8). Anal appendages (Figs 9, 10): Superiors brownish black, upper branch much longer than hooked lower branch; inferiors slightly shorter than upper branch of superiors; upper branch of superiors and inferiors apically very thin. Dorsal appendage of S10 (epiproct) widely subtriangular with narrow apex, its apical portion split.



Figures 1–3. *Teinobasis cuneata* sp. nov., male holotype in life, near Tabubil, PNG. Photos SJR (10-ii-2013): 1 – habitus, lateral; 2 – frontal; 3 – abdominal segment 7, lateral.



Figures 4–10. *Teinobasis cuneata* sp. nov., male: 4 – posterior lobe of pronotum, dorsal; 5 – pterostigma of forewing; 6 – abdominal segment 1, dorsal; 7 – abdominal segment 7, dorsal; 8 – abdominal segment 9, valvae, ventral; 9, 10 – anal appendages: 9 – dorsal; 10 – lateral.

Measurements [mm] – Hind wing 24.7; abdomen including anal appendages 40.8.

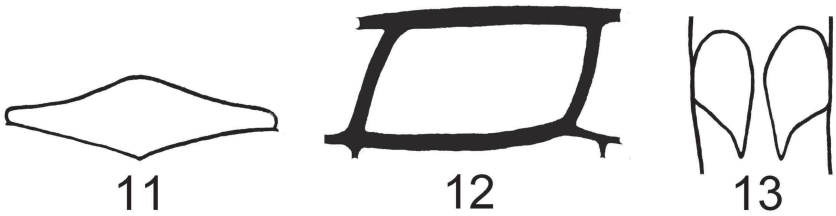
Female
Unknown.

Distribution
Currently known only from the type locality in the upper Ok Tedi headwaters near Tabubil Town in Western Province, Papua New Guinea.

Notes on biology
The holotype and only known specimen was perched about 30 cm above the ground in dense remnant riparian vegetation approximately 20 m upstream of the point where Umansim Stream intersects, and passes beneath, the Kiunga-Tabubil road. At this point the stream, which drains the southern ridges of the Hindenburg Range, was approximately 10 m wide, shallow (<50 cm deep), clear and flowing swiftly over a rocky substrate. The forest along the stream had been severely disturbed, with canopy cover near the stream largely removed for at least 50 m upstream and downstream of the road. A number of large *Pandanus* trees were observed in the heavily disturbed nearby forest but the holotype was not closely associated with them.

Differential diagnosis
A rather large, very slender species that can be distinguished from all congeners by the following combination of characters: male (Figs 1–3) with largely yellow/orange face and legs, with black mid-dorsal stripe on the otherwise largely orange synthorax, and with largely black abdomen. A black dorsal wedge is present on the otherwise yellow abdominal S1 and a subapical yellow mark each side extends close to mid-dorsum of S7. The male of *Teinobasis cuneata* sp. nov. (Figs 1–10) is most similar to *Teinobasis angusticlavia* Ris, 1915 (Figs 11–13) from the Aru Islands in colouration and in shape and proportions of the anal appendages. However the two species differ in the following characters: the dark stripe along mid-dorsal carina covers only a third of the width of the front of the synthorax in *T. angusticlavia* (vs almost half the width in *T. cuneata* sp. nov), the pterostigma of fore wing (Fig. 12) is

sub-rectangular and only about 1.6 times as long as wide in *T. angusticlavia* (vs shaped as a distinctly slanting parallelogram and about twice as long as wide in *T. cuneata* sp. nov.) (Fig. 5), and the apical half of S7 is largely light greyish brown in *T. angusticlavia* (vs S7 with a rather narrow yellow subapical mark that is connected with the yellow ventral margin (Fig. 7) in *T. cuneata* sp. nov.). The superior anal appendages are also somewhat shorter and less curved in *T. cuneata* than in *T. angusticlavia* (paratype studied). It will be interesting to find out if the shape of the male valvae – the inner corner is apparently strongly produced in *T. angusticlavia* (Fig. 13), but not so in *T. cuneata* (Fig. 8) – is reflected in the development of the female valves once the female of *T. cuneata* is known.



Figures 11–13. *Teinobasis angusticlavia* Ris, male: 11 – posterior lobe of pronotum, dorsal; 12 – pterostigma of fore wing; 13 – abdominal segment 9, valvae, ventral.

Teinobasis flavolineata **sp. nov.**
(Figs 14–21)

Material studied

Holotype ♂. Papua New Guinea, small stream draining into Ok Menga near junction with Kiunga-Tabubil Road south of Tabubil Town (5.3702°S, 141.2947°E; 282 m a.s.l.), 27-ii-2013, M. Hammer leg. (SAMA 07-001422).
Paratype. 1♀ (SAMA 07-001423), same data as holotype.

Etymology

The specific name is a composite of two Latin adjectives, *flavus*, *-a*, *-um*, meaning yellow, and *lineatus*, *-a*, *-um*, meaning lined, owing to the yellow intersegmental membrane of abdominal segments 7, 8, and 9 that in dorsal view appears as three yellow transverse lines.

Male (holotype)
Head – Labium pale brownish yellow; labrum, base of mandibles, genae, clypeus and anterior frons including frontal face of antennal base, scape (+ apex) and pedicel and a rather small ventral portion of subgenae orange/yellow; top of frons, vertex, post-ocular lobes, larger, more dorsal portion of subgenae, and remainder of antennae black with only a thin line each side between antennal base and lateral ocellus.

Thorax – Prothorax pale orange. Synthorax almost entirely pale orange; only ante-alar ridge, spots on top of both mesepimeron and metepimeron and rim of metapostepimeron black. Terga largely yellow, but some sclerites at wing base greyish brown. Postcoxae and poststernum pale orange. Legs yellow to pale orange with knees, apex of tibiae and terminal tarsal segments narrowly blackened and claws brown.

Wings – Membrane hyaline, venation black; pterostigma (Fig. 19) dark grey, an approximate rhombus, scarcely longer than wide; postnodals 14–15/15.

Abdomen – Largely black. A narrow short black wedge in the apical half of the otherwise pale orange S1; S2 with sides and connecting narrow transverse dorsal stripe at the very base pale orange; a small subapical yellow line each side on black dorsal patch; S3–10 latero-ventrally pale yellow, this colour connected with yellow basal spot at least in S3–6; intersegmental membrane of S7, 8, and 9 yellow. Anal appendages (Figs 20, 21): superiors with upper branch black, hook-like, incurved at apex and markedly longer than the hooked blackish brown lower branch which is hardly shorter than the apically rounded brown inferior appendages. Dorsal appendage of S10 (epiproct) broadly subtriangular with narrow apex; apical portion split.

Measurements [mm] – Hind wing 28.0; abdomen including anal appendages 43.3.

Female (paratype)
Head – Much as in male but colouration even less vivid.

Figures 14–16. *Teinobasis flavolineata* sp. nov., male holotype in life, near Tabubil, PNG. Photos: SJR (27-ii-2013): 14 – habitus, lateral; 15 – frontal; 16 – abdominal segments 7–10, dorsal/lateral.

Thorax – Prothorax largely as in male but median lobe of notum with narrow dark line along midline and with a tiny dark spot each side, close to posterior lobe (Figs 17, 18). Posterior lobe widely rhomboidal and smooth with an ill-defined dark patch on each side close to midline and to the dark spot on median lobe. Synthorax similar to male but very narrowly black along mid-dorsal carina; also dark along spiracular dorsum and distal to the black mid-dorsal stripe in the second quarter of its length from ante-alar ridge; ante-alar ridge and sinus medially bright yellow, laterally black. Legs with black colour at knees and at apex of tibiae and terminal tarsal segments even less extensive than in male.

Wings – Much as in male with the same short square/rhomboidal pterostigma; postnodals 13/13.

Abdomen – Much as in male but basal lateral yellow spots dorsally more widely separated and therefore even more inconspicuous; a small and ill-defined brown lateral patch on S9, S10 ventrally brownish yellow. Anal appendages black. Valves basally yellow merging to brown and black apically, reaching very slightly beyond end of S10 and with ventral margin smooth; terebra pale to medium brown.

Measurements [mm] – Hind wing 27.4; abdomen 38.5.

Distribution

Presently known only from the type locality in the upper Ok Tedi headwaters near Tabubil Town in Western Province, Papua New Guinea.

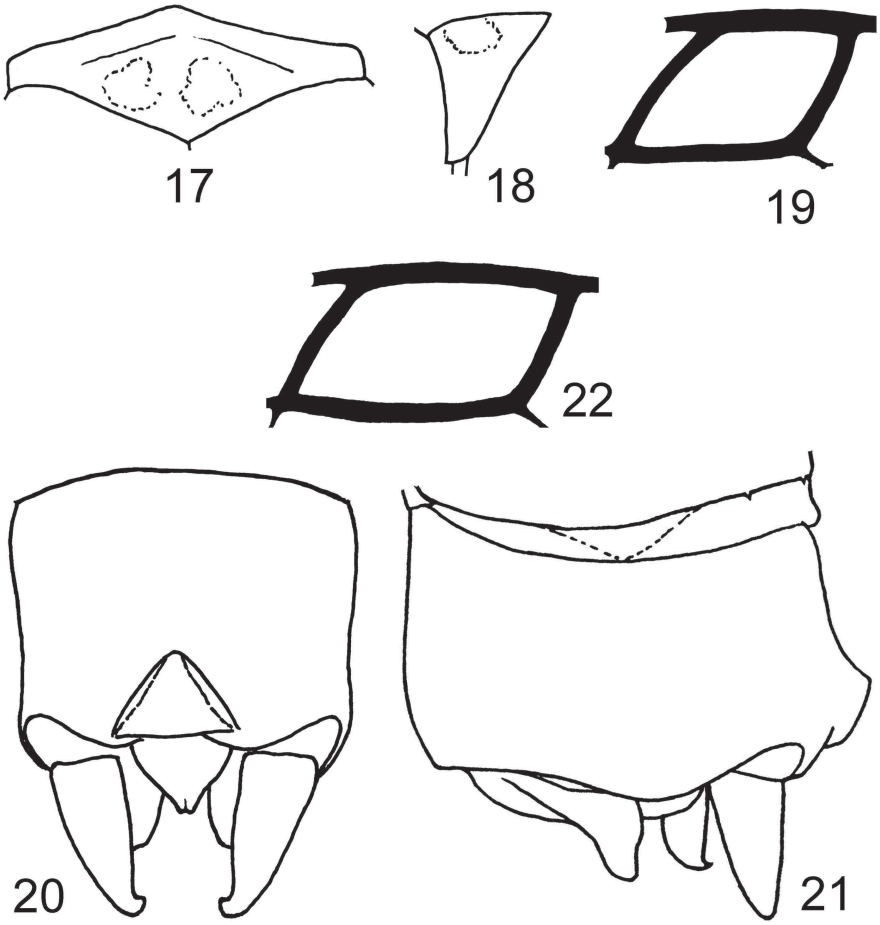
Notes on biology

The two specimens of this species were perched in dense low foliage along a small, clear, shallow stream draining into the Ok Menga, a major tributary of the Ok Tedi near the confluence of these two rivers.

Differential diagnosis

A rather large, very slender species of *Teinobasis* that is distinguished from all congeners by the following combination of characters: face, thorax, and

legs largely yellow/orange, pterostigma equilateral-rhomboidal and abdomen largely black (but intersegmental membrane of abdominal S7, 8, and 9 yellow), the male (Figs 14–16) without black stripe along midline of front of synthorax, the female with widely triangular posterior lobe of pronotum and with narrow black mid-stripe on the front of synthorax. Eyes of



Figures 17–21. *Teinobasis flavolineata* sp. nov.: 17, 18 – female, posterior lobe of pronotum: 17 – dorsal; 18 – lateral; 19–21 – male: 19 – pterostigma of forewing; 20, 21 – anal appendages: 20 – dorsal; 21 – lateral.
Figure 22. *Teinobasis albula* Ris, male, pterostigma of fore wing.

male and female green in life. The male of *Teinobasis flavolineata* sp. nov. is most similar to *Teinobasis albula* Ris, 1913 (photos of holotype studied) from Lorentz River in Papua Province, Indonesian New Guinea. Both species have the front of the synthorax orange without a black stripe in the middle, and the shapes and proportion of their anal appendages are similar. However *T. flavolineata* sp. nov. has legs with the knees, apex of tibiae, and terminal segments of tarsi blackened (Figs 14, 15) (vs simply reddish yellow in *T. albula*), a short square/rhomboidal pterostigma (Fig. 19) (vs an elongate sub-rectangular pterostigma in *T. albula*: Fig. 22) and apically rather rounded inferior anal appendages (Fig. 21) (vs rather narrowly pointed inferior anal appendages in *T. albula*).

***Nososticta oculata* sp. nov.**
(Figs 23–27)

Material studied

Holotype ♂. Papua New Guinea, Western Province, Tulenbeng Wok (stream) where stream intersects Kiunga-Tabubil Road south of Tabubil Town (5.3082°S, 141.2528°E; 433 m a.s.l.), 02-iii-2013, M. Hammer leg. (SAMA 07-001424).

Paratype. 1 ♂ (SAMA 07-001425), same details as holotype but collected 10-ii-2013, S.J. Richards leg.

Etymology

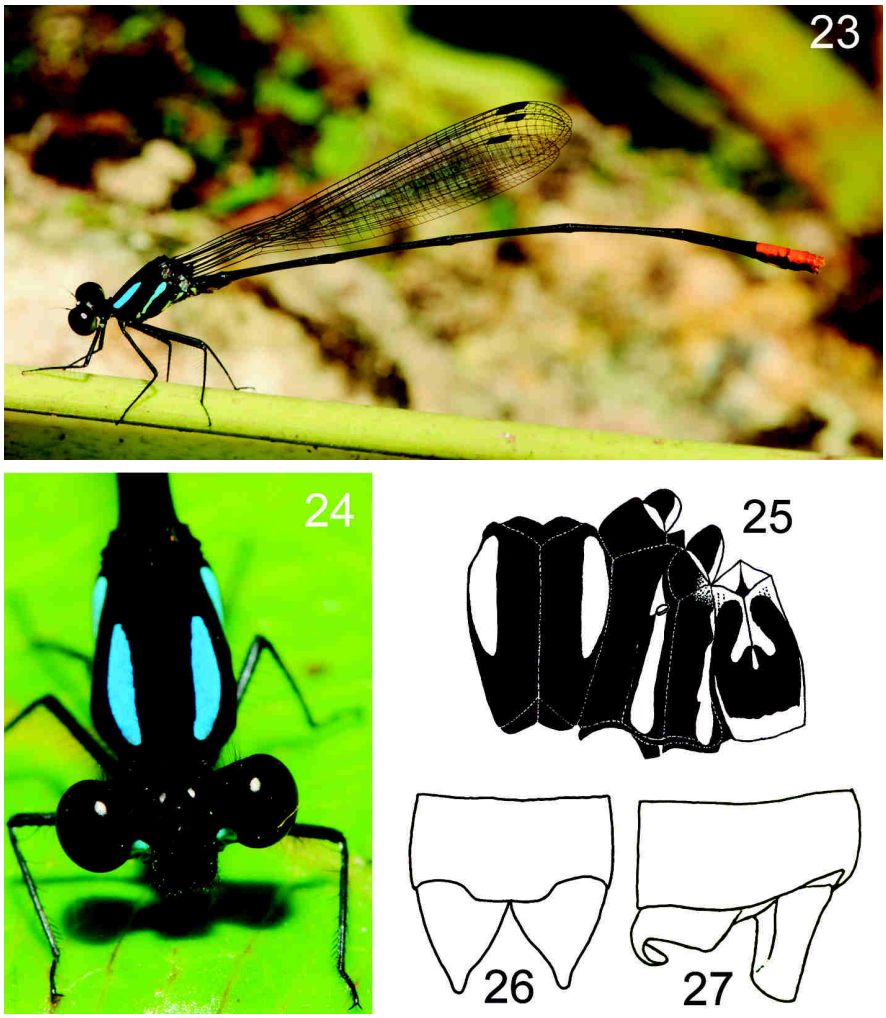
The specific name *oculatus*, *-a*, *-um* is a Latin adjective meaning »with eyes visible« and refers to the distinct lateral pale blue spots on the face that resemble eyes.

Male (holotype)

Head – Black with only base of mandibles, genae and lateral corners of post and ante-frons pale blue.

Thorax – Prothorax black with a tiny and well-defined, very pale spot in postero-ventral corner of episternum. Synthorax (Fig. 25) black with bright blue ante-humeral patches about ⅔ the length and ⅖ the width of each mesanepisternum, a lighter blue tapered metepisternal stripe, fading ventrally,

and even lighter tapered metepimeral patch; an ill-defined lighter area in posterior corner of metakatepisternum and in ventral corner of metepimeron. Mesopostcoxae black, metapostcoxae largely bluish white to yellow,



Figures 23–27. *Nososticta oculata* sp. nov.: 23, 24 – male holotype in life, near Tabubil, PNG. Photos: SJR (02-iii-2013): 23 – lateral; 24 – frontal; 25 – synthorax, frontal, lateral, ventral; 26, 27 – anal appendages: 26 – dorsal; 27 – lateral.

poststernum largely black. Legs black except for posterior edge of meso- and metacoxa.

Wings – Membrane hyaline, venation black; pterostigma at least twice as long as wide, parallelogram-shaped, strongly slanting, black with fine thin whitish line along delimiting veins; postnodals 21–22/18; no transverse cross-vein from distal margin of discoidal cell to wing margin.

Abdomen – Largely black; S1 with two, and S2 with one, bluish white to yellow lateral patches; S3–8 pale yellowish along most or part of lateral margin; S8–10 dorsally bright reddish-orange, laterally wholly or largely black. Anal appendages (Figs 26, 27) reddish-orange to brownish yellow; superiors short and plump, in dorsal view subtriangular with tip somewhat compressed, in lateral view sub-rectangular with rather small inner tooth, inferiors with base wide-angled and apically strongly curved.

Measurements [mm] – Hind wing 23.6; abdomen including anal appendages 37.6.

Variability in paratype male
Postnodals of hind wing 18–19 (vs 18 in the holotype); abdominal S1 with one complex bluish white to yellow lateral patch (vs 2 smaller simple patches in the holotype); hind wing length 23.8 mm, abdomen including anal appendages 38.0 mm (vs 23.6 and 37.6 respectively).

Female
Unknown.

Distribution
Presently known only from the type locality in the upper Ok Tedi headwaters near Tabubil Town in Western Province, Papua New Guinea.

Notes on biology
Nososticta oculata were perched in dappled sunlight on small twigs a few centimeters above the water along the Tulenbeng Wok, a small (<10 m

wide) steep stream flowing over a rocky substrate through remnant foothill rainforest. The stream originates on the southern slopes of the Hindenburg Range south of Tabubil Town so the water is cool and clear. Most of the rainforest around the collection locality, where the Tulenbeng Wok intersects the Kiunga-Tabubil road, has been severely disturbed.

Differential diagnosis

A rather large, dark, very slender species (Figs 23, 24) distinguished from all congeners by the following combination of characters: male with head black with pale blue patch each side of the anterior frons, prothorax black with tiny white spot, synthorax black with bright blue ante-humeral and lighter narrow tapered metepisternal and metepimeral patch and largely black abdomen with dorsal face of terminal segments and anal appendages bright orange. The male of *Nososticta oculata* sp. nov. (Figs 23, 24) is most similar to *Nososticta finisterrae* (Förster, 1897) as studied from numerous localities over a wide range in southern New Guinea. However the two species can be clearly distinguished by the shape and extent of the blue markings on the face; whereas there is a blue bar from eye to eye and a rather wide (wider than the metastigma) parallel sided metepisternal stripe in *N. finisterrae*, there are only two widely separated pale blue spots on the anterior frons and a narrow (not wider than metastigma) tapered metepisternal stripe in *N. oculata*.

Acknowledgements

Field work in Papua New Guinea by SJR was supported by the Wildlife Conservation Society-PNG through a grant and logistical support from the PNG Sustainable Development Program (PNGSDP), and he is particularly grateful to Nathan Whitmore, Ross Sinclair, John Kuange, and John Par Kagl from WCS, and to Stanis Tao and Kaia Songoa from PNGSDP, for their assistance. The local communities of Wangbin and Tabubil provided access to, and hospitality on, their land, and SJR is most grateful to the community members of these areas for their support and field assistance. Permission to conduct research in Western Province, and other assistance, was provided by the PNG Department of Environment and Conservation, the National Research Institute, the Western Province Provincial Government, and the

Star Mountains Local Level Government. We wish to thank V.J. Kalkman (Leiden) for providing photos of the holotype of *Teinobasis albula*, and W.A. Nässig and W. Schneider (Frankfurt am Main) for making available type material of *Teinobasis angusticlavia*. GT wishes to acknowledge ongoing support by the management of the Office of Environment and Heritage, NSW Department of Planning and Environment.

References

Chao H.F. 1953. The external morphology of the dragonfly *Onychogomphus ardens* Needham. *Smithsonian miscellaneous Collections* 122/6: 1-56

Kalkman V.J. & Orr A.G. 2013. Field guide to the damselflies of New Guinea. *Brachytron* 16, Supplement: 3-120

Orr A.G., Kalkman V.J. & Richards S.J. 2014. Four new species of *Palaiargia* Förster, 1903 (Odonata: Platycnemididae) from New Guinea with revised distribution records for the genus. *International Journal of Odonatology* 16 [2013]: 309-325

Michalski J. 2012. A manual for the identification of the dragonflies and damselflies of New Guinea, Maluku and the Solomon Islands. Kanduanum Books, Morristown, NJ

Richards S.J. & Theischinger G. 2015. Chapter 5. Odonata (dragonflies and damselflies). In: Richards S.J. & Whitmore N. (Eds), A rapid biodiversity assessment of Papua New Guinea's Hindenburg Wall Region: 75-83. Wildlife Conservation Society, Goroka

Theischinger G. & Kalkman V.J. 2014. The genus *Teinobasis* on the Bird's Head Peninsula and the Raja Ampat Islands, Indonesia (Odonata: Coenagrionidae). *Odonatologica* 43: 143-168

Theischinger G. & Richards S.J. 2007. *Teinobasis kiautai* spec. nov., a new species from Papua New Guinea (Zygoptera: Coenagrionidae). *Odonatologica* 36: 85-88

Theischinger G. & Richards S.J. 2013. Three new species of *Teinobasis* Kirby from Papua New Guinea (Zygoptera: Coenagrionidae). *Odonatologica* 42: 359-367

Theischinger G. & Richards S.J. 2014 *Drepanosticta machadoi* spec. nov. from New Guinea (Odonata: Platystictidae). *Zootaxa* 3866: 145-150

Theischinger G. & Richards S.J. 2015. The genus *Nososticta* Hagen (Odonata: Platycnemididae) from the Papuan region with descriptions of ten new species group taxa. *Odonatologica* 44: 153-224

Theischinger G., Gassmann D. & Richards S.J. 2015. *Macrocnemis gracilis*, a new genus and species of Idiocnemidinae (Zygoptera: Platycnemididae) from Papua New Guinea. *Zootaxa* 3990: 429-436

Watson J.A.L. & O'Farrell F.A. 1991. Odonata (dragonflies and damselflies). In: CSIRO Division of Entomology (Ed.), The insects of Australia. A textbook for students and research workers. 2nd ed.: 294-310. Melbourne University Press, Carlton