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To cite this article: Petr Janšta , Gérard Delvare , Hannes Baur , Benjamin Wipfler & Ralph S. Peters (2020) Data-rich description of a new genus of praying mantid egg parasitoids, *Lasallegrion* gen. n. (Hymenoptera: Torymidae: Podagrionini), with a re-examination of *Podagrion* species of Australia and New Caledonia, Journal of Natural History, 54:9-12, 755-790, DOI: 10.1080/00222933.2020.1778112

To link to this article: <https://doi.org/10.1080/00222933.2020.1778112>



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Published online: 23 Sep 2020.



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# Data-rich description of a new genus of praying mantid egg parasitoids, *Lasallegrion* gen. n. (Hymenoptera: Torymidae: Podagrionini), with a re-examination of *Podagrion* species of Australia and New Caledonia

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## ABSTRACT

The genus *Lasallegrion* gen. n. is described, and three species, *Lasallegrion koebelei* (Crawford 1912), **comb. n.**, *Lasallegrion virescens* (Strand 1911), **comb. n.**, and *Lasallegrion washingtoni* (Girault 1915), **comb. n.**, are redescribed and transferred to it. *Podagrion holbeini* Girault 1923, **syn. n.**, and *Podagrion metatarsum* Girault 1929, **syn. n.**, are synonymised here with *Lasallegrion koebelei*. Further, 14 species from Australia and New Caledonia are confirmed as belonging to *Podagrion* Spinola, 1811. The classic morphological approaches are combined with multivariate ratio analysis and molecular and additional morphological methods for (re-)descriptions. A comprehensive set of morphometric data, COI barcode sequences, a fully sequenced transcriptome and detailed  $\mu$ CT data are provided. An updated key to the Australasian genera of Podagrionini and to the *Lasallegrion* species is given. Additionally, we present some discussion on the collisions of the concepts of modern taxonomy, and the restrictions caused by poorly conditioned old type material.

## ARTICLE HISTORY

Received 31 October 2019  
Accepted 7 May 2020  
Published online  
23 September 2020  
Published in print  
23 September 2020

## KEYWORDS

Podagrioninae; *Lasallegrion*;  
*Podagrion*; Mantodea;  
integrative taxonomy;  
taxonomy challenges

## Introduction

The tribe Podagrionini Bouček, 1976 belongs to the subfamily Podagrioninae Ashmead, 1904 (Torymidae) and includes about 135 described species in nine genera (Grissell 1995; Janšta et al. 2018). The main distribution is in the pan-tropical area, with most described species occurring in the Afrotropics, the Neotropics and Australia. Almost all Podagrionini species for which reliable host associations are recorded are parasitoids of Mantodea eggs. Mantodea eggs are laid in clutches surrounded by hardened structural proteins, the so-called oothecae. Members of the tribe Podagrionini can be easily identified not only by their specific host association but also by a number of striking morphological features (for

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details see Grissell 1995). However, the classification of Podagrionini genera still requires taxonomic revision (Janšta et al. 2018).

Currently, there are 27 species of the tribe described from Australia and New Caledonia, 19 classified in the genus *Podagrion*, four in *Palmon*, three in *Propachytomoides* and one in *Podagrionella*. The remaining genera of Podagrionini have not yet been recorded from Australia or New Caledonia (Grissell 1995). However, Janšta et al. (2018) mentioned one more undescribed genus from Australia (quoted as 'PJAN1079 Podagrionini n. gen. sp. Australia' in their study). Here, we revise part of the Podagrionini species described from Australia and New Caledonia based on newly collected material and material found in scientific collections. We follow an integrative approach, and study qualitative and quantitative morphological characters and COI sequence data. Based on these results of Janšta et al. (2018), we describe a new genus, transfer three described species into this new genus, and make two new synonymies. In addition to the classical taxonomic description of the genus, we provide  $\mu$ CT data of two species included in the new genus as well as transcriptome sequence data of one of the species.

Using the next-generation morphology (Hita Garcia et al. 2017) or twenty-first century taxonomy (Fontaine et al. 2012; Bik 2017) we would like to point out some difficulties caused by the condition of the available type material that collide with our primary aim of providing unambiguous, objective taxonomic actions complemented by rich data sources. This problem is not restricted to Hymenoptera or insects, and will multiply in the near future with new morphological and molecular techniques becoming standard and available also to most taxonomists. As an example, we will discuss these problems here in addition to the actual taxonomic part of our study.

## Material and methods

### Abbreviations and collection depositories

This study is based on material borrowed from the following museums (with abbreviations following Evenhuis (2017) used in the text): American Museum of Natural History, New York, U.S.A. (AMNH); Australian National Insect Collection, Canberra, Australia (ANIC); Charles University in Prague, Faculty of Science, Department of Zoology, Prague, Czech Republic (CUPC); Centre de Biologie pour la Gestion des Populations, Montferrier-sur-Lez, France (CBGP); Hope Department, Oxford University, U.K. (HDOU); National Museum of Victoria, Melbourne, Australia (NMVM); Natural History Museum, London, U.K. (NHMUK); Queensland Museum, Brisbane, AUS (QMB); South Australian Museum, Adelaide, Australia (SAMA); United States Museum of Natural History, Washington D.C., U.S.A. (USMN); Waite Insect and Nematode Collection, University of Adelaide, Adelaide, SA (WINC); Zoological Museum, Humboldt University, Berlin, Germany (ZMHU); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

### Measurements and character abbreviations

We measured 90 characters with an Olympus SZX 12 stereomicroscope equipped with a Carl Zeiss scale ocular and a calibrated eyepiece micrometre (S48–StageMic). Each character was measured at a particular magnification. For a complete list of measurement and

ratio data, including character definition of characters not listed in Table 1, see Supplementary Table 1. In addition, we use OI (ovipositor index) = ratio of ovipositor length to length of metatibia.

A subset of 19 characters (characters marked with an asterisk in Table 1 and in Supplementary Table 1) was used for the multivariate ratio analysis (MRA). In particular, we calculated a shape principle component analysis (shape PCA) and looked for the best separating ratios using the LDA ratio extractor (for details, see Baur and Leuenberger 2011). All multivariate statistical analyses were done with R (version 3.3.3, R Core Team 2017) using slightly modified R scripts provided by Baur et al. (2014).

Terminology of morphological structures in this study mostly follows Gibson et al. (1997), terms for surface sculpture follow Steinmann and Zombori (1985).

### **Molecular analysis**

The initial morphological examination revealed two groups with a different morphological appearance, morphospecies 1 and morphospecies 2. For DNA extraction, 23 specimens were randomly taken from the material preserved in 99% ethanol. For morphospecies 2, only one male specimen (lc\_20) was available for DNA sequencing. From morphospecies 1, 17 females (lc\_1–lc\_10, lc\_15–lc\_19, GEL3175, GDEL3176) and 5 male specimens (lc\_11–lc\_14, GDEL3177) were chosen. To retain the sequenced material for morphological examination and as voucher specimens, the extraction of all specimens was done non-destructively using the DNeasy Blood & Tissue Kit from Qiagen. For amplification of most of the specimen's barcode region LCO1490–JJ (5'–CHACWAAAYCATAAAGATATYGG–3') and HCO2198–JJ (5'–AWACTTC VGGRTGVCCAAARAATCA–3') primers (Astrin and Stüben 2008) were used. Specimens GDEL3175–3177 were amplified using LCO1490 (5'–GGTCAACAAATCATAAAGATATTGG–3') and HCO2198 (5' – TAAACTTCAGGGTGACCAAAAATCA–3') primers (Cruaud et al. 2010).

For amplification, a touchdown PCR program was chosen. DNA thermal cycling was performed as follows: initial denaturation step of 15 min at 95°C followed by first cycle set (15 repeats, 94°C for 35 s, 55°C for 90 s and 72°C for 90 s), second cycle set (25 repeats, 94°C for 35 s, 40°C for 90 s and 72°C for 90 s) and final elongation step of 10 min at 72°C and cooling at 10°C. Specimens GDEL3175–3177 were amplified using slightly different conditions (initial denaturation step of 3 min at 94°C followed by 30 repeats, 92°C for 30 s, 48°C for 90 s and 72°C for 210 s, final elongation step of 10 min at 72°C) (Cruaud et al. 2010). For control of success an agarose gel electrophoresis was used. PCR products were sequenced either by MacroGen Europe Amsterdam or (GDEL3175–3177) by Genoscope, Evry, France.

Multiple sequence alignment of all sequences plus one previously published (MF956323 of PJAN1079, Janšta et al. 2018) was done using the MAFFT algorithm implementation in Geneious Prime 2019.2.1 (Biomatters Ltd.) with default settings. The multiple sequence alignments were used to generate an alignment heatmap using a standard feature in Geneious Prime 2019.2.1. The heatmap indicates the genetic distances as percentages of positive base matches for each single alignment. Further, the phylogenetic tree of all COI sequences including three outgroups was reconstructed to see how specimens of morphospecies 1 group together. All outgroups (*Podagrion bouceki* Delvare, *P. pachymerum* Walker, *Propachytomoides* sp1) included in the analysis were selected based on the most recent phylogeny of Torymidae (Janšta et al. 2018). The molecular tree



**Table 1.** Definition of characters used for diagnoses, descriptions and morphometric part of study (characters marked with an asterisk were used in a multivariate ratio analysis (MRA) including a shape principle component analysis (shape PCA) and a PCA ratio spectrum).

Abbreviation	Character name	Character definition
bod.l	Body length	Sum of lengths of head, mesosoma and metasoma (Janšta et al. 2016)
*eye.l	Eye length	Length of eye, dorsal view (Graham 1969)
*eye.h	Eye height	Greatest length of eye height, lateral view (Baur 2015)
*hea.l	Head length	Length of head, dorsal view (Graham 1969)
*hea.b	Head breadth	Greatest breadth of head, dorsal view (Baur 2015)
*hea.h	Head height	Sum of heights of upper and lower face (for definition of upper and lower face see Supplementary table 1)
*msp.l	Malar space length	Distance between the point where malar sulcus enters mouth margin and malar sulcus enters lower edge of eye, lateral view (Graham 1969)
*of.o.b	Oral fossa breadth	Intermalar distance, ventral view (Graham 1969)
frv.b	Frontovertex breadth	Minimal distance between compound eyes at level of median (= anterior) ocellus (Janšta et al. 2016)
pol.l	POL	Shortest distance between posterior ocelli, dorsal view (Graham 1969)
ool.l	OOL	Shortest distance between posterior ocellus and eye margin, dorsal view (Graham 1969)
pod.d	POD	Posterior (=lateral) ocellus longest diameter, dorsal view
psp.h	Parascrobal protuberance height	Height of parascrobal protuberance, lateral view
scp.l	Scape length	Length of scape exclusive of radicle, outer aspect (Graham 1969)
scp.b	Scape breadth	Greatest breadth of scape, outer aspect (Baur 2015)
pdl.l	Pedicellus length	Length of pedicel, outer aspect (Baur 2015)
pdl.b	Pedicellus breadth	Greatest breadth of pedicel, outer aspect (Baur 2015)
*flg.l	Flagellum length	Sum of lengths of anellus, funicle and clava
fl1.l	Anellus length	Greatest length of anellus (= first flagellar segment)
fl1.b	Anellus breadth	Greatest breadth of anellus (= first flagellar segment)
fl2.l – fl8.l	First – seventh funicular segment length	Greatest length of first – seventh funicular segment (= second – eighth flagellar segment) (Baur 2015)
mss.l	Mesosoma length	Sum of length of pronotum, mesoscutum and propodeum (for definition of propodeum length see Supplementary table 1)
*pnt.l	Pronotum length	Length of pronotum, measured along median line, dorsal view
*pnt.b	Pronotum breadth	Greatest breadth of pronotum, dorsal view
*msc.l	Mesoscutum length	Length of mesoscutum along median line from posterior edge of pronotum to posterior edge of mesoscutum, dorsal view (Baur 2015)
msc.b	Mesoscutum breadth	Greatest breadth of mesoscutum just in front of level of tegula, dorsal view (Baur 2015)
*sct.l	Mesoscutellum length	Length of mesoscutellum (=scutellum) along median line from posterior edge of mesoscutum to posterior edge of mesoscutellum, dorsal view (Baur 2015)
*sct.b	Mesoscutellum breadth	Greatest breadth of mesoscutellum (=scutellum), dorsal view (Janšta et al. 2016)
fre.l	Frenal area length	Length of frenal area along median line from posterior edge of frenum to posterior edge of frenum, dorsal view
*fm3.b	Metafemur breadth	Greatest breadth of metafemur, outer aspect (Baur 2015)
*tb3.l	Metatibia length	Length of metatibia, measured along midline, outer aspect (Baur 2015)
ta3.l	Metatarsus length	Length of hind tarsus, including pretarsus (Baur 2015)
*fwi.l	Fore wing length	Greatest length of fore wing, measured from end of humeral plate to tip of wing (Baur 2015)
fwi.b	Fore wing breadth	Greatest breadth of fore wing, measured at about right angle to marginal and postmarginal veins (Baur 2015)
*cc1.l	Costal cell of fore wing length	Length of costal cell of fore wing, measured from end of humeral plate to the point at which the submarginal vein touches the leading edge of the wing (Janšta et al. 2016)
*mgv.l	Marginal vein length	Length of marginal vein, distance between the point at which the submarginal vein touches the leading edge of the wing and the point at which stigmal vein and postmarginal vein unite (Graham 1969)
stv.l	Stigmal vein length	Length of stigmal vein, distance between the point at which stigmal vein and postmarginal vein unite apically, and the distal end of the stigma (Graham 1969)

(Continued)

**Table 1.** (Continued).

Abbreviation	Character name	Character definition
mts.l	Metasoma length	Length of metasoma, measured from anterior margin of petiolus to the tip of the last gastral tergite, dorsal view (Janšta et al. 2016)
ovi.l	Ovipositor length	Length of ovipositor, measured as the part of the ovipositor sheaths that extend beyond the tip of the last gastral tergite (Janšta et al. 2016)

was reconstructed using the Maximum Likelihood method (ML) in RAXML 8.2.12 using GTRCAT approximation with 1000 bootstrap replicates (Stamatakis 2006) and conducted on the CIPRES Science Gateway (Miller et al. 2010). Bootstrap percentages (BP)  $\geq 70\%$  were considered as strong support. All COI sequences are deposited at NCBI under the accession numbers: MF956194, MF956202, MF956323, MF956381, MN822803 – MN822824.

### **Transcriptome sequencing**

Eight adult females (entire bodies) of morphospecies 1 collected in Australia (ATC, Canberra, National Botanical Garden, 35.279831°S 149.110501°E, 575 m a.s.l., 5. Feb. 2014, em. Feb.–Mar. 2014, ex *Archimantis* sp. ootheca, leg. P. Janšta) were ground and preserved in RNAlater (Qiagen, Hilden, Germany) and stored at +4°C or – 80°C until further processing.

Transcriptome sequencing, de novo assembly, and identification and removal of contaminating sequences were done as described in Peters et al. (2017).

Comparison of the COI sequence data included in the transcriptome sequences with those of the targeted sequencing of COI for the integrative taxonomy part (see below) allowed us to identify that the transcriptome sequence corresponds to *Lasallegrion koebelei* (see below for the taxonomic treatment of this species). The COI sequence extracted from the transcriptome will be deposited alongside the other COI sequences at NCBI (for details see above).

The assembly and raw data (reads) are available at NCBI via the Umbrella BioProject accession number NCBI: PRJNA183205 ('The 1KITE project: evolution of insects'). The accession number of the *L. koebelei* data is PRJNA299163.

### **Micro x-ray computed tomography**

We applied high resolution micro x-ray computed tomography ( $\mu$ CT). Two specimens selected for optimal morphological condition (morphospecies 1: lc\_157 for group A, lc\_49 for group B; for description of groups see below) were transferred to 100% ethanol and subsequently critical point dried using a Leica EM CPD300. As specimens needed to be mounted on specific sample holders, card mounted specimens or any materials of high density such as metal insect pins were ineligible. Instead, we glued the dried specimens beneath their posterior metasomal apex with a minute spot of shellac insect glue to fine, straight cactus needles. The needles were fixed with a hot glue gun to the specific sample holders of the  $\mu$ -CT. This setup resulted in an upright vertical position of the specimens that allowed a minimal distance to the radiation source, and thus higher magnifications (and a higher spatial resolution) during the scanning process. Shellac is soluble in ethanol, which allowed us, due to the careful

fixing with a minimal amount of glue to easily detach and card-mount the specimens after completion of the  $\mu$ CT scans.

All scans were performed with a Skyscan 1272 (Bruker Corporation, Billerica, USA) with the following basic settings (for a detailed list of settings see Supplementary file 1): 30 kV, 200  $\mu$ A, 1400 ms of exposure time, rotation steps of 0.25° over 360°, frame averaging: 5, random movement 10, spatial resolution: 1.300910  $\mu$ m.

Segmentation of the projections was performed with NRecon (Bruker Software Solutions). The resulting .tif files were imported into Amira 5.3 (ThermoFisher, Waltham, USA) where the needles and dirt were virtually removed from the data set using the segmentation and arithmetic functions. Subsequently, volume rendering was performed in VG Studiomax 3.2 (Volume Graphics, Heidelberg, Germany). Final images were adjusted, assembled and labelled in Adobe Photoshop CS6 and Illustrator CS6.

The  $\mu$ CT scans are available at morphobank (<https://morphobank.org>) under project number P3746.

## Results

### Molecular results

The DNA extraction failed for the only available fresh specimen (male) of morphospecies 2 (*Lasallegrion washingtoni*, hereinafter), but extraction, amplification and sequencing was successful for 22 samples of morphospecies 1 (*L. koebelei* and *L. virescens*, hereinafter).

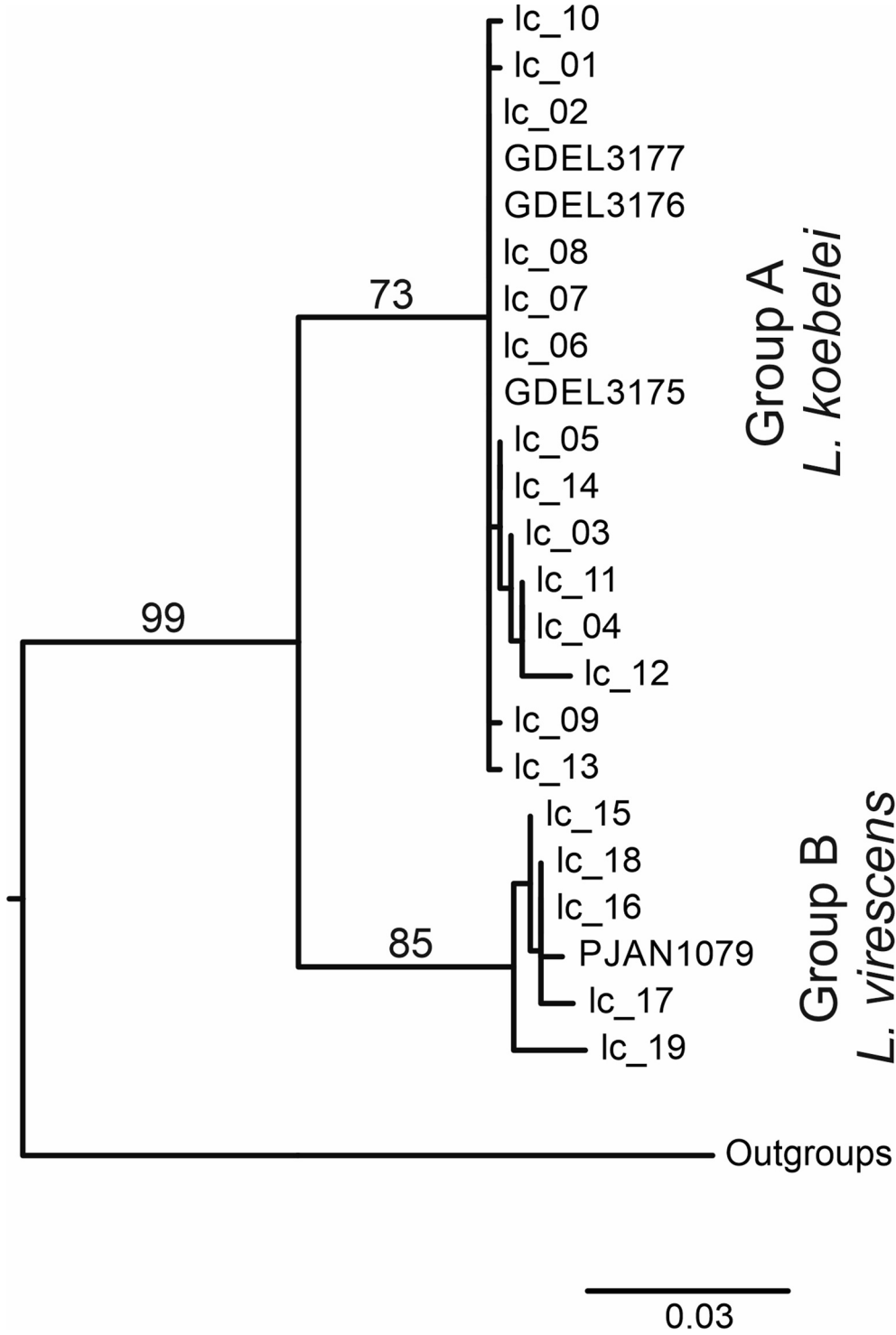
Based on the COI sequence analysis in the form of an alignment heatmap of genetic distances as percentage of positive base matches for each single alignment, the analysed specimens of morphospecies 1 form two groups (group A and group B) of relatively high genetic dissimilarity (Table 2). Group A comprises the specimens lc\_01–lc\_14 and GDEL3175–GDEL3177, group B specimens lc\_15–lc\_19 and PJAN1079. The genetic similarity within group A ranges between 98.74% and 100%, within group B between 98.26% and 100% and between group A and B between 94.08% and 94.83%. The results shown in the alignment heatmap are interpreted as interspecific differences with more than 5% dissimilarity between group A and B. Similar grouping is shown in the phylogenetic tree reconstructed using COI sequences (Figure 1).

The collection sites map (Figure 2) of all studied specimens shows some congruence between the molecular results and the origin of the specimens. All sequenced specimens within group A (lc\_01–lc\_14, GDEL 3175–3177) plus others morphologically assigned to group A were collected in coastal regions with a temperate to tropical climate. All sequenced specimens within group B (lc\_15–lc\_19 and PJ1079) plus most (all except four) of the specimens morphologically assigned to group B originate from an arid to hyper arid region in the north of Western Australia.

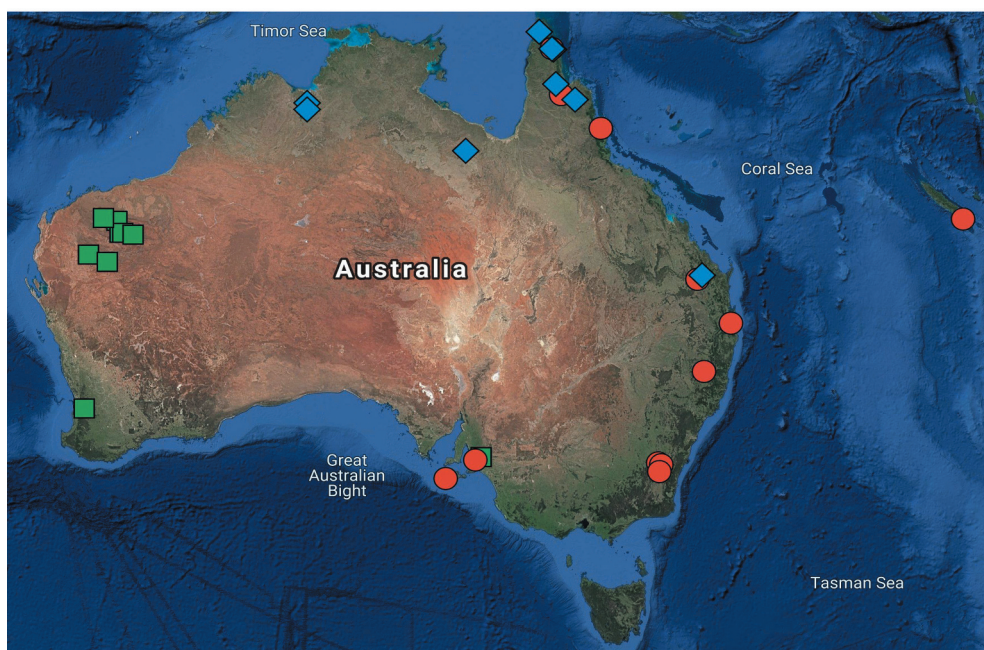
In summary, the molecular results suggest the existence of two species within morphospecies 1, with one mostly originating from Western Australia and the other from eastern parts of Australian regions. As an additional line of evidence, morphological and morphometric analyses are integrated for a final species delimitation (see below).

**Table 2.** Heatmap of COI sequences distances indicates (in %) the genetic similarity of positive base matches for each single alignment of *Lasallegrion koebelei* and *L. virescens* specimens. Interspecific similarity is dark-grey highlighted and intraspecific similarity is clear (for *L. koebelei*, group A) and light-grey highlighted (for *L. virescens*, group B).

	GDEL 3175	GDEL 3176	GDEL 3177	lc_12	lc_01	lc_02	lc_03	lc_04	lc_05	lc_06	lc_07	lc_08	lc_09	lc_10	lc_11	lc_13	lc_14	lc_15	lc_16	lc_17	lc_18	lc_19	PJT 079	
<b>GDEL</b>	100.00	100.00	100.00	98.99	99.76	100.00	99.68	99.45	99.84	100.00	100.00	100.00	99.76	99.75	99.75	99.45	99.84	99.84	94.78	94.83	94.70	94.78	94.30	94.78
<b>3175</b>																								
<b>GDEL</b>	100.00			98.99	99.76	100.00	99.68	99.45	99.84	100.00	100.00	100.00	99.76	99.75	99.75	99.45	99.84	99.84	94.78	94.83	94.70	94.78	94.30	94.78
<b>3176</b>																								
<b>GDEL</b>	100.00	100.00		98.99	99.76	100.00	99.68	99.45	99.84	100.00	100.00	100.00	99.76	99.75	99.75	99.45	99.84	99.84	94.78	94.83	94.70	94.78	94.30	94.78
<b>3177</b>																								
<b>lc_12</b>	98.99	98.99	98.99		99.08	98.99	99.16	99.33	98.99	98.99	98.99	98.99	98.74	98.91	99.33	98.83	98.99	94.46	94.46	94.38	94.46	94.13	94.30	
<b>lc_01</b>	99.76	99.76	99.76	99.08		99.76	99.45	99.37	99.61	99.76	99.76	99.76	99.53	99.75	99.37	99.61	99.61	94.71	94.74	94.63	94.71	94.23	94.55	
<b>lc_02</b>	100.00	100.00	100.00	98.99	99.76		99.68	99.45	99.84	100.00	100.00	100.00	99.76	99.75	99.45	99.84	99.84	94.79	94.83	94.71	94.79	94.31	94.79	
<b>lc_03</b>	99.68	99.68	99.68	99.16	99.45	99.68		99.76	99.84	99.68	99.68	99.68	99.68	99.45	99.43	99.76	99.53	99.84	94.79	94.83	94.71	94.79	94.31	
<b>lc_04</b>	99.45	99.45	99.45	99.33	99.37	99.45	99.76		99.61	99.45	99.45	99.45	99.21	99.34	99.92	99.29	99.61	94.63	94.65	94.55	94.63	94.15	94.63	
<b>lc_05</b>	99.84	99.84	99.84	98.99	99.61	99.84	99.84	99.61		99.84	99.84	99.84	99.61	99.59	99.61	99.68	100.00	94.63	94.65	94.55	94.63	94.15	94.63	
<b>lc_06</b>	100.00	100.00	100.00	98.99	99.76	100.00	99.68	99.45	99.84		100.00	100.00	99.76	99.75	99.45	99.84	99.84	94.79	94.83	94.71	94.79	94.31	94.79	
<b>lc_07</b>	100.00	100.00	100.00	98.99	99.76	100.00	99.68	99.45	99.84	100.00		100.00	99.76	99.75	99.45	99.84	99.84	94.79	94.83	94.71	94.79	94.31	94.79	
<b>lc_08</b>	100.00	100.00	100.00	98.99	99.76	100.00	99.68	99.45	99.84	100.00	100.00		99.76	99.75	99.45	99.84	99.84	94.79	94.83	94.71	94.79	94.31	94.79	
<b>lc_09</b>	99.76	99.76	99.76	98.74	99.53	99.76	99.45	99.21	99.61	99.76	99.76	99.76		99.51	99.21	99.61	99.61	94.55	94.56	94.47	94.55	94.08	94.55	
<b>lc_10</b>	99.75	99.75	99.75	98.91	99.75	99.75	99.43	99.34	99.59	99.75	99.75	99.75	99.51		99.34	99.59	99.59	94.66	94.56	94.58	94.66	94.33	94.50	
<b>lc_11</b>	99.45	99.45	99.45	99.33	99.37	99.45	99.76	99.92	99.61	99.45	99.45	99.45	99.21	99.34		99.29	99.61	94.63	94.65	94.55	94.63	94.15	94.63	
<b>lc_13</b>	99.84	99.84	99.84	98.83	99.61	99.84	99.53	99.29	99.68	99.84	99.84	99.84	99.61	99.59	99.29		99.68	94.63	94.83	94.55	94.63	94.15	94.63	
<b>lc_14</b>	99.84	99.84	99.84	98.99	99.61	99.84	99.84	99.61	100.00	99.84	99.84	99.84	99.61	99.59	99.61	99.68		94.63	94.65	94.55	94.63	94.15	94.63	
<b>lc_15</b>	94.78	94.78	94.78	94.46	94.71	94.79	94.79	94.63	94.63	94.79	94.79	94.79	94.55	94.66	94.63	94.63	94.63		99.82	99.29	99.84	98.74	99.53	
<b>lc_16</b>	94.83	94.83	94.83	94.46	94.74	94.83	94.83	94.65	94.65	94.83	94.83	94.83	94.56	94.56	94.65	94.83	94.65	99.82		99.35	100.00	98.52	99.82	
<b>lc_17</b>	94.70	94.70	94.70	94.38	94.63	94.71	94.71	94.55	94.55	94.71	94.71	94.71	94.47	94.58	94.55	94.55	94.55	99.29	99.35		99.45	98.34	99.13	
<b>lc_18</b>	94.78	94.78	94.78	94.46	94.71	94.79	94.79	94.63	94.63	94.79	94.79	94.79	94.55	94.66	94.63	94.63	94.63	99.84	100.00	99.45		98.58	99.68	
<b>lc_19</b>	94.30	94.30	94.30	94.13	94.23	94.31	94.31	94.15	94.15	94.31	94.31	94.31	94.08	94.33	94.15	94.15	94.15	98.74	98.52	98.34	98.58		98.26	
<b>PJ1079</b>	94.78	94.78	94.78	94.30	94.55	94.79	94.79	94.63	94.63	94.79	94.79	94.79	94.55	94.50	94.63	94.63	94.63	99.53	99.82	99.13	99.68	99.68		



**Figure 1. Maximum likelihood tree.** The tree was reconstructed based on COI of *Lasallegrion koebelei* and *L. virescens* using RaxML with 1000 bootstrap replications. Only support values  $\geq 50$  are shown.



**Figure 2. Map of collection sites.** Red – *Lasallegrion koebelei*; green – *L. virescens*; blue – *L. washingtoni* (MyMaps by google).

### Morphometric results

For the multivariate ratio analysis (MRA) of morphospecies 1, specimens were labelled according to the molecular analysis as either *L. koebelei* or *L. virescens*. The shape PCA revealed two clusters. A scatterplot of isosize versus shape PC1 (the second and all further shape PCs were not significant) showed that the clusters were almost distinct in shape but strongly overlapping in size (Figure 3). Hence, allometric scaling as cause for the separation can be ruled out.

For finding out what are the best separating ratios of the two groups we applied the LDA ratio extractor. It was evident (from Figure 4) that the ratio head height to marginal vein length ( $hea.h/mgv.l$ ; standard distance = 5.042, delta = 0.037) gave an almost complete separation. Therefore, we used this ratio in the identification key.

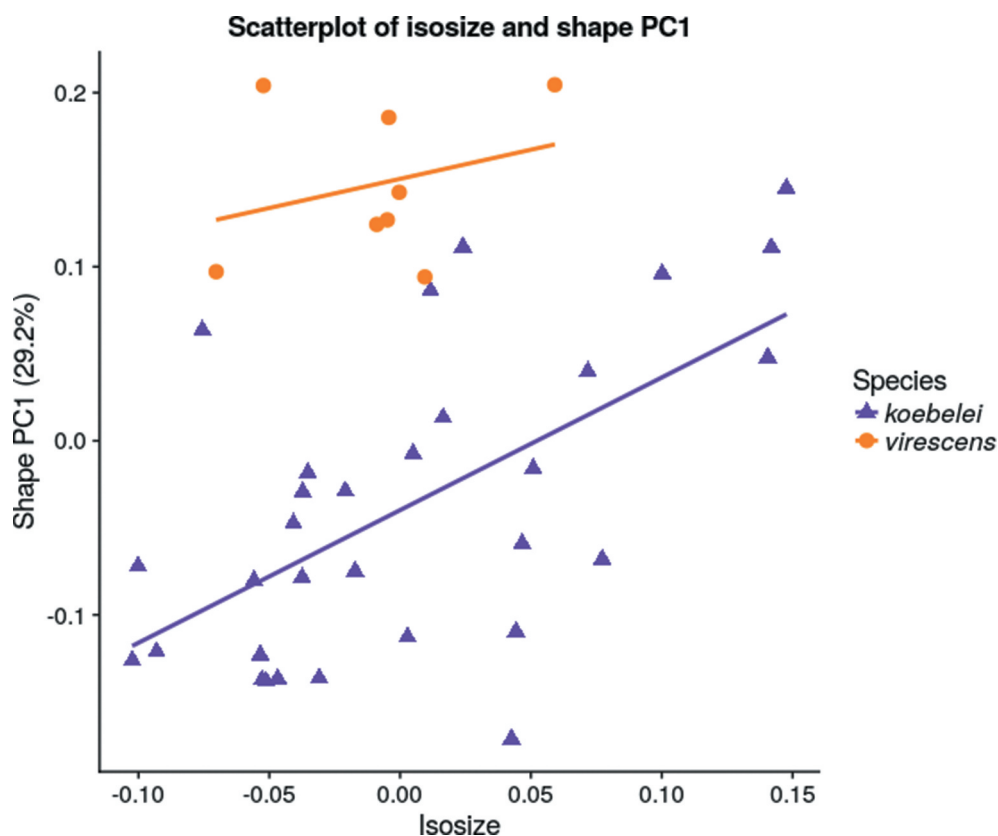
### Generic description

***Lasallegrion* Janšta, Delvare, Peters, gen. n.** (Figs 5–6, 7a–c, 8–13)

#### Type species

*Podagrion koebelei* Crawford, 1912: 4–5, Figure 2; Bouček (1988): 141, Fig. 201

**Etymology.** The genus is named in honour of our late colleague John La Salle. The first part of the generic name refers to his family name, the latter ('grion') is the Latin word for

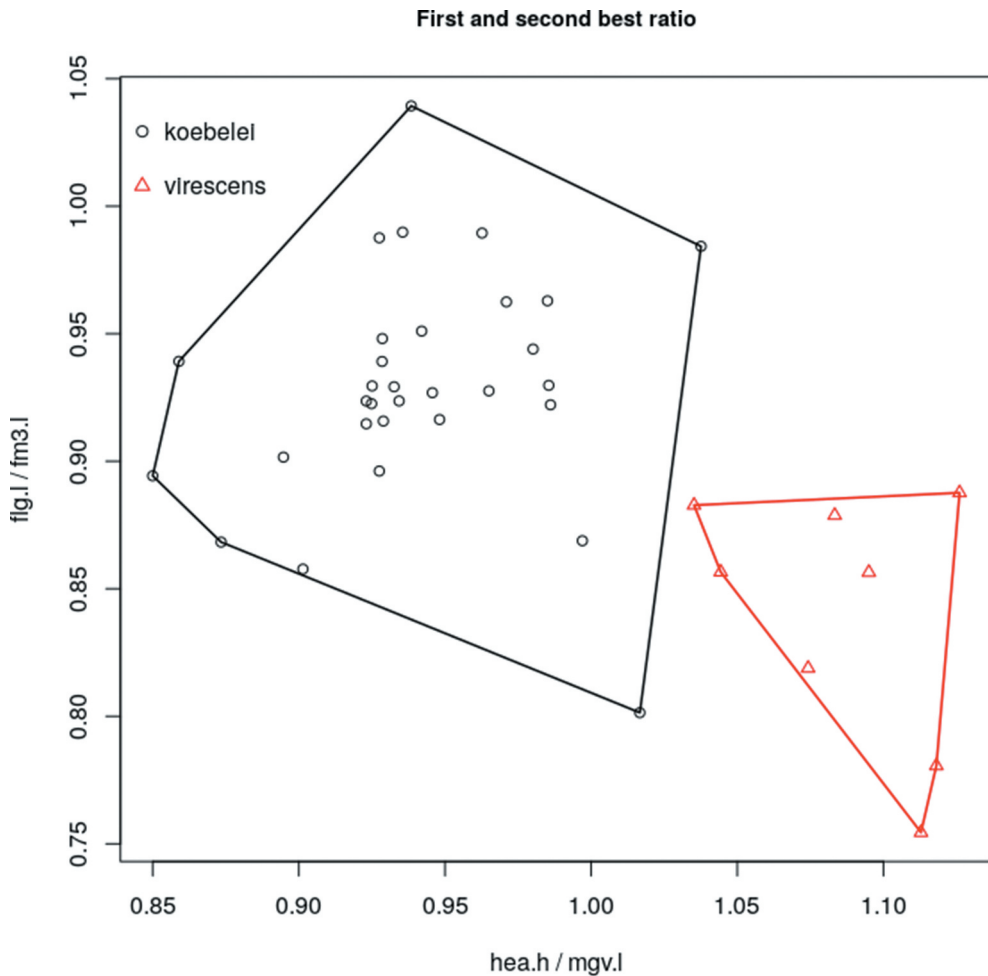


**Figure 3.** Shape PCA of *L. koebelei* and *L. virescens*. The scatterplot shows isosize versus shape PC1.

crest (of teeth on the hind femora) and refers to the genus *Podagrion* Spinola, 1811 that most closely resembles the new genus.

**Diagnosis (females and homeomorph males only).** *Lasallegrion* (Figure 6a) is readily distinguished from the other *Podagrionini* genera based on the following characters: Antenna filiform with antennal formula 11173; single anellus transverse; clava not enlarged and distinctly 3-segmented, with segments completely encircled by fine sutures, clava of female with only narrow strip of micropilosity on 2<sup>nd</sup> and 3<sup>rd</sup> segment ventrally (Figure 6b); pronotum with a sharp carina delimiting collar anteriorly; neck short, with posterior part forming almost a right angle (Figure 6c); propodeum with a median carina originating anteriorly, and dividing into two transverse branches at an obtuse inner angle approximately in the middle of propodeum, two lateral carinae originating from spiracular sulci and joining transverse branches posteriorly at about 2/3 of the propodeum length, the area bordered by transverse branches and by posterior 1/3 of lateral carinae originating from propodeal spiracle (adpetiolar area) with irregular rugulose carinae, the rest of propodeum dorsum reticulate to rugulose reticulate (Figure 6d); metepimeron slender, anteriorly pointed, entirely reticulate and setose, without a polished median area, ventral margin carinate (Figure 6c); metacoxal foramen largely surrounded by translucent integument anteriorly and medially; metadiscimen as median stripe narrowing





**Figure 4.** The scatterplot of best ratios for separating *L. koebelei* and *L. virescens* based on the LDA ratio extractor.

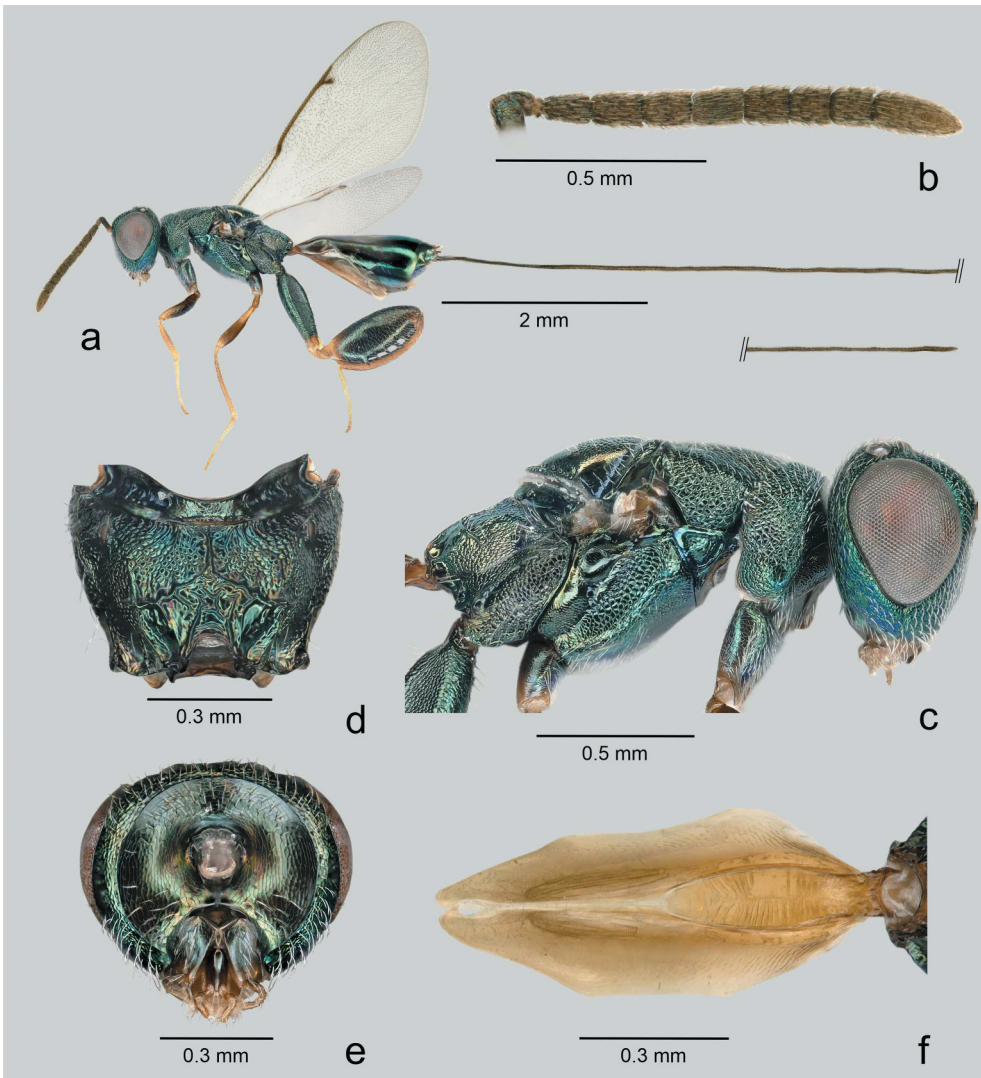
posteriorly, with transverse crests and delimited by irregular, sometimes broken, submedian ridges (Figure 7a–c). Petiolar foramen of propodeum large in connection with the large and upturned condyle of the petiolus. Body of petiolus with a fine medioventral carina (Figure 6f).

**Description.** Head. Head broader than high. Face, vertex, and temples shallowly reticulate with fine, short, and pale setae, about as long as 3–4 meshes of the reticulation, setation denser and longer on lower face than rest of head. Antennal scrobes without setae, more shallowly and more finely reticulate than rest of face, interantennal projection greatly protruding. Anterior margin of clypeus slightly convex to broadly toothed, slightly recessed relative to corners of oral fossa. Malar sulcus weakly present. Occipital carina completely encircling the back of the head, joining the hypostomal carina above the base of mandible (Figure 6e). Toruli inserted high on head, their lower margins above median level of eye. Scape short and thick,



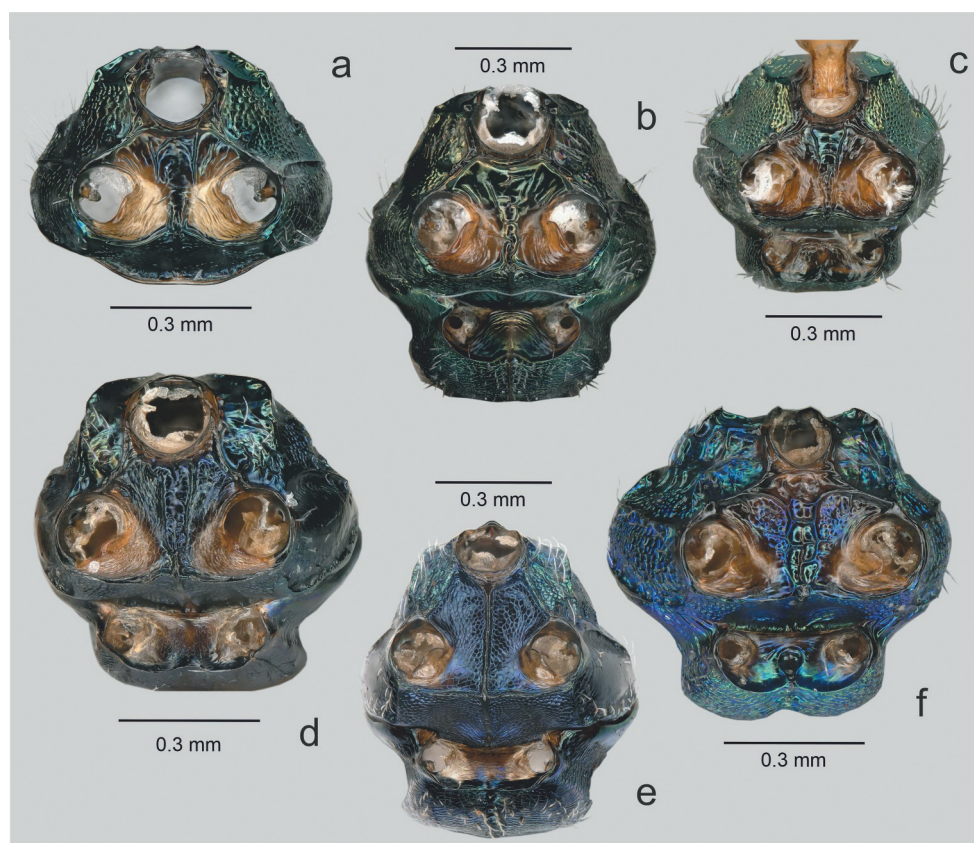
**Figure 5.** Volume renders of the  $\mu$ -CT scans of *Lasallegriion* gen. n.; (a), *L. virescens*, lateral; (b), *L. koebelei*, lateral. Midsagittal sections showing the inner anatomy. Scale bars: 0.5 mm.

reaching anterior margin of median ocellus. Flagellum with a single strongly transverse anellus, seven funicular segments and distinctly three-segmented clava with only narrow strip of micropilosity on 2nd and 3rd segment ventrally (micropilosity only present in females).



**Figure 6. Diagnostic characters of *Lasallegrion* gen. n.;** *L. koebelei* (a – e), *L. washingtoni* (f). (a), habitus, lateral; (b), antenna, lateral; (c), head and mesosoma, lateral (arrows indicate pronotal collar carina and metapleuron); (d), propodeum, dorsal; (e), head, posterior; (f), petiolus and first sternite, ventral.

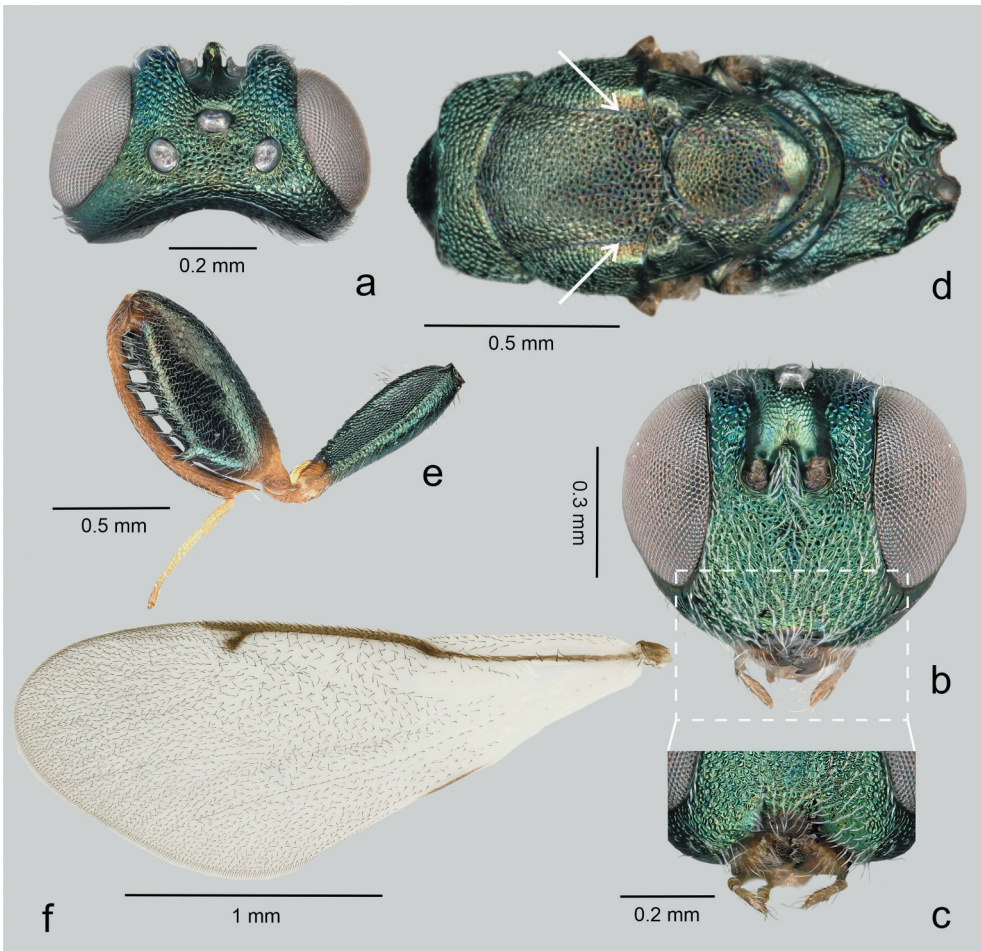
Mesosoma. Pronotum and mesoscutal midlobe slightly flattened dorsally (Figure 6c), and alveolate to areolate, lateral lobes of pronotum scabriculous to areolate. Pronotum and mesoscutum covered with fine, pale setae. Pronotal collar carinately delimited anteriorly on most of its width. Notauli complete, moderately converging, widely separated at transscutal line, shallowly impressed, and of contrasting colour, weakly obliterated by sculpture. Mesoscutellum with frenal line absent, frenal area well indicated by smoothly alutaceous sculpture without setae (Figures 8d, 11e, 12e). Axilla less reticulate than rest of mesoscutum, especially lateral parts rather smooth with imbricate sculpture, sparsely covered with setae. Propodeum alveolate to areolate and without



**Figure 7. Metepisternum, posteroventral, females.** (a), *Lasallegrion koebelej*; (b), *L. virescens*; (c), *L. washingtoni*; (d), *Podagrion idomene* sp. gr.; (e), *P. pachymerum*; (f), *Mantiphaga gongylusae* Risbec.

setae, sides of propodeum laterally to lateral carina steep and with no spiracular sulcus (Figures 6d, 8d, 11d–e, 12d–e). Posterior ventral margin of the mesepimeron not reaching the metapleural venter. Metepisternum (Figure 7a–e) with propodeal foramen placed posteriorly, not touching imaginary line drawn across the posterior margin of metacoxal foramina, distance between anterior margin of propodeal foramen and imaginary line between posterior margin of metacoxal foramina slightly less than diameter of propodeal foramen; outer ventral edge of propodeal foramen connected with outer posterior edge of metacoxal foramen by a distinct single carina; metacoxal foramen largely surrounded by translucent integument anteriorly and medially. Metacoxa long, almost as long as metafemur, areolate to punctate laterally, without setae, dorsally and ventrally setose with imbricate sculpture. Metafemur (Figures 8e, 9e, 11c, 12f) enlarged, bearing strong teeth, imbricate and covered with pale setae. Metatibia greatly curved with a carinate crest ventrally, metatibial apex diagonally truncated and ventrally slightly produced, truncation length subequal to the width of tibia, with a single setose metatibial spur at apex of truncation. Fore wing with basal cell and speculum bare, basal vein and cubital vein indicated by a row of dense brown setae (Figures 8f, 11f).

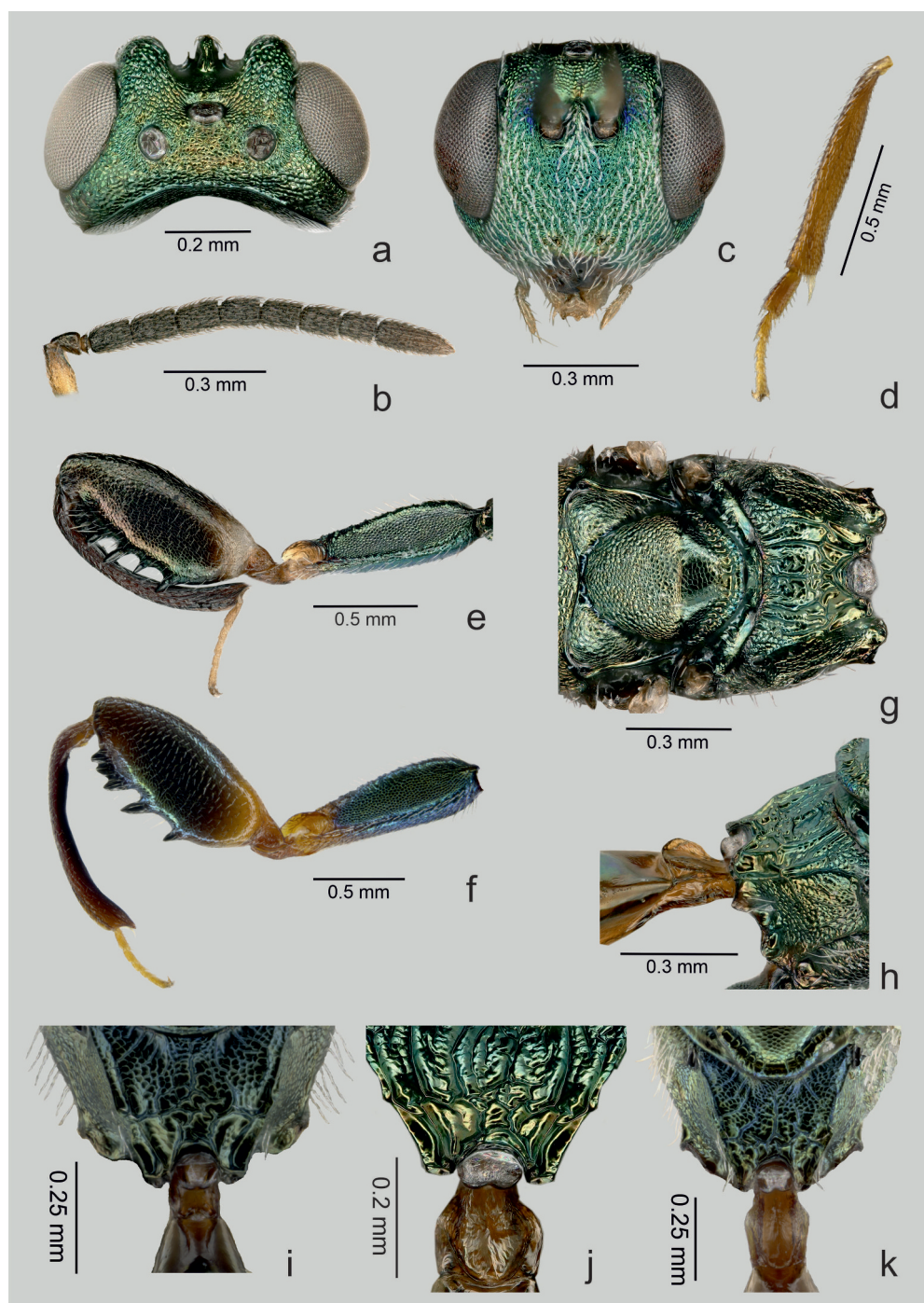




**Figure 8.** *Lasallegrion koebele*, female. (a), head, dorsal; (b), head, frontal; (c), lower face, detail; (d), mesosoma, dorsal (arrows indicate notauli in their posterior part); (e), right hind leg, outer aspect; (f), left fore wing, ventral.

Metasoma. petiolus quadrate to subquadrate with fine transverse medioventral carina (Figure 9i). Metasomal tergites dorsally and laterally with faint imbricate sculpture, and sparsely and unevenly covered with only few long setae. Gt<sub>1-4</sub> laterally and dorsomedially emarginate.

**Recognition.** In the key of Grissell (1995) *Lasallegrion* would key out as *Podagrion* Spinola (in couplet 14) but *Lasallegrion* differs from *Podagrion* as well as from the other Podagrionini genera by the anteriorly sharply carinate pronotal collar, which is not carinate in all other genera. *Lasallegrion* also differs from other Podagrionini by a characteristic propodeal surface sculpture (Figures 6d, 8d, 11e, 12e). In all other Podagrionini, three basic propodeal states can be found that are all very different from the structure seen in *Lasallegrion*. *Palmon* has no carination on propodeum, *Iridophagoides* is characterised by having almost no carination on the disc of propodeum except posterior lateral



**Figure 9.** *Lasallegrion koebelej*, intermediate (a – c, e, g, h, j), heteromorph (d, f, k) and homeomorph (i) male. (a), head, dorsal; (b), antenna, lateral; (c), head, frontal; (d), left midtibia and midtarsus, outer aspect; (e), right hind leg, outer aspect, intermediate male; (f), right hind leg, outer aspect, heteromorph male; (g), mesoscutellum and propodeum, dorsal; (h), part of propodeum and petiolus, dorsolateral; (i), propodeum and petiolus, dorsal; (j), propodeum and petiolus, dorsal; (k), propodeum and petiolus, dorsal.

vestigial carinae, and *Mantiphaga*, *Podagrion*, *Micropodagrion*, *Podagriomicron* and *Podagrionella* have reversed V or U-shaped carina. Further *Propachytomoides* have no carination but exhibits a flattened median plate and *Iridophaga* has strongly curved, lyriform carinae delimiting a subelliptic median area. *Lasallegrion* can be further distinguished from *Palmon*, *Podagrion*, *Micropodagrion* and *Mantiphaga* by the condition of the metadiscimen of the metepisternum. *Lasallegrion* has a median strip delimited by irregular submedian ridge (metadiscimen is broader, with one median or two submedian carinae in *Palmon*, *Podagrion* and *Micropodagrion* and broader and more sclerotised in *Mantiphaga*, Figure 7a–e). Almost all genera of Podagrionini, excluding *Lasallegrion* and *Mantiphaga*, share a metepimeron with a polished median area without setation. The metepimeron in *Mantiphaga* is less elongate than in *Lasallegrion* and anteriorly bent. In *Micropodagrion* and *Palmon* the metepimeron is very broad, in *Palmon* it is almost as broad as long. In *Propachytomoides* the mesepimeron is bulged outwardly and raised as a flange above the surface of the metapleuron.

Furthermore, *Podagrionella*, *Iridophaga* and *Iridophagoides* have the apex of the metatibia expanded in a curved long spine, much longer than that of *Lasallegrion*, and *Palmon* is characterised by the complete setation of the fore wing, an autapomorphy of the genus.

Females of *Podagrion* usually do not have the antennal clava distinctly 3-segmented in combination with a narrow line of micropilosity on apical claval segments two and three.

Grissell (1995) already stated that *P. koebelei* (now transferred to *Lasallegrion*) might need to be transferred from *Podagrion* into a new genus. He already noticed the sharply margined pronotal collar, the 3 segmented filiform clava and the narrow strip of micropilosity on apical claval segment 2 and 3 and noted that these characters are different from both *Podagrion* and *Palmon*. However, because he apparently knew that some of those characters (segmentation of clava and condition of micropilosity on apical claval segment) are rather homoplastic within Podagrionini, he did not follow up on this, and the presumed new genus has not been described to date. Further, Janšta et al. (2018) mentioned 'PJAN1079 Podagrionini n. gen. sp. Australia' as an undescribed genus from Australia. In their phylogenetic analysis, it was inferred as sister group (but with almost no support) of two *Mantiphaga* species. Sequence of COI (MF956323) of this specimen is highly similar to the COI sequences of specimens of morphospecies 1 group B. The present study confirms the findings of Grissell (1995) and Janšta et al. (2018) and adds several generic diagnostic characters, which corroborate the present designation of *Lasallegrion*.

## Key to Australasian genera of Podagrionini and species of *Lasallegrion*

- 1 Hind tibia with apex elongately produced, the truncation at least 2x width of tibia and with spur at base of truncation near basitarsus ***Podagrionella*** Girault
- Hind tibia with apex diagonally truncated and ventrally not or only slightly produced; the truncation subequal in length to width of tibia and with spur at apex of truncation ..... 2
- 2 (1) Mesepimeron bulged outwardly and raised into lamelliform plate above surface of metapleuron and overhanging (partially obscuring) ventral shelf of metepisternum; fore wing with well delimited spot..... ***Propachytomoides*** Girault



- Mesepimeron not bulged, abutting metepimeron and not overhanging ventral shelf of metepisternum; fore wing without delimited spot, rarely with diffuse stain..... 3
- 3 (2) Anellus elongate, as long as broad, fore wing entirely covered with setae, without distinct vein tracts, cells or speculum..... **Palmon** Dalman
  - Anellus transverse, fore wing with distinct vein tracts, cells and speculum..... 4
- 4 (3) Pronotum with a sharp and carinate pronotal collar; antennal clava distinctly 3-segmented, females with a narrow line of micropilosity on apical claval segment 2 and 3; metadiscimen as median strip delimited by irregular submedian ridges..... **Lasallegrion** gen n., 5
  - Pronotum round and without a carinate collar; antennal clava not distinctly 3-segmented, females with a large micropilosity area covering the ventral side of the clava; metadiscimen broader, with one median or two submedian carinae..... **Podagrion** Spinola
- 5 (4) Ventral margin of clypeus with small median tooth; metafemur with 6–8, moderately short, teeth plus one composite tooth distally (Figure 12f); ovipositor sheaths short, 0.9–1.5× as long as body; OI = 3.3–5.0; relatively smaller species (2.9–3.7 mm without ovipositor)..... **L. washingtoni** (Girault, 1915), **comb. n.**
  - Ventral margin of clypeus hardly convex; metafemur with 5 or 6 stout teeth ventrally plus one composite tooth distally (Figures 8e, 11c); ovipositor sheaths 1.6–2.5× as long as body; OI = 5.2–7.6; relatively bigger species (3.5–4.4 mm without ovipositor)..... 6
- 6 (5) Combined length of pedicel and flagellum 1.45–1.65× breadth of head; head height 0.85–1.02× (in one marginal case up to 1.04) as long as marginal vein; antennae inserted high on the head, distance from lower edge of toruli to ventral margin of clypeus 1.1–1.6× as long as distance from lower edge of toruli to anterior ocellus; parascrobal area remarkably raised above the outline of head anteriorly (best seen from dorsal view, Figure 8a); setae on lower face not so dense, long and wide than in alternate (Figure 8b–c); propodeum with adpetiolar area (behind posterior branches of carinae) coarsely rugose (Figure 6d), metafemur with 5 teeth preceding the composite terminal one, at least length of 3<sup>rd</sup> and 4<sup>th</sup> tooth same as or longer than breadth of tibia opposite to tooth (Figure 8e); costal cell of fore wing with 2 complete rows of setae on the underside (Figure 8f);..... **L. koebelei** (Crawford, 1912), **comb. n.**
  - Combined length of pedicel and flagellum 1.1–1.4× breadth of head; head height 1.04–1.13× as long as marginal vein; antennae inserted less high on the head, distance from lower edge of toruli to ventral margin of clypeus 1.0–1.2× as long as distance from lower edge of toruli to anterior ocellus; parascrobal area not so remarkably raised above the outline of head anteriorly (Figure 11a); setae on lower face very dense, long and lanceolate (Figure 11b); propodeum with adpetiolar area rugulose reticulate (Figure 11e); metafemur with 4 stout teeth preceding the composite terminal one; length of 2<sup>nd</sup> – 4<sup>th</sup> tooth longer than breadth of tibia opposite to tooth (Figure 11c); costal cell of fore wing at most with one incomplete row of setae on the underside (Figure 11f)..... **L. virescens** (Strand, 1911), **comb. n.**

## Species redescriptions

### *Lasallegrion koebelei* Crawford, 1912, comb. n.

(Figures 5b, 6a–e, 7a, 8, 9, 10a–c, 13a–b)

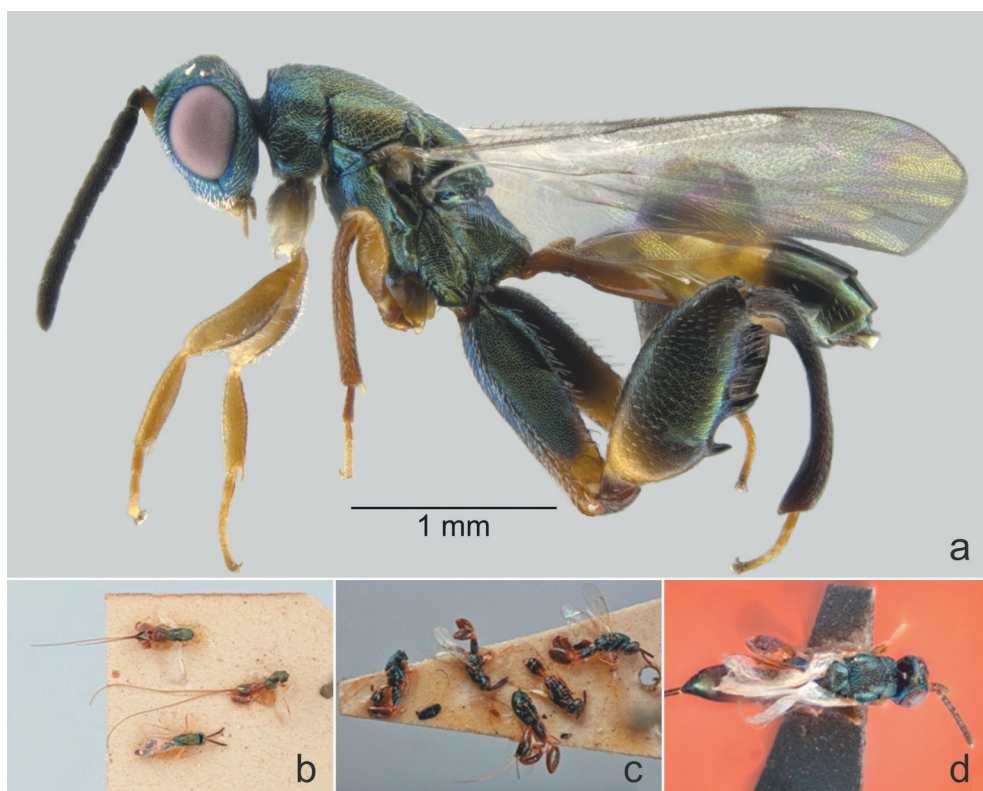
*Podagrion koebelei* Crawford, 1912: 4–5, [Figure 2](#); ♀ holotype (examined), Australia–South Australia (USNM). Label: 606, Australia Koebele, Type No. 14342 U.S.N.M., *Podagrion koebelei* ♀ Type, Cwfd. Bouček (1988): 141.

*Podagrion grotii* Girault, 1915: 291–292. ♀ holotype (examined), Australia–Queensland (QMB); Label: HOLOTYPE Hy. 3319, E.C.D. 1983, Photographed Specimen, *Podagrion grotii* Girault ♀ Type, ENTI 6.12. Bouček (1988): 141 (synonymy under *P. koebelei*).

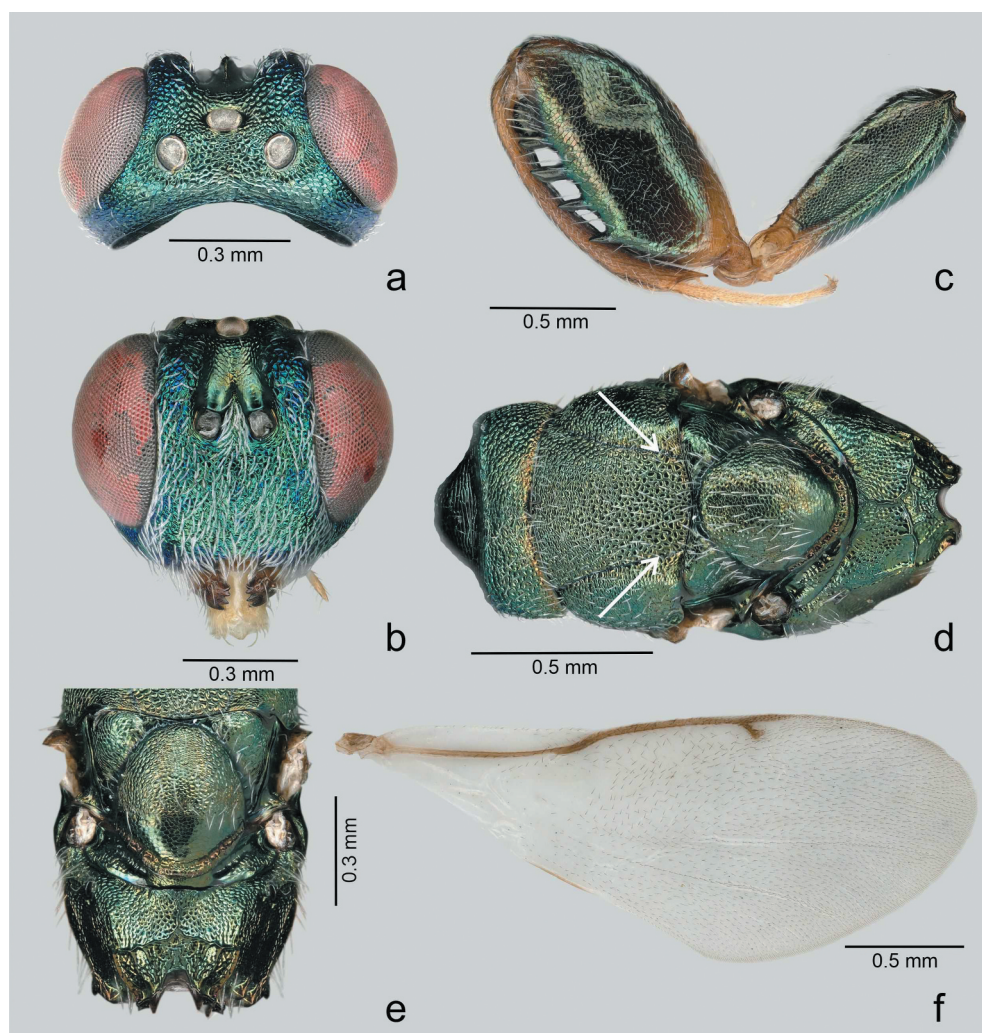
*Podagrion dolichurum* Cockerell, 1930: 2–3, [Figures 1–5](#). ♀ holotype (examined), New Caledonia (AMNH); Label: *Podagrion dolichurum*, Ckll. TYPE, Noumea, New Caledonia. Bouček (1988): 141 (synonymy under *P. koebelei*).

*Podagrion holbeini* Girault, 1923: 8; syntypes (examined), Australia–Victoria (QMB); Label: SYNTYPES T. 5090 E.C.D. 1983, *Podagrion holbeini* Gi. ♀ ♂ Types, Brighth Bred from egg capsule of large mantis, Photographed specimen. Bouček (1988): 141. **Syn. n.**

*Podagrion metatarsum* Girault, 1929: 341–342; syntypes (examined), Australia–Victoria (QMB); Label (QMB): SYNTYPES T. 5097 E.C.D. 1984, Photographed specimen, *Podagrion metatarsum* ♀ ♂ Gi. Type. Bouček (1988): 141. **Syn. n.**



**Figure 10.** (a), *Lasallegrion koebelei*, heteromorph male habitus, lateral; (b), syntype of *P. holbeini*, syn. n.; (c), syntype of *P. metatarsum*, syn. n.; (d), holotype of *L. virescens*.

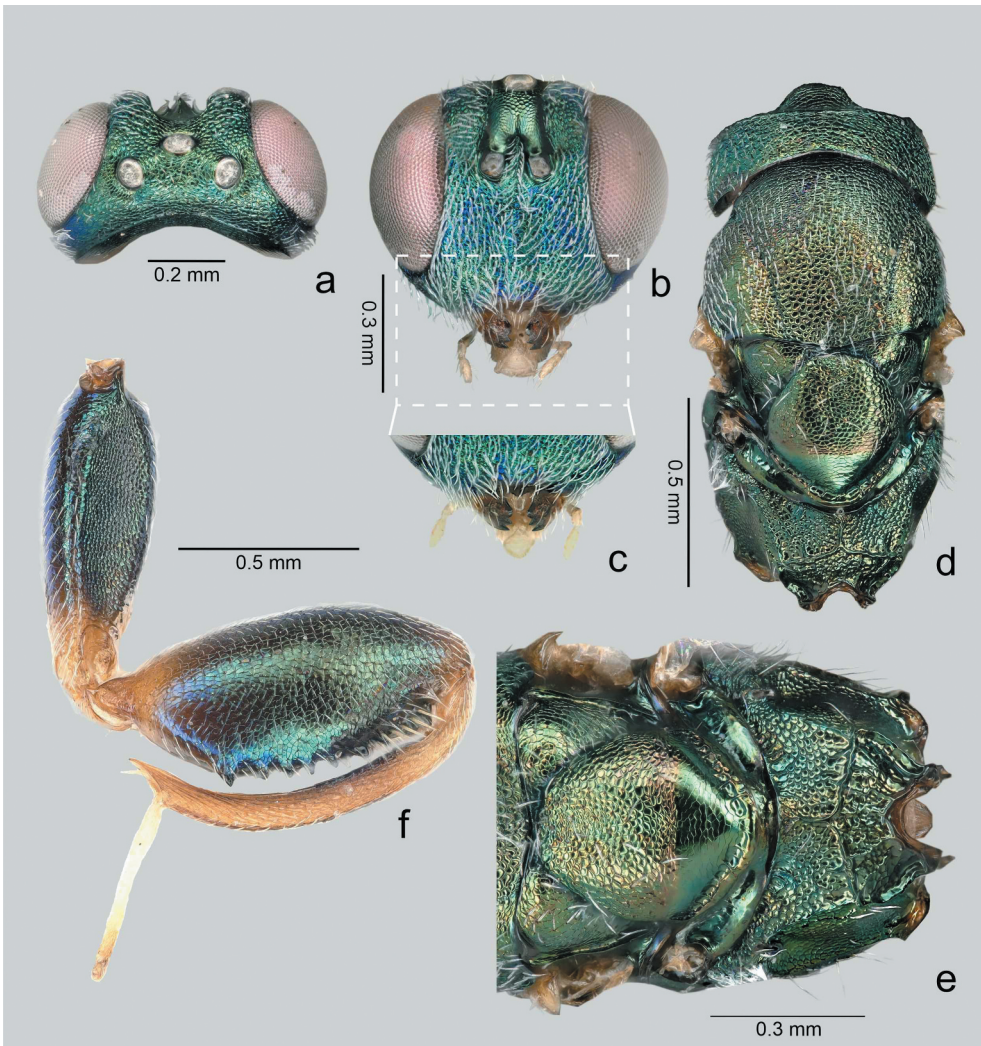


**Figure 11.** *Lasallegrion virescens*, female. (a), head, dorsal; (b), head, frontal; (c), right hind leg, outer aspect; (d), mesosoma, dorsal (arrows indicate notauli in their posterior part); (e), mesoscutellum and propodeum, dorsal; (f), left fore wing, ventral.

### *Non-type material examined*

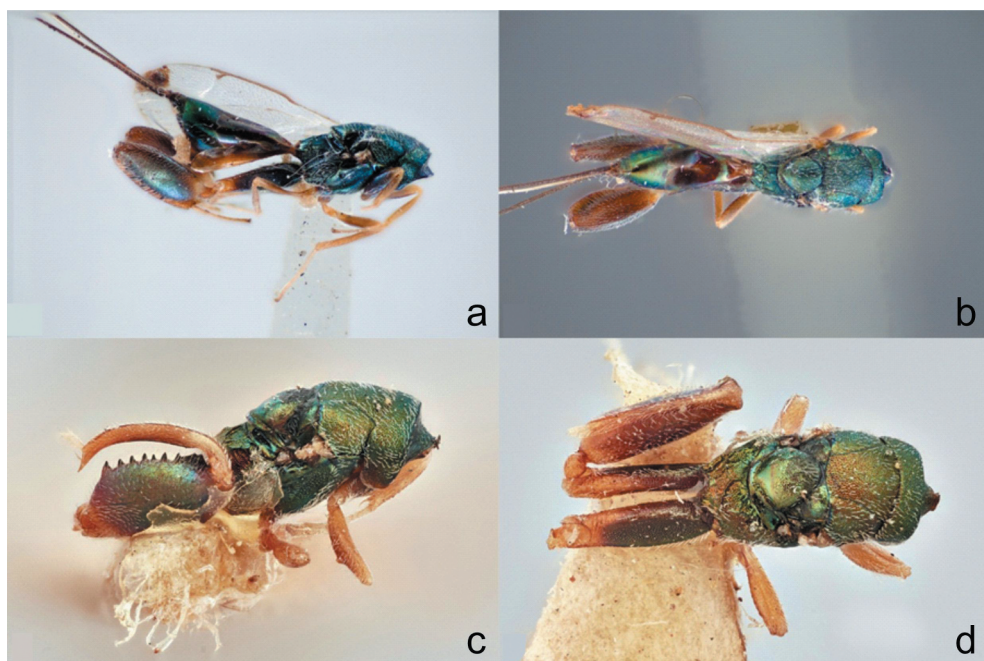
Australia, ATC, Canberra, National Botanical Garden, 35.279831°S 149.110501°E, 575 m a.s.l., 5. Feb. 2014, em. Feb.–Mar. 2014, ex *Archimantis* sp. ootheca, leg. P. Janšta (7 ♀♀, **lc\_01–03**, **lc\_05–08**, ZFMK; 6 ♀♀, **lc\_33–34**, **lc\_43–44**, **lc\_46**, **lc\_55**, CUPC; 4 ♀♀, **GDEL3175–GDEL3177**, **lc\_04**, CBGP); Australia, ATC, Canberra, Black Mtn., 1.–14. Dec. 2001, leg. NA (1 ♀, **lc\_09**, ANIC); Australia, ATC, Canberra, Black Mtn., 35.16°S, 149.06°E, 1.–14. Feb. 1999, Malaise trap, leg. G. Gibson (1 ♀, **lc\_10**, ANIC); Australia, ATC, Canberra, Black Mtn., 35.16°S, 149.06°E, 15.–28. Feb. 1999, Malaise trap, leg. G. Gibson (1 ♀ **lc\_45**, ANIC); Australia, ATC, Canberra, Black Mtn., Dec. 1982, Malaise trap, leg. I.D. Naumann & J.C. Cardale (1 ♀, **lc\_36**, ANIC); Australia, ATC, Canberra, Apr. 1948, ex mantid ootheca, ex ethanol, leg. NA, (1 ♀, **lc\_37**, ANIC); Australia, ATC, Tharwa, coll. 28. Feb. 1988 emg. 1. Mar. 1988, ex ootheca





**Figure 12.** *Lasallegrion washingtoni*, female. (a), head, dorsal; (b), head, frontal; (c), lower face, detail; (d), mesosoma, dorsal; (e), mesoscutellum and propodeum, dorsal; (f), left hind leg, outer aspect.

*Archimantis* sp., leg. J. Balderson, (1 ♀♀, **lc\_40**, ANIC); Australia, QLD, Hann River, 15.11°S 143.52°E, 18. Dec. 1993–14. Jan. 1994, Malaise trap, leg. P. Zborowski & Edwards, (1 ♀, **lc\_29**, ANIC); Australia, QLD, Hann River, 15.11°S 143.52°E, 20. Mar.–24. Apr. 1994, Malaise trap, leg. P. Zborowski & G. Turner, (1 ♀, **lc\_31**, ANIC); Australia, QLD, 13 km E. by S. of Weipa, 12.40 S, 143.00E, 16. Jan.–16. Feb. 1994, Malaise trap, leg. P. Zborowski & D. Khalu, (1 ♀, **lc\_30**, ANIC); Australia, QLD, 13 km E. by S. of Weipa, 12.40 S, 143.00E, 15. Nov.–16. Dec 1993, Malaise trap, leg. P. Zborowski, (1 ♀, **lc\_32**, ANIC); Australia, NSW, Whiskers, 7 km W NW of Hoskinstown, 35.24 S, 149.23E, 8. Jan. 1993, leg. M. S. Upton, (1 ♀, **lc\_35**, ANIC); Australia, NSW, Armidale, Sep. 1991, ex mantid ootheca, leg. H. Coombs, (1 ♀, **lc\_38**, ANIC); Australia, NSW, 4.1 km W of Williamsdale, 19. Dec. 1994, on Eucalyptus flower, leg. G. Maynard & G. Davis, (1 ♀, **lc\_41**, ANIC); Australia, ATC, Canberra, National



**Figure 13.** (a) – holotype of *L. koebelei*, lateral aspect; (b) – holotype of *L. koebelei*, dorsal aspect; (c) – holotype of *L. washingtoni*, lateral aspect; (d) – holotype of *L. washingtoni*, dorsal aspect.

Botanical Garden, 35.279831°S 149.110501°E, 575 m a.s.l., Feb.–Mar. 2014, ex *Archimantis* sp. ootheca, leg. P. Janšta (4 ♂♂, **lc\_11–14**, CUPC; 3 ♂♂, **lc\_50–52**, ZFMK); Australia, SE Queensland: Tambourine Mts., 11.–18.iv.1935, R.E.Turner, B.M. 1935–240, ♀ *Podagrion koebelei* Crawf., det. Z. Bouček 1978 (1 ♀, **lc\_74**, ANIC); Australia: QLD, 0.5 km S Gordonvale, 10 m, 27.iv.1990, J. Heraty, H90/036, edged sugarcane field, Univ. Calif. Riverside Ent. Res. Mus. UCRC ENT 78401 (1 ♀, **lc\_75**, UCRC); Australia: QLD, Munduberra, 13.iv.–12.v.2000, C. Freebairn, MT, Univ. Calif. Riverside Ent. Res. Mus. UCRC ENT 147599 (1 ♀, **lc\_76**, UCRC); Australia: SA, Belair NP, gate 9 MT, 21.–27.i.2008, J.T. Jennings (1 ♀, **lc\_77**, SMNS); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_01, in EtOH (20 ♀♀, **lc\_78–lc\_97**, CUPC); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_2 (10 ♀♀, **lc\_98–107**, CUPC; 10 ♀♀, **lc\_108–117**, CBGP); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_3 (6 ♀♀, **lc\_118–123**, CUPC; 6 ♀♀, **lc\_124–129**, ZFMK); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_4, homeomorph males (3 ♂♂, **lc\_130–132**, CUCP); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_5, heteromorph males (4 ♂♂, **lc\_133–136**, CUCP; 5 ♂♂, **lc\_137–141**, CBGP; 5 ♂♂, **lc\_142–146**, ZFMK); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta,

Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_7, in EtOH heteromorph males (10 ♂♂, **lc\_147–156**, CUCP); Australia: SA, Kangaroo Island, Flinders Chase NP, Gosselands, 35.93325°S, 136.9326°E, 16.i.2019, Janšta, Böhmová, ex *Archimantis* sp. ootheca, em. ii.–iv. 2019, PJ19020\_8\_8, in EtOH (3 ♀♀, **lc\_157, lc\_159**, 2 ♂♂, **lc\_160–161**, ZFMK), card-mounted (1 ♀, **lc\_158**, ZFMK).

**Diagnosis.** Antenna ([Figure 6b](#)) with all funicular segments slightly or distinctly longer than broad, length of segments decreasing from proximal to distal, F7 at least 1.1× as long as wide. Combined length of pedicel and flagellum 1.45–1.65× breadth of head. Antenna inserted high on the head, distance from lower edge of toruli to ventral margin of clypeus 1.1–1.6× as long as distance from lower edge of toruli to anterior ocellus. Parascrobal area remarkably raised above the outline of head anteriorly (best seen in dorsal or lateral view) and scrobal depression deep with interantennal process long, raised slightly above outline of parascrobal area ([Figure 8a](#)). Head height 0.85–1.02× as long as marginal vein. Notauli almost parallel posteriorly ([Figure 8d](#) – indicated by arrows). Propodeum with adpetiolar area (behind posterior branches of carinae) coarsely rugose. Metafemur large, 1.88–2.73× as long as broad, with five long ventral teeth plus one composite terminal one, at least length of 3<sup>rd</sup> and 4<sup>th</sup> tooth same as or longer than width of tibia opposite to tooth ([Figure 8e](#)). Costal cell of fore wing with two complete rows of setae on the underside ([Figure 8f](#)). Ovipositor very long, between 1.6 and 2.5× as long as body ([Figure 6a](#)).

**Additional characters.** FEMALE (N = 90): Body length excluding ovipositor between 3.3 mm and 4.4 mm; length of ovipositor 5.3–9.8 mm.

Colour. Head, meso- and metasoma entirely metallic bronze blue to green with coppery reflections. Scape, pedicel and flagellum dark brown. Pro-, meso- and metacoxa and outer side of metafemur metallic bronze blue to green with coppery reflections, inner median areas of pro- and metacoxa brown, paramedian parts yellow. Median areas of outer side of pro- and mesofemur and of inner side of metafemur brown with coppery reflections, paramedially yellow. Pro-, meso- and metatibia yellow. All tarsi yellow but pretarsi brown. Ovipositor pale yellow to white, sheaths brown. Fore wing hyaline, wing venation pale to slightly brown, setae brown.

Head. Head 1.15–1.28× as broad as high ([Figure 8b](#)) and 1.6–2.2× as broad as long ([Figure 8a](#)); 1.17–1.32× as broad as pronotum breadth. Frontovertex 0.83–0.96× as broad as eye height. Eye 1.16–1.35× as high as long. Parascrobal protuberance 0.04–0.11× as high as head height. Malar space 0.44–0.6× as long as breadth of oral fossa and 0.28–0.37× as long as eye height. Clypeus slightly convex ([Figure 8c](#)). Antenna with scape 2.24–2.88× and pedicel 1.13–1.57× as long as broad. Flagellum 1.30–1.46× as long as breadth of head. Anellus 0.2–0.5× as long as broad. F1 1.13–1.98×, F2 1.3–1.88×, F3 1.22–1.86×, F4 1.13–1.74×, F5 1.20–1.71×, F6 1.1–1.6×, F7 1.1–1.42× as long as broad. POL 2.63–4.00× OOL, OOL 0.56–0.89× POD.

Mesosoma ([Figure 8d](#)). Pronotum 0.83–0.95× as broad as mesoscutum and 0.43–0.63× as long as mesoscutum. Mesoscutellum 1.07–1.2× as long as broad, with frenal area covering about 0.21–0.30× of mesoscutellum length. Metatarsus 0.53–0.68× as long as metatibia. Fore wing 2.60–2.96× as long as broad; marginal vein 3.28–4.33× as long as postmarginal vein and 6.00–8.63× as long as stigmal vein ([Figure 8f](#)).

Metasoma. Metasoma 0.89–1.2× as long as mesosoma. OI = 5.2–7.6.



Variation (females). Some specimens have entire scapus yellow to light brown, some have scapus yellow laterally; basal part of metafemur of some specimens are yellow to very light yellow. Of the examined 90 females, about 10 specimens vary in number of teeth on hind femora, i.e. some of them are missing the second (the smallest) teeth on right metafemur, some of them are missing the second teeth on left metafemur.

MALE (N = 35): Length of body 2.7–3.26 mm. Similar to females except as follows: head 1.14–1.3x as broad as high; frontovertex 0.78–1.04x as broad as eye height; eye 1.20–1.44x as high as long; parascrobal protuberance 0.16–0.22x as high as head height; malar space 0.48–0.73x as long as breadth of oral fossa and 0.32–0.39x as long as eye height; flagellum longer, 1.43–1.63x as long as breadth of head, pedicel 0.93–1.48x and F7 1.20–1.61x as long as broad; POL 2.24–3.21x OOL, OOL 0.50–0.71x POD; metasoma with yellow subbasal ring extend to 4/5 of metasoma; parascrobal protuberance more raised than in females, about 0.2x as long as eye length (only about 0.13x in females).

Variation (males). There have been reported so called homeomorph and heteromorph (or even their intermediates) males to be found within various genera of Podagrionini (for more details see Delvare 2005). We have found homeomorph and heteromorph males, including some intermediates, within our samples. Most of the examined males have been reared from the same egg case of *Archeomantis* sp. (lc\_11–14, lc\_50–52, and lc\_130–146, respectively). Homeomorph males are similar to females with slightly different sculpture on propodeum (Figure 1i). The intermediates and true heteromorph (Figure 10a) males differ in having slightly enlarged all tibiae and mesobasitarsus (Figure 9d), in number of teeth on metafemur and shape of metatibia (Figure 9e–f), in sculpture of propodeum, and shape of petiolus (Figure 9g, h, j, k). Within all examined males 5 specimens were true homeomorphs, 20 specimens true heteromorphs, and 10 intermediates.

**Distribution.** Australia (Queensland, Australian Capital Territory, New South Wales, South Australia, Victoria) and New Caledonia.

**Biology.** All specimens with known host associations were reared from egg cases of *Archimantis* sp.

**Taxonomic remarks.** The comparison of the material preliminarily named morphospecies 1 group A with the type material of the Australian members of the genus *Podagrion* revealed that morphospecies 1 group A corresponds to *P. koebelei* Crawford, 1912 and its synonyms *P. dolichurum* Cockerell, 1930 and *P. grotii* Girault, 1915. The remnant of holotype (for holotype condition see below) as well as the non-type material show all generic characters of *Lasallegrion*. Accordingly, the above redescribed species is transferred into *Lasallegrion*.

The holotype of *L. koebelei* lacks head and antennae, the left fore wing is partially covered with glue, the right fore wing and the right hind wing are missing. Unfortunately, the holotype of *L. koebelei* was damaged during examination for this study, when the plastic card it was mounted on broke at the point where the pin went through. Right hind leg, part of the left hind leg, left fore wing and metasoma were detached from the rest of the body and were mounted on a separate card. The *P. grotii* type is completely fragmented. It consists of one card-mounted metacoxa, a severely damaged head, antennal parts and a metatibia mounted on a broken slide. It cannot be stated with certainty that all



of these fragments actually belong to the same specimen. The type of *P. dolichurum* is complete and intact. Thus, a complete set of diagnostic characters can only be obtained by combining the types of *P. koebelei* and *P. grotii* with the type specimen of *P. dolichurum*.

Additionally, we identified two new synonyms of *L. koebelei*, *P. holbeini*, and *P. metatarsum* (Figure 10b–c).

The three syntypes of *P. holbeini* (two females and one male mounted on one single card) partially lack heads, but the rest of the body allows us to reliably assign all three specimens to the same species that matches our concept of *L. koebelei*. The synonymy of *P. holbeini* with *L. koebelei* had been suggested already by Bouček (1988).

The five syntypes of *P. metatarsum* (three females and two males mounted on one single card (SAMA); plus two slides – one (SAMA) with two antennae mounted separately on a slide, labelled '*Podagrion metatarsus* Gir., Type ♀'; second (QMB) with fragmented head and antennae on it, labelled '*Podagrion metatarsus* Gir., Type ♀', 5097) are also partially damaged or fragmented, yet there are enough characters visible that allow assignment to the same species which matches our concept of *L. koebelei*. Similar to *P. holbeini*, the synonymy of *P. metatarsum* with *L. koebelei* had been suggested already by Bouček (1988).

Although *L. koebelei* is fairly similar to *L. virescens*, it can be easily distinguished from the third species of the genus, *L. washingtoni*, by its very long ovipositor, the funicular segments being always longer than broad, and by the number and shape of the meta-femoral teeth. In *L. washingtoni* the ovipositor is distinctly shorter, the antennal funicle is stouter with its distal segments being quadrate to subquadrate, and the metafemur bears more and smaller ventral teeth than the metafemur of *L. koebelei* (and *L. virescens*). A molecular delimitation of *L. koebelei* plus *L. virescens* and *L. washingtoni* was not possible, because for *L. washingtoni* no COI sequence data could be obtained.

*Lasallegrion koebelei* and *L. virescens* can be differentiated either based on genetic divergence of COI sequences (94.08–94.83%) or morphologically, even if some specimens of both species overlap in some characters, and a combination of all characters is needed to reliably distinguish both species. Furthermore, the multivariate ratio analysis (MRA) resulted in a useful separation of *L. koebelei* from *L. virescens* and gave further evidence to separate taxa.

### ***Lasallegrion virescens* (Strand, 1911), comb. n. (Figures 5a, 7b, 10d, 11a–f)**

*Podagrion virescens* Strand, 1911: 156; ♀ holotype (examined), Australia – Western Australia, (ZMHU); Label: Type, *Podagrion virescens* m. Strand det. ♀, 13482, GBIF–ChalcidSD ID: ChalD0137, Zool. Mus. Berlin. Bouček (1988): 141.

### ***Non-type material examined***

Australia, WA, Wagin, 5. May 1954, ex ethanol, leg. M.M.H. Wallace, (1 ♀, **lc\_39**, ANIC); Australia, WA, Mt. Augustus National Park, 9 km S of tourist camp, 24.228°S 116.542°E, 394 m a.s.l., 24. Mar.–5. May 2003, Malaise trap, leg. M.E. Irwin & F.D. Parker, (1 ♀, **lc\_15**, ANIC); Australia, WA, Karijini NP, Hamersley, Mt. Bruce Rd., 22.3414°S, 118.1752°E, leg. NA, (1 ♀, **lc\_16**, ANIC); Australia, WA, E slope of Mt. Robinson at rest stop on Great Northern Hwy., 23.02°S, 18.35°E, 722 m a.s.l., 7. Jun. 2003, leg. M.E. Irwin & F.D. Parker, (1 ♀, **lc\_17**, ANIC); Australia, WA, Mt. Augustus National Park, 9 km S of tourist camp, 24.228°S 116.542°E, 394 m a.s.l., 9.–22. May 2003, Malaise trap, leg. M.E. Irwin & F.D. Parker, (2 ♀♀, **lc\_18**, **lc\_47**, ANIC); Australia, WA, 23.026°S, 118.502°E, 23. Apr.–6. May 2003, leg. M.E. Irwin & F.D.

Parker, (1 ♀, **lc\_19**, ANIC); Australia, WA, 60 km N of Tom Price on Hamersley Iron Road, 22.188°S 117.405°E, 600 m a.s.l., 20. Apr.–4. May 2003, Malaise trap on meadow, leg. F.D. Parker & M.E. Irwin (2 ♀♀, **lc\_48–49**, ANIC); Australia, WA, Mt. Cooke, 40 km SE of Armadale, M.T., 7.–22.xii.90, A.D. Austin, Banksia/Jarrah forest, *Podagrion obscurum* (Westwood) det. Eric Grissell 1993 (1 ♀, **lc\_66**, WINC); Australia, WA, Mt. Cooke, 13.–28. i.91, M.S. Harvey, J.M. Waldoock, M.T. (1 ♀, **lc\_67**, WINC); Australia, WA, Mt. Cooke, 28.i.–17. ii.91, M.S. Harvey, J.M. Waldoock, M.T. (2 ♀, **lc\_68–69**, WINC); [Australia, SA], Mt. Torrens, 10. v.85, C.W. Feutrill, emerged from mantig egg case, *Podagrion obscurum* (Westwood) det. E. Grissell 1993 (3 ♀♀, 1 ♂, **lc\_70–71**, WINC; **lc\_72–73**, CUPC); Australia, WA, 82 km S from jct. Karijini Drive on Great Northern hwy., 694 m, 23°07.3'S, 119°05.5'E, 23.iv.–16.v.2003, wash with drying pools, M.E. Irwin, F.D. Parker (1 ♀, **PJ19125\_01**, CUPC); AUSTRALIA: WA, 158 km S Newman, 9 km N Kumarina Rd. House, 24°37.8'S, 117°36.8'E, 638 m, 7.–18. v.2003, M.E. Irwin, F.D. Parker, MT in wide sandy wash (1 ♀, **PJAN1079**, CUPC).

**Diagnosis.** Antenna with all funicular segments slightly or distinctly longer than broad, length of segments decreasing from proximal to distal, F7 at least 1.08 as long as wide. Combined length of pedicel and flagellum 1.1–1.4× breadth of head. Antenna inserted almost in centre of face, distance from lower edge of toruli to ventral margin of clypeus 1.0–1.2× as long as distance from lower edge of toruli to anterior ocellus. Setation of lower face dense, setae long and slightly lanceolate ([Figure 11b](#)). Head height 1.04–1.13× as long as marginal vein. Notauli convergent along entire length ([Figure 11d](#) – indicates by arrows). Propodeum with adpetiolar area (behind posterior branches of carinae) rugulose reticulate ([Figure 11e](#)). Metafemur with four stout teeth preceding the composite terminal one, length of 2<sup>nd</sup> – 4<sup>th</sup> tooth longer than breadth of tibia opposite to tooth ([Figure 11c](#)). Costal cell of fore wing at most with one incomplete row of setae on the underside ([Figure 11f](#)). Ovipositor very long, between 1.77 and 2.14× as long as body.

**Additional characters.** FEMALE (N = 19): Body length excluding ovipositor between 3.5 mm and 3.8 mm; length of ovipositor 6.2–8.2 mm.

Colour. Head, mesosoma entirely metallic blue or dark blue to green with coppery to dark coppery reflections. Metasoma pale brown to brown with metallic reflection, at least distally. Proximal half of scape yellow or pale brown, distal half of scape, pedicel and flagellum dark brown. Pro-, meso- and metacoxa and outer side of metafemur metallic blue to green with coppery reflections. Median areas of outer side of pro- and mesofemur and of inner side of metafemur brown with coppery reflections, paramedially yellow. Pro- and mesotibia yellow, metatibia brown. Pro-, meso- and metatarsal segments yellow, pretarsi brown. Scapula pale brown. Fore wing hyaline, wing venation pale to lightly brown, setae brown. Ovipositor pale yellow to white, sheaths brown.

Head. Head 1.19–1.43× as broad as high and 1.95–2.20× as broad as long; 1.23–1.27× as broad as pronotum breadth. Frontovortex 0.79–0.93× as broad as eye height. Eye 1.07–1.39× as high as long. Parascrobal area not remarkably raised above the outline of head anteriorly (best seen from dorsal or lateral view) and interantennal process not raised above outline of parascrobal area ([Figure 11a](#)). Parascrobal protuberance 0.06–0.13× as high as head height. Malar space 0.47–0.54× as long as breadth of oral fossa and 0.29–0.37× as long as eye height. Antenna with scape 2.41–2.88× and pedicel 1.31–1.45× as long as broad. Flagellum 1.08–1.29× as long as breadth of head. Anellus 0.31–0.38× as long as

broad. F1 1.16–1.97x, F2 1.3–1.76x, F3 1.22–1.71x, F4 1.22–1.69x, F5 1.11–1.70x, F6 1.11–1.50x, F7 1.08–1.52x as long as broad. POL 3.00–4.08x OOL, OOL 0.5–0.71x POD.

Mesosoma. Pronotum 0.89–0.95x as broad as mesoscutum and 0.51–0.67x as long as mesoscutum. Mesoscutellum 1.07–1.15x as long as broad, with frenal area covering about 0.28–0.33x of mesoscutellum length. Metatarsus 0.57–0.65x as long as metatibia. Fore wing 2.55–2.76x as long as broad; marginal vein 2.72–3.80x as long as postmarginal vein and 5.83–6.86x as long as stigmal vein.

Metasoma. Metasoma 0.89–1.15x as long as mesosoma. OI = 6.1–7.4.

MALE (N = 1): Length of body 2.69 mm. Similar to females except as follows: pedicel only 1.29x as long as broad, F1 1.10x, F2 1.15x, F3 1.40x, F4 1.10x, F5 1.15x, F6 1.05x, F7 1.05x as long as broad.

**Distribution.** Australia (Western Australia, South Australia).

**Biology.** Unknown.

**Taxonomic remarks.** The holotype of *P. virescens* is in fairly good condition. The specimen is complete but the wings are crumbled and seem to be covered by some sort of varnish-like layer (Figure 10d). All specimens initially grouped into morphospecies 1 group B match the holotype of *P. virescens*. The holotype as well as the non-type material shows all generic characters of *Lasallegrion*. Accordingly, the above redescribed species is transferred into *Lasallegrion*. Beside above discussed characters, *L. virescens* is recognisable from the other two species by dense white pilosity covering especially the lower face of females. Those setae are slightly longer and slightly lanceolate and sometimes so dense that the lower margin of clypeus and oral fossa are hidden (Figure 11b).

***Lasallegrion washingtoni* Girault, 1915, comb. n.**  
(Figures 6f, 7c, 12a–g, 13c–d)

*Podagrion washingtoni* Girault, 1915: 290; ♀ holotype (examined), Australia–Queensland (QMB). Label: *Podagrion washingtoni* ♀ Girault Type, Ny. 3317, E.C.D. 1985, Photographed Specimen. Bouček (1988): 141.

Additional non-type material examined. Australia, QLD, 9 km SE by E of Musselbrook Camp, 18.38°S 138.12°E, 20. May 1995, light trap, leg. I.D. Naumann, (1 ♀, **lc\_21**, ANIC); Australia, QLD, Coleman River, 14.48°S 143.22°E, 26. Jun. 1993, leg. I.D. Naumann & P. Zborowski (1 ♀, **lc\_22**, ANIC); Australia, QLD, Split Rock, 15.39°S 144.31°E, 24. Aug.–21. Sep. 1992, Malaise trap, leg. P. Zborowski & L. Miller, (1 ♀, **lc\_23**, ANIC); Australia, QLD, 9 km W by N of Mt. Tozer, 12.44°S 143.08°E, 30. Jun.–7. Jul. 1986, Malaise trap, leg. J.C. Cardale, (1 ♀, **lc\_24**, ANIC); Australia, QLD, Cockatoo Creek Xing, 17 km NW of Heathlands, 11.39°S 142.27°E, 22. Mar.–25. Apr. 1992, Malaise trap open forest #5, leg. T. McLeod, (1 ♀, **lc\_25**, ANIC); Australia, QLD, 13 km E by S of Weipa, 12.40°S 143.00°E, 15. Aug.–12. Sep. 1993, Malaise trap, leg. P. Zborowski & S. Shattuck, (1 ♀, **lc\_26**, ANIC); Australia, QLD, Musselbrook Camp, 18.36°S 138.08°E, 8.–21. May 1995, Malaise trap, leg. I.D. Naumann, (1 ♀, **lc\_27**, ANIC); Australia, QLD, 5.5 km SW by S of Mt. Biggenden, 25.35°S 151.57°E, 11. Oct. 1984, at light, leg. I.D. Naumann & J. Cardale (1 ♀, **lc\_28**, ANIC); Australia, NT, Keep River NP, Bail–Me–Up Creek, 23.7 km S by SW of Jarnarm Camp, 15.5755°S 129.0152°E, 3.–8.

Jun. 2001, Malaise trap in dry creek bed, leg. M.E. Irwin & F.D. Parker & C. Lambkin (1 ♂, **lc\_20**, ANIC); Australia, NT, Keep River NP, Bail–Me–Up Cr. 23.7 km SSW Jarrnarm Camp Ground, 15°57'55"S, 129°01'52"E, 3.–8.vi.2001, MT in deep creek bed, M.E. Irwin, F.D. Parker, C. Lambkin, MT (1 ♀, **PJ19131\_01**, CUPC).

**Diagnosis.** Antenna with all funiculars quadrate, subquadrate or at maximum slightly longer than broad. Clypeus with one broad tooth (Figure 12c). Metafemur large, 2.29–2.50x as long as broad, imbricate and covered with pale setae, with nine or ten ventral teeth (Figure 12f). The most distal three teeth coalesced basally and with a successively decreasing size. All other teeth similar in size and shape, about 0.10x as high as the metafemur breadth. Ovipositor between 0.97x and 1.54x as long as body.

**Additional characters.** FEMALE (N = 10): Body length excluding ovipositor between 2.98 mm and 3.67 mm (mean 3.4 mm); length of ovipositor 3.51–5.57 mm.

Colour. Head, meso- and metasoma entirely metallic bronze blue-green to virescent with coppery reflections. Metafemur, pro- and metacoxa exteriorly metallic bronze blue-green to virescent with coppery reflections, interior median areas brown, paramedian parts yellow. External median areas of pro- and mesofemur and metafemur on inner side brown with coppery reflections, paramedian areas yellow. Pro-, meso- and metatibia yellow. Pro-, meso- and metatarsal segments yellow, pretarsi brown. Scape, pedicel and flagellum brown. Ovipositor pale yellow or bright red, sheaths brown. Fore wing hyaline, wing venation pale to lightly brown, setae brown.

Head. Head 1.14–1.28x as broad as high (Figure 12b) and 1.72–2.12x as broad as long (Figure 12a); 1.21–1.44x as broad as pronotum breadth. Frontovertex 0.74–0.92x as broad as eye height. Eye 1.21–1.31x as high as long. Parascrobal protuberance 0.045–0.099x as high as head height. Malar space 0.46–0.55x as long as breadth of oral fossa and 0.23–0.29x as long as eye height. Antenna with scape 2.44–3.0x and pedicel 1.14–1.71x as long as broad. Flagellum length 1.09–1.27x as long as breadth of head; with a single transverse anellus, 0.2–0.5x as long as broad, and seven funicular segments (F1: 1.00–1.29x, F2: 1.00–1.25x, F3: 0.92–1.25x, F4: 0.92–1.11x, F5: 0.90–1.00x, F6: 0.80–1.00x, F7: 0.80–1.00x). POL 2.62–4.25x as long as OOL, OOL 0.4–0.8x as long as POD.

Mesosoma. Pronotum 0.77–0.97x as broad as mesoscutum and 0.50–0.71x as long as mesoscutum (Figure 12d). Mesoscutellum 1.07–1.22x as long as broad, with frenal area covering about 0.2–0.34 of its length (Figure 12e). Metatarsus 0.5–0.61x as long as metatibia. Fore wing 2.49–2.83x as long as broad, marginal vein 2.42–4.69x as long as postmarginal vein and 7.33–8.85x as long as stigmal vein.

Metasoma. Metasoma 0.89–1.02x as long as mesosoma. OI = 3.64–5.00.

Variation. One female specimen (lc\_23) has the metasoma light brown in anterior two thirds, dark brown with blue reflections in dorsal half of posterior third. Two of the total 10 female specimens (lc\_23, lc\_28) show a rather filiform funicle with basal segments significantly elongate. One specimen (lc\_22) shows the right metafemur bearing 10 ventral teeth while the left metafemur bears nine ventral teeth.

MALE (N = 1): Similar to females, except as follows: Length of body 2.6 mm. Head and mesosoma entirely metallic dark blue-green; metasoma brown in anterior half, dark brown with some blue reflections in posterior half. Pro-, meso-, and metacoxa concolorous with mesosoma. Outer side of pro-, meso-, and metafemur brown with few blue

reflections, inner side lighter brown. Flagellum length 0.97x as long as breadth of head. Fore wing 2.42x as long as broad.

**Distribution.** Australia (Queensland and Northern Territory).

**Biology.** Unknown.

**Taxonomic remarks.** The specimens of what used to be called morphospecies 2 match the holotype of *P. washingtoni* Girault, 1915. The card-mounted holotype is in poor condition and lacks head, wings, metasoma, right mid leg, right metafemur, metatibia and metatarsi, and part of the left metatarsus. The slide with the type (labelled as Queensland Museum, 5092, *Podagrion washingtoni*, ♀, 5092, Gir.) is divided into two pieces (fixed together by two pieces of tape) and includes fragmented head (several pieces), metafemur and antenna (without scape). Remnants of the holotype as well as the non-type material show all generic characters of *Lasallegrion*. Accordingly, the above redescribed species is transferred into *Lasallegrion*.

*Lasallegrion washingtoni* can be easily distinguished from the other species within *Lasallegrion* (*L. koebelei* and *L. virescens*, see above) by the shorter ovipositor, the funicular segments being stouter with its distal segments quadrate, by the number and the shape of nine or 10 uniform and relatively small metafemoral teeth. In *L. koebelei* and *L. virescens* the ovipositor is significantly longer, the funicle is more filiform with all segments being distinctly longer than broad and the metafemur only bears less metafemoral teeth of different size and shape.

The DNA extraction failed for the only ethanol-preserved specimen of *L. washingtoni*. Accordingly, we have no inferences from nucleotide sequence data analysis regarding the delimitation of *L. koebelei* plus *L. virescens* and *L. washingtoni*.

### Comments on *Podagrion* species of Australia and New Caledonia

Because the most similar genus to *Lasallegrion* (described herein) is the genus *Podagrion* and we have found the species belonging to this genus within the described species of *Podagrion*, we decided to examine the accessible type material of all described species of *Podagrion* (14 species that are not part of *Lasallegrion*) from Australia and New Caledonia (Bouček 1988). These species were examined for generic assignment not for species-level revision, but their condition is commented upon.

#### *Podagrion abbreviatum* Cockerell, 1930

*Podagrion abbreviatum* Cockerell, 1930: 3–4. New Caledonia: Noumea. Bouček (1988): 140.

Material examined: 1 ♀ holotype (card), NMV; labelled: *Podagrion abbreviatum*, Ckll., TYPE, Noumea, New Caledonia.

Remarks. The holotype of *P. abbreviatum* is card-mounted, complete and in good condition. The species clearly belongs to the genus *Podagrion*.

***Podagrion batesi* Girault, 1915**

*Podagrion batesi* Girault, 1915 [243]: 292. QLD: Cloncurry. Bouček (1988): 140.

Material examined: 1 ♀ holotype (card), QMB; labelled: *Podagrion batesi* Hy. 3320, E.C.D. 1982, Australia–Queensland.

Remarks. The holotype of *P. batesi* is card-mounted and lacks head, antennae and right hind leg. Based on the still visible characters the species belongs to the genus *Podagrion*.

***Podagrion beneficium* Girault, 1915**

*Podagrion beneficium* Girault, 1915 [243]: 289–290. QLD: Gordonvale. Bouček (1988): 140.

Material examined: 1 ♀ lectotype (card, designated herein), USNM; labelled: *Podagrion beneficium*, Nr. 15,361, Cotype, Nelson near Cairns, N. Queensland, Australia. 2 ♀♀, 1 ♂ paralectotypes (card, designated herein), QMB; labelled: *Podagrion beneficium*, Hy. 1170, E. C.D. 1982. 1 ♀ paralectotype (slide, designated herein), QMB; labelled: *Podagrion beneficium* ♀ Type, 5100, varitarsus Gir., from mantid ootheca, 5103, Type ♀, loc. Kuranda, N.Q.

Remarks. The single female specimen from USNM is card-mounted and partially fragmented. No fragments are missing, they are all glued to the same card. This specimen is designated here as lectotype. The two female specimens from QMB are mounted on one card, one specimen is complete and in good condition, the other specimen is fragmented and lacks head and metasoma. The male specimen from QMB is card-mounted and lacks the head including antennae. The slide from QMB contains two coverslips. One square and larger coverslip contain an undescribed species of *Podagrion* (Dahms 1983) (two females and one male), and one small complete circular coverslip contains a fragmented head and two incomplete antennae (one fragmented) of *P. beneficium* paralectotype. All examined material of *P. beneficium* belongs to the genus *Podagrion*.

***Podagrion flabellatum* Girault, 1929**

*Podagrion flabellatum* Girault, 1929 [431]: 342. TAS: Launceston. Bouček (1988): 141.

Material examined: 1 ♀ lectotype (card; designated herein), SAMA; labelled: *Podagrion flabellatus* Girault, Launceston T., FM Littler., 'TYPE ♀', SAMA Database No. 32–035305. 1 ♂ paralectotype (card), SAMA; labelled: *Podagrion flabellatus* Girault, Tasmania, Launceston T., FM Littler., 'TYPE ♀', SAMA Database No. 32–035304. ♂ ♀ types" (slide), SAMA; labelled 'Podagrion flabellatus Girault ♂ ♀ types'.

Remarks. Both card-mounted specimens are accompanied by their host mantid egg-cases; both are in good condition. Three antennae are present on a separate slide labelled: TYPE, Ent. Div. Dep. Ag. & Stk., Qld., *Podagrion flabellatus* Girault ♂ ♀ types, S. Aus. Mus. *P. flabellatum* clearly belongs to the genus *Podagrion*.

***Podagrion hyalinum* (Girault, 1913)**

*Podagrionella hyalina* Girault, 1913 [175]: 80. QLD: Longreach. Transferred to *Podagrion* by Girault, 1915 [243]: 292. Bouček (1988): 141.



Material examined: 1 ♀ holotype (card and slide), SAMA; card labelled: *Podagrionella hyalina* Girault, 'TYPE' ♀, Longreach, Q.; A.M. Lea, SAMA Database No. 32-035303; slide labelled: *Podagrionella hyalina* Girault, TYPE, ♀.

Remarks. The specimen is card-mounted, fragmented and partially destroyed. It lacks the head, but an apical part of one antenna is present. One hind leg is present, the other legs are missing or are covered by glue. A hind leg, a complete antenna, two fore wings and one hind wing are present on a separate slide. *P. hyalinum* clearly belongs to the genus *Podagrion*.

### ***Podagrion julia* (Girault, 1927)**

*Podagrionella julia* Girault, 1927 [416]: 330. SA: Adelaide. Transferred to *Podagrion* by Bouček (1988): 141.

Material examined: 1 ♀ lectotype (card; designated by Dahms 1984), SAMA; labelled: *Podagrionella julia* Girault, TYPE, ♀.

Remarks. The lectotype is card mounted and lacks the head and right fore wing. The species clearly belongs to *Podagrion*. Bouček (1988) stated that *P. julia* is probably best placed in *Podagrion* subg. *Propodagrion*. This subgenus classification, however, was later rejected by Grissell (1995, p. 164).

### ***Podagrion magniclavum* (Girault, 1913)**

*Pachytomoidella magniclavus* Girault, 1913 [172]: 40–41. QLD: Gordonvale (Nelson). Bouček (1988): 141.

Remarks. The type specimen of *Podagrion magniclavum* is lost. It was previously deposited in the QMB and was apparently examined by Bouček (1988), but it could not be traced and examined for the present study.

### ***Podagrion nigriclava* Dodd, 1917**

*Podagrion nigriclava* Dodd, 1917: 360. NT: Darwin. Bouček (1988): 141.

Material examined: 1 ♀ type (slide), QMB; labelled: *Podagrion pax* Girault, *nigriclavum* Dodd, ♀ types, 5093. 5094.

Remarks. There are two coverslips on the slide. According to Dahms (1986) one almost complete coverslip belongs to the holotype of *Podagrion pax* (for details see *P. pax* paragraph) and the second (just a fragment) coverslip belongs to the syntypes of *Podagrion nigriclava* Dodd. We clearly identified parts of a destroyed head, two female antennae and one hind female leg under this coverslip which most probably belongs to a (syn)type of *P. nigriclava*. Examination of these fragments can still clearly assign this species to the genus *Podagrion*.

### ***Podagrion obscurum* (Westwood, 1847)**

*Palmon obscurus* Westwood, 1847: 260. WA King George's Sound. Transferred to *Podagrion* by Dalla Torre, 1898: 370. Bouček (1988): 141, 152 (Fig. 202).



Remarks. Bouček (1988) and Grissell (1995, referring to Bouček (1988)) mention that *P. obscurum* (Westwood, 1847) is close to *P. koebelei* by sharing the carinate pronotal collar. Thus, *P. obscurum* most probably belongs to *Lasallegrion*. Based on the collecting locality and other characters given by Bouček (1988), *P. obscurum* is most probably conspecific with *L. virescens*. The latter therefore could be considered as junior synonym of *P. obscurum*. However, we were unable to locate the single specimen that had been designated as lectotype by Bouček (1988) and which should be located at the Oxford Museum. It bears a label written by Graham (Bouček 1988). We also tried to locate it at the Natural History Museum London, because parts of the Graham collection are located there, but without success. We decided to keep those two species as separate species and leave the status of *P. obscurum* unclear until the type will be found.

### ***Podagrion olenus* (Walker, 1839)**

*Palmon olenus* Walker, 1839b: 7–8. NSW: Sydney. Transferred to *Podagrion* by Dalla Torre, 1898: 370. Bouček (1988): 141.

Remarks. Bouček (1988) designated a lectotype but stated that ‘unfortunately only the gaster and one hind leg (on a slide) remain’. This incomplete type, however, could not be located at NHMUK. Bouček (1988) does not provide any further discussion on this species, which we interpret as him being fine with the classification of the species in *Podagrion* (albeit with some uncertainty because he already could only examine some fragments).

### ***Podagrion pavo* Girault, 1915**

*Podagrion pavo* Girault, 1915 [243]: 291. VIC: Melbourne; ex *Tenodera australasiae* Leach. Bouček (1988): 141.

Material examined: 1 ♀ lectotype (card; designated herein), NMVM; labelled: ‘TYPE’, T–11648 *Podagrion pavo* Syntypes, MUS. VIC. (NMVM) ENTO 2016–11 L, Syntype T–22112–164; lectotype, desig. P. Janšta 2019. 3 ♀♀, 2 ♂♂ paralectotypes (on one card; designated herein), NMVM; labelled: ‘TYPE’, T–11648 *Podagrion pavo* Syntypes, MUS. VIC. (NMVM) ENTO 2016–11 L, Syntype T–22112–164; paralectotypes, desig. P. Janšta 2019. ♂, ♀ paralectotypes (slide, designated herein), NMVM; labelled: T–11648, *Podagrion pavo* (one label); *Podagrion pavo* Gir. ♂, ♀ Types; paralectotypes, desig. P. Janšta 2019.

Remarks. The lectotype on card is complete, paralectotypes on card are partly missing antennae and some legs. The slide contains one female hind leg (in two parts – metacoxa plus metafemur and metatibia), one female antenna and two male antennae. All card-mounted type specimens are in good condition and can be clearly assigned to the genus *Podagrion*.

### ***Podagrion pax* Girault, 1915**

*Podagrion pax* Girault, 1915 [243]: 291. QLD: Gordonvale.

Material examined: 1 ♀ holotype (card and slide), QMB; card labelled: *Podagrion pax* Girault, ‘TYPE ♀’, Hy. 3318, E.C.D. 1985; slide labelled: *Podagrion pax* Girault, nigriclavum Dodd, ♀ types, 5093. 5094.

Remarks. The holotype is card-mounted and lacks head, pronotum, some legs and part of the fore wing. The slide contains two coverslips; one almost complete coverslip with the fragmented head, separated fragmented and incomplete antennae and one hind leg from the holotype of *Podagrion pax*. The second (fragment of) coverslip contains supposedly parts of *Podagrion nigriclava* Dodd (Dahms 1986). *Podagrion pax* can still be clearly assigned to the genus *Podagrion*.

### ***Podagrion risbeci* (Cockerell, 1930)**

*Pachytomus risbeci* Cockerell, 1930: 4–5. New Caledonia: Noumea. Transferred to *Podagrion* by Bouček (1988): 141.

Material examined: 1 ♂ holotype, ANMH, labelled: *Pachytomus risbeci* Ckll, TYPE, Noumea, New Caledonia.

Remarks. The holotype of *P. risbeci* is card-mounted and in a good condition, only the antennae are missing. *P. risbeci* belongs to the genus *Podagrion*.

### ***Podagrion worcesteri* Girault, 1913**

*Podagrion worcesteri* Girault, 1913 [159]: 97–98. QLD: Gordonvale (Nelson). Bouček (1988): 141.

Material examined: 1 ♀ holotype (card and slide), QMB; card labelled: *Podagrion worcesteri* Girault, TYPE ♀, Hy. 3316, E.C.D. 1985, ENT 16.12; 1 ♂; slide labelled: *Podagrion worcesteri* Girault, Type ♀ 5109.

Remarks. The card-mounted holotype of *P. worcesteri* is fragmented and lacks head and hind legs. All these missing parts are on slide (head including both antennae and complete hind legs). *P. worcesteri* belongs to the genus *Podagrion*.

## **Discussion**

The integrative approach of modern taxonomy extends the classical morphological analysis to, among others, molecular methods, multivariate ratio statistics and state-of-the-art image computing. The aim is to develop an accurate classification and to provide extensive material that allows for further scientific work. Also, concepts that focus on standardised molecular methods to save time and increase efficiency (turbo-taxonomy) are becoming increasingly important in the face of a drastic decline in insect numbers and presumably insect species as recently shown by Hallmann et al. (2017). However, recent results using state-of-the-art integrative approaches and providing newly available data resources, such as µCT scan images and transcriptome assemblies, always have to be incorporated into the existing taxonomic system and the often old and sometimes damaged type material, which sometimes, as in this study, will raise some serious problems.

In this study, the description of the new genus as well as the transfer of the three valid species are based on clear morphological diagnostic characters. However, the assignment of the examined material to the lost or existing types (and hence existing names) proved to be rather difficult. The unequivocal matching of the new material to old type material of *P. koebelei* (Figures 11a–b, 22a–b), and *P. washingtoni* (Figures 22c–d) cannot be done. Both types are lacking body parts bearing characters that are relevant for genus and species

diagnoses, and reliable taxonomic work is not possible with these types. Especially the lack of a head with antenna in both types, and of the metasoma with ovipositor in the *L. washingtoni* type is fraught with problems for reliable identification. In the case of *L. koebelei*, there are two previously established synonyms: *P. dolichurum* Cockerell, 1930 and *P. grotii* Girault, 1915 which in combination show all diagnostic characters. Our assignment of the new material to the name *L. koebelei* therefore highly depends on the assumption that the previous synonymy (Bouček 1988) was correct, and on the basis of formerly complete type material. The condition of the *L. washingtoni* type is even worse, and there are no synonyms to try a reliable assignment of new material to the type. As a result, we are facing a significant uncertainty that we will never be able to solve that the new material we have at hand actually might not belong to the described species. All data for the redescription are collected from non-type material that cannot be undoubtedly associated to the original type specimens. In this case, all new taxonomic work on this species breaks the taxonomic rule of unambiguity. The designation of a neotype seems to be the most appropriate solution of the dilemma in respect of taxonomic unambiguity. However, according to article 75 of the International Code of Zoological Nomenclature the designation of a neotype by a scientific authorship is only allowed, if the original type is assumed to be irretrievably lost (Article 75.1, ICZN). As long as one last fragment of the original type is present, the International Committee of Zoological Nomenclature (ICZN) reserves the right to designate a neotype under its plenary power (Article 75.5, ICZN). According to the ICZN guidelines for case preparation, the designation procedure takes the committee at least eight months for a final decision. For efficient taxonomic work involving old material, as will be necessary in many cases in the future, such a lengthy process certainly is not an adequate solution. Alternatively, we could have described the new material as new species, while keeping the old species with its damaged type material. This is not a good solution either because we would not be able to formulate diagnoses and identification keys for the valid species, because characters that are needed for a precise distinction of the old and the new species are missing. Another possible approach would be to describe a new species and declare the existing species as *nomina dubia*. However, *nomina dubia* are still existing names which have to be considered in all future work on the taxa, yet the identity of the names or species will – in our case – probably never be solved, and accordingly, these species can never be used in any study relying on correct species (e.g., in conservation, phylogenetics, evolutionary biology). Applicability in other disciplines is increasingly recognised as one of the main goals of taxonomic work, rendering any decision leaving too much uncertainty highly undesirable. Considering these alternatives, it seems the most practical approach to accept the uncertain identification mentioned above, and to provide an accurate, comprehensive and future-proof redescription. An additional argument backing this approach is that both species have wide geographic distributions which makes it more likely that they have already been described in the past and that our new material really corresponds to the previously described species.

The above outlined taxonomic dilemma is neither new nor exclusive for our studied taxa, yet we felt a troubling discrepancy between our attempts to perform modern comprehensive integrative taxonomy and the very basic uncertainties caused by type material in poor condition. We deliberately and explicitly add this discussion of the taxonomic dilemma to stress that – unlike other scientific disciplines – taxonomy will always have to face a struggle between modern approaches and the work that has been

done in the past.

## Acknowledgements

We are indebted to curators who provided material and information for our study, namely Susan Wright and Geoff Thompson (QMB), Natalie Dale-Skey (NHMUK), Christine LeBeau (AMNH), Viola Richter (ZMHU), Simon Hinkley (NMVM), Peter Hudson (SAMA), Michael Gates (USMN), and James Hogan (HDOU). We thank Claudia Etzbauer and Bernhard Misof (ZFMK) for help with generating COI sequences, and Hajo Krammer, Phil Erkeling, Ximo Mengual (ZFMK), and Kristýna Bubeníková (CUPC) for assistance with imaging of specimens. Alex Donath und Lars Podsiadlowski (ZFMK) cleaned and submitted the included transcriptome. Peter Rühr, Claudia Koch, and Juliane Vehof (ZFMK) assisted in generation of  $\mu$ CT data. Maximilian Weber made most of the morphometric measurements. This work has been supported by a grant of the Ministry of Education, Youth and Sports of the Czech Republic no. SVV 260571/2019 and J. William Fulbright Commission no. 2019-21-04 (both to PJ).

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by the Ministry of Education, Youth and Sports of the Czech Republic [SVV 260571/2020] and J. William Fulbright Commission [2019-21-04].

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