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Habitat requirements affect genetic variation in three species of mayfly (Ephemeroptera, Baetidae) from South Africa

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Abstract

This study investigates genetic diversity in three species of Ephemeroptera, one eurytopic and therefore widespread (*Afroptilum sudafricanum*) and two stenotopic and thus endemic (*Demoreptus natalensis* and *Demoreptus capensis*) species, all of which co-occur in the southern Great Escarpment, South Africa. Mitochondrial DNA was analysed to compare the genetic diversity between the habitat generalist and the two habitat specialists. *Afroptilum sudafricanum* showed no indication of population genetic structure due to geographic location, while both *Demoreptus* species revealed clear genetic differentiation between geographic localities and catchments, evident from phylogenetic analyses and high F_{ST} values from AMOVA. In addition, the phylogenetic analyses indicate some deeper haplotype divergences within *A. sudafricanum* and *Demoreptus* that merit taxonomic attention. These results give important insight into evolutionary processes occurring through habitat specialisation and population isolation. Further research and sampling across a wider geographic setting that includes both major mountain blocks of the Escarpment and lowland non-Escarpment sites will allow for refined understanding of biodiversity and associated habitat preferences, and illuminate comparative inferences into gene flow and cryptic speciation.

Keywords

cytochrome oxidase 1, genetic diversity, habitat specialisation, haplotype, phylogeography, mayfly

Introduction

Greater genetic diversity within a lineage is regarded as increasing its resilience to environmental change (Jump et al. 2009, Razgour et al. 2019), which gives contemporary relevance to insights into the mechanisms shaping genetic diversity of populations. Genetic diversity between populations is, in part, a reflection of their members' dispersal activity through space and time (Slatkin 1985, Bohonak 1999, Avise 2009). Theoretically, if widespread intermigration between populations of a species occurs, then levels of genetic differentiation will be relatively low, whereas if dispersal is restricted by physical barriers or limitations to mobility, then genetic differentiation is likely to be higher (Slatkin 1993). The relationship between dispersal ability and genetic population structure of a species can provide important insights into micro-evolutionary processes, phylogeography (Hanski and Gaggiotti 2004, Avise 2009), and resilience to environmental change.

Aquatic insects have a winged adult stage that is generally considered to have relatively strong dispersal ability (Hughes and Mather 1995, Bunn and Hughes 1997). This is reflected in the ability of stream organisms to recover from disturbance (Wallace 1990, Yount and Niemi 1990) and the widespread geographic distribution of many aquatic species across catchments. Consequently, many such insects show low levels of genetic differentiation among populations, both within and between catchments, attributed to the extensive dispersal of adults by flying (Schmidt et al. 1995, Hughes et al. 1998, 2000, Miller et al. 2002, Monaghan et al. 2002, Pereira-da-Conceicoa et al. 2012, Gattolliat et al. 2018). Despite the apparent mobility of these species, their need for persistent waters for breeding tends to fragment their distribution into metapopulations (Avise 2009). The patchiness of lakes, the linear, unidirectional, hierarchical character of rivers, and the topographical structure of catchments tend to structure the dispersal of aquatic organisms between breeding sites or local populations (Wishart et al. 2003, Kaltenbach and Gattolliat 2018). The population genetic variance of certain species is structured significantly according to drainage basin, especially in mountainous landscapes with rugged topography (Hughes et al. 1999, 2003, Wishart and Hughes 2001, 2003, Monaghan et al. 2002, Price et al. 2010, Toussaint et al. 2013, 2014, Barber-James and Pereira-da-Conceicoa 2016). Ecologically, aquatic habitats within terrestrial landscapes can therefore be conceptualised as functional islands for some aquatic organisms.

Genetic variation between populations is related to the ability of their members to disperse, and a high degree of genetic structure has been observed among populations of some South African winged aquatic (Wishart and Hughes 2001, 2003) and terrestrial (Price et al. 2007, 2010) insects. This has been attributed to habitat-specificity that imparts a high cost to unsuccessful dispersal, so that stronger associations with restricted habitats, such as particular aquatic conditions, result in increasingly limited potential for successful dispersal (Price et al. 2007). Aquatic invertebrate species, including Ephemeroptera, show varied degrees of habitat-specificity, with some species being completely restricted to a certain habitat and others occurring in a range of habitat types (Barber-James and Lugo-Ortiz 2003).

The aim of this study is to use three model species of mayfly to test the hypothesis that habitat-restricted taxa have greater phylogeographical structure than habitat-generalist species. *Afroptilum sudafricanum* Lestage is a common, widespread African species, occurring in a range of ecological conditions, including different flow regimes and a wide altitude range (Barber-James and Lugo-Ortiz 2003). *Demoreptus natalensis* Crass and *Demoreptus capensis* Barnard have very specific habitat requirements, being most commonly found on rock faces associated with waterfalls in fast-flowing mountain streams (Barber-James and Lugo-Ortiz 2003).

Materials and methods

Study region

The southern Great Escarpment forms an 800-km-long stretch of mountain complexes extending from the Nuweveldberge in the west to the Eastern Cape Drakensberg in the east. Ancient erosional features divide the mountains into five main blocks that range in altitude from 1 600–3 000 m a.s.l., making the area interesting for study of dispersal-limited groups.

Taxon sampling

Nymphs of *A. sudafricanum*, *D. capensis*, and *D. natalensis* were collected from 21 rivers in the Eastern Cape Great Escarpment, relating to 12 study areas within the Escarpment and non-Escarpment sites (Table 1). An additional six rivers were sampled for *A. sudafricanum* in lower-altitude (non-Escarpment) areas in the Eastern Cape and KwaZulu-Natal (Table 1). All specimens were preserved in 80% ethanol.

A related species of Baetidae, *Baetis rhodani* Pictet, was used as the outgroup for phylogenetic analyses, and relevant sequence data (Rutschmann et al. 2014) were obtained through Genbank (Benson et al. 2012) for both cytochrome c oxidase subunit I (COI) (KP438135 and KP438160) and 16S rRNA (16S) (KP438109 and KP438119) gene regions.

DNA extraction, amplification, and sequencing

DNA was extracted using the Invisorb Spin Tissue Mini Kit following manufacturer's protocol (Invitek, Berlin, Germany). Extraction was non-destructive, using internal body digestion, which ensured the preservation of the exoskeleton for future morphological analysis (housed in the Albany Museum, Makhanda, South Africa, along with additional material that is stored in the collection, listed under the GEN catalogue.)

Two mitochondrial gene regions were amplified: cytochrome c oxidase subunit I (COI) and small subunit ribosomal RNA (16S). A 528-bp section of the COI regions of *D. natalensis* and *D. capensis* was successfully amplified with the standard 'universal' primer pair, LCO1490 and HCO2198 (Folmer et al. 1994), which worked with only limited initial success with *A. sudafricanum*. A new forward primer (5'–GGT GGA TGG GCA GGA ATG GTA GGA–3') was designed and used with HCO2198 to successfully sequence the remaining samples of *A. sudafricanum*. The 16S region was amplified with the primer pair 16Sar (5'–CGC CTG TTT ATC AAA AAC AT–3') and 16Sbr (5'–CCG GTC TGA ACT CAG ATC ACG T–3') (Palumbi 1996). However, these primers proved problematic for the *Demoreptus* samples, and this region is thus excluded from subsequent analyses for this taxon.

The polymerase chain reaction (PCR) was performed in a 50 µl volume using the following thermal regime: 95 °C for 5 min, 35 cycles of 95 °C for 45 s, 50 °C for 45 s, and 72 °C for 90 s, followed by a final extension period of 72 °C for 5 min. PCR amplifications were checked for the presence of amplified PCR products by gel electrophoresis (0.5% agarose gel stained with SYBR green) and viewed with a UV-transilluminator. Successful PCR products were cleaned up using the Invisorb PCRapace® Quick purification kit (Invitek, Berlin, Germany) and cycle-sequenced in both directions using the primers used for amplification, the ABI Big Dye Sequencing kit v.3.1 (following manufacturer's instructions (Applied Biosystems)), and a ABI Genetic Analyzer 3500 (Applied Biosystems).

Sequence trace files were assembled and edited using Sequencher 3.0 (DNA sequence analysis software, Gene Code Corporations, Ann Arbor, MI USA, http://www.genecodes.com). The sequences were then aligned in MEGA v.6 (Tamura et al. 2013) using the ClustalW algorithm and subsequently each non-synonymous mutation was manually cross-checked in the original trace files.

Phylogenetic analyses

Each gene was tested for substitution saturation using plots of transitions and transversions against F84 distance in DAMBE v7.0.58 (Xia et al. 2003, Xia and Lemey 2009, Xia 2017).

Congruence between the COI and 16S datasets was assessed using the partition homogeneity test (PHT) in PAUP* (Swofford 2002) with 1000 replicates to verify that the gene sections could be combined for analysis.

Bayesian Inference (BI) analyses were conducted with MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001) using the GTR+I+G model since it is the most complex model, allowing the nesting of simpler models that could be estimated through the Bayesian sampling. Each analysis comprised two independent runs with random starting trees and four chains (three heated and one cold) each, sampled every 200 generations for 20 million generations per run. The cumulative sample sizes were plotted against the likelihood scores and tree length using Tracer v1.7.0 (Rambaut et al. 2018), to ascertain when the analysis reached stationarity after the first 10% of the trees were discarded as burn-in. The analysis was run on the CIPRES Science Gateway (Miller et al. 2010) using default parameters for variables not mentioned above.

Maximum likelihood (ML) analyses were conducted with 2 000 bootstrap replicates using the GARLI (Genetic Algorithm for Rapid Likelihood Inference) on XSEDE via the CIPRES (Cyberinfrustructure for Phylogenetic Research) Science Gateway v3.3 (Miller et al. 2010), which is supported by the San Diego Supercomputer Center (SDSC) and the University of California (UC San Diego). Models of molecular evolution for each dataset were selected using the Akaike information criteria (AIC) as implemented by jModeltest 2.1.6 (Darriba et al. 2012) (Table 2). The COI and COI+16S ML phylograms were compared and presented using Phylo.io software (Robinson et al. 2016).

Parsimony analyses were performed in PAUP* version 4.0b10 (Swofford 2002) using the heuristic search option with 100 random addition replicates. A search with TBR (Tree Bisection and Reconnection) branch-swapping was used to find the approximate length of the shortest trees, with one tree kept with each random addition. To investigate nodal support, all of the trees from this search were used as starting trees for a second heuristic search with MAXTREES set to 5 000. The *Demoreptus* analysis used FASTBOOTSTRAP with 10 000 replicates.

Phylogeographical structure and variation

Molecular diversity was investigated using the COI datasets. The number of variable sites (S), number of haplotypes (Hap) and haplotype diversity (Hd), Nucleotide diversity (p) and neutrality tests (Tajima's D and Fu's F_S) were calculated in DNAsp (Rozas et al. 2017). Population structures within each species were estimated using one-level Analyses of Molecular Variance (AMOVA) in ARLEQUIN ver. 3.5.2 (Excoffier and Lischer 2010). F_{ST} (fixation index) values were calculated between localities to determine whether putatively conspecific populations differed significantly in their genetic composition. For all AMOVA analyses (listed in Table 4), *a priori* groups were defined by each site where the insects were collected. Haplotype networks were illustrated with a median-joining network (MJN) algorithm ($\varepsilon = 0$) (Bandelt et al. 1999) using the software PopART v. 1.7 (Leigh and Bryant 2015) to analyse haplotype genealogy.

Results

Data characteristics

COI sequences (649 bp) were obtained from 86 individuals and 16S sequences (542 bp) obtained from 59 individuals of *A. sudafricanum*. Shorter (528 bp) COI sequences were obtained for 24 *Demoreptus* individuals (for *D. natalensis*, *N* = 12; *D. capensis*, *N* = 11; unidentified, *N* = 1). DNA characteristics for each gene dataset are summarised in Table 2. The Partition Homogeneity Test for incongruency (Swofford 2002) showed that the combined COI and 16S datasets were not significantly incongruent (P = 0.3890) and could therefore be combined for analysis. The COI+16S molecular dataset consisted of 59 specimens and 1191 nucleotides including the outgroup. No evidence of saturated substitution was found for either gene (data not shown).

Phylogenetic analyses

The parsimony analyses' results are summarised in Table 2. Phylogenetic analyses of the habitat generalist *A. sudafricanum* consistently retrieved six distinct clades and an unresolved grade of specimens (referred to hereafter as the "widespread grade") from a wide range of sites for all analyses (Fig. 1). The tree comparison shows that the relationships between these clades in the analysis of the CO1 data and the CO1+16S data sets were consistent, with improved support for the combined dataset. The well-supported clades did not conform to the mountain blocks described in Table 1 and included specimens from across these ranges. The clades were roughly separated into overlapping geographic groups: Southern Montane, Stormberg/Barkly East, and Eastern Cape, while more restricted geographic areas included KwaZulu-Natal and Eastern Cape Drakensberg, the latter clade showing a longer stem branch compared to other clades (Fig. 1).

The phylogenetic analysis of the habitat-restricted *D. capensis* and *D. natalensis* clearly indicated strong genetic structure corresponding to geographic location (Fig. 2). Both species had genetically distinct populations with strong support from parsimony, Bayesian and maximum likelihood analyses. The clades found for *D. capensis* and *D. natalensis* were more closely aligned with the mountain ranges described in Table 1 and appear to be site-restricted, apart from one instance where individuals of *D. natalensis* from Rhodes and Barkly Pass fell into the same well-supported clade. For *D. capensis* the Rhodes clade had a long branch and is clearly distinct from the other clades, which is noteworthy considering the close geographic proximity to Barkly East, which formed a separate well-supported clade nested with other clades (Fig. 2). This pattern was not apparent in *D. natalensis*, where the Barkly East specimen was clearly separate from the *D. natalensis* clade; morphological re-examination suggests that it does not belong to any described *Demoreptus* species.

Population genetics

MJN analysis collapsed the 86 *A. sudafricanum* COI sequences into 60 haplotypes (Fig. 3, Table 3), 45 of which were singletons or private haplotypes. Haplotype 17 was the most abundant (N = 8) and occurred in three of the 12 study areas (Fig. 4), which included non-Escarpment Grahamstown and two main mountain Escarpment blocks (Sneeuberg and Winterberg–Amathole). Haplotype 20 was next-most-abundant (N = 4) and exclusive to non-Escarpment Makhanda (= Grahamstown). Haplotype 10 (N = 3) was found in one non-Escarpment site (KwaZulu-Natal) and one main moun-

Table 1. Collecting localities (Site and river name) and non-zero sample sizes for each species from each site. The GenBank sequence accession numbers for each sample are listed in Suppl. material 1.

Locality	Longitude/ Latitude	*A. sudafricanum*	*D. capensis*	*D. natalensis*	*Demoreptus* sp.
Escarpment sites					
Eastern Cape Drakensberg					
Barkley East 1: Diepspruit	-30.751, 27.546	3	1		
Barkley East 2: Diepspruit	-30.757, 27.552	3			
Barkley East 3: Diepspruit	-30.718, 27.54	3			1
Barkley Pass 1: Marais Hoek	-31.215, 27.686	3			
Barkley Pass 4: Ben Wyvie	-31.173, 27.971	3		3	
Barkley Pass 5: Lymore Lodge	-31.172, 27.854		2		
Rhodes 1: Hawkshead	-30.676, 27.884	3	2		
Rhodes 2: Tiffindell	-30.674, 27.904	3	1		
Rhodes 3: Tenahead	-30.696, 28.150	3		1	
Maclear 1: Vuvu River	-30.603, 28.216	5			
Stomberg					
Stomberg 3: Lana River	-31.163, 26.602	3			
Stomberg 4: Lemonfountain	-31.416, 26.842	3			
Winterberg-Amatole					
Elansberg 1: Elandsberg	-32.506, 26.903	3			
Winterberg 1: Fanella falls	-32.363, 26.385	2		3	
Winterberg 2: Fanella falls	-32.380, 22.967	3			
Winterberg 3:	–	5			
Sneeuberg					
Sneeuberg 1: Fish River	-32.227, 24.954	2			
Sneeuberg 2: Melkriver	-32.243, 24.941	2	3	3	
Kamdeboorberg 1: Buffelsrivier	-32.177, 24.016	3		2	
Kamdeboorberg 3: Waterkloof	-32.353, 23.890	2	2		
Nuweveldberge					
Nuweveldberge 1: Maijiesvlei	-32.102, 22.636	1			
Non-Escarpment sites					
Grahamstown					
Grahamstown CR: Coleridge River	-33.349, 26.618	2			
Grahamstown KP: Kap River	-33.351, 26.858	5			
Grahamstown KR: Kowie River	-33.349, 26.560	5			
Grahamstown PM: Palmiet River	-33.370, 26.476	5			
KwaZulu-Natal					
KwaZulu-Natal KK: Karkloof River	-29.338, 30.307	5			
KwaZulu-Natal LR: Lions River	-29.492, 30.108	5			
KwaZulu-Natal UM: Umgeni River	-29.477, 30.261	1			
		86	11	12	1

Table 2. Data characteristics and summary of the parsimony analysis. The number of specimens with sequence data (ntax), total number of base pairs (bp), parsimony informative (# Pi), and percent parsimony informative (% Pi) is reported. The results of the parsimony are summarised with the number of trees retained (# trees), tree length (score), Consistence Index (CI) and Retention Index (RI). The summary of the models for the Maximum Likelihood analysis (ML) selected by jModeltest.

Species	Dataset	ntax	Characters				Parsimony analysis				Model	
			bp	#Var	# Pi	% Pi	# trees	Score	CI	RI	ML analysis	BI analysis
A. sudafricanum	COI	88	649	217	192	29.6	5 000	421	0.601	0.932	GTR+I+G	GTR+I+G
	COI+16S	88	1191	380	336	28.2	5 000	645	0.662	0.939	TIM3+I+G	GTR+I+G
Demoreptus spp.	COI	24	528	164	159	30.1	8	302	0.745	0.922	TVM+G	GTR+I+G

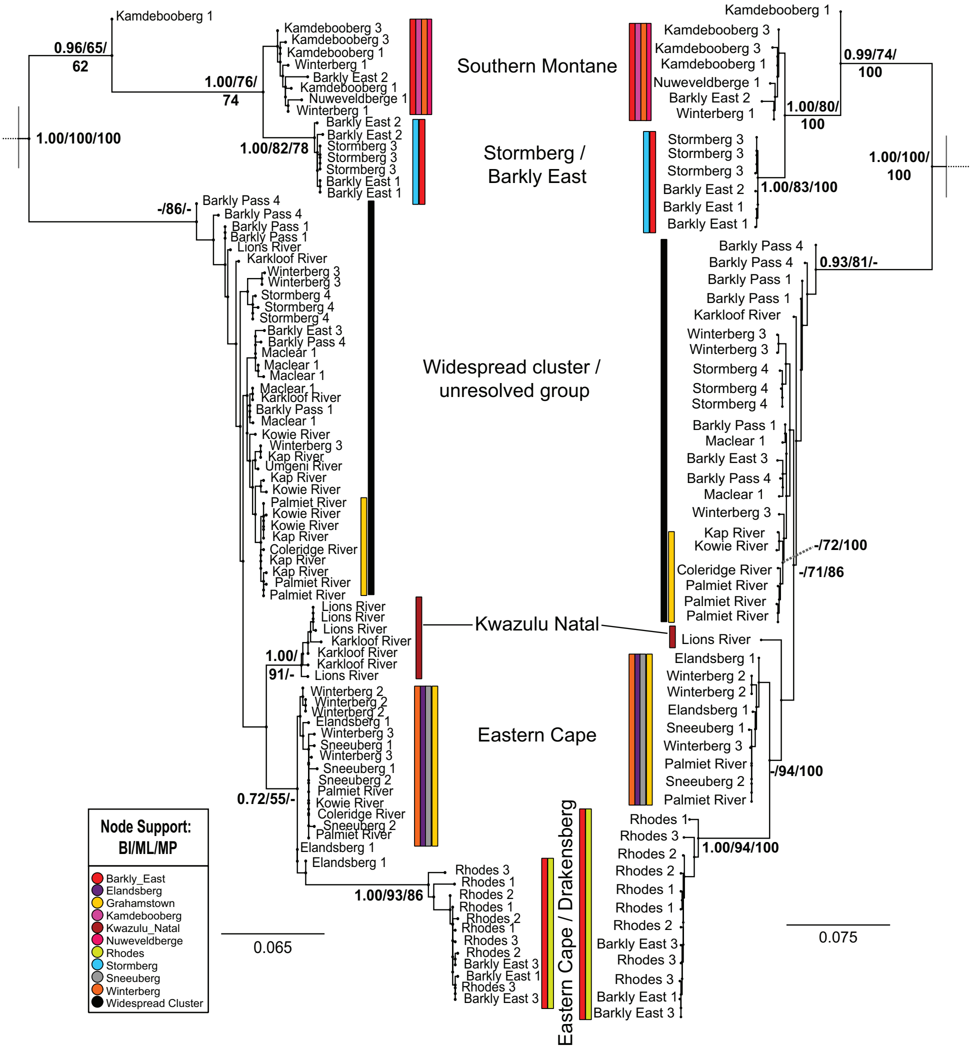

Figure 1. Bayesian inference phylograms of *A. sudafricanum* for gene markers COI (left) and COI + 16S (right). Support for major nodes shown in the order Bayesian Inference / Maximum Parsimony / Maximum Likelihood (BI/ML/MP). Bars next to clades refer to distinct clades that are colour-coded according to the study areas found within that clade (see colour legend), except for the widespread grade which is designated by a solid black line. Branches bearing outgroups have been omitted to save space and their position is depicted by a dashed line.

tain Escarpment block (Eastern Cape Drakensberg, in two study areas: Barkly Pass and Maclear; Figs 3, 4). Haplotypes were clustered according to a broad geographical structure, which correspond to clades from the phylogenetic analyses (Fig. 1). The numerous missing mutational steps in the haplotype network (Fig. 3) suggest that more sampling is needed for some clusters, particularly between sites that are separated by long sampling gaps (for example, the non-Escarpment sites). Other clusters that are separated

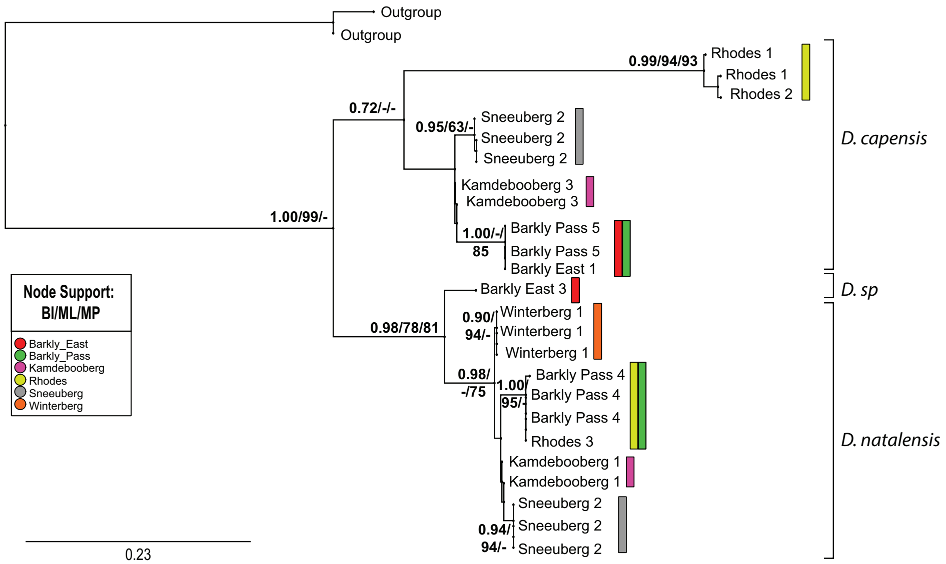

Figure 2. Bayesian inference phylogram of *Demoreptus* spp for the COI gene marker. Support for major nodes is shown in the order Bayesian Inference / Maximum Parsimony / Maximum Likelihood (BI/ML/MP). Bars next to clades refer to distinct clades that are colour-coded according to the study areas found within that clade (see colour legend). *Baetis rhodani* Pictet was used as the outgroup.

by numerous missing intermediates could represent cryptic species or relict lineages that have re-joined the metapopulation (Hinojosa et al. 2019) (encircled with dashes in Fig. 3). The divergent Haplotype 27 from the Kamdebooberg did not cluster with the other haplotypes from the same area and may represent such a lineage. The widespread grade showed little geographic structure, and all haplotypes from Stormberg (Hap 51, 52 and 53) grouped together exclusively, otherwise all other sites are mixed.

The MJN analyses for *D. capensis* retrieved eight haplotypes (Hd = 0.9273, S = 101), six of which were singletons and *D. natalensis* retrieved six haplotypes (Hd = 0.8636, S = 21) including three singletons (Fig. 5). Haplotypes were largely site-restricted for both species with the exception of Haplotype 1 ($N = 3$) for *D. capensis* and Haplotype 4 ($N = 3$) for *D. natalensis* (study areas Barkly Pass and Rhodes), which are both found in the Eastern Cape Drakensberg main mountain block in the Escarpment (Fig. 4). Both networks show many missing mutational steps between haplotypes grouped by locality, which could result from undersampling or haplotype filtering.

Nucleotide diversities (P_i) are reported in Table 3 and are not interpreted further because the small sample sizes for *Demoreptus* spp. make the estimates imprecise. Neutrality tests (Tajima's D and Fu's F_S) were not significant for *A. sudafricanum*, *D. capensis* or *D. natalensis* indicating that the nucleotide patterns of variation are consistent with the neutral theory of evolution. Fu's F_S statistic for the widespread grade of *A. sudafricanum* was negative ($F_S = –11.544$) and significant ($P < 0.02$), indicating a recent population expansion (Table 3). The Fu's F_S statistics for *D. capensis* and *D. natalensis* were

Table 3. Haplotype characteristics and Neutrality tests for *A. sudafricanum*, *D. capensis* and *D. natalensis*.

Species	Haplotype characteristic		
	Number of haplotypes (Hap)	Nucleotide diversity (Pi)	Number of variable sites (S)
A. sudafricanum	60	0.07508	129
A. sudafricanum (unresolved)	28	0.01998	67
D. capensis	8	0.08592	101
D. natalensis	6	0.01881	21

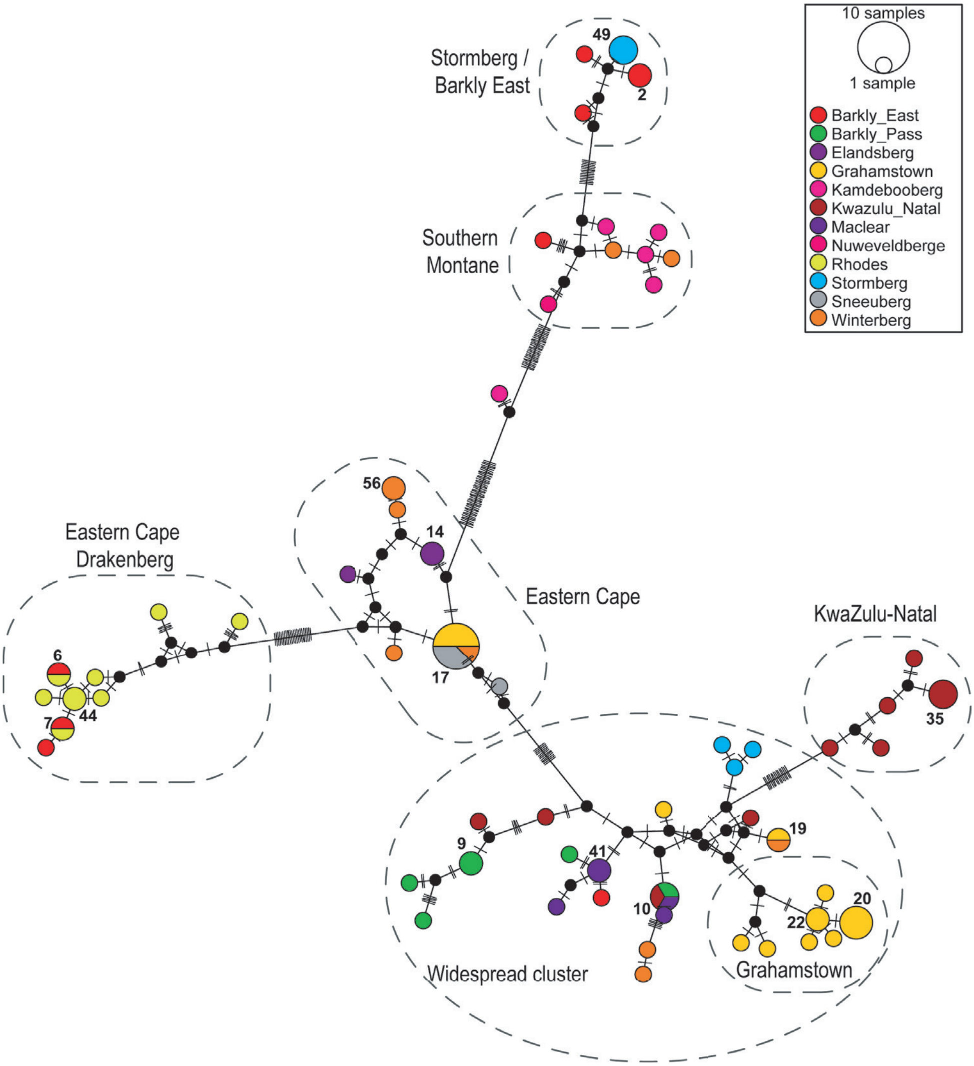

Figure 3. Median-joining network of *A. sudafricanum* based on COI haplotypes generated in this study. The network was estimated using the median-joining algorithm in PoPArt v.1.7 with epsilon = 0. Each circle represents a different haplotype and the size of a circle correlates with the number of individuals assigned to that haplotype. Only haplotypes found in more than one sample are numbered. Colours indicate the geographic origin of sequences; black dots indicate unsampled or extinct haplotypes.

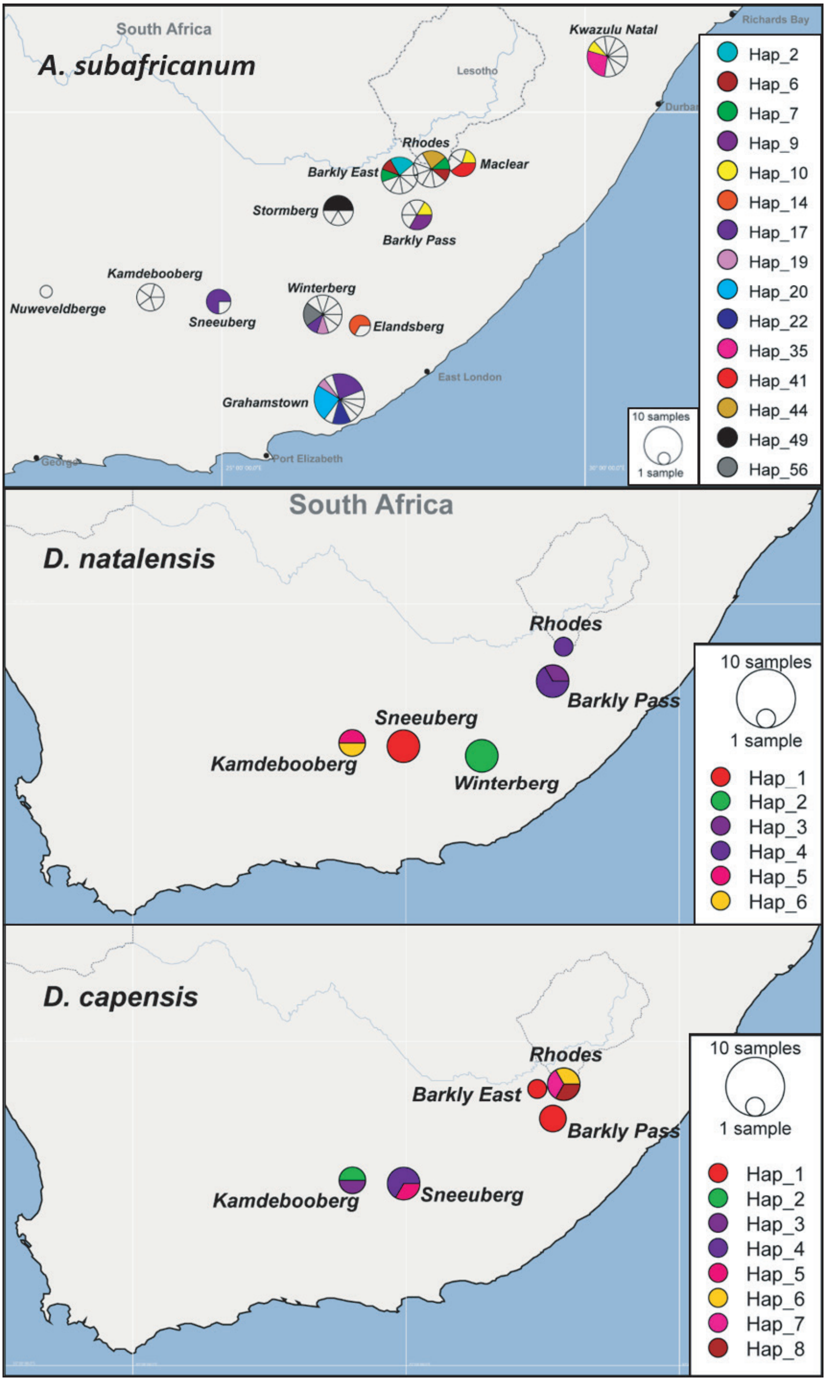

Figure 4. Distribution of *A. sudafricanum*, *D. natalensis* and *D. capensis* COI haplotypes across the study area. The map shows the study areas defined in Table 1, and the pie charts indicate the haplotype composition of the population from each area. Each colour represents a shared haplotype found across the study area; private haplotypes (singletons found in the samples from one particular population and are absent in the samples from other populations) are represented as clear sections within the pie charts.

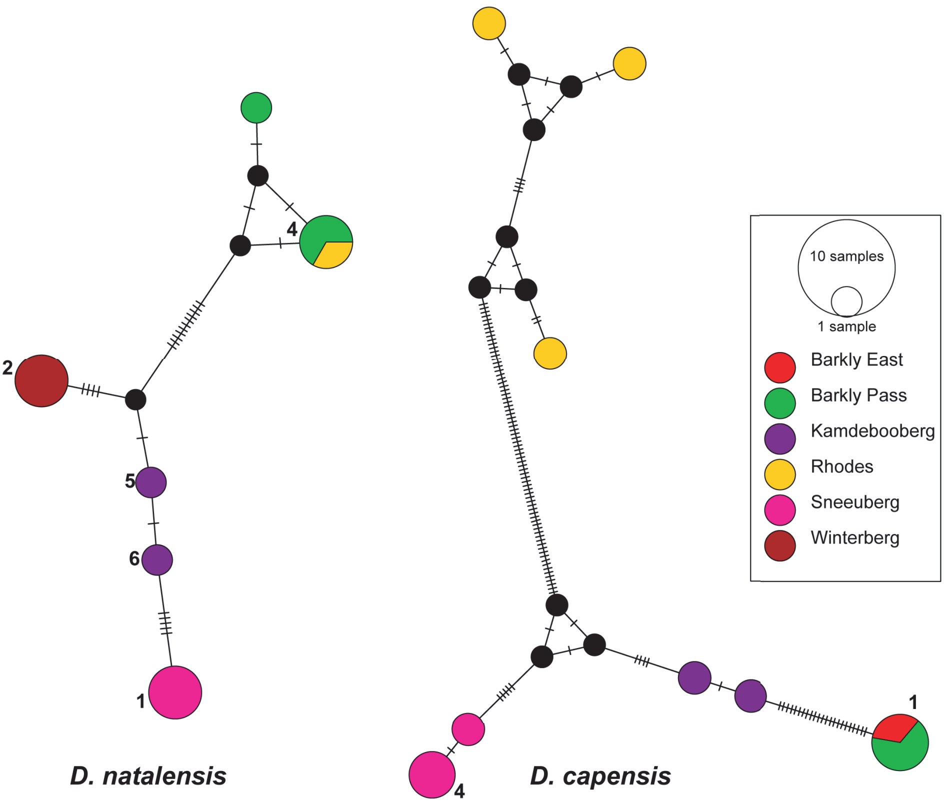

Figure 5. Median-joining networks of *D. natalensis* and *D. capensis* based on COI haplotypes generated in this study. The network was estimated using the median-joining algorithm in PoPArt v.1.7 with epsilon = 0. Each circle represents a different haplotype and the size of a circle correlates with number of individuals belonging to that given haplotype. Only haplotypes found in more than one sample are numbered. Colours indicate the geographic origin of sequences; black dots indicate unsampled or extinct haplotypes.

positive, indicating a deficiency of alleles as expected from a population bottleneck, but they were not significant and need a larger sample size to confirm these results.

The AMOVA results for *A. sudafricanum* revealed that over all localities, 52.33% of the total variance was explained by variation among populations (df = 10, Va = 12.073) while 47.67% (df = 75, Vb = 10.998) was explained by variation within populations (Table 4). A similar result was found with the widespread grade of *A. sudafricanum*, with 39.43% of the total variance explained by variation among populations (df = 5, Va = 2.238) and 60.57% (df = 28, Va = 3.438) explained by variation within populations. In contrast, the AMOVAs for the habitat-restricted species, *D. capensis* and *D. natalensis*, indicated a higher proportion of variation among populations: 94.83% (df = 4, Va = 24.950) and 95.39% (df = 4, Va = 5.423), respectively (Table 4). The total variance explained by variation within populations was only 5.17% (df = 6, Vb = 1.361) for *D. capensis* and 4.61% (df = 7, Vb = 0.262) for *D. natalensis*.

Table 4. One-level AMOVA results for *A. sudafricanum*, *D. capensis* and *D. natalensis* showing percentage variation among and within populations and the fixation index (F_{ST}). Significant p-values (< 0.05) are set in bold.

Species/clade	% variation		F_{ST}
	Among	Within	
A. sudafricanum	52.33	47.67	**0.52327**
A. sudafricanum unresolved group	39.43	60.57	**0.39426**
D. capensis	94.83	5.17	**0.94827**
D. natalensis	95.39	4.61	**0.95393**

The measure of population differentiation due to genetic structure (F_{ST}) was much lower for *A. sudafricanum* compared to the *Demoreptus* species (Table 4). The widespread grade for *A. sudafricanum* had a very low F_{ST} value of 0.39 while *D. natalensis* and *D. capensis* had very high F_{ST} values of over 0.94 (Table 4).

Discussion

This study considered evidence of the phylogenetic structure of three species of Baetidae corresponding to two different habitat requirements. Results indicate that habitat-restricted *Demoreptus* species have greater maternal genetic structure than widespread *A. sudafricanum*, showing notable genetic differentiation associated with geographic localities and catchments. This is evident from the haplotype networks in a MJN analysis, F_{ST} values from an AMOVA and the phylogeographical structure indicated by phylogenetic trees.

Phylogeographical structure of habitat generalist, *A. sudafricanum* retrieved six distinct, well-supported clades and one widespread grade of individuals from widespread (Escarpment and non-Escarpment) sites across the sampling area. *Afroptilum sudafricanum* was best represented with a haplotype network (Fig. 3), particularly for the widespread grade as the samples have evolved over such a short time that ancestral and descendant haplotypes exist concurrently, and so it remains unresolved in the hierarchical tree. The species occupies a range of habitats from still to flowing rivers. Remarkably, shared haplotypes (Haps 10, 17, and 19) were identified between Escarpment and non-Escarpment sites, some over 300 km apart (Hap 10), across various mountain chains and differing in altitude by over 900 m (Fig. 4). The genetic differentiation within *A. sudafricanum* is not attributed to purely geographic location or catchments. Most clades seen in both the hierarchical trees and haplotype networks include sites that are widely spread across sampled catchments and mountain blocks, with the exception of one clade that occurs only in the Eastern Cape Drakensberg (Rhodes and Barkly East). Even if *A. sudafricanum* is treated as a species complex and assessed for mitochondrial genetic differentiation, results indicate low divergence between populations, suggesting that gene flow is not particularly limited within catchments and across the geographic range. Although mayflies are traditionally thought to have limited dispersal ability due to weak flight and short adult lifespans (Brittain and

Sartori 2003, Monaghan et al. 2005, Gattolliat et al. 2008), some mitochondrial clades within *A. sudafricanum* are remarkably widespread. These results support studies indicating that long-distance dispersal is in fact more prevalent in mayflies than previously thought (Monaghan et al. 2005, Gattolliat and Staniczek 2011, Pereira-da-Conceicoa et al. 2012, Vuataz et al. 2013, Rutschmann et al. 2016).

The habitat specialist species, *D. natalensis* and *D. capensis* are rheophilic and found on rock faces associated with waterfalls and large bedrock sections in shallow but fast-flowing sections of mountain streams. Analyses indicate restricted gene flow over distance and across catchments, a possible consequence of isolation by habitat limitations in mountainous areas. Distinct clades retrieved from phylogenetic analyses show a close association with geographic locality. *Demoreptus natalensis* returned clades and haplotypes exclusive to Sneeuberg and Winterberg areas; the Eastern Cape Drakensberg clade included two study areas (Barkly Pass and Rhodes areas); and Kamdebooberg was unresolved. *Demoreptus capensis* had a similar result, but the Rhodes area returned a separated clade with a well-supported, long branch. Suggestively, the samples of *A. sudafricanum* and *D. capensis* collected at Rhodes both occupy long branches in their respective phylogenetic analyses (Figs 2, 3). These sites are from the highest regions of the study (2600 m.a.s.l.) on the slopes of Ben MacDhui. This may indicate a historical isolation event or an accelerated local rate of molecular evolution (perhaps through faster fixation in smaller populations) responsible for the pattern observed.

Preliminary re-examinations indicate morphological differences between *D. capensis* from Rhodes and *D. capensis* from other localities, and between *D. natalensis* from Barkly East and *D. natalensis* from other localities (HMBJ, pers. obs.); these characters will be documented in a subsequent taxonomic study. Other areas in the Drakensberg range in KwaZulu-Natal and Lesotho should be sampled to investigate the range of this mitochondrial clade and whether it occurs throughout high altitude, mountainous areas. A caveat is that the *Demoreptus* population analyses involve limited sample sizes from few localities, which can produce misleading clustering (Phiri and Daniels 2014, Hinojosa et al. 2019), and that sampling more localities can address this concern (Phiri and Daniels 2014). Furthermore, mitochondrial genes are inherited asexually and maternally, and may represent gene flow differently from sexually-inherited, recombining nuclear genes (Hinojosa et al. 2019), so quantifying nuclear gene diversity is also necessary to clarify this situation.

Previous studies on South African species have found genetic differentiation according to catchments in both animals with limited dispersal ability (Wishart and Hughes 2001, 2003, Daniels et al. 2009, McDonald and Daniels 2012, Tolley et al. 2014, Barber-James and Pereira-da-Conceicoa 2016) and terrestrial insects with high vagility (Price et al. 2007, 2010). The unexpected limited dispersal potential of cicadas was attributed to their habitat philopatry (Price et al. 2010) and host-plant specificity (Price et al. 2007). Similarly, *D. natalensis* and *D. capensis* are restricted by their habitat, and subsequently show high levels of genetic differentiation. Similar limitations to gene flow have been found in various other mountain-restricted aquatic insects (Hughes et al. 2003, Wishart and Hughes 2003, Finn et al. 2006, Lehrian et al. 2010).

The high support values for some geographically localised clades within *A. sudafricanum* and the two *Demoreptus* species could indicate the presence of cryptic species or local haplotype filtering and mutation due to protracted isolation (Hinojosa et al. 2019). Mountain-dwelling populations are often fragmented and under-sampled (Phiri and Daniels 2013), and the reported low diversity of Baetidae in most areas of Africa has been attributed to the lack of data and comprehensive analysis of material collected by taxonomists (Gattolliat et al. 2008). Intensive sampling over large geographical ranges usually results in the discovery of numerous new taxa and the extension of distribution ranges (Gattolliat et al. 2008). Cryptic taxa are not uncommon in aquatic insects (Wishart and Hughes 2003, 200, Pereira-da-Conceicoa et al. 2012). Since the 1980s there has been an exponential increase in the number of studies on cryptic species, partly due to the introduction of the PCR, which resulted in the increasing availability of DNA sequences (Bickford et al. 2007). Molecular (DNA) methods are valuable in resolving morphologically cryptic lineages and have been used extensively in discriminating species with few or no morphological differences (Jackson and Resh 1998, Rutschmann et al. 2014, Leys et al. 2016, Tenchini et al. 2018). Within the Ephemeroptera, cryptic lineages have been discovered in numerous families through electrophoretic studies (Sweeney and Funk 1991, Zloty et al. 1993, Funk and Sweeney 1994) and, more recently, DNA sequence data (Williams et al. 2006, Ståhls and Savolainen 2008, Pereira-da-Conceicoa et al. 2012).

The observed deep haplotype divergences in all three species studied and the recent population expansion in *A. sudafricanum* may be explained by possible Quaternary glaciation in the Drakensberg area, where small glaciers formed as low as 2100 m on south-facing slopes (Lewis and Hanvey 1993, Lewis and Illgner 2001, Grab 2002, Mills and Grab 2005, Lewis 2011, Mills et al. 2012). Small remnant populations in non-glaciated areas at high altitude would have been isolated for some time which may explain the long branch patterns seen in *D. capensis* and *A. sudafricanum* for high altitude populations from Rhodes in the Eastern Cape Drakensberg. Glaciation would exacerbate the difficulty of finding suitable habitats more for *Demoreptus* spp. than for *A. sudafricanum*, which can find suitable habitats at lower altitudes). However, the evidence available for this niche glaciation is considered by some as ambiguous and unclear (Osmaston and Harrison 2005). Cyclical climate changes from the Pleistocene to present interglacial (Dingle and Rogers 1972, Siesser and Dingle 1981) could have resulted in historic population fluctuations including expansions, bottlenecks, drift and allele fixation (especially for *A. sudafricanum*).

However, because they are asexually and maternally inherited, strongly divergent haplotypes that originated in relict populations may not reflect contemporary mating pattern if those isolated populations' ranges subsequently expand to restore potential panmixis (Hinojosa et al. 2019). More samples and an investigation of nuclear genetic diversity are necessary to get any further resolution into the patterns observed.

Perspectives

These results help to illuminate some of the evolutionary processes occurring in mayfly species and highlight the effect of habitat-specificity on haplotype diversity and partitioning within a species. While all three species have qualitatively similar levels of dispersal potential in terms of flight, they show differences in gene flow, suggesting that other processes, such as species-specific habitat requirements, may contribute to genetic population structure. These results have implications for the conservation of riverine organisms, the reintroduction of locally extinct taxa and the rehabilitation of disturbed environments (Jump et al. 2009, Razgour et al. 2019).

In South Africa, it is legislated that catchments are used as management units (Republic of South Africa 1998). Previous studies on the genetic population structure of winged aquatic insects in South Africa have further supported the use of catchments as units for conservation (Wishart and Hughes 2003, Wishart et al. 2003, Price et al. 2010). The results found here for *D. capensis* and *D. natalensis* further highlight the genetic distinctiveness of populations between catchments, further corroborating the value of using catchments in conservation, management and legislative frameworks. These genetically distinct populations form an important component in the evolutionary legacy of a species. Therefore, the development of inter-basin water transfer schemes poses a threat to both *D. capensis* and *D. natalensis* and many other species by potentially connecting historically isolated and genetically distinct populations (Snaddon and Davies 1998, Davies et al. 2000)

In addition, dispersal among adjacent catchments has implications for the recovery of lotic systems following disturbance (Wishart and Davies 2003, Bellingan et al. 2019, Razgour et al. 2019). These factors should be considered in the development of strategies for the conservation of aquatic biodiversity (Wishart 2000, Thieme et al. 2007, Castello et al. 2013, Bellingan et al. 2019), and most particularly for high altitude catchments.

This study highlights the importance for future studies on community structure, biodiversity, and biomonitoring, where the taxonomic accuracy of species identification is crucial (Hajibabaei et al. 2016). The identification of possible cryptic species in *A. sudafricanum* and new species of *Demoreptus* affect the field of aquatic research in South Africa. Mayflies form a very important component of applied aquatic biology, particularly biomonitoring, the presence of cryptic taxa is being discovered at an increasing rate and poses challenges for some aquatic ecosystem monitoring methods. With bioassessment methods gaining increasing popularity, a detailed understanding of commonly collected species will aid in further development of assessment methods and clarify species identification (Delić et al. 2017, Suh et al. 2019). In addition, a deeper understanding of evolutionary processes and gene flow with regard to commonly occurring mayfly taxa contributes to broader research on ecosystem functioning and environmental processes. The utility of DNA barcoding for elucidating such phenomena is already proven (Jackson and Resh 1998, Plaisance et al. 2009, Raupach and Radulovici 2015) and widely used, with new technologies allowing for the rapid assessment of biodiversity using DNA metabarcoding (Pavan-Kumar et al. 2015, Elbrecht et al. 2017, Daravath et al. 2018, Alvarez-Yela et al. 2019). This approach to rapid biodiversity assessment has the potential to revolutionise and streamline management and conservation practices by providing detailed data for informed decision- and policy-making.

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Supplementary material 1

List of GenBank sequence accession numbers for each sample

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RESEARCH ARTICLE

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Island mysteries in the spotlight: *Barbitistes kaltenbachi* and *Rhacocleis buchichii*, the only bush-cricket species endemic to Croatia (Orthoptera, Tettigoniidae)

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Abstract

Hvar Saw Bush-cricket *Barbitistes kaltenbachi* Harz, 1965 (Phaneropterinae: Barbitistini) and Lesina Bush-cricket *Rhacocleis buchichii* Brunner von Wattenwyl in Herman 1874 (Tettigoniinae: Platycleidini) are flightless orthopterans restricted to a narrow area in the Mediterranean part of Croatia, both originally described from Hvar Island. In this study, all available information on these two interesting species is presented: data on morphology, bioacoustics, distribution, habitat, and a key to identification of the species belonging to genera *Barbitistes* and *Rhacocleis* in Croatia. The songs of both *B. kaltenbachi* and *R. buchichii* are described here for the first time, with the former one being the second known example of a synchronising and presumably duetting species. Both species were reassessed according to the IUCN Red List criteria, where *B. kaltenbachi* should be considered an endangered species, while *R. buchichii* is suggested to be downgraded to a less threatened category. Biogeography and evolution of the species are briefly discussed.

Keywords

Adriatic, Barbitistini, bioacoustics, Biokovo, Dalmatia, duet, ecology, Endangered, flightless, Hvar, IUCN Red List, Platycleidini, systematics, Vis Island, Vulnerable

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* Authors of equal contribution.

Introduction

Despite two centuries of research on Orthoptera in Croatia (Skejo et al. 2018), the only two bush-crickets endemic to the country, Hvar Saw Bush-cricket *Barbitistes kaltenbachi* Harz, 1965 and Lesina Bush-cricket *Rhacocleis buchichii* Brunner von Wattenwyl in Herman 1874, have escaped the eyes and ears of many researchers for quite some time. The knowledge of their distribution and biology is based merely on scattered documentation, with temporally and spatially well separated findings (Herman 1874; Harz 1965, 1969; Gausz 1970; Warchałowska-Śliwa et al. 2013; Wagner 2015; Puskás et al. 2018; Skejo et al. 2018).

Both species were originally described from the Island of Hvar (*Lesina* in Italian), one of Croatia's Adriatic islands, belonging to the Central Dalmatian archipelago. Until now *Barbitistes kaltenbachi* has been regarded as a Hvar-endemic, while *Rhacocleis buchichii* has been found on other Dalmatian islands (Puskás et al. 2018) as well as in mainland Croatia (Gausz 1970, Wagner 2015, Skejo et al. 2018). The same is true for most other Orthoptera species that were originally regarded as Hvar-endemics, such as *Paramogoplistes novaki* (Krauss, 1888), *Chorthippus mollis lesinensis* (Krauss, 1888) and *Pholidoptera dalmatica maritima* Zeuner, 1931 (Willemse et al. 2009; Rebrina and Brigić 2017; Puskás et al. 2018; Skejo et al. 2018).

Since so little has been published about *Barbitistes kaltenbachi* and *Rhacocleis buchichii*, the authors of the current paper felt the need to present a comprehensive overview of the information available. This paper is written around RF's finding of both species on the Island of Vis, well outside their formerly known distribution areas (briefly mentioned in Skejo et al. 2018). KGH's records of *B. kaltenbachi* from two sites on Hvar Is. (briefly mentioned in Warchałowska-Śliwa et al. 2013; Rebrina 2014; Skejo et al. 2018) are presented in more detail, together with a comprehensive analysis of the bioacoustics of the species. Unpublished records of *R. buchichii* are presented, together with an overview of the published data. Distribution, habitat, ecology, and possible evolutionary patterns of *B. kaltenbachi* and *R. buchichii* are discussed. To facilitate recognition in the field, an identification key to the Croatian species of *Barbitistes* and *Rhacocleis* is provided.

Materials and methods

Study area

The Central Dalmatian islands (Fig. 1) form a tectonic unit composed of the geomorphologically similar islands of Vis, Hvar, and Brač (Borović et al. 1977). Unlike the typical *Dalmatian orientation* (direction NW to SE) exhibited by the majority of islands in the Adriatic Sea, these islands show *Hvar orientation* (direction W to E), witnessing their shared geological history. The Central Dalmatian islands harbour diverse habitats, e.g., rocky hills, small patches of forest, meadows (karst-poljes), ponds, and dry valleys. The backbone of the islands is formed by Mesozoic ridges of limestone and/or dolomite rock. The islands were connected to the Croatian and Italian mainland, by the ancient Po or Adriatic valley until approximately 11000–12000 years ago, when the sea level rose and the islands became separated (Lozić et al. 2012, Maselli et al. 2014). The Dalmatian coast is, just like the islands, warm and dry, with annual precipitation of only 700–900 mm. Isolated mountains (Svilaja Mt., Mosor Mt., and Biokovo Mt.) in the mainland have a mixed upper belt, rich in Mediterranean biota, with rare continental and oro-Mediterranean elements (Skejo et al. 2018).

Identification and taxonomy

Specimens were identified using Harz (1969), the original species descriptions (Herman 1874; Harz 1965) and photographs of the type material on the Orthoptera Species File (Cigliano et al. 2019). Taxonomy follows the Orthoptera Species File (Cigliano et al. 2019).

Institutional abbreviations

Specimens mentioned in this paper are deposited in the following collections:

KGHC	Klaus-Gerhard Heller Collection
MfN	Museum für Naturkunde, Berlin, Germany
NBC	Naturalis Biodiversity Center, Leiden, the Netherlands
NHMUK	Natural History Museum, London, UK
NMW	Naturhistorisches Museum Wien, Vienna, Austria
RFPC	Rob Felix Collection, Nijmegen, the Netherlands
ZSZJS	Natural History Museum Split: Josip Skejo Collection, Split, Croatia

Measurements

Body length (from the frons to the tip of the abdomen), pronotum length in dorsal view, hind femora length, and ovipositor length (in females), were measured with a calliper of 0.1 mm precision.

Analyses of *Barbitistes* bioacoustics

Male song (including the male-versus-male-interaction duets) was usually recorded in the evening, using a Sony WM-D3 cassette recorder and a SONY TCD-D7 DAT recorder with microphones Uher M 645 (Uher, Munich, Germany) and Sony ECM-121 (Sony, Tokyo, Japan). For the interactions (20 min duet recordings; 6 males) two males were placed separately, each in a plastic tube (Drosophila tube 28.5 × 95 mm, Biosigma, Cona (VE), Italy), standing side by side and each with a microphone placed inside (or on top of) the tube. Both microphones typically picked up both male sounds, but with quantifiable differences in amplitude. The output of each microphone was registered as a track of a stereo recording. After digitising the songs on a computer (sampling rate 44.1 kHz), oscillograms (after high pass filtering, typically around 1 kHz) and sound analyses were made using the following software: Turbolab (TL 4.0, Stemmer, Puchheim, Germany), Amadeus (Amadeus II, Martin Hairer, http://www.hairersoft.com), Audacity (Audacity 2.1.0; http://audacity.sourceforge.net) and Canary (Canary 1.2.4; Cornell Laboratory of Ornithology) on Apple. Due to the recorders' restricted frequency response, data on frequency were not evaluated. Each data point for the time pattern is based on not less than 20 independent measurements (except series data), given as mean ± standard deviation (SD) and coefficient of variance (CV) (see Suppl. material 3).

Analyses of *Rhacocleis* bioacoustics

Two sound recordings of two different individuals of this species have been made by Roy Kleukers (see Material examined under *Rhacocleis buchichii*), using a DCC-recorder (Philips DCC175) with a Shure Prologic condenser microphone. Sound recordings have been made in simple studio conditions at night, at 26–27 °C. Although the recordings are digital, some frequencies inaudible to humans were automatically removed before digitisation. Also, frequencies above ca. 20kHz are missing completely. The sound recordings are therefore not very useful for the analysis of frequencies. Yet, they are useful for temporal analysis of the song.

Temporal characters have been measured for both sound recordings using Wavelab 10 software (www.steinberg.net). A high pass filtering at 500Hz using phonetic software Praat 6.0.39 (www.praat.org) preceded the preparation of oscillograms for the Pitve specimen only.

Bioacoustic data of other *Rhacocleis* species has been derived from Ragge and Reynolds (1998), Heller (1988), and Massa et al. (2012) (analysis of the song of *R. japygia* by Paolo Fontana).

Bioacoustics terminology

Syllable. sound produced during one cycle of wing movements. In *Barbitistes* only pulse-like closing hemi-syllables are known (Heller 1988) (Fig. 5A). In *Rhacocleis* both opening and closing hemi-syllables can be recognised; **trigger syllable**: pronounced syllable (*sensu* Stumpner and Meyer 2001); **syllable period**: time period measured from the beginning of a syllable to the beginning of the next; **echeme** (*sensu* Ragge and Reynolds 1998) or **chirp** (*sensu* Stumpner and Meyer 2001): a first-order assemblage of syllables; **verse**: a combination of echeme and trigger syllable; **verse period**: time period measured from the beginning of a trigger syllable to the beginning of the next (reciprocal value verse repetition rate). Details on songs of other *Barbitistes* and *Rhacocleis* species used for comparison can be found in Heller (1988), Ragge and Reynolds (1998) and Massa et al. (2012). For details on when and where *Barbitistes*-recordings were made see Suppl. material 3.

IUCN Red List Assessment

Data from the previous IUCN assessments for *B. kaltenbachi* (Chobanov et al. 2016) and *R. buchichii* (Skejo 2014; Hochkirch 2016a) were used, together with the new data presented in this study to calculate new values of AOO (area of occupancy) and EOO (extent of occurrence) using GeoCAT Editor (Bachman et al. 2011) (available at http://geocat.kew.org). IUCN criteria were applied to suggest new Red List status qualifications for both species (IUCN 2001).

Results

Family Tettigoniidae Krauss, 1902
Subfamily Phaneropterinae Burmeister, 1838
Tribe Barbitistini Jacobson, 1905

Barbitistes kaltenbachi Harz, 1965

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:10819
Figures 1–8
eng. Hvar Saw Bush-cricket, *hrv.* Kaltenbachov ljuskokrili konjic, *deutsch.* Hvar Säbelschrecke

Barbitistes kaltenbachi Harz, 1965: Harz (1965): 443 (description of the species from Brunner von Wattenwyl's collection, 12 ♂♂ syntypes, and 16 ♀♀ syntypes, depicted in details, measured, based on males and females from Hvar Is., and a female from Trieste) (see Fig. 2);

Barbitistes kaltenbachi Harz, 1965: Harz (1969): 75 (included in the key to species of the genus in Europe, depicted in details in figs 224, 237, 242–243, described and measured, cited from Hvar Is., and mentioned from a few mainland localities: Lukovo, Rijeka, Trieste);

Barbitistes kaltenbachi Harz, 1965: Galvagni and Fontana (1993): 204 (comparison with newly described *B. vicetinus*);

Barbitistes kaltenbachi Harz, 1965: Heller et al. (1998): 25 (listed in the checklist of European Orthoptera);

Barbitistes kaltenbachi Harz, 1965: Massa et al. (2012): 521 (presence in Italy, in the region of Trieste, unlikely);

Barbitistes kaltenbachi Harz, 1965: Warchałowska-Śliwa et al. (2013): 668–669, 671 (reported from Hvar Is., Bogomolje, number and shape of chromosomes determined, as well as sex determination system X0);

Barbitistes kaltenbachi Harz, 1965: Rebrina (2014): 4, 10–11, 14–16, 19, map Karta 1, Photo 1 (distribution in Croatia, Hvar cited as the only confirmed locality, new data from Bogomolje and Sućuraj, E corner of the island of Hvar, presence in Lukovo and Rijeka unlikely, Heller's findings are the first since the description);

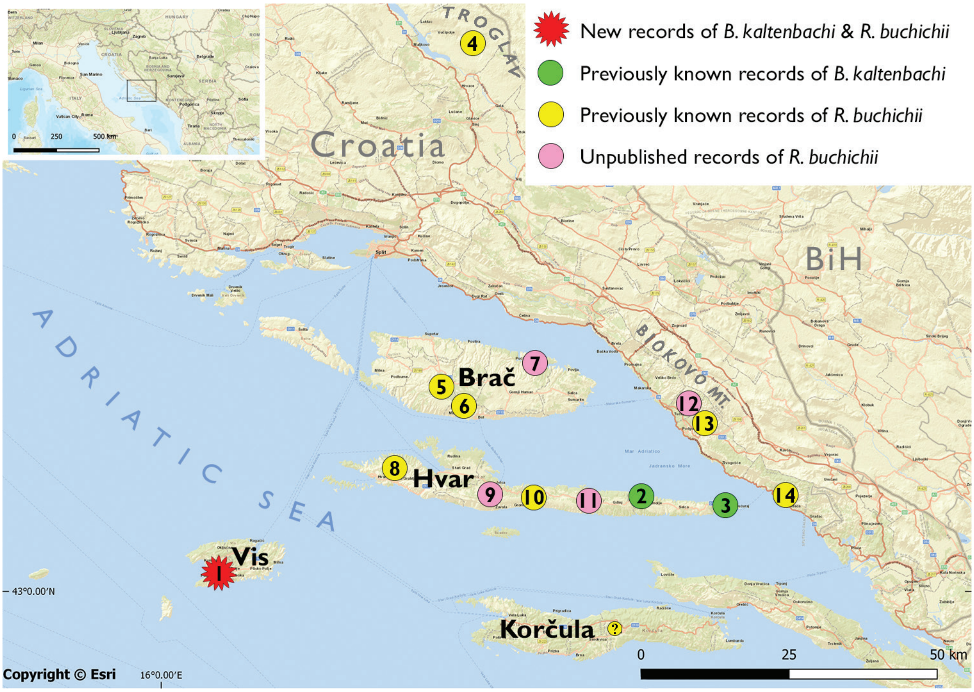

Figure 1. Distribution of the only known endemic bush-crickets (Tettigoniidae) of Croatia: *Barbitistes kaltenbachi* (localities **1**–**3**) and *Rhacocleis buchichii* (localities **1**, **4**–**14**, **?**) **1** new records from Vis Is., Mt. Hum (present paper) **2** Hvar Is., Likova Glava, Bogomolje (present paper; Warchałowska-Śliwa et al. 2013; Rebrina 2014) **3** Hvar Is., Sućuraj (present paper; Rebrina 2014) **4** Velika Greda, Troglav Mt. (Skejo et al. 2018) **5** Brač Is., south of Nere-žišća (Werner 1919) **6** Brač Is., Vidova Gora Mt. above Bol (Puskás et al. 2018) **7** new record from Brač Is., valley near Pučišća (present paper, leg., coll. KGH, 31 May 2006) **8** Hvar Is., Brusje (Novak 1888; Ramme 1951) **9** new record form Hvar Is., Pitve and Vrisnik (leg. R. Kleukers, 13 Aug. 1996, NBC) **10** Hvar Is, Mt. Humac (Novak 1888) **11** new record Hvar Is., between Jelsa and Gdinj (present paper, leg., coll. KGH, 25 Jul. 1982) **12** new record from Biokovo Mt., above Tučepi (present paper, leg., coll. KGH, 28 May 2006) **13** Biokovo Mt. (Wagner 2015) **14** Zaostrog (Gausz 1970) "**?**" presence on Korčula Is. has never been confirmed (Harz 1969).

Barbitistes kaltenbachi Harz, 1965: Hollier and Bruckner (2015): 192 (Reported that type series should consist of 12 ♂♂ syntypes and 16 ♀♀ syntypes labelled 'Insel Lesina' and no specimens are deposited in Natural History Museum in Geneva. Since Harz did not designate a holotype all of the specimens in type series should be considered syntypes. Orthoptera collection in Vienna harbours 31 specimens identifiable as possible syntypes, of which one has been labelled as the holotype, one as allotype, and 16 as paratypes);

Barbitistes kaltenbachi: Chobanov et al. (2016) (assessed as Near Threatened in IUCN Red List);

Barbitistes kaltenbachi: Hochkirch et al. (2016b): 67 (listed among Near Threatened Orthoptera of Europe);

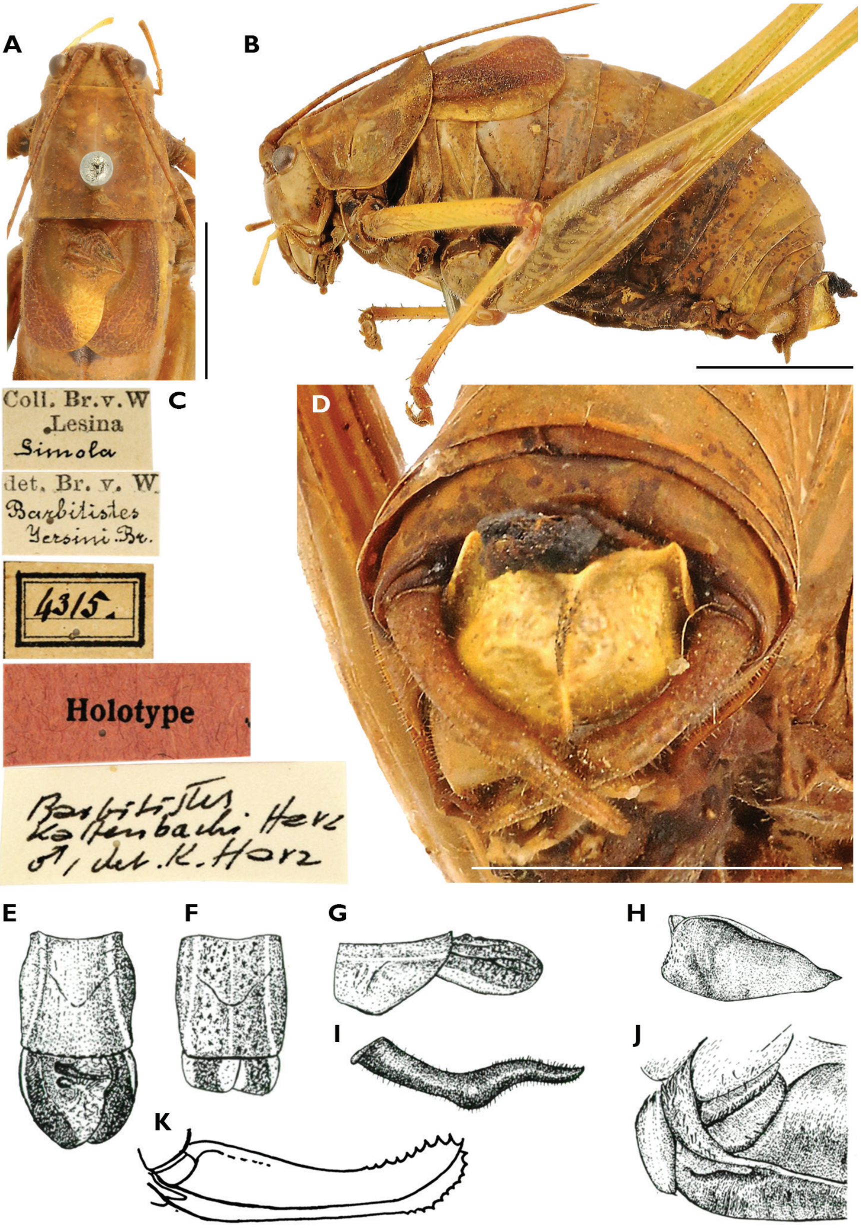

Figure 2. Photos of a syntype male of *Barbitistes kaltenbachi* by G. Puskás taken from OSF (Cigliano et al. 2019) (**A–D**) and drawings from Harz (1965, 1969) (**E–J**). The male specimen is labelled as a holotype, but since Harz (1965) did not designate a holotype, it should be labelled as syntype **A** pronotum and elytra of the syntype male in dorsal view **B** habitus of the male **C** labels of the male syntype **D** tip of abdomen with cerci and subgenital plate of the male **E** dorsal view of pronotum and elytra of a male **F** dorsal view of pronotum and elytra of a female **G** pronotum and elytrae of a male in lateral view **H** subgenital plate of a male seen from rear right **I** cercus of a male **J** base of ovipositor **K** ovipositor. Scale bars: 5 mm. Drawings are not to scale.

Barbitistes kaltenbachi Harz, 1965: Skejo et al. (2018): 19, 21 (endemic to Croatia, distribution in the country presented, as well as Rob Felix's photograph from Hum, Vis Is.).

Type material. Type specimens of *B. kaltenbachi* are deposited in NMW, Vienna. Harz's (1965) description is based on 31 syntypes: 12 males (10 from Lesina (*Italian* for Hvar), 2 from an unknown locality, probably "Dalmatia"), 16 females (12 from Hvar, 1 from Trieste (Italy), 3 with unknown locality) and 3 nymphs from Lesina. A male syntype is erroneously labelled as holotype (Fig. 3).

Material examined. Croatia • 2♂, 1♀; Vis Is., Mount Hum, Crikvica Sv. Duha; alt. 545 m a.s.l.; 43°02.13'N, 16°06.92'E; 21 Jul. 2011; R. Felix leg.; RFPC • 4♂, 2♀; Hvar Is., near Bogomolje, Likova Glava; 30 May 2006; M. & K.-G. Heller leg.; KGHC CH6738, CH6739, CH6740, CH6751, CH6752, CH6754 • 1♂; same data as for preceding; NBC CH6735 • 3♂, 1♀; Hvar Is., Sucuraj; 30 May 2006; M. & K.-G. Heller leg.; KGHC CH6736, CH6737, CH6755, CH6759.

New record on Vis Island. Hvar Saw Bush-cricket was found on 20 and 21 July 2011, near the Chapel of St. Spirit (Crikvica Sv. Duha) at Mount Hum, in the southwestern corner of Vis (43°02.13' N, 16°06.92' E, 545 m a.s.l.) (Figs 1, 3, 4A). Hum is the highest mountain on the island, with a peak reaching 587 m a.s.l. The observed specimens represent the first record of *B. kaltenbachi* on the Island of Vis, and outside of Hvar Is. Four individuals were observed, of which three were collected (see Material examined). Individuals were observed basking in the morning sun on outer leaves of Holm Oak (*Quercus ilex*), at a height of ca. 1.5 meters. *Barbitistes* was accompanied by Long-tailed Speckled Bush-cricket, *Leptophyes laticauda* (Frivaldszky, 1868) and Schmidt's Marbled Bush-cricket, *Eupholidoptera schmidti* (Fieber, 1861) in the same habitat. The collecting site was inspected for only an hour, and a more comprehensive survey would probably have yielded more sightings.

Additional information on morphology. The right tegmen of the female has several rows of stridulatory pegs, in resting position covered by the upper left tegmen. To produce sound, the pegs are probably contacted by the slightly enhanced inner edge or a sclerotised vein on the lower side of the left tegmen.

Distribution. Harz (1965) originally described *B. kaltenbachi* from Hvar Is., Trieste (mainland Italy), and an unspecified locality (see Type material). Later, Harz mentions the species from Rijeka and Lukovo in mainland Croatia (Harz 1969). Massa et al. (2012) point out that the occurrence of *B. kaltenbachi* in mainland Italy (Trieste) is based solely on a female specimen. Since female specimens of *Barbitistes* are very hard to identify to species level, because of a high degree of overlap in interspecific characteristics (Nadig 1987), the record from Trieste is considered unreliable. Furthermore, Harz's records from mainland Croatia are assumed to be based on females and are therefore regarded as doubtful. Therefore, we consider *B. kaltenbachi* as being absent from mainland Croatia and endemic to the Dalmatian Islands.

All known records of *B. kaltenbachi* are shown on the map in Fig. 1 and presented in Table 1. The first records of *B. kaltenbachi* after its description by Harz (1965,

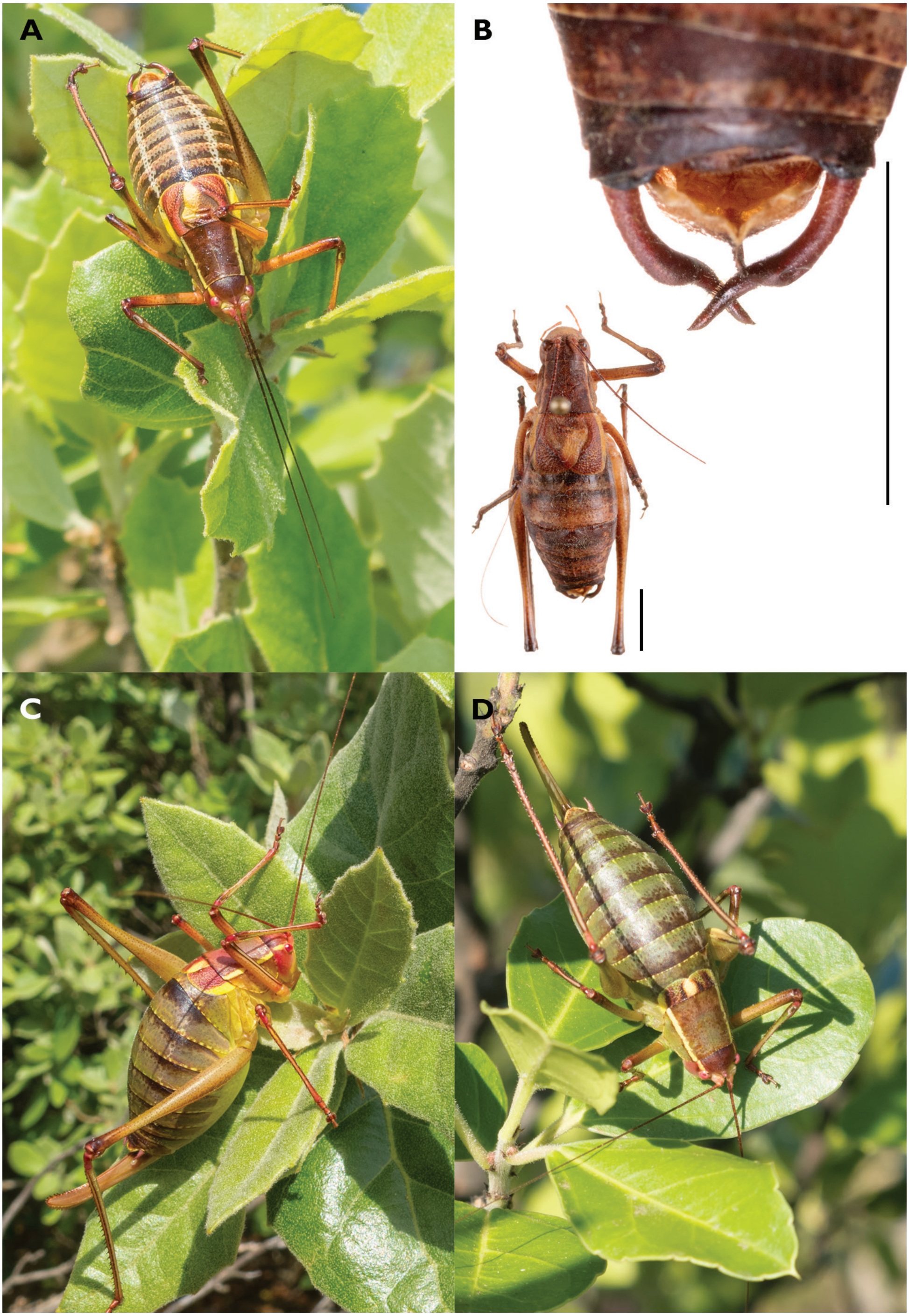

Figure 3. Habitus of *Barbitistes kaltenbachi*, Croatia, Vis Is., Mount Hum, 21 Jul. 2011 **A** male **B** collected male specimen and its cerci **C, D** females (photographs R. Felix). Scale bars: 5 mm.

Table 1. Known records of *Barbitistes kaltenbachi* with data on the sites and collection events. The #map correspond with the numbers in Fig. 1. Type specimens collected by various persons in different events (Harz, 1965) on Lesina (Hvar) are not included in the table, nor are depicted on the map in Fig. 1.

# map	Specimens	Location	Date of collection	Coll.	Reference
1	2♂, 2♀	Vis Is., Mt. Hum, Crikvica Sv. Duha, 43°02.13'N, 16°06.92'E, 545 m a.s.l.	20, 21 Jul. 2011	RFPC	This study
2	5♂, 2♀	Hvar Is., Bogomolje, Likova Glava	30 May 2006	KGHC	Warchałowska-Śliwa et al. (2013), Rebrina (2014)
3	3♂, 1♀	Hvar Is., near Sućuraj	30 May 2006	KGHC	Rebrina (2014)

1969) were the ones by KGH in 2006, on Likova Glava, near Bogomolje, and near Sućuraj, both on Hvar Is. (Fig. 1, 4B). In Warchałowska-Śliwa et al. (2013) and Rebrina (2014) coordinates are provided but after mapping, those appear to be incorrect, and are therefore omitted from Table 1. The distribution on both Hvar Is. and Vis Is. is probably much wider and the presence of the species on nearby islands such as Brač Is., Korčula Is., as well as neighbouring islets, is also possible.

Habitat. No published data on the habitat of *B. kaltenbachi* are available. On Vis Is. the species has been found on bushes and small trees of Holm Oak, in maquis intercepted with scattered patches of grassy vegetation and bare limestone rock (Fig. 4A). The habitat on Hvar Is. is similar to that on Vis Is. but lacks rocky outcrops (Fig. 4B). *Barbitistes* is an arbusticolous genus, as its members are usually living in bushes, shrubs and on low trees (Galvagni and Fontana 1993; Pavićević et al. 2014). Thus, Hvar Saw Bush-cricket inhabits typical *Barbitistes*-habitat.

Song description. The male calling song consists of short (up to ca. 10 ms), pulse-like syllables without clearly recognisable impulses (tooth impacts). Syllables are arranged in a stereotyped pattern. One loud syllable, the *trigger syllable*, assumed to be the marker for female response (Stumpner and Meyer 2001), is followed by a group of two or three (rarely one or four) 'softer' syllables (echeme) (Fig. 5A). The trigger syllables are 6 to 16 dB louder than syllables within the echeme (Suppl. material 3: Table S3.1). After a short interval, the same pattern (verse) is repeated again and again (Fig. 5B). Periods range from 280–400 ms for the verse (verse repetition rate ca. 3 Hz), 120–160 ms for the post- and pre-trigger periods, to 40–50 ms for the syllables in the echeme (Suppl. material 3: Table S3.2). These sequences of verses are variable in duration but may last more than 30 s (Suppl. material 3: Table S3.3), at least while two males are in acoustic contact. During interactions males seem to prefer singing during the other male's song pauses, but they are not inhibited. Songs overlap quite often, even for many seconds. In situations of overlap, males typically synchronise the pattern: they produce trigger syllables nearly at the same time (Fig. 5B, C). The delay between the trigger syllables of two synchronising males is typically below 20 ms (Fig. 5E) and the roles of leader and follower

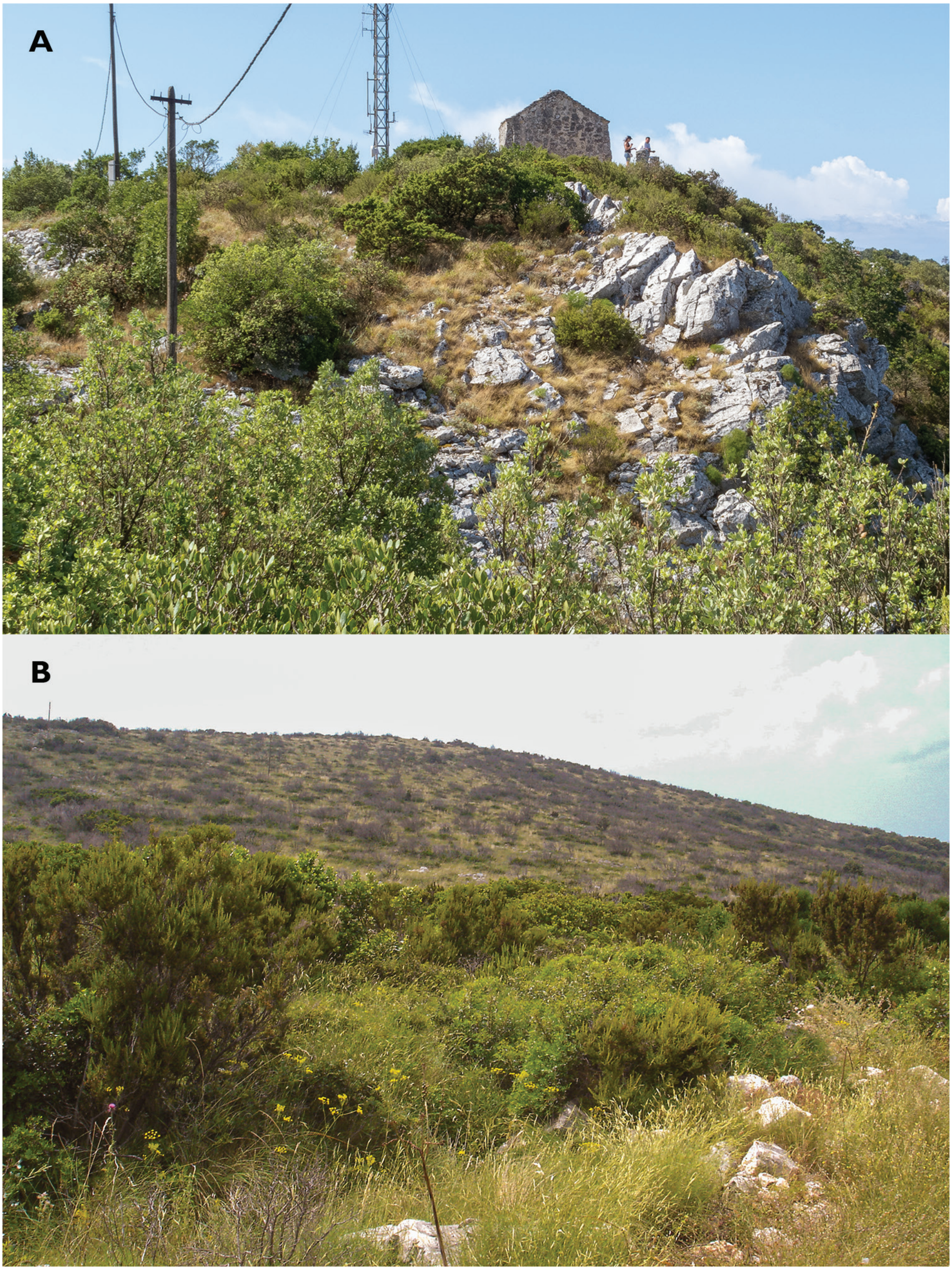

Figure 4. Collecting sites on Vis Is. and Hvar Is., Croatia **A** Vis Is., Mount Hum, St. Spirit Chapel (21 Jul. 2011). This locality is inhabited by both *Barbitistes kaltenbachi* and *Rhacocleis buchichii*. The vegetation is rich in Holm Oak bushes (*Quercus ilex*) (photograph R. Felix) **B** Hvar Is., Likova Glava, Bogomolje (30 May 2006), the habitat of *B. kaltenbachi* (photograph K.-G. Heller).

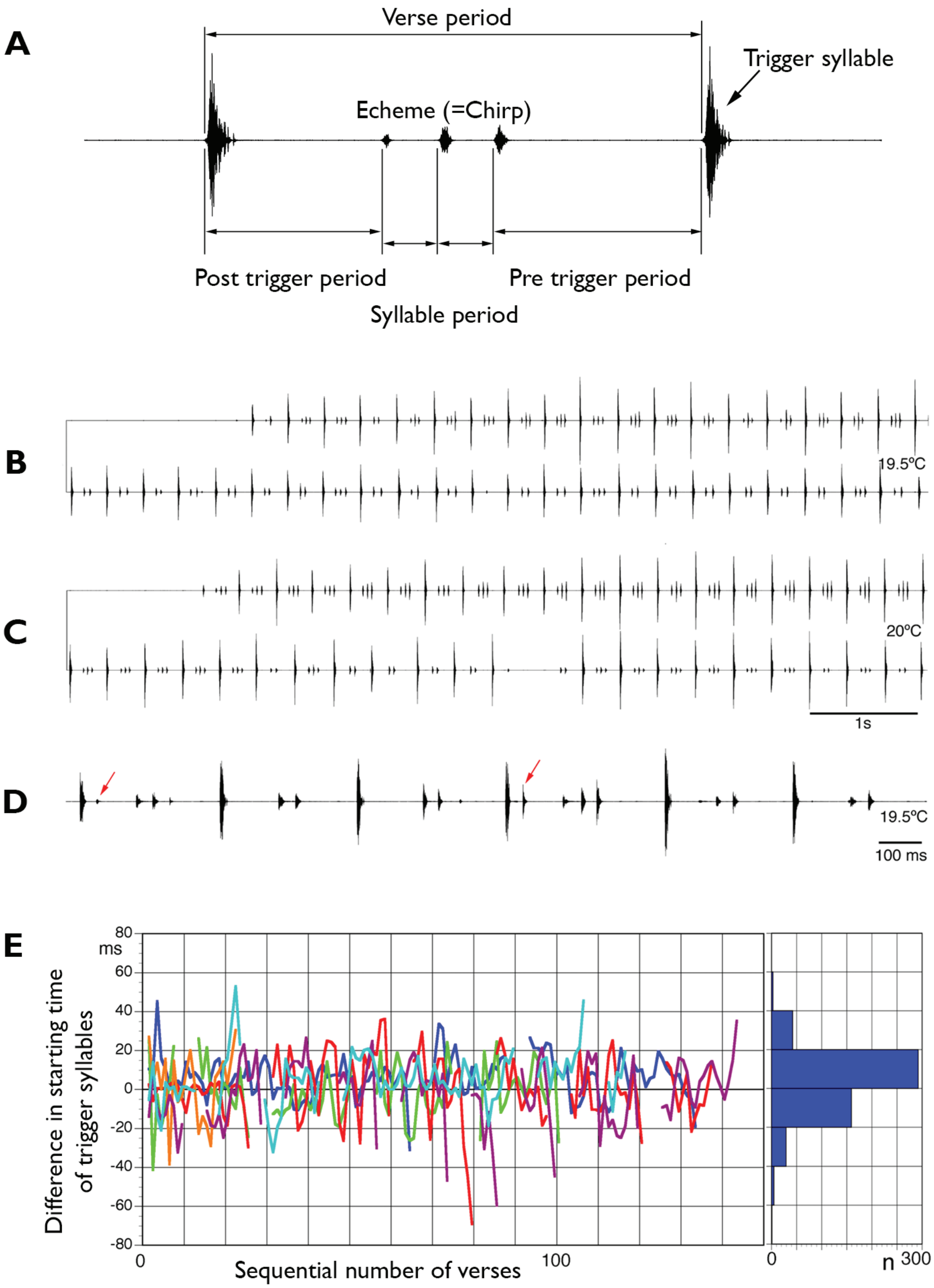

Figure 5. Bioacoustic data of *Barbitistes kaltenbachi* **A** oscillogram showing bioacoustics terminology used in our study **B, C** details of the calling song (sections of 8 seconds) **B** second male starting in synchrony **C** second male starting anti-phasic, first male switching to synchrony **D** male song with extra syllables (red arrows, see text) **E** difference in starting time between the trigger syllables of two duetting males, always referring to a focal male; different colours indicate different male combinations; intervals in the lines mark duet pauses.

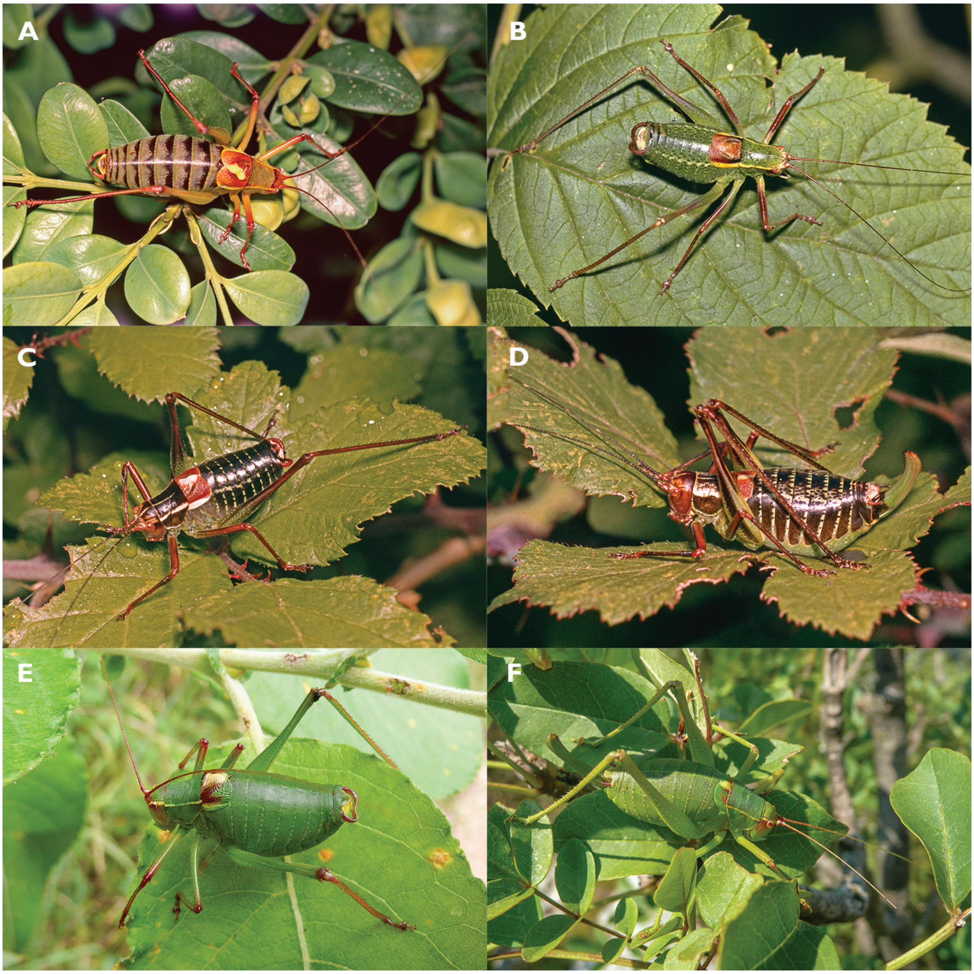

Figure 6. All *Barbitistes* species occurring in Croatia **A** *B. kaltenbachi* (Croatia, Hvar, 30 May 2006) **B** *B. serricauda* (Austria, Obir near Klagenfurt, 13 August 1980) **C** Male *B. ocskayi* (Montenegro, Lovćen pass above Kotor, 26 July 1982) **D** Female *B. ocskayi* (same locality as male) **E** Male *B. yersini* (Croatia, Grabovača, 7 Aug. 2018) **F** Female *B. yersini* (Croatia, Sniježnica, 20 Aug. 2018) (**A–D** photos K.-G. Heller **E, F** photos F. Rebrina).

change often. After disturbances males are able to reach synchronicity within a few periods. Quite rarely, males add extra syllables (*sensu* Stumpner and Meyer 2001), ca. 50 ms after the trigger syllable (Fig. 5D). These song structures are known from several other *Barbitistes*-species and are interpreted as female response mimicking (Stumpner and Meyer 2001).

Species diagnosis. Males of *Barbitistes kaltenbachi* can be distinguished from its Croatian congeners, *B. ocskayi* Charpentier in Ocskay et al., 1850, *B. serricauda* (Fabricius, 1794), and *B. yersini* Brunner von Wattenwyl, 1878 (Fig. 6), by the shape of the cerci (Fig. 7A). Male cerci in *B. kaltenbachi* are thickened in their mid-part. The

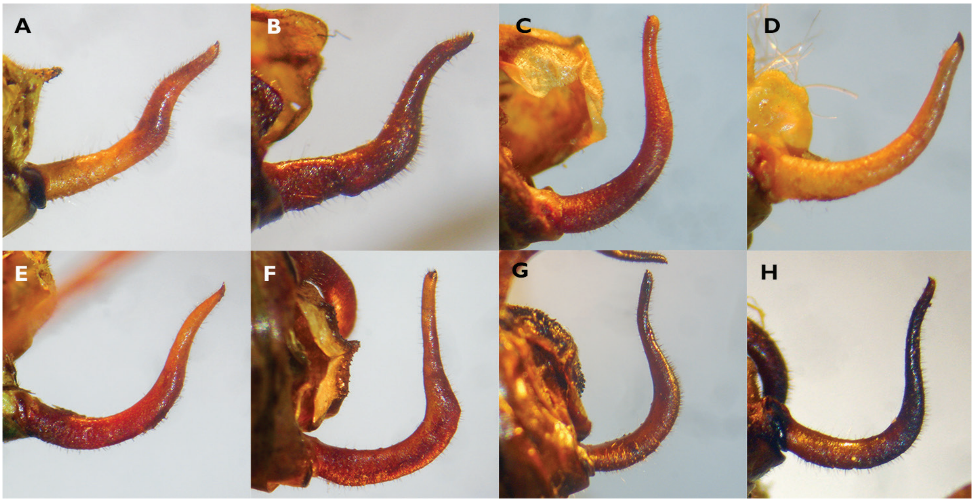

Figure 7. Male cerci of all members of the genus *Barbitistes* **A–E**, **G, H** left cercus **F** right cercus flipped vertically **A** *B. kaltenbachi* **B** *B. constrictus* **C** *B. alpinus* **D** *B. fischeri* **E** *B. serricauda* **F** *B. vicetinus* **G** *B. ocskayi* **H** *B. yersini* (photographs K.-G. Heller). Based on cercal morphology, *B. kaltenbachi* is most similar to *B. constrictus*.

proximal half of a cercus is in an abrupt but obtuse angle with the distal half, giving the cercus an angular sinuosity, like that of an open elbow. *Barbitistes constrictus* has nearly identically shaped cerci (Fig. 7B). All the other species of the genus have cerci of a different shape, in the absence of a thickened mid-part and in being more gradually curved, showing a smoother sinuosity in the apical part (Figs 7C–H), except for *B. vicetinus*, which has uniquely shaped cerci (Fig. 7F).

The song of *B. kaltenbachi* differs distinctly from the songs of all other *Barbitistes*-species in the temporal pattern of the syllables (Fig. 8). Definite diagnostic differences between females cannot be given. Females of different species of *Barbitistes* show many similarities, some exhibiting intermediate characters (see e.g., Nadig 1987). In this paper, the photos of females are of specimens present together with males in the same bush and hence are identified as belonging to *B. kaltenbachi*. See Suppl. material 1:Table S1 for measurements of specimens in collections and literature data.

Key to the species of the genus *Barbitistes* in Croatia (males only)

In Croatia, four species of *Barbitistes* occur, namely *Barbitistes kaltenbachi*, *B. ocskayi*, *B. serricauda*, and *B. yersini* (Rebrina 2014; Skejo et al. 2018). Males are easily identified to species level, but females are not. The key to males presented below is based on the morphology of cerci (angle and thickness) and subgenital plate (presence or absence of nose-like projection), and is adapted after Harz (1969). The key to the identification of females published by Harz (1969) has proven to be unreliable in practice, so it is not presented here.

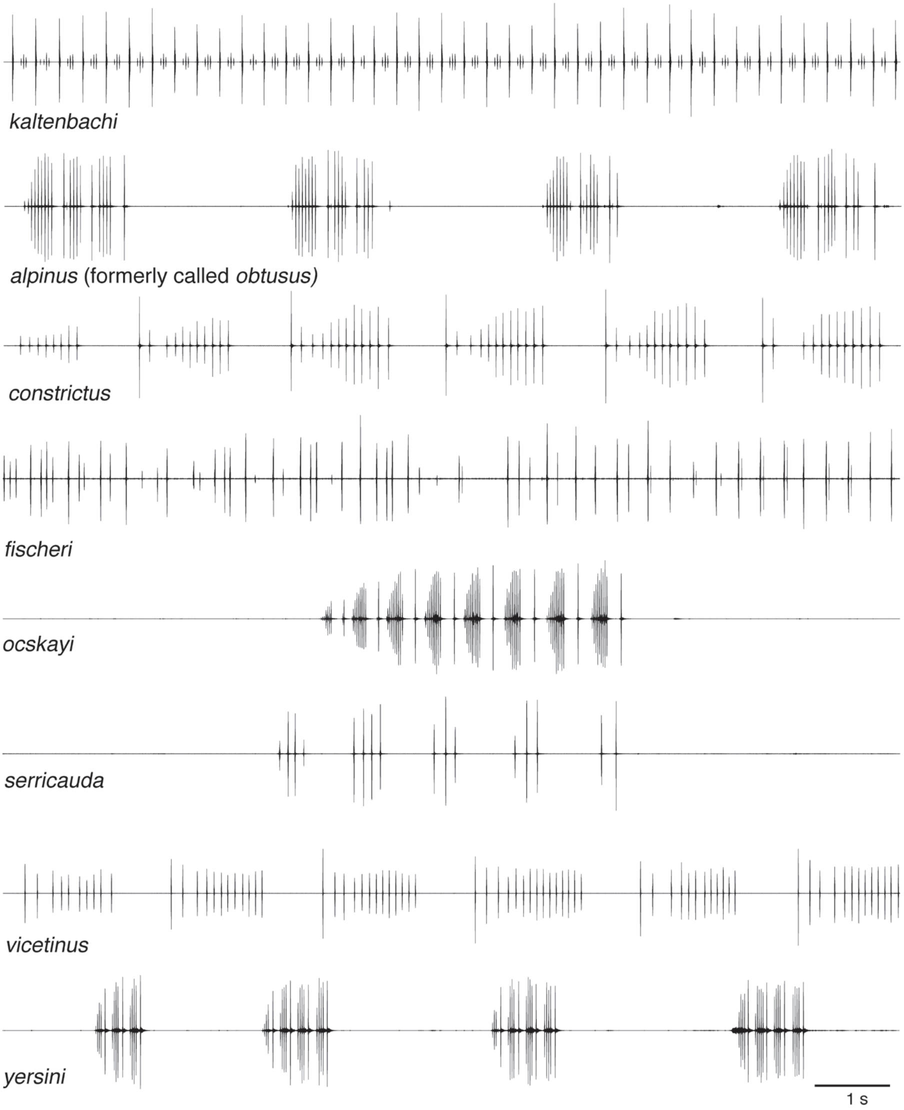

Figure 8. Oscillograms of male calling song (12 s sections) of all members of the genus *Barbitistes* (temperature range 21.5–25 °C).

1 Cercus thickened in the middle, proximal half in an abrupt but obtuse angle with the distal part, giving the cercus an elbow-like appearance. Distal half angularly sinuous (Fig. 8) [currently known only from Hvar Is. and Vis Is.]… ………………………………………………… ***Barbitistes kaltenbachi*** **Harz, 1965**

– Cercus not thickened in the middle, but gradually narrowing from base to apex. Distal part slightly and smoothly sinuous…………………………………**2**

2 Subgenital plate with a nose-like projection, visible in lateral view. [Dubrovnik region; Istria, Kvarner with adjacent islands] ....***Barbitistes ocskayi*** **Charpentier in Ocskay et al., 1850**

– Subgenital plate without a nose-like projection, almost flat.........................**3**

3 Cercus halfway strongly incurved, with proximal and distal halves in an almost right angle (Fig. 8). Pronotum almost flat. Tegmina with a yellow triangle in the middle. [Common in the Dinaric Alps and Mediterranean Croatia] ....***Barbitistes yersini*** **Brunner von Wattenwyl, 1878**

– Cerci gradually curved (Fig. 8). Pronotum saddle-shaped. Tegmina dorsally uniformly reddish brown. [Pannonian Croatia; NW Dinaric Alps] .... ***Barbitistes serricauda*** **(Fabricius, 1794)**

Reassessment IUCN Red List status of *Barbitistes kaltenbachi*

Current status. Near Threatened in Europe and EU28 (Chobanov et al. 2016).

Area of occupancy (AOO): calculated from the known data (ca.) 12 km^2, maximal estimation 72–80 km^2.

Extent of occurrence (EOO): calculated from the known data 90 km^2, maximal estimation ca. 780 km^2 (if all the hilly habitats in Hvar Is. and Vis Is. are included).

Newly proposed status. The species is reassessed here as Endangered. Up to now, the species has been known from only two Adriatic islands (Hvar and Vis). Inhabiting a restricted number of sites, it has an AOO of 12 km^2 to maximally 80 km^2, and a known EOO of 90 km^2 (maximally estimated less than 800 km^2). This makes it qualify for EN, following the criteria B1ab(iii)+B2ab(iii). Since there are only three sites at which this species occurs with certainty, only a few threat events may be enough to wipe out or threaten proportional parts of the population. Forest fires, for example, occur quite often on the Adriatic islands and can damage important parts of the species' habitat, as can touristic and recreational developments and clear cutting of maquis and scrubland.

Subfamily Tettigoniinae Krauss, 1902
Tribe Platycleidini Brunner von Wattenwyl, 1893

Rhacocleis buchichii Brunner von Wattenwyl in Herman 1874

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:2709
Figures 1, 9–12
eng. Lesina Bush-cricket, *hrv.* Bučićev konjic grmušar, *deutsch.* Lesina Strauchschrecke

Rhacocleis Buchichii Br.: Herman (1874): 201–202, plate III, figs 8–12 (original Brunner von Wattenwyl's description accompanied with figures; erroneously calls *buchichii* type species of the genus) (see Figs 9, 10 in this paper);

Rhacocleis Bucchichii (O. Herman): Dubrony (1878): 21 (misspelled; reported the species from Liguria, based on misidentification of another *Rhacocleis* sp.);

Rhacocleis Bucchici Br.: Brunner von Wattenwyl (1882): 321 (misspelled; included in key), 322 (description, measurements, and Hvar, Lesina, designated as distribution);

Anterastes Bucchichi: Bucchich (1886): 382 (misspelled; Bucchich wrote a remark "In Luglio nei cespugli specialmente di erica; nei campi non si vede", "In July found in bushes, especially of Erica; but not observed in fields" [= karst poljes]);

Rhacocleis Bucchici Br. 1874: Novak (1888): 129 (misspelled; provides first exact localities, Brusje and Humac on Hvar Is., and added data on Bucchic's comments on species' habitat: "Io ne ho trovato nel bosco ordinariamente fra il *Cystus monspeliensis* dal mese di giugno all' ottobre, in agosto in casa introdotto forse colla frasca, negli orti fra i rosai, a Brusje e monte Humac in ottobre (25) sul *Quercus*", "Usually I found them in bushes [or forest], under *Cystus monspeliensis* from June to October. In August in houses, probably with branches. Found in gardens under roses. In Brusje and Humac found on *Quercus* on October 25th");

Rhacocleis bucchici Herman 1874: Redtenbacher (1900): 107 (misspelled; gives a short morphological description of the species with measurements and mentions the species to occur on the island of Lesina);

Rhacocleis bucchici Herm.: Jacobson and Bianki (1905): 400 (misspelled; colouration and morphology described in Russian, measurements provided, distribution cited 'Dalmatia');

Rhacocleis Buchichii, Herm.: Kirby (1906): 187 (listed in catalogue);

Rhacocleis Buchicii Br. 1874: Karny (1907a): 26 (misspelled; lists sp. in catalogue, citing Brunner von Wattenwyl, Novak and Redtenbacher);

Rhacocleis Bucchici: Karny (1907b): 131 (misspelled; mentions that the species has been known only from Hvar Is.);

Rhacocleis buchichii Herman: Caudell (1908): 5 (listed in the catalogue of Decticinae species, mentioned as endemic to Hvar Is.);

Rhacocleis bucchici Herm.: Werner (1919): 217 (misspelled; mentions species to occur on Brač Is., "south of Neresi, near the water tanks in the bushes, not common". Also mentions "species until then only known from Lesina");

Rhacocleis buchichii Herm.: Salfi (1924): 43, 45 (key to species);

Rhacocleis bucchichi Br.: Ramme (1951): 118 (reported to have found the species in hilly terrain under *Pistacia terebinthus* L. and noted that the species was timorous and difficult to catch);

Rhacocleis bucchichi Br.: La Greca (1959): 43, 148, fig. 115 (148) (misspelled; treats all the species of the genus and mentions *buchichii* to be present on Lesina Is., also shown on a distribution map of Italian species);

Rhacocleis bucchichi Hermann, 1874: Us (1967): 23 (misspelled; checklist of Yugoslavian Orthoptera, cited from Hvar, Brač and Korcula);

Rhacocleis bucchici Herm. 1874: Harz (1969): 429–441 (misspelled; included in key to European species, depicted in detail, figs 1343, 1361, 1396–1400, described and measured, distribution Hvar, Brač and probably also Korčula);

Rhacocleis buchichi Herm.: Gausz (1970): 131 (misspelled; first mainland record at Zaostrog along the Dalmatian coast);

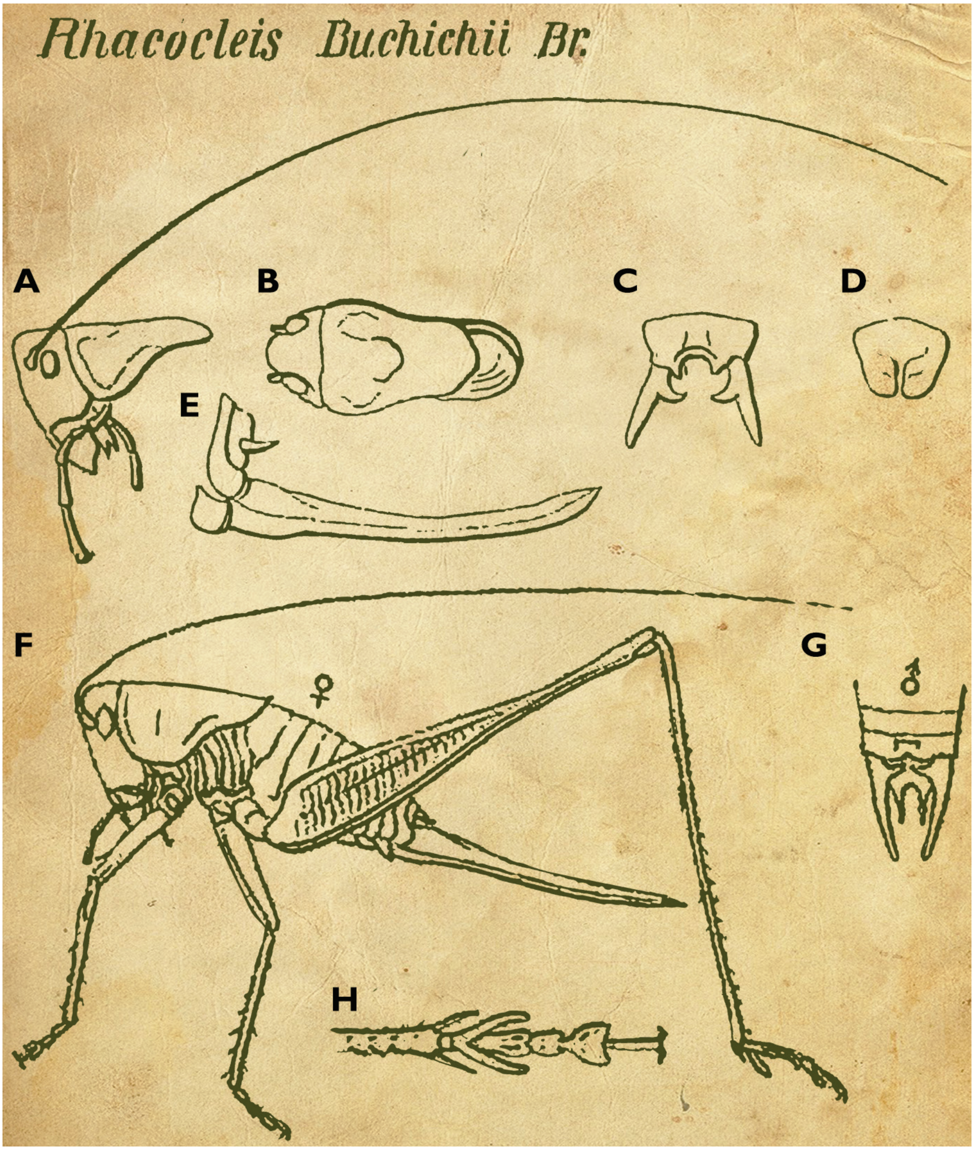

Figure 9. The first published spelling and the oldest drawings of *Rhacocleis buchichii* after Herman (1874) (**A–E**) and Brunner von Wattenwyl (1882) (**F–H**) **A** head and pronotum in lateral view **B** head and pronotum in dorsal view **C** cerci of a male **D** subgenital plate of a female **E** ovipositor **F** habitus of a female in lateral view **G** cerci of a male **H** hind leg details, apex of tibia and tarsus. Drawings not to scale.

Rhacocleis bucchicii Hermann, 1874: Heller (1988): 147, Abb. 146 F, I (F) (misspelled; mentions the species to occur on Hvar Is., lists a collecting event on 25 July 1982 and depicts the stridulatory file)

Pterolepis bucchicii (Herman, 1874): Heller et al. (1998): 37 (misspelled; species listed in checklist of European Orthoptera);

Rhacocleis bucchichi Herman, 1874: Willemse and Willemse (2005): 269 (misspelled; listed in checklist of *Rhacocleis* and *Pterolepis* species, 6 specimens from Dalmatia examined, in R. Kleukers and K.-G. Heller's collections);
Rhacocleis buchichii: Skejo (2014) (assessed as Endangered species in IUCN Red list);
Rhacocleis buchichii Herman 1874: Wagner (2015): 37–41 (new record from Biokovo Mt., photographs provided);
Rhacocleis buchichii: Hochkirch et al. (2016a) (assessed as Endangered species in IUCN Red list, distribution Hvar, Brač and probably Korčula);
Rhacocleis buchichii: Hochkirch et al. (2016b): 20, 76 (listed among Endangered species in European Orthoptera fauna);
Rhacocleis buchichii Brunner von Wattenwyl in Herman 1874: Skejo et al. (2018): 33 (author corrected to Brunner von Wattenwyl, species distribution in Croatia and Europe presented).

Historical misspellings. Historically, the species name of *Rhacocleis buchichii* was misspelled a lot, for obvious reasons. It was even misspelled more often than cited correctly (see above). One specific misspelling, *bucchichi*, can be explained by the fact that the person after whom the species was named is Grgur/Gregorio Bučić/Bucchich (1829–1911), a Croatian naturalist with a surname that contains two consonants (voiceless postalveolar affricate consonant *č*, pronounced /tʂ/; and voiceless alveolo-palatal affricate ć, pronounced /tɕ/). These consonants were written in Croatian language in many different ways (ch, cch, ci, cci, chi) in the past, which has probably caused the confusion.

Type material. Syntypes of *Rhacocleis buchichii*, one male and one female, are deposited in MfN, Berlin (Fig. 10). In the collection of NMW, Vienna, there are three specimens from the collection of Brunner von Wattenwyl (pers. comm. S Randolf). These three specimens are not labelled as types, but since they are part of the type-collection, they should be considered syntypes too.

Material examined. Croatia • 1♂; Vis Is., Mount Hum; 43°02.13'N, 16°06.92'E; alt. 545 m a.s.l.; 21 Jul. 2011; R. Felix leg.; RFPC • 2♂; Hvar Is., between Jelsa and Gdinj; 25 Jul. 1982; K.-G. Heller leg.; KGHC CH0531 and CH2167 • 1♀; Biokovo Mt., above Tučepi; alt. 500 m a.s.l.; 43°16'N, 17°05'E 28 May 2006; M. & K.-G. Heller leg.; KGHC CH6779 • 1♂, nymph; Brač Is., near Pučišća; 31 May 2006, M. & K.-G. Heller leg.; KGHC CH6783 • 1♀; Troglav Mt., southern slope; alt. 850 m a.s.l.; 29 Aug. 2014; J. Skejo leg.; ZSZJS • 2♀; Hvar Is., 500 m south of Pitve; alt. 300 m a.s.l.; 13 Aug. 1996; R. Kleukers leg.; NBC RMNH.INS.960939 and RMNH.INS.1259083 • 1♂; Hvar Is., 500 m east of Vrisnik; alt. 150 m a.s.l.; 13 Aug. 1996; R. Kleukers leg.; NBC RMNH.INS.1259084; sound recorded • 1♂; Hvar Is., 500 m south of Pitve; alt. 300 m a.s.l.; 13 Aug. 1996; R. Kleukers leg.; sound recorded; specimen lost.

New record from Vis Island. A single male individual of *Rhacocleis buchichii* was found under a *Juniperus* bush near the Chapel of St. Spirit (Crikvica Sv. Duha) at Mount Hum, in the southwestern corner of Vis Is. (N43.036°, E16.116°, 545 m a.s.l.) (Figs 1, 2A, 11). Several photographs of the specimen were taken in its natural habitat

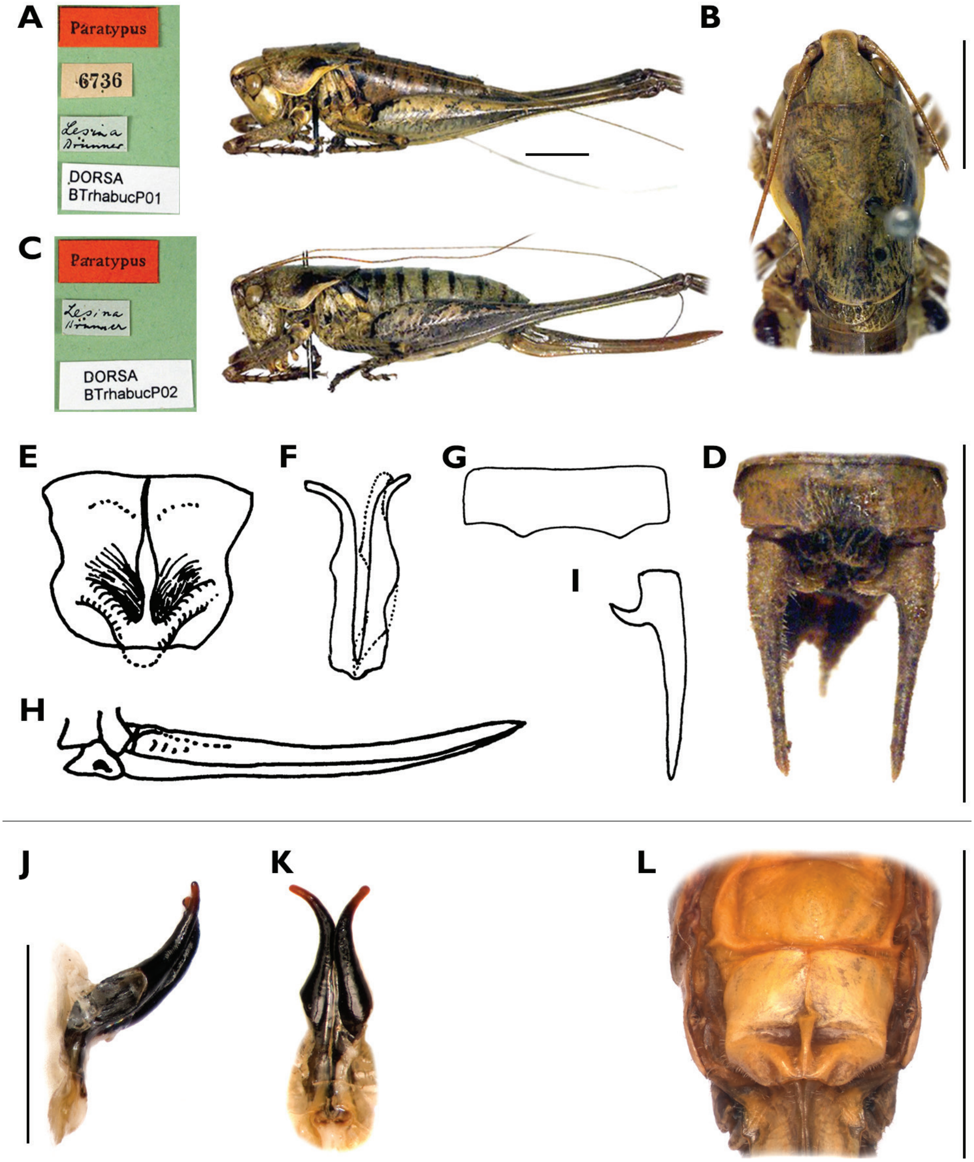

Figure 10. Photos of syntype male and female of *Rhacocleis buchichii* by Naskrecki, taken from OSF (Cigliano et al. 2019) (**A–D**) drawings from Harz (1969) (**E–I**) and details of specimens from Croatia, Hvar Is., near Pitve and Vrisnik, 13 Aug. 1996 (collection NBC) (**J–L**) (photos Luc Willemse, NBC) **A** male syntype and its label **B** pronotum and tegmina of the male in dorsal view **C** female syntype and its label **D** cerci and 10th tergite of the male **E** subgenital plate of a female **F** titillators **G** 10th tergite of a male **H** ovipositor **I** right cercus of a male **J** titillators lateral view **K** titillators caudal/posterior view **L** subgenital plate of a female. Scale bars: 5 mm (**A–D, L**); 1 mm (**J, K**). Drawings not to scale.

(Fig. 11C), and it was subsequently collected (Fig. 11). As in the case of Hvar Saw Bush-cricket, this is the very first record of Lesina Bush-cricket for the island of Vis. It was recorded in the direct vicinity of the collecting site of *Barbitistes kaltenbachi*.

Distribution. All known records of *R. buchichii* are depicted on the map in Fig. 1 and presented in Table 2. After its description from Hvar Is., the species has been found at scattered localities on the island and in a wide area outside the island: Zaostrog (Gausz 1970), Biokovo Mt. (present paper; Wagner 2015), Brač Is. (present paper; Puskás et al. 2018) and Troglav Mt. within the Dinara Massif (Skejo et al. 2018). Harz (1969) mentions the species' occurrence on Korčula Is., but its presence on the island has never been confirmed.

Habitat. The first information on the habitat of *R. buchichii* was given by the name bearer himself; Bucchich (1886) found the species in July in a hilly terrain in bushes, especially *Erica*. He mentions that the species does not occur in fields (see Bibliography). Novak (1888) also mentions hilly areas as the prime habitat, adding that the species can be found from June to October under *Cistus monspeliensis*. Some individuals entered the house, probably as stowaways in collected firewood. In gardens, it was found under roses. Ramme (1951) reported the species to live under *Pistacia terebinthus* and noted that it was timorous and difficult to catch. Gausz (1970) found a specimen in the littoral zone near Zaostrog, in the undergrowth (karst-steppe vegetation of 3–10 cm high) in a stand of *Ficus carica* and *Olea europaea*. Kleukers (pers. comm.) found *R. buchichii* in 1996 on a rocky slope with low bushes around the villages of Pitve and Vrisnik, Hvar Is. Wagner (2015) found *R. buchichii* on Biokovo Mt., under Black Pine, *Pinus nigra*, while JS found it on Troglav Mt. under *Pistacia* sp. On 25 Jul. 1982, KGH found many specimens at night, walking and jumping on the road between Jelsa and Gdinj.

Song description. We regard this song description as preliminary, as we were able to analyse the sound recordings of only two males. The calling song of *R. buchichii* consists of echemes that are repeated in a series of 4–13. However, in one of the recordings only the series of 2–5 occur. Echemes are repeated at a rate of ca. one or two echemes/s. In the available recordings, no continuous repetition of echemes is found. Echemes seem to have a more or less fixed structure, last ca. 160–220 ms and contain 7–9 syllables. Syllables are repeated at a rate of 40–50/s (26–27 °C).

Species diagnosis. Within Tettigoniidae, the members of the Platycleidini tribe have either an unarmed prosternum or the prosternum bears two spines (Massa et al. 2012). The *Rhacocleis* genus belongs to the latter group, together with *Pterolepis* Rambur, 1838, *Antaxius* Brunner von Wattenwyl, 1882, *Anterastes* Brunner von Wattenwyl and *Yersinella* Ramme, 1933, among others.

Based on the shape of the cerci of the male and the subgenital plate of the female, La Greca (1959) placed *R. buchichii* into the *Rhacocleis neglecta*-species group (La Greca 1959), composed of *R. neglecta* (Costa, 1863), *R. japygia* La Greca, 1959 (both from central and southern Italy) and *R. buchichii* (Croatia). These species are

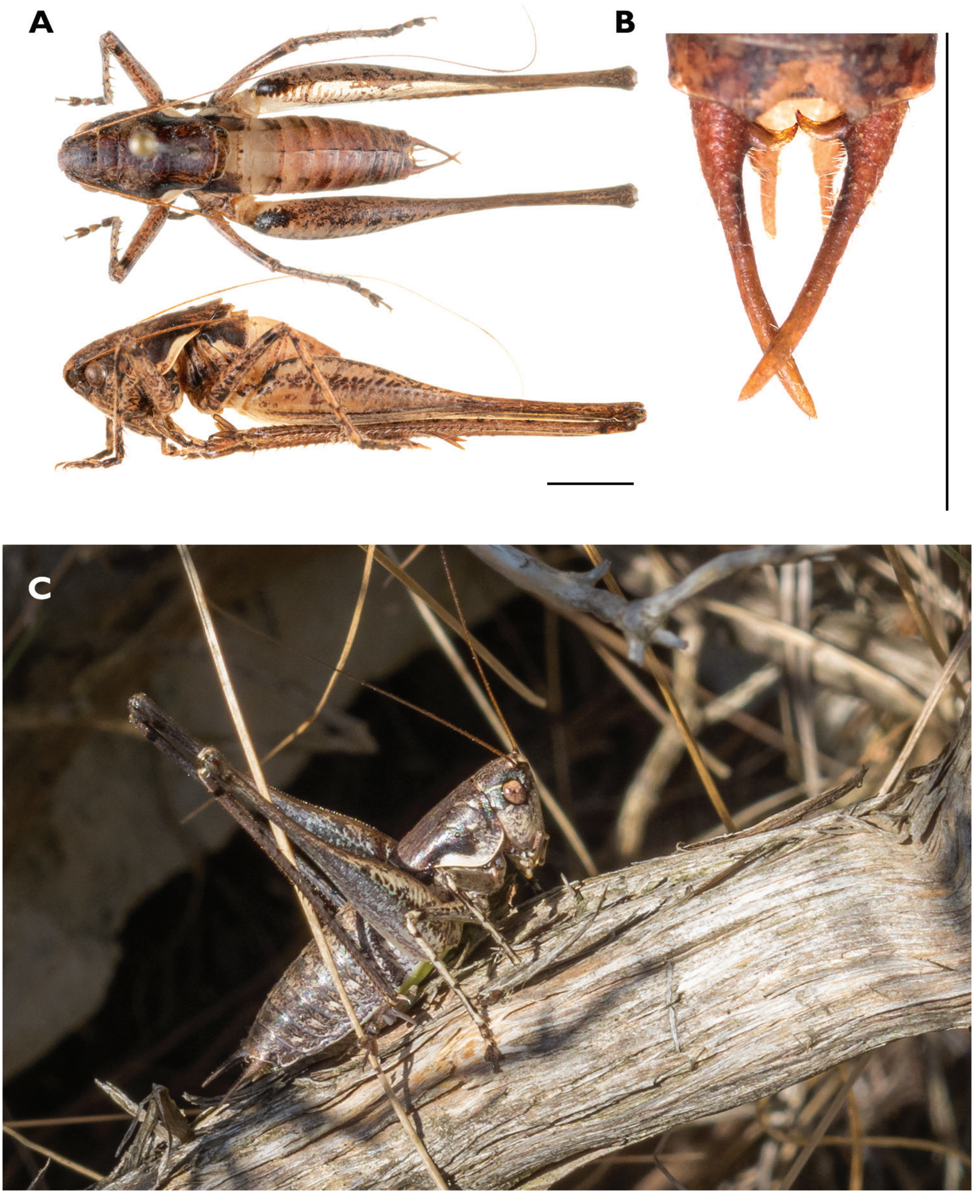

Figure 11. Habitus of *Rhacocleis buchichii*, Croatia, Vis Is., Mount Hum **A** male **B** cerci of the male **C** the same specimen in situ. Scale bars: 5 mm.

characterised by 1) slender cerci with a decurved inner tooth close to the base (♂♂) and 2) a quadrate subgenital plate with a central keel and lateral depressions (♀♀). *Rhacocleis buchichii* is characterised by very small, *neglecta*-type titillators (Fig. 10J, K), but with a blunt and rounded apex (La Greca 1959). Cerci of the male are coni-

Table 2. Known records of *Rhacocleis buchichii*, with data on the sites and collection events. Type specimens collected on 'Lesina' (Hvar Is.) and labelled as such are not included in the table, nor are depicted on the map in Fig. 1. Key: n/c, not collected.

Date of collection	map	Specimens	Location	Coll.	Reference
25 Oct. 1875	8	n/c?	Hvar Is., Brusje		Novak (1888)
25 Oct. 1875	10	n/c?	Hvar Is., Mt. Humac		Novak (1888)
20 Jul. 1912	5	n/c?	Brač Is., south of Nerežišća		Werner (1919)
18 – 25 Aug. 1939	8	7	Hvar Is., Brusje, below 500 m. a.s.l.		Ramme (1951)
Aug. 1964–1966	14	1	Zaostrog		Gausz (1970)
25 Jul. 1982	11	2♂	Hvar Is., between Jelsa and Gdinj	KGHC	
13 Aug. 1996	9	1♂ 2♀	Hvar Is., Pitve, 300 m a.s.l.	NBC	
13 Aug. 1996	9	1♂	Hvar Is., Vrisnik, 150 m a.s.l.	NBC	
18 Aug. 2002	6	1♂	Brač Is., Bol, Mt. Vidova Gora, 43°16.77'N, 16°37.14'E, 770 m a.s.l.		Puskás et al. (2018)
28 May 2006	12	1♀	Biokovo Mt., above Tučepi, 43°16'N, 17°5'E, 500 m a.s.l.	KGHC	
31 May 2006	7	1♂ juv	Brač Is., near Pučišća	KGHC	
21 Jul. 2011	1	1♂	Vis Is., Mt. Hum, Crikvica Sv. Duha, 43°02.13'N, 16°06.92'E, 545 m a.s.l.	RFPC	
29 Aug. 2014	4	1♀	Southern slope of Mt. Troglav, Greda, 43°49.33'N, 16°38.48'E, 850 m a.s.l.	ZSZJS	Skejo et al. (2018)
13 Oct. 2015	13	10♂♀	Biokovo Mt., 43°15.59'N, 17°05.57'E, 650 m a.s.l.		Wagner (2015)
16 Oct. 2015	13	5♂♀	Biokovo Mt., 43°15.32'N, 17°06.02'E, 650 m a.s.l.		Wagner (2015)

cal, delicate, very long and have a medial tooth protruding ca. 1/5 from their base (Figs 10, 11). La Greca (1959) provides a detailed description of the subgenital plate of the female: it presents a median carina and two lateral carinulas arranged obliquely and converging to the centre, towards the apex of the median carina. Transversal grooves on both sides of the median carina are situated more towards the apex of the subgenital plate than towards its base, and are limited posteriorly by the two lateral carinulas (Fig. 10L).

Rhacocleis buchichii is easily distinguished from its only congener in Croatia, *R. germanica* (Herrich-Schäffer, 1840). The cerci of *R. buchichii* males are very slender, while the males of *R. germanica* have more robust cerci, with a less elongated distal part. Each cercus of male *R. germanica* has a long and straight inner tooth. Females of *R. buchichii* have a rectangular subgenital plate with a median keel, which is armed at the tip (Fig. 10L), while *R. germanica* females have a prolonged, oval subgenital plate with an apical incision. The two Croatian species also differ in colouration. *Rhacocleis germanica* is more reddish and brownish tinted, without a white band on the paranota of the pronotum. *Rhacocleis buchichii* has darker and greyer tints and has a clear pale paranotal band (Figs 10, 11). See Suppl. material 2: Table S2 for the measurements of specimens in collections and literature data.

The song (Table 3) is different from the song of *R. germanica* in the number of syllables per echeme, being ca. ten in *R. germanica*, and 7–9 in *R. buchichii*. In *R. japygia* echemes are repeated in short series (2–8 echemes) or more or less continuously, with a repetition rate of ca. 1–2.5 echemes/s. Echemes consist of 5–7 syllables which are repeated at a rate of ca. 30/s. In *R. neglecta*, echemes are produced in long series or continuously, at a rate of 1–3 echemes/s. Echemes consist of 3–5 syllables. Syllables are repeated at a rate of ca. 25–40/s.

Echeme repetition rate and the number of syllables per echeme are considered to be the main distinguishing features of different species.

Table 3. Bioacoustic data of *R. buchichii*, *R. germanica*, *R. japygia*, and *R. neglecta*. Presented are echeme repetition rates per second, number of syllables per echeme, and syllable repetition rate per second. Data of *R. germanica* and *R. neglecta* obtained from Ragge and Reynolds (1998) and Heller (1988), data of *R. japygia* obtained from Massa et al. (2012).

Species	Echeme repetition rate (/s)	Syllables per echeme	Syllable repetition rate (/s)
R. buchichii	1–2	7–9	40–50
R. germanica	0,3–1	10	40
R. japygia	1–2,5	5–7	30
R. neglecta	1–3	3–5	25–40

Key to the species of the genus *Rhacocleis* in Croatia

1 Male cerci long and slender, inner tooth positioned at the basal fifth of the cercus, the apex of the tooth curved inward. Female subgenital plate rectangular, with a median keel thickened towards the apex. [currently known only from Brač Is., Hvar Is., Vis Is., and some inland and coastal mountains]....... .... ***Rhacocleis buchichii* Brunner von Wattenwyl in Herman 1874**

– Male cerci robust, inner tooth positioned just at the basis of the cercus, long and straight, in a right angle with the cercus. Female subgenital plate elongated, without a median keel and with an apical incision. [Common in the whole Mediterranean part of Croatia, including islands, and mountains; less common in Panno-nian region]... .... ***Rhacocleis germanica* (Herrich-Schäffer, 1840)**

Reassessment IUCN Red List status of *Rhacocleis buchichii*

Current status. Endangered (EN) in Europe and EU28 (Hochkirch et al. 2016a).

Area of occupancy (AOO): calculated from the known data (ca. 10 sites) 60 km^2, maximal estimation 400 km^2.

Extent of occurrence (EOO): calculated from the known data 3700 km^2, maximal estimation ca. 7400 km^2.

Newly proposed status. Lesina Bush-cricket inhabits the Adriatic islands of Hvar, Brač and Vis, as well as certain mountains in mainland Dalmatia. Since the species has recently been found on Vis Is. and its presence on Troglav Mt. has now been confirmed, its known range has extended significantly compared to the previous assessment. Based on the above calculations, we propose the species to be downgraded to a less threatened category.

The species occurs in Natura 2000 protected areas (Vis Is., Hvar Is., Brač Is.) and in a protected natural park (Biokovo Natural Park), but it is expected to occur outside the protected areas as well, where the main threats to the species' survival persist. Based on numerous references, the habitat type of the species, to be considered in a future reassessment, has to be extended with scrubland (see above, under Habitat).

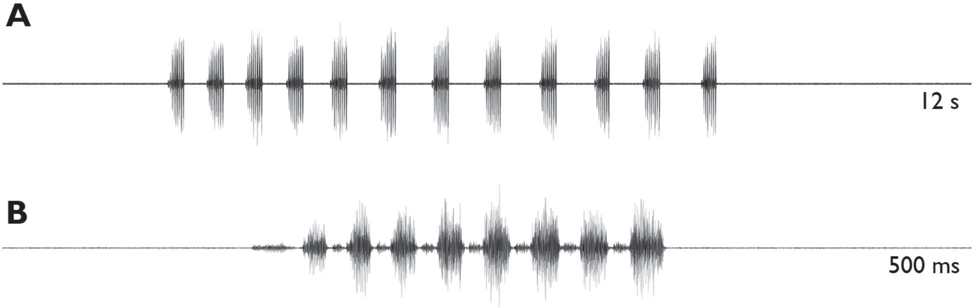

Figure 12. Bioacoustic data of *Rhacocleis buchichii* **A** oscillogram showing one series of echemes (12 s) **B** oscillogram showing one echeme (500 ms).

Discussion

Dalmatian endemics from a biogeographical perspective

The Adriatic islands are of a rather young evolutionary age (Malvić 2016) compared to large Mediterranean or Greek islands (Robertson and Dixon 1984, Willemse et al. 2018). Therefore, the rate of endemism on the Adriatic islands is relatively low (Kenyeres et al. 2009). During most of the time from Oligocene to Pleistocene, the Adriatic islands seem to have been a part of the mainland Balkans (Giuli et al. 1987). From the lower Pliocene, when the Adriatic sea was large and extended far into the northwest, through the Würm ice age (ca. 100,000–11,700 years ago), when the sea level was low, as well as in the early Holocene, when the sea level increased, the islands were connected to the mainland (Velić & Malvić 2011, Malvić 2016). They may have been isolated during some interglacials, but these periods were probably short.

Nevertheless, a few endemics known from the central Dalmatian islands, mainly documented in plants (Bogdanović et al. 2014), may justify the status of this island group as a distinct biogeographic unit. Among animals, however, very few examples are known, most of which refer to troglobitic taxa. Of particular note is the troglobitic beetle genus *Spelaeobates* Müller, 1901, endemic to the central Dalmatian islands and adjacent Croatian mainland. *S. kraussi* Müller, 1903 and *S. pharensis* Müller, 1901 are Brač and Hvar endemics, respectively (Pretner 1968, Gottstein Matočec et al. 2002) while *S. novaki* Müller, 1901 is found on Dugi otok Is. and adjacent Croatian mainland, at the foot of Velebit Mt. (Jalžić 1983). Allegrucci et al. (2017) recently mentioned a new, yet undescribed species of *Troglophilus* (T. sp. 1) from the caves on Mljet Is. However, these troglobitic and troglophilous forms live in special habitat 'islands', not necessarily related to true islands.

The terrestrial fauna of most Croatian islands still remains profoundly understudied and the Orthoptera of the Central Dalmatian islands, in particular, have never been studied systematically (Skejo et al. 2018). At the present state of knowledge, however, the occurrence of endemic or subendemic Orthoptera species is surprising and noteworthy. How and when could these forms speciate? Surprisingly, the available data indicate rather different histories for the two species studied in this paper.

To start with the less complex case, the Lesina Bush-cricket *Rhacocleis buchichii* is endemic to Dalmatian islands (Brač, Hvar, Vis) and mountains (e.g., Troglav and Biokovo), and occurs sympatrically with *R. germanica*, the latter being very common in the Mediterranean region of Croatia. The two species show clear morphological differences and do not seem to be closely related. On the other side of the Adriatic Sea, in Italy, two species presumably closely related to *R. buchichii* and each other occur, namely *R. neglecta* and *R. japygia* (La Greca 1959). *Rhacocleis neglecta* is widespread in the Italian mainland, while *R. japygia* occurs in a small area between Basilica and Puglia (Massa et al. 2012). All three species of the so-called *neglecta*-group (*neglecta*, *buchichii*, *japygia*; La Greca 1959) have similar cerci in males and quadrate subgenital plates in females. Thus, it is highly probable that these species share the most recent common ancestor. La Greca (1959) considers *R. buchichii* as originating from the Apennines, Italy. The ancestor of *R. buchichii* may have inhabited the area currently covered by the Adriatic Sea during one of the periods when the sea level was low (e.g., during Würm; Malvić 2016). After the sea level rose and the Balkan Peninsula became separated from the Italian Peninsula, speciation became possible.

Despite the fact that the similarity between the three species was mentioned as early as 60 years ago (La Greca 1959), a comprehensive comparative study has never been conducted. In terms of bioacoustics, the songs of the three allopatric *Rhacocleis* species are relatively similar, but all four mentioned species of this genus can be identified by their songs. However, very few sound recordings of these species exist and a more thorough study of their bioacoustics, including female behavioural response experiments, is required to test this hypothesis.

The situation with Hvar Saw Bush-cricket *Barbitistes kaltenbachi* is quite different and much more complex. This flightless bush-cricket is endemic to two Dalmatian islands (Hvar Is. and Vis Is.). The song of *B. kaltenbachi* is unique within the genus and does not resemble that of any other known species (Figs 5, 6). On Hvar Is., *B. kaltenbachi* occurs sympatrically with *B. yersini*, a common and widespread species in the Western Balkans (Hochkirch et al. 2016a, Skejo et al. 2018), with an isolated, trans-Adriatic occurrence in Central Italy (Massa et al. 2012). The true origin of this isolated population would be an interesting subject for a bioacoustic/genetic study.

According to the cercal morphology, *B. kaltenbachi* could be closely related to *B. constrictus*, their cerci being nearly identical (Fig. 8). On the other hand, *B. constrictus* has a completely different distribution and habitat. It inhabits central, northern and eastern Europe (Harz 1969) and is typically found in coniferous forests (Hochkirch et al. 2016b), whereas *B. kaltenbachi* is a species of dry and hot maquis.

Looking at the distribution ranges of other *Barbitistes* species, one can recognise an intriguing gap between the northern and southern distributional areas of *B. ocskayi* (see Hochkirch et al. 2016b, Skejo et al. 2018), in which the distribution of *B. kaltenbachi* seems to fit perfectly. If *B. kaltenbachi* were an offshoot of *B. ocskayi*, it would be relatively young (perhaps isolated during one of the interglacials), but in this case it means that its unique song and distinctive cercal morphology evolved very fast. Since both characters are known to be under sexual selection (Lehmann 1998), a rapid evolution seems possible. Under these premises, it would be particularly interesting to get a molecularly based estimate of the age of the species involved. If the distribution of *kaltenbachi* is restricted to Hvar Is. and Vis Is. – during a quick search we only found *B. yersini* on Brač Is. and the mainland opposite to Hvar Is. – this could be ascribed to its occurrence (or origin?) in only one of the two separate local Würm glacial refugia, that were situated south of the Neretva River (see Podnar et al. 2004).

Based on the shape of the subgenital plate, *B. kaltenbachi* is similar to *ocskayi*. Based on cercal morphology, however, *B. ocskayi* and *B. yersini* seem to resemble each other more. *Barbitistes vicetinus* is a species restricted to Northern Italy, which exhibits an isolated occurrence comparable to that of *B. kaltenbachi*. Despite a superficial resemblance of the male cerci of *B. kaltenbachi* and *B. vicetinus* (the latter also has a somewhat thickened mid-part; Fig. 7F) the authors consider the cerci of the two species very different from each other. *Barbitistes vicetinus'* cerci show a right angle between the proximal and distal parts, and almost lack any sinuousity in the distal part (compare *B. kaltenbachi* in Key to the species). Furthermore, their songs are different (Fig. 8).

Acoustic behaviour of *Barbitistes kaltenbachi*

Barbitistes kaltenbachi belongs to Phaneropterinae, a bush-cricket subfamily in which females of most species do not respond to male songs only by phonotactic approach, but also react with their own acoustic signals. These sounds are used by males for locating females (see Heller et al. 2015 for a review). Female responses are often short, occur very fast after releasing male the song element (in less than 100 ms; see Heller et al. 2018) and are scarcely detectable by predators, but can be exploited by conspecific males (Villarreal and Gilbert 2014). Therefore, it is not surprising that a variety of song modifications which can be interpreted as forms of defense against eaves-dropping rivals, are known (Heller and Hemp 2017, Heller et al. 2017). The rivals, on the other hand, can attempt to mask female response (Bailey et al. 2006).

Male calling songs of all species belonging to Barbitistini *sensu stricto* (genera *Barbitistes*, *Metaplastes*, and *Ancistrura*) are characterised by short, isolated syllables showing a species-specific pattern (Heller 1988). They mostly contain a short sequence of syllables (up to ten) followed by a larger interval, after which an isolated syllable is produced. This syllable is called trigger syllable, because a female ready to mate responds directly to it. *Barbitistes* males (e.g., *B. serricauda* and *B. kaltenbachi*; Fig. 5) sometimes produce so-called "extra syllables" (Stumpner and Meyer 2001) at the time of an expected female response, possibly to hinder the rivals' ability to locate answering females. However, there are almost no data describing the calling behaviour of two or several males singing together. A rival male could e.g., disturb the silent interval (before the next trigger syllable of another male) by sounds reducing the probability of female response. In some species, trigger periods are certainly long enough for such attempts (e.g., *Ancistrura nigrovittata*, *B. constrictus*, *B. serricauda*), but in others, sequences of verses are probably too short (e.g., *B. alpinus*, *B. yersini*), making the prediction of the trigger periods difficult. *Barbitistes kaltenbachi* songs are relatively long, so the rivals' disruption attempts should not be difficult. However, a rival would arguably not gain much from such behaviour, because its own song could be disturbed by the song of the 'attacked' male in a similar way. Thus, it could be more worthwhile to synchronise the song as closely as possible with the song of a neighbour.

During the duets of *B. kaltenbachi*, trigger syllables/verses of both males started within only 20 ms (Fig. 5). Some duetting frogs have a mean difference of 79 ms (Legett et al. 2019). The shortest onset difference tested by Snedden and Greenfield (1998) in a synchronising tettigoniid was 26 ms. When synchrony is near-perfect (*sensu* Legett et al. 2019; delays of 5 ms or less), as observed here in many instances, males increase the amplitude of their signals by overlapping. In any case, both males are still able to hear female responses, provided the female is in the hearing range of both. This system works even if males use auditory time windows, as reported from other Barbitistini (Heller and von Helversen 1986). To our knowledge, synchronising in duetting bush-cricket species has been observed only in *Amblycorypha parvipennis* (Shaw et al. 1990). This species has syllables (called phonatomes in Shaw et al. 1990) with a duration of 100 ms. Female responses follow ca. 120 ms after the beginning of a male syllable. In Barbitistini, synchronising would have been considered unlikely due to the fast female response and narrow auditory time windows.

Unfortunately, as nothing is known about female acoustic behaviour or the potential male reaction, the hypotheses regarding *B. kaltenbachi* acoustic behaviour can only be based on what is known of other species. *Barbitistes* females respond to the trigger syllable after a delay of ca. 40 ms (Stumpner and Meyer 2001), probably caused by an audio-motoric reflex (named acousto-motorical reflex in *Ancistrura nigrovittata* by Dobler et al. 1994). In this case, a preference for the leading call would be obvious. Females would (and can only) respond to the first sound. This is comparable to a precedence effect discussed in the context of synchrony and alternation in chorusing animals (Greenfield 2002). However, males are not necessarily under pressure to call first. This depends a lot on the specific borders of the auditory time window. The trigger syllable of the leading male may start the auditory time window not only in the female, but also in the male follower. Ideally, it should not be reset by the follower's own trigger syllable. On the other hand, singing at a different time from the leading male may result in covering the female response. Thus, exact synchronisation might be the optimal strategy. Of course, much more data, especially from females, are necessary to prove this hypothesis, but it seems a fascinating prospect for acoustic co-operation – even if it is considered to 'make the best of a bad situation'.

Concluding remarks

With this paper, we attempted to enhance the information on the distribution of two Croatian endemic bush-crickets, as well as the knowledge of their morphology and bioacoustics. The songs of *Barbitistes kaltenbachi* and *Rhacocleis buchichii* are described here for the first time. The IUCN Red List status has been reassessed here for both species; we suggest *R. buchichii* to be downgraded to a less threatened category, while *B. kaltenbachi* should be upgraded to 'Endangered'.

The knowledge of the biology of both species is still scarce. *Barbitistes kaltenbachi* is suspected to be active early in the season, while *R. buchichii* is probably active late in the season, based on many records of this species from October (see Tables 1, 2). JS visited Hvar Is. two times, in late July and late August 2017, focusing on finding both species, but without success. Both dates were apparently too late in the season for *B. kaltenbachi*, taking into account that KGH collected specimens of this species on Hvar Is. at the end of May, without observing nymphs at that time.

The fact that the type series of *B. kaltenbachi* consists of a fairly large number of specimens (22) from the same locality (Hollier and Bruckner 2015) could suggest that the species exhibits gradations in certain years. Gradations are a well-known aspect of the biology of other *Barbitistes* species (Galvagni and Fontana 1993, Stumpner et al. 2015), some of which were, and still are, sometimes characterised as pest species (e.g., Bei-Bienko 1954, Cavaletto et al. 2019). However, outbreaks of *B. kaltenbachi* have never been reported.

To enrich the knowledge of the Orthoptera fauna of Vis Is. and other Adriatic islands, the authors would like to suggest visiting entomologists to pay attention to these and other species, and enter their sightings, accompanied by photos, on websites such as Observation (www.observation.org) or iNaturalist (www.iNaturalist.org).

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The general idea for the study was initialised by JS and RF. JS, RF, and KGH conducted field research on the two endemic species on Hvar Is. (KGH with success, JS without success), Brač Is. (KGH with success, JS without success), Vis Is. (RF), Biokovo Mt. (KGH with success, JS without success), and Troglav Mt. (JS). KGH, FR, and JS conducted research on other *Barbitistes* and *Rhacocleis* species in Croatia. All the authors compiled literature data, discussed the data, and photographed material. KGH conducted bioacoustics analysis of *B. kaltenbachi* and wrote that part of the study. BO did the same for *R. buchichii*. The rest of the study was written mainly by RF, JS, and KGH, with the help of FR.

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Supplementary material 1

***Barbitistes kaltenbachi* morphometrics**

Authors: Rob Felix, Klaus-Gerhard Heller, Baudewijn Odé, Fran Rebrina, Josip Skejo

Data type: Microsoft Word Document (.docx)

Explanation note: Table S1. Morphometrics of Hvar Saw Bush-cricket. Published measurements (Harz 1965, 1969) are compared with the measurements of specimens collected on Vis Is. and Hvar Is. Shown are body length (from the frons to the tip of abdomen), pronotum length (in dorsal view), length of the visible part of tegmina, hind femur, and ovipositor length (in females). All measurements are in mm. [* the tip of abdomen of the other male was eaten by a wasp during preparation]

Link: https://doi.org/10.3897/zookeys.936.51599.suppl1

Supplementary material 2

***Rhacocleis buchichii* morphometrics**

Authors: Rob Felix, Klaus-Gerhard Heller, Baudewijn Odé, Fran Rebrina, Josip Skejo

Data type: Microsoft Word Document (.docx)

Explanation note: Table S2. Morphometrics of Lesina Bush-cricket. Published measurements (Herman 1874, Brunner von Wattenwyl 1882, Redtenbacher 1900, Jacobson and Bianki 1905, Harz 1969) are compared with measurements of a male specimen collected on Vis Is. Shown are body length (from the frons to the tip of abdomen), pronotum length (in dorsal view), length of the visible part of tegmina, hind femur, and ovipositor length (in females). All measurements are in mm.

Link: https://doi.org/10.3897/zookeys.936.51599.suppl2

Supplementary material 3

***Barbitistes kaltenbachi* bioacoustics and comparative morphology**

Authors: Rob Felix, Klaus-Gerhard Heller, Baudewijn Odé, Fran Rebrina, Josip Skejo

Data type: Microsoft Word Document (.docx)

Explanation note: Table S3.1. Measurements of the amplitudes in the song of *Barbitistes kaltenbachi*; Table S3.2 Measurements of the species-specific time pattern in the song of *Barbitistes kaltenbachi*; Table S3.3 Measurements of the parameters of calling activity of *Barbitistes kaltenbachi*; Table S3.4 Sampling locality data for the specimens used in Fig. 7 (cercus morphology).

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RESEARCH ARTICLE

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Two new species of the genus *Formosatettix* Tinkham, 1937 (Orthoptera, Tetrigidae) from Guizhou and Chongqing, PR China

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Abstract

Two new pygmy grasshopper species are described from PR China and are assigned to *Formosatettix* Tinkham, 1937, a large Asian tetrigin genus composed of species with reduced tegmina and hind wings: *F. leigongshanensis* Zha & Ding, **sp. nov.** from Guizhou and *F. wulongensis* Zha & Ding, **sp. nov.** from Chongqing. We provide descriptions of morphology and habit, supplemented with photographs. Flying organs of the genus *Formosatettix* are discussed and the genus is compared with other Asian genera with reduced flying organs, such as *Formosatettixoides* Zheng, 1994 and *Alulatettix* Liang, 1993 in Tetriginae, *Deltonotus* Hancock, 1904, *Epitettix* Hancock, 1907 and *Pseudepitettix* Zheng, 1995 in Cladonotinae, and *Macromotettixoides* Zheng, Wei & Jiang, 2005 and *Pseudomacromotettix* Zheng, Li & Lin, 2012 in Metrodorinae.

Keywords

ecology, habit, Karst Region, taxonomy, Tetriginae, Tetrigoidea

Introduction

The genus *Formosatettix* Tinkham, 1937 (subfamily Tetriginae) was originally established for only two species from Taiwan, China – *F. arisanensis* Tinkham, 1937 (type species) and *F. karenkoensis* Tinkham, 1937, but today it is a large genus composed of 68 known species in China, Japan, Korea, Nepal, Pakistan and Russia (Wei et al. 2019, Cigliano et al. 2020). *Formosatettix* is similar to the Tetriginae genera *Alulatettix* Liang, 1993 and

Formosatettixoides Zheng, 1994. Members of *Alulatettix* have a pair of conspicuous tegminal sinus (Zhang et al. 2014), while those of *Formosatettixoides* have visible tegmina and hind wings (Zha and Zheng 2014). Member of *Formosatettix*, on the other hand, lack a pair of tegminal sinus and both tegmina and hind wings are invisible (Wei et al. 2019). *Formosatettix* is also similar to the Cladonotinae genera *Deltonotus* Hancock, 1904, *Epitettix* Hancock, 1907, and *Pseudepitettix* Zheng, 1995 [which is a likely synonym of *Epitettix* as suggested by Deng (2016) and Zha et al. (2017b)], and to the Metrodorinae genera *Macromotettixoides* Zheng, Wei & Jiang, 2005 and *Pseudomacromotettix* Zheng, Li & Lin, 2012 [syn. of *Macromotettixoides* as suggested by Zha et al. (2017a)]. Relations among the aforementioned genera have never been systematically investigated.

During investigations of pygmy grasshoppers in PR China, we have collected new data on members of the genus *Formosatettix*. In this study, we introduce two new members of the genus *Formosatettix*, namely *F. leigongshanensis* Zha & Ding, sp. nov. and *F. wulongensis* Zha & Ding, sp. nov., from Southwest China. At the same time, we provide brief discussion on the morphology of the flying organs of *Formosatettix*, and compare the genus to allied genera.

Material and methods

Photography. Specimens were photographed using Canon EOS 800D with 100 mm macro lens, and partial images were stacked using Photoshop CS6. Photographs of the habitat were made using Nikon Coolpix P520.

Terminology. Morphological terminology and measurements follow Zheng (2005), Tumbrinck (2014) and Muhammad et al. (2018). Measurements are given in millimeters (mm).

Depository. Type and voucher specimens are deposited in the Specimen Room of the School of Life Sciences, Huaibei Normal University (HNU), Huaibei, Anhui Province, China.

Taxonomy. Taxonomy follows Cigliano et al. (2020) (= Orthoptera Species File).

Taxonomy

Formosatettix Tinkham, 1937

Formosatettix leigongshanensis Zha & Ding, sp. nov.

http://zoobank.org/894716AD-59D6-40D5-8283-C5737BD64A21
Figs 1, 2

Diagnosis. *Formosatettix serrifemora* Deng, 2019 was reported from Liupanshui (Yushe) and Suiyang (Kuankuoshui), Guizhou, China (Wei et al. 2019), and is geographically closest to our new species. We have collected the species (9♂20♀) from the Tongzi County (Baiqing Natural Reserve), also in Guizhou. Apart from the number of antennal

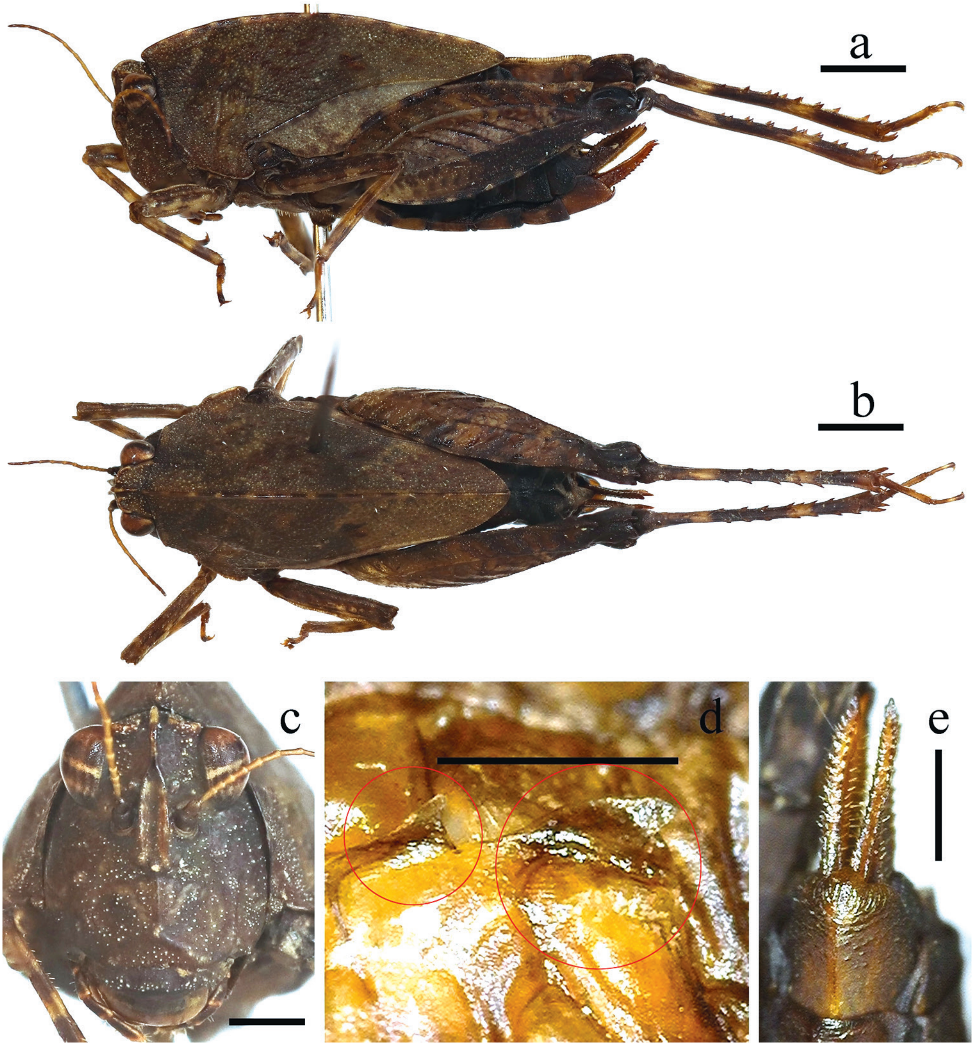

Figure 1. Female of *Formosatettix leigongshanensis* sp. nov. **a** body in lateral **b** body in dorsal view **c** head in frontal view **d** wings in lateral view (tegmenulum in the smaller circle, hind wing in the bigger circle) **e** subgenital plate in ventral view. Pictures **a, b** were stacked using Photoshop CS6. Scale bars: 2 mm (**a, b**), 1 mm (**c–e**).

segments (14 or 15) and presented tegmina and hind wings (closely similar to *F. leigongshanensis* sp. nov.), our collections are identical to the description and photographs of *F. serrifemora* (14-segmented, tegmenulum and hind wing absent; Wei et al. 2019).

Formosatettix leigongshanensis sp. nov. is similar to *F. serrifemora*, but the latter has a narrower scutellum, an acutely angled anterior margin of the pronotum in dorsal view, undulate ventral margins of the fore and mid femora, and undulate dorsal margin of the hind femur (Wei et al. 2019, fig. 7b). The main differences between the two species are outlined in Table 1.

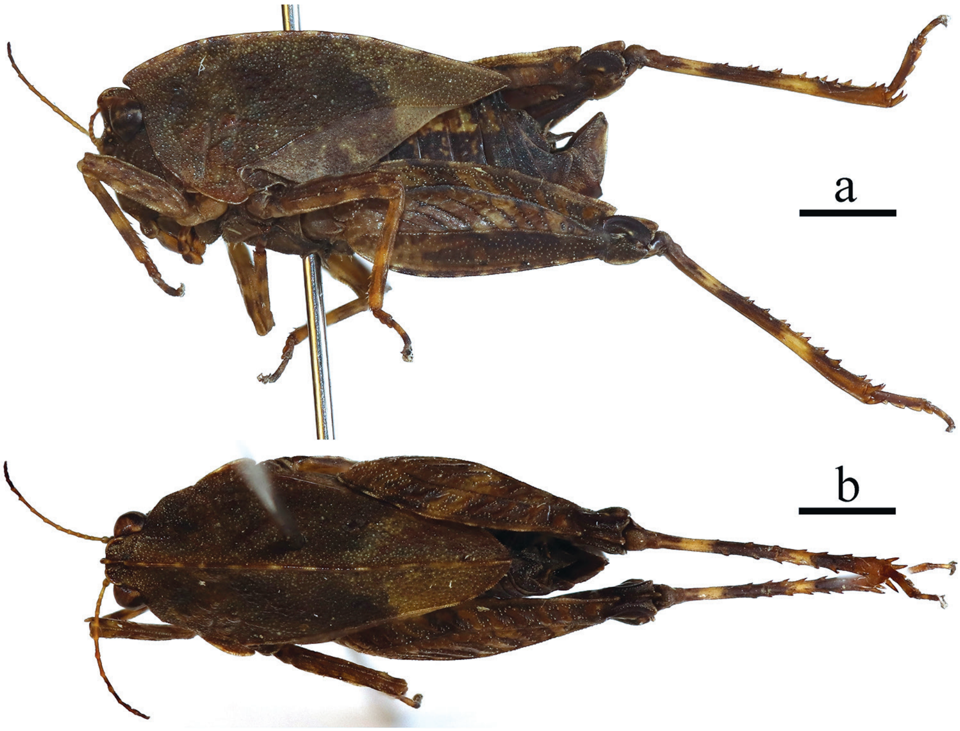

Figure 2. Male of *Formosatettix leigongshanensis* sp. nov. **a** body in lateral view **b** body in dorsal view. Pictures were stacked using Photoshop CS6. Scale bars: 2 mm.

Formosatettix leigongshanensis sp. nov. is also similar to *F. changbaishanensis* Yuan et al., 2006 from Jilin, *F. yunnanensis* Zheng, 1992 from Yunnan, China, and *F. martensi* Ingrisch, 2001 from Nepal (Panchthar). Some of the main diagnostic differences are that in *F. changbaishanensis*: 1) vertex is 1.67♂–1.76♀ times as wide as one eye; 2) middle segments of the antennae are 5.16♀–6.3♂ times as long as wide; 3) prozonal carinae are contracted backwards; and 4) apex of the posterior angle of the lateral lobe is rounded (Yuan et al. 2006); in *F. yunnanensis*: 1) facial carinae before the eyes are indistinctly concave; 2) antennae are inserted slightly above the lower margin of the eyes; 3) scutellum is as wide as the diameter of scapus; 4) ventral margins of the fore and mid femora are undulate; and 5) apex of the posterior angle of the lateral lobe is rounded (Zheng 1992); and in *F. martensi*: 1) face is distinctly inclined and the frontal costa together with the medial carina of the vertex forms an acute angle; 2) anterior margin of the pronotum is slightly projected forwards and only reaches the posterior margin of the eyes; 3) ventral margin of the mid femur is undulate; and 4) the area between the internal and external lateral carinae of the pronotum is much narrower (Ingrisch 2001, Cigliano et al. 2020).

The new species is the second *Formosatettix* species, after *F. serrifemora*, reported in Guizhou Province, China.

Table 1. Main differences between *Formosatettix serrifemora*, *F. leigongshanensis* sp. nov. and *F. wulongensis* sp. nov.

	F. serrifemora	*F. leigongshanensis* sp. nov.	*F. wulongensis* sp. nov.
Anterior margin of the vertex	Elevated, arcuate, strongly surpassing the anterior margin of the compound eyes	Elevated, arcuate, strongly surpassing the anterior margin of the compound eyes	Low, straight, slightly surpassing the anterior margin of the compound eyes
Antennae	14–15 segments (♂, ♀), mid segments 2.5–3.0× as long as wide	15(♂)–16(♀) segments, mid segments 4–5× as long as wide	15(♂)–16(♀) segments, mid segments 4–5× as long as wide
Scutellum between the antennal grooves	Visibly narrower than diameter of scapus	Visibly wider than diameter of scapus	Visibly wider than diameter of scapus
Anterior margin of the pronotum	Acutely angled	Obtusely angled	Acutely angled
Median carina of the pronotum in lateral view	Low and arcuate	Low and arcuate	High and arcuate
Apex of hind pronotal process from dorsal view	Pointed-rounded	Pointed-rounded	Broadly arcuate
Ventral margins of fore and mid femora	Teeth present	Straight	Teeth present
Dorsal margin of the hind femur before the antegenicular tooth	Three teeth present clearly	Teeth absent	Three teeth present clearly

Detailed description of females. ***General appearance.*** Body stout and short, size moderate, surface smooth and covered with numerous fine granules.

Head. Vertex slightly below the anterior margin of the pronotum, slightly roof-like, anterior part higher than posterior part and center part higher than both sides, 2 times as wide as a compound eye; anterior margin somewhat arcuate, clearly surpasses the anterior margin of eyes; lateral carinae distinct, folded upwards and slightly over the top of eyes; medial carina distinct and compresso-elevated in anterior half, almost touching the median carina of the pronotum; paired fossulae distinct, rounded. In lateral view face nearly vertical, frontal costa together with medial carina rounded; facial carinae above superior ocelli concave, between antennal grooves arcuate forwards. In frontal view frontal costa bifurcates into facial carinae at the lower one-third of between anterior margin of vertex and upper margin of superior ocelli, and run nearly parallel downwards; scutellum deep and wide, between grooves 1.3–1.4 times as wide as the diameter of scapus. Eyes globose and elevated over the anterior margin of the pronotum, but clearly lower than top of vertex; superior ocelli placed at the level of lower one-third of the inner margins of eyes. ***Antenna.*** Antenna filiform, 16-segmented, inserted slightly below the lower margin of eyes, with 9–11th segments longest and 4–5 times as long as wide.

Pronotum. Pronotum distinctly compresso-elevated, surface smooth, between sulci somewhat swollen at the base of median carina and a little concave on both sides of the discus. The anterior margin projected forwards and reaching the middle of eyes, in dorsal view obtusely angled; prozonal carinae extend to the anterior sulcus, parallel, indistinct; hind pronotal process short, only reaching 3/4 of hind femur, apex pointed-rounded. Median carina of pronotum lamellate, in lateral view low arcuate; lower margin of hind process curved, internal lateral carina slightly incurved, the area between internal and external lateral carinae of the pronotum about 1.4 mm wide. Posterior angles of the lateral lobes of the paranota extend obliquely, downwards and backwards, with rounded-truncated apices; ventral sinus present while tegminal sinus absent.

Wings. Tegmina and hind wings reduced, very small, triangular, hidden beneath pronotum and invisible (the 'abbreviated' type after Zha et al. 2016).

Legs. Dorsal and ventral margins of all femora finely serrate; fore and mid femora compressed, dorsal and ventral margins nearly straight; hind femur robust, about 2.6 times as long as wide, dorsal and ventral margins entire; antegenicular tooth slightly folded outwards with acute apex, apex of the genicular tooth obtuse; hind tibia with finely serrate inner margins, terminal part slightly wider than basal part, outer/inner side with 7–9/6–8 spines; first segment of hind tarsus 1.8 times as long as third, the first pulvillus short, while the second and third long, tips of all the pulvilli obtuse.

Abdomen. Ovipositor narrow and long, upper valvae about 3.2 times as long as wide, outer margins of upper and lower valvae armed with saw-like teeth. Subgenital plate in ventral view: median carina entire and distinct; posterior margin truncated, in the middle has a broadly triangular protrusion which is folded inwards, base of the protrusion elevated and slightly higher than posterior margin.

Coloration. Body dark brown. Antennae brown to dark brown. Pronotum behind shoulder usually has a pair of blackish spots (posthumeral spots), median carina of pronotum dotted with yellowish-brown. Ventral external area of hind femur mainly black, ventral margin of hind femur has a series of small yellow spots. Fore and mid tibiae with 3 yellowish-brown rings each, hind tibia with 2 elongate yellowish-brown rings.

Brief description of the males. Slightly smaller than female. Antenna 15-segmented, with 8–10th segments longest. The area between internal and external lateral carinae of the pronotum about 1.2–1.3 mm wide. Subgenital plate short and cone-shape, distal end nearly obliquely truncated in lateral view, apex bifurcate and forms into two short and obtuse teeth. Other characters same as females.

Measurements (mm). Length of body♂10–11.5, ♀11–13.5; length of pronotum ♂7.5–8.0, ♀8.5–9.1; length of hind femur ♂6.4–6.9, ♀7.1–7.7, width of hind femur ♂2.5–2.7, ♀2.7–2.9; length of antenna ♂3.8–4.0, ♀4.1–4.5.

Type material. *Holotype* female, PR CHINA, Guizhou Province, Leishan County (Leigong-shan Mt.), 26°22'45.69"N, 108°11'42.83"E, 1460 m alt., 2 Aug. 2016, collected by Ling-Sheng Zha. ***Paratypes*:** 15 males and 6 females, Leigong-shan Mt., 1400–1600 m alt., 1–3 Aug. 2016, collected by Ling-Sheng Zha.

Ecology and habits. Individuals of *Formosatettix leigongshanensis* sp. nov. inhabit fall-leaf layers in humid subtropical rainforests of Karst Region (Fig. 3a, c, d). They move slowly and can easily be caught. They mainly feed on humus. Specimens are capable of burrowing their bodies in shallow soil layer.

Etymology. The new species is named after the type locality, Leigong-shan Mt., Leishan, Guizhou, China. The specific epithet is a third Latin declension adjective.

Distribution. China (Guizhou). For now, only found in Leigong-shan Mt. in Leishan County (Fig. 4).

Figure 3. Habitats of two new *Formosatettix* species in PR China **a** habitat of *F. leigongshanensis* sp. nov. **b** habitat of *F. wulongensis* sp. nov. **c, d** female *F. leigongshanensis* sp. nov. standing on fall-leaf layers. Pictures **a, c, d** were photographed in Leigong-shan Mt., Leishan, Guizhou, China; while picture **b** was taken in Wulong, Chongqing, China.

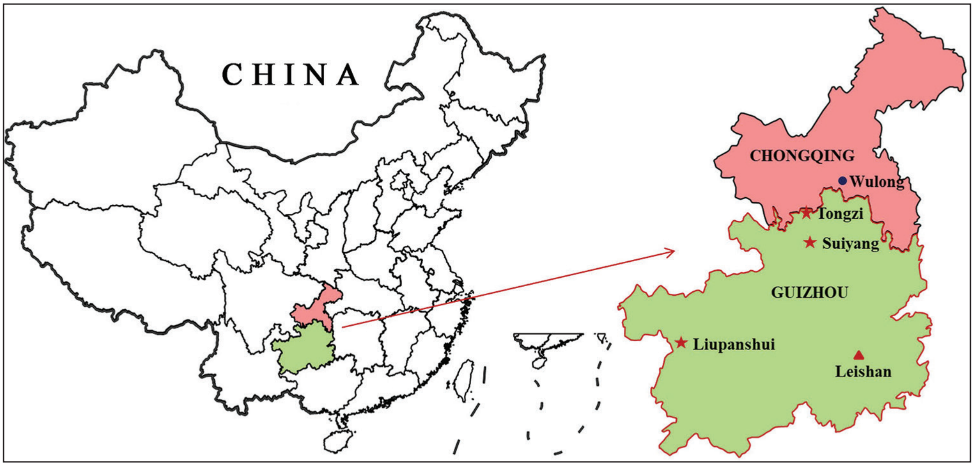

Figure 4. *Formosatettix* species inhabiting Guizhou and Chongqing, PR China. Red star: *F. serrifemora* from Liupanshui, Suiyang and Tongzi, Guizhou; Red triangle: *F. leigongshanensis* sp. nov. from Leishan, Guizhou; Blue circle: *F. wulongensis* sp. nov. from Wulong, Chongqing.

Formosatettix wulongensis Zha & Ding, sp. nov.

http://zoobank.org/A40391D1-ED6F-44DB-8317-1124F0A2F54B
Figs 5, 6

Diagnosis. *Formosatettix wulongensis* sp. nov. is similar to *F. serrifemora*, but the latter has elevated, arcuate and much more projected anterior margin of the vertex, narrower scutellum, lower arcuate median carina of pronotum in lateral view, and pointed-rounded apex of hind pronotal process (Wei et al. 2019, fig. 7b). Main differences between *F. serrifemora* and *F. wulongensis* sp. nov., together with *F. leigongshanensis* sp. nov., are outlined in Table 1.

Formosatettix wulongensis sp. nov. is also similar to *F. omeiensis* Zheng, 2009 from Sichuan and *F. baishuijiangensis* Zheng, 1999 from Gansu, China. *Formosatettix omeiensis* differs from our new species in 1) frontal costa together with the medial carina of the vertex acutely angled; 2) superior ocelli situated between the lower margin of the eyes; 3) anterior margin of the pronotum reaching only the level of the half length of the compound eyes; and 4) parallel prozonal carinae (Zheng 2009); while *F. baishuijiangensis* can be separated from the new species in 1) vertex 3.6 times as wide as one eye; 2) vertex strongly surpassing the anterior margin of the compound eyes; 3) scutellum 2 times as wide as the diameter of the scapus; and 4) anterior margin of the pronotum reaching only the posterior one-third of the compound eyes length (Zheng et al. 1999).

The new species is the first *Formosatettix* species known from Chongqing Autonomous Region, China.

Detailed description of female. ***General appearance.*** Body stout and short, size moderate; surface coarse, covered with numerous fine granules.

Head. Vertex clearly below anterior margin of pronotum, 2.5 times as wide as a compound eye; middle portion higher than surrounding area; anterior margin straight and low, a little surpasses the anterior margin of the compound eyes; lateral carinae distinct, folded upwards and up to the top of eyes; medial carina distinct and compresso-elevated in the anterior half; paired fossulae distinct, rounded. In lateral view face nearly vertical; frontal costa together with medial carina rounded; facial carinae above superior ocelli distinctly concave, between the antennal grooves nearly obtusely triangular (strongly arcuate) forwards. In frontal view frontal costa bifurcates into facial carinae at the lower one-third of between anterior margin of vertex and upper margin of superior ocelli, and run nearly parallel downwards; scutellum deep and wide, between grooves 1.2–1.3 times as wide as the diameter of the scapus. Eyes globose and elevated over the anterior margin of pronotum, but clearly lower than vertex; superior ocelli placed slightly above the lower margin of eyes. ***Antenna.*** Antenna filiform, 16-segmented, inserted distinctly below the lower margin of eyes, segments 10–12th longest and 4–5 times as long as wide.

Pronotum. Pronotum strongly compresso-elevated, surface coarse, bearing small tubercles and wrinkles; between sulci a little swollen at the base of median carina and a little concave on both sides of the discus. Anterior margin projected forwards and nearly reaches the level of the anterior margin of eyes, in dorsal view acutely angled; prozonal carinae distinct, but short, slightly contracted backwards;

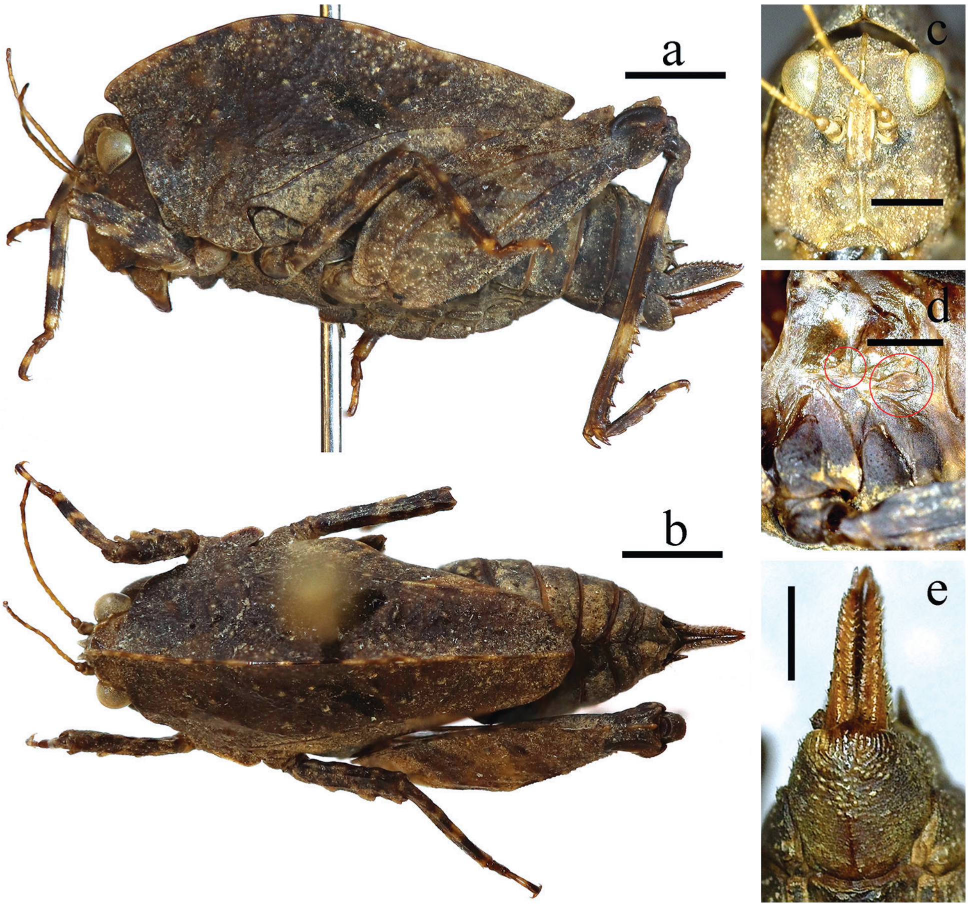

Figure 5. Female of *Formosatettix wulongensis* sp. nov. **a** body in lateral view **b** body in dorsal view **c** head in frontal view **d** reduced wings in lateral view (tegmenulum in the smaller circle, hind wing in the bigger circle) **e** subgenital plate in ventral view. Pictures **a, b** were stacked using Photoshop CS6. Scale bars: 2 mm (**a, b**), 1 mm (**c–e**).

hind pronotal process short, reaching 3/4 of the hind femur; apex broadly arcuate in dorsal view. Median carina of pronotum strongly compresso-elevated, in lateral view highly arcuate; lower margin of hind pronotal process curved, interlal lateral carinae incurved, the area between internal and external lateral carinae of the pronotum about 1.4 mm wide. Posterior angles of the lateral lobes of paranota directed downwards and backwards, with truncated or nearly truncated apices; ventral sinus present, tegminal sinus absent.

Wings. Tegmina and hind wings extremely degenerated and very small, scaly, hidden beneath pronotum and invisible (the 'abbreviated' type after Zha et al. 2016).

Legs. Dorsal and ventral margins of all the femora finely serrated; fore and mid femora compressed, dorsal margins almost straight, ventral margins with 3 teeth each (at the base, in the middle and at the end). Hind femur robust, about 2.8 times as

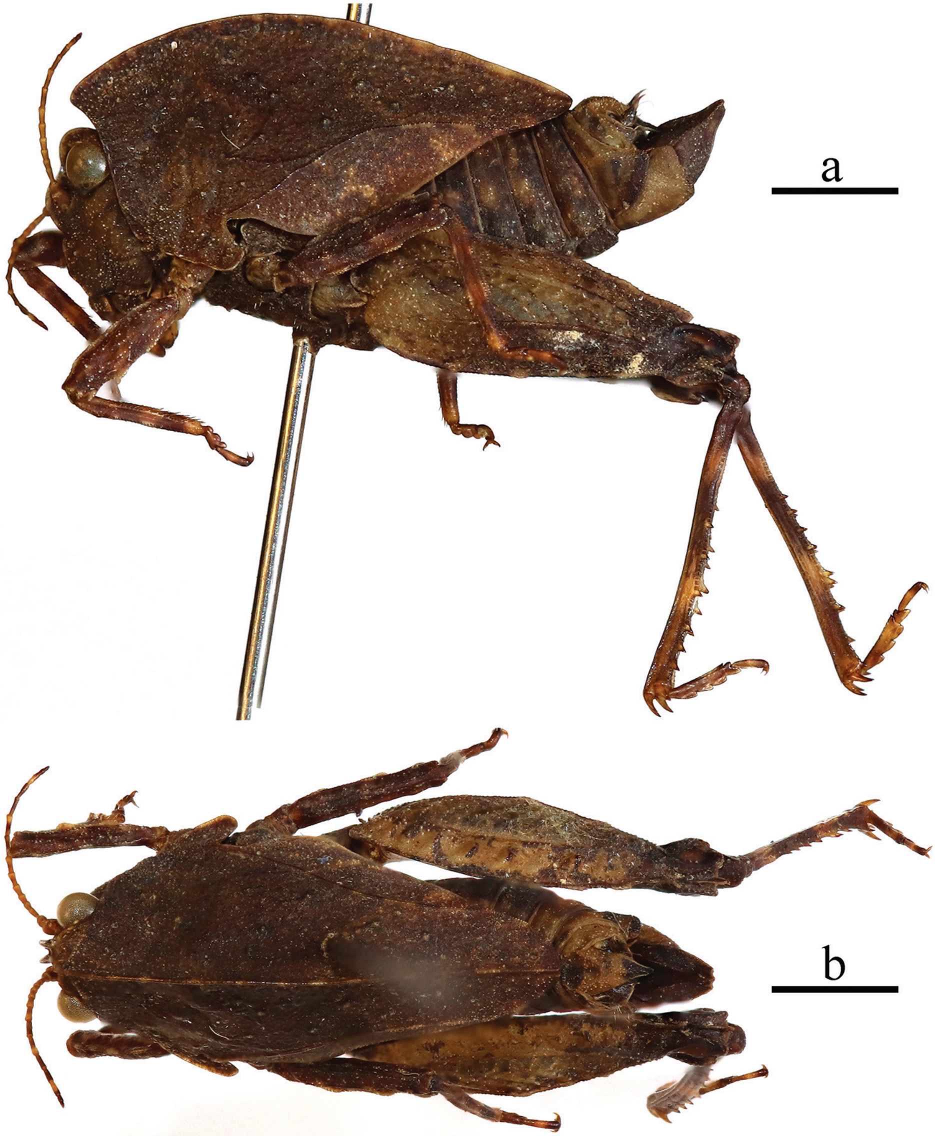

Figure 6. Male of *Formosatettix wulongensis* sp. nov. **a** body in lateral view **b** body in dorsal view. Pictures were stacked using Photoshop CS6. Scale bars: 2 mm.

long as wide, dorsal margin before antegenicular tooth bearing three lappets; ventral margins with a series of small teeth, three to four visible; ventro-external carina bearing a series of small teeth, 2–3 larger and evident; antegenicular tooth slightly folded outwards with apex acute, apex of genicular tooth obtuse; hind tibia with finely serrate inner margins, terminal part slightly wider than basal part, outer and inner sides with 5–7 spines each; first segment of hind tarsus 1.8 times as long as third, three pulvilli nearly equal in length and with obtuse apices.

Abdomen. Ovipositor narrow and long; upper valvae about 3.2 times as long as wide; outer margins of upper and lower valvae armed with slender, saw-like teeth. Subgenital plate in ventral view: median carina evident in the anterior half while obscure in the posterior part; posterior margin truncated, in the middle with a broad triangular protrusion which is folded inwards.

Coloration. Body dark brown. Antennae brown to dark brown from base to distal end, except for the pale colored 14th segment; pronotum behind shoulder in some specimen has a pair of blackish spots (posthumeral spots); anterior margin, median carina and lateral carinae of pronotum covered in yellowish-brown dots; teeth on femora generally yellowish-brown; fore and mid tibiae with three yellowish-brown rings each; hind tibia with two elongate yellowish-brown rings.

Brief description of males. Slightly smaller than female. Vertex 2.3 times as wide as one eye; antennae 15-segmented, segments 9–11th longest; 13th segment light colored. The area between internal and external lateral carinae of the pronotum 1.3 mm wide. Subgenital plate short cone-shape, distal part abruptly narrowed, distal end obliquely truncated in lateral view, but apex bifurcates into two distinct and obtuse teeth. Other characters same as females.

Measurements (mm). Length of body ♂10.8, ♀12–14; length of pronotum ♂7.5, ♀8.2–9.2; length of hind femur ♂5.9, ♀6.3–6.8, width of hind femur ♂2.2, ♀2.3–2.5; length of antenna ♂3.5, ♀3.8–4.

Type material. *Holotype* female, PR CHINA, Chongqing Autonomous Region, Wulong County, 29°20'32.27"N, 107°45'23.35"E, 470 m alt., 11 July 2016, collected by Ling-Sheng Zha. ***Paratypes*:** 1 male and 2 females, same data as holotype.

Ecology and habits. Individuals of *F. wulongensis* sp. nov. inhabit slopes of bamboo forest in humid subtropical rainforests (Fig. 3b). They move slowly on fall-leaf layers among bushes. They may feed on mosses and/or humus. Most of their life cycles, they maybe burry their bodies in shallow soil layer.

Etymology. The new species is named after the type locality, Wulong, Chongqing, China. The specific epithet is a third Latin declension adjective.

Distribution. China (Chongqing). For now, only found in Wulong County (Fig. 4).

Discussion

There has been a lot of discussion on how to properly describe the tegmina and hind wings of *Formosatettix*. Tinkham (1937) and Zheng (2005, 2009) described them as 'absent or degenerated', while Wei et al. (2019) referred to 'tegmina' as absent, while hind wings as 'absent or very short'. Authors in other continents have similar issues, such as North America (Hancock 1902) or Europe (Skejo et al. 2014), and have already proven that the flying organs of some Tetriginae species are degenerated, not absent. We have now also checked the flying organs of the *Formosatettix* specimens (ten species altogether). Specimens of *Formosatettix* indeed have tegmina and hind wings present, but degenerated, very small, triangular and scaly or long-ovate, hind wind being distinctly longer than tegmenulum (Figs 1d, 5d). *Formosatettix* thus, has reduced tegmina and hind wings, not absent, just as members of the genus *Nomotettix* (Hancock 1902) in North America or *Tetrix nodulosa* and *Tetrix transsylvanica* in Europe (Skejo et al. 2014). We now have reasons to doubt that tegmina and hind wings of many brachypterous species in Tetrigidae taxonomy do exist, in reduced fashion, as they originated from winged ancestors. According to the classification standard of the hind wings of pygmy grasshoppers suggested by Zha et al. (2016, 2017a), flying organs of the members of the genus *Formosatettix* should be assigned to the 'abbreviated' type (hind wings never reach middle of hind pronotal process, but are distinctly longer than tegmina).

Formosatettix is morphologically similar to members of the genera *Alulatettix* and *Formosatettixoides* (Tetriginae), *Deltonotus* and *Epitettix* (with *Pseudepitettix* syn.) in (Cladonotinae), and *Macromotettixoides* (with *Pseudomacromotettix* syn.) (Metrodorinae). Based on previous work (Zheng 2005, Tumbrinck 2014, Zha et al. 2016, 2017a, b) and specimens in our hands, we provide brief comparison between *Formosatettix* and aforementioned genera, including summarized differences among Tetriginae, Cladonotinae and Metrodorinae (see Tables 2, 3; Fig. 7).

Table 2. Differences between Tetriginae, Cladonotinae and Metrodorinae (summarized based on Tumbrinck (2014) and our collections).

	Tetriginae	**Cladonotinae**	**Metrodorinae**
Medial carina of vertex in dorsal view	Reaching middle of vertex or more	Reaching one-third of vertex or less	Generally reaching 1/3–1/2 of vertex
Scutellum relationship to scapus	Narrower to slightly wider	In a few species slightly wider, in most species much wider	In some members narrower, in most slightly to clearly wider
Surface of pronotum	Generally smooth, humps absent, sometimes wrinkles present	Coarse, high or low humps present, sometimes wrinkles present	Relatively coarse, wrinkles generally present, humps absent
Direction of the lateral lobes of the paranota	Close to the body (downwards), sometimes indistinctly turned sidewards	From sidewards, to indistinctly or distinctly turned outwards	Directed sidewards or outwards

Table 3. Differences between *Formosatettix* and its allied genera (together with the differences among the subfamilies outlined in Table 2, Fig. 7).

	Alulatettix **(Tetriginae)**	***Formosatettix*** **and** ***Formosatettixoides*** **(Tetriginae)**	***Deltonotus*** **(Cladonotinae)**	***Epitettix*** **and** ***Pseudepitettix*** **(Cladonotinae)**	***Macromotettixoides*** **and** ***Pseudomacromotettix*** **(Metrodorinae)**
Tegminal sinus	Visible	Absent or weak	Absent	Absent or weak	Absent or weak
Tegmina and hind wings (uncovering pronotum needed!)*	Abbreviated	Abbreviated	Apterous	Vestigial (?)	Abbreviated
Anterior margin of the pronotum	Weakly elevated, not reaching the level of the anterior margin of the compound eyes	Weakly elevated, not reaching the level of the anterior margin of the compound eyes	Strongly elevated, in most species surpasses the level of the anterior margin of the compound eyes	Not at all or weakly elevated, not reaching the level of the anterior margin of the compound eyes	Not elevated, not reaching the level of the anterior margin of the compound eyes

* Hind wings of Tetrigidae can be divided into four types: 'normal' (developed, surpassing middle of hind pronotal process), 'abbreviated' (never reaching middle of hind pronotal process, but distinctly longer than tegmina), 'vestigial' (equal to or shorter than tegmina) and 'apterous' (completely absent) (Zha et al. 2016, 2017a). *Deltonotus* is considered as the 'apterous' type based on Storozhenko (2011) and confirmed by us on *Deltonotus hainanensis* Zheng & Liang; *Epitettix*, as well as *Yunnantettix* Zheng (Zha et al. 2016), is probably the 'vestigial' type, observed on *Epitettix obtusus* Storozhenko & Dawwrueng.

Figure 7. *Formosatettix* and its allies, comparison in lateral view **a** *Alulatettix anhuiensis* Zheng **b** *Formosatettix serrifemora* **c** *Deltonotus hainanensis* Zheng & Liang **d** *Epitettix obtusus* Storozhenko & Dawwrueng **e** *Macromotettixoides hainanensis* (Liang). Pictures were stacked using Photoshop CS6. Scale bars: 2 mm.

We furthermore suggest that the length of the medial carina of the vertex could be one of the important traits that could help in separating Cladonotinae from other related subfamilies (Table 2). *Alulatettix* differs from *Formosatettix* by clear tegminal sinus, usually absent or weak in *Formosatettix* (Table 3). Future research may discover numerous synonyms in Chinese Tetrigoidea, as already proposed in some studies. *Formosatettixoides* and *Formosatettix* could represent synonyms of each other, as well as *Epitettix* and *Pseudepitettix*, but also *Macromotettixoides* and *Pseudomacromotettix* (Table 3). Many *Formosatettix* species were either described as having wings absent, or lack photographs to be checked. Revisions are necessary in the future, as is good taxonomic practice (Lehmann et al. 2017).

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A review of the genus *Sinocymbachus* Strohecker & Chûjô with description of four new species (Coleoptera, Endomychidae)

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Abstract

This work presents a review of species of the Asian genus *Sinocymbachus* Strohecker & Chûjô, 1970. Four new species are described from China: *S. fanjingshanensis* Chang & Bi, **sp. nov.**, *S. longipennis* Chang & Bi, **sp. nov.**, *S. sinicus* Chang & Bi, **sp. nov.**, and *S. wangyinjiei* Chang & Bi, **sp. nov.** *Cymbachus koreanus* Chûjô & Lee, 1993 is transferred to *Sinocymbachus* as *S. koreanus* (Chûjô & Lee) **comb. nov.** *Sinocymbachus bimaculatus* (Pic, 1927) is reported for the first time from China. The male of *S. parvimaculatus* (Mader, 1938) is discovered and described for the first time. Illustration, diagnosis and distribution are provided for each species. Prior to the present study, *Sinocymbachus* included ten species. An updated key to the species of *Sinocymbachus* is given.

Keywords

Coleoptera, Endomychidae, new species, taxonomy

Introduction

The genus *Sinocymbachus* is exclusively known in Southeast Asia and was established by Strohecker and Chûjô (1970) with *Engonius excisipes* Strohecker, 1943 from China (Sichuan) as the type species. It is a member of the largest endomychid subfamily Lycoperdininae, the monophyly of which was tested and confirmed by the phylogenetic analyses of morphological characters by Tomaszewska (2000, 2005). Robertson et al. (2015) presented a large-scale phylogenetic study for the Cucujoidea, using molecular evidence to rebuild the relationship tree of this superfamily and established a new superfamily, Coccinelloidea, with Endomychidae placed within it. This study further confirmed the monophyly of the subfamily Lycoperdininae and established its sister relationship with the subfamily Epipocinae (Robertson et al. 2015).

Tomaszewska (2005) recognised five generic groups among 38 genera of Lycoperdininae known at that time; she placed *Sinocymbachus* with eight other genera in the *Amphix*-group containing *Amphix* Laporte, 1840 (returned to *Corynomalus* Chevrolat (Bousquet 2004, Arriaga Varela et al. 2007, Shockley et al. 2009)), *Acinaces* Gerstaecker, 1858 (11 species), *Beccariola* Arrow, 1943 (31 species), *Dryadites* Frivaldszky, 1883 (8 species), *Cymbachus* Gerstaecker, 1857 (5 species), *Pseudindalmus* Arrow, 1920 (13 species), *Aphorista* Gorham, 1873 (3 species) and *Mycetina* Mulsant, 1846 (70 species) widely distributed in the Holarctic, Oriental, and Afrotropical regions. This group is supported by a larval synapomorphy: labrum with sinuate or multi-denticulate apical margin (Tomaszewska 2005).

Apart from *Engonius excisipes*, Strohecker and Chûjô (1970) transferred seven other species to *Sinocymbachus*: *Cymbachus humerosus* Mader, 1938, *C. parvimaculatus* Mader, 1938, *Engonius luteomaculatus* Pic, 1921, *E. angustefasciatus* Pic, 1940, *Amphisternus bimaculatus* Pic, 1927, *A. quadrimaculatus* Pic, 1927, and *A. quadriundulatus* Chûjô, 1938. Moreover, *Amphisternus quadrinotatus* Chûjô, 1938 was recognised as a synonym of *S. humerosus* (Mader, 1938) by the same authors, and *Sinocymbachus politus* (Taiwan) and *S. decorus* (Yunnan) were described as new species (Strohecker and Chûjô 1970).

Prior to the present study, *Sinocymbachus* included ten species (Shockley et al. 2009): *S. angustefasciatus*, *S. bimaculatus*, *S. decorus*, *S. excisipes*, *S. humerosus*, *S. luteomaculatus*, *S. parvimaculatus*, *S. politus*, *S. quadrimaculatus* and *S. quadriundulatus*. During the examination of Endomychidae collected in China, four new species were recognised and are described here. An updated key to species of *Sinocymbachus* is given.

Materials and methods

Type specimens of the new species described here and examined specimens are deposited in the following institutions and private collections:

CBWX	Collection of Wen-Xuan Bi, Shanghai, China
CCCC	Collection of Chang-Chin Chen, Tianjin, China
CCLX	Collection of Ling-Xiao Chang, Beijing, China
IZCAS	Chinese Academy of Sciences, Institute of Zoology, Beijing, China
MHBU	Museum of Heibei University, Baoding, China
SHNU	Shanghai Normal University, China, Shanghai

The specimens were examined, dissected, and measured using a Olympus SZX10 dissecting microscope. The measurements are standardised as follows: body length from the apical margin of the clypeus to the apex of the elytra; body width across both elytra at widest part; pronotal length from anterior angle to posterior margin; elytral length along the suture, including the scutellum. After observation, the dissected parts were mounted on the same card with the specimen. The abdomen was boiled in 10% NaOH solution, cleaned, and the aedeagus was dissected in distilled water. Habitus photographs were taken using a Canon EOS 5D III SLR camera and Canon MP-E 65 mm macro lens, and an Olympus OM-D E-M1 camera and Olympus ED 60 mm macro lens. Photographs of male genitalia and aedeagi were taken using a Canon EOS 5D III SLR camera and Canon MP-E 6 5mm macro lens. All photographs were refined in Adobe Photoshop CC 2015.

Taxonomy

***Sinocymbachus* Strohecker & Chûjô**

Sinocymbachus Strohecker & Chûjô, 1970: 511.

Type species. *Engonius excisipes* Strohecker, 1943.

Diagnosis. The species of *Sinocymbachus* appear to be closely related to *Cymbachus*. However, *Sinocymbachus* can be distinguished from *Cymbachus* in having the body more elongate in most cases (except *S. parvimaculatus* and *S. sinicus* sp. nov.); intercoxal process of mesoventrite distinctly longer than wide (except *S. parvimaculatus* and *S. sinicus* sp. nov.), and with median ridge or tubercle at base; mesotibiae sexually dimorphic, toothed and excised on inner edge in male, straight in female (modified based on Tomaszewska 2005).

Remarks. There is distinct sexual dimorphism in the species of the genus *Sinocymbachus*. The species of the genus *Sinocymbachus* bear distinct characters of sexual dimorphism. The mesotibiae of males usually have variously developed teeth and excisions. Besides, median lobe of the aedeagus is usually less complicated apically in the species with teeth and excisions symmetric on mesotibiae while it is more complicated in the species with teeth and excisions placed asymmetrically on tibiae and usually have a wide concavity on the ventral side of antenna. However, there are also exceptions. For example, the median lobe is complicated in the males of *S. excisipes* with symmetric teeth and excisions on mesotibiae while there is a wide concavity on the ventral surface of antenna in the males of *S. humerosus* with symmetrically placed teeth and excisions on mesotibiae.

***Sinocymbachus fanjingshanensis* Chang & Bi, sp. nov.**

http://zoobank.org/0022ECFA-7F83-4A4F-A3AC-57CEFDAB78F8
Figures 1A, 2A, 3A, 4A, 5A, 6A

Type material. ***Holotype.*** Male, China: Guizhou Province: Jiangkou, Fanjingshan, 1775 m, 23–27.VII.2016, Yu-Tang Wang leg. (SHNU); ***Paratypes.*** 1 male, 1 female, Jiangkou, Fanjingshan, 1775 m, 11.VII.2009, Wen-Hsin Lin leg. (CCCC).

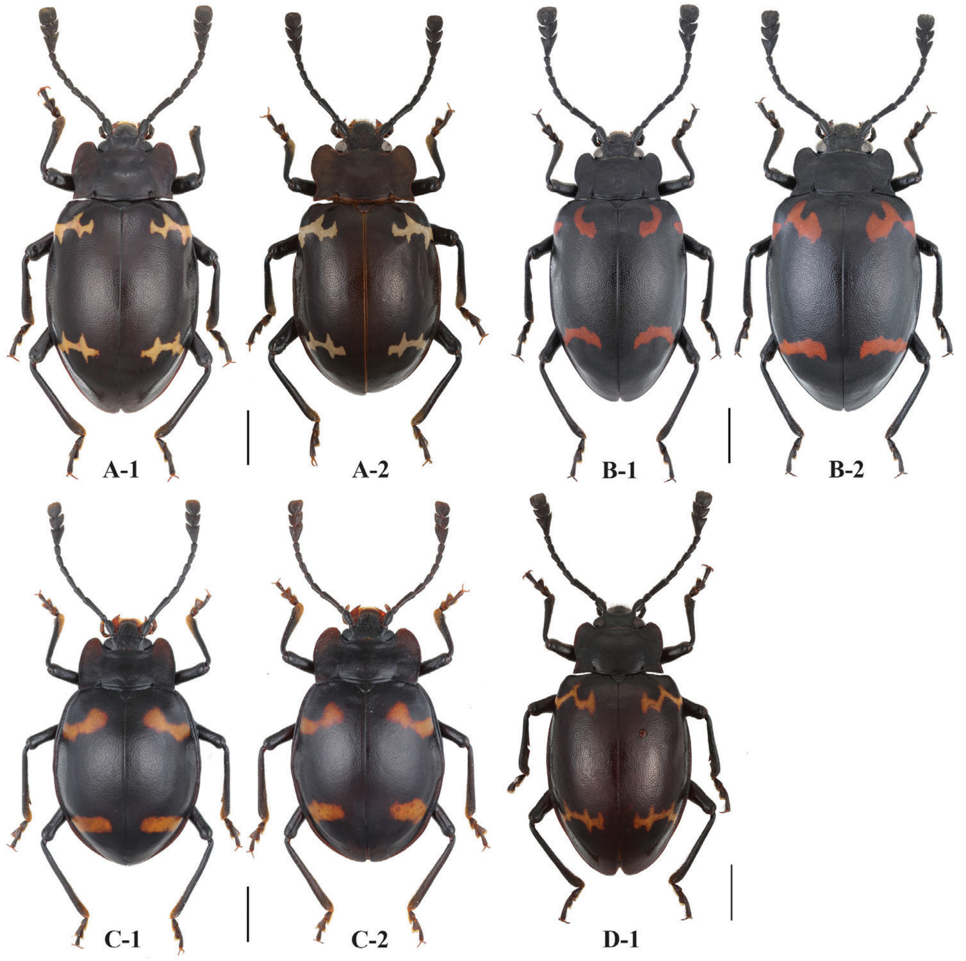

Figure 1. Habitus of *Sinocymbachus* spp. nov. **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov. **1** male **2** female. Scale bar: 2 mm.

Etymology. The name refers to the type locality.

Diagnosis. *Sinocymbachus fanjingshanensis* sp. nov. is most similar to *S. angustefasciatus*, *S. longipennis* sp. nov., *S. quadriundulatus* and *S. wangyinjiei* sp. nov. in appearance. However, *S. fanjingshanensis* sp. nov. differs from *S. angustefasciatus* by the shiny body (vs. body opaque); left mesotibia in male widely excised (vs. not excised); from *S. longipennis* sp. nov. by the body dark brown, shiny (vs. black, opaque); elytra oval with sides curved (vs. long oval, weakly curved); right mesotibia in male not excised (vs. with shallow and weakly undulate excision); from *S. quadriundulatus* by the body without cupreous sheen (vs. with cupreous sheen); left mesotibia in male widely excised (vs. not excised); from *S. wangyinjiei* sp. nov. by the mesoventral process with anterior and posterior margins nearly equally wide (vs. anterior margin

Figure 2. Left antenna of *Sinocymbachus* spp. nov. (ventral view) **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov.

much wider than posterior); mesotibia in male with shallow but broad excision (vs. with deep and narrow excision).

Description. Length 9.7–10.9 mm. Body oval, approximately 1.9–2.0 times as long as wide; convex; shiny. Colour dark brown, shiny, with four irregular orange transverse maculae on the elytra.

Head. Antenna (Fig. 2A) long, rather slender, extending to ca. 1/2 body length, with antennomeres 1–8 distinctly longer than wide; scape ca. 3.0 times as long as pedicel; pedicel wider than long; antennomere 3 nearly as long as 4 and 5 combined; antennomere 4 as long as 5; antennomeres 5–8 gradually shorter; club rather broad, moderately flat, loosely articulated; antennomeres 10 and 11 ventrally with wide concavity.

Thorax. Pronotum 2.4–2.9 mm long, 3.5–3.8 mm wide; widest near 1/2 of pronotal length; rather coarsely and densely punctate; lateral and anterior margins narrowly bordered; anterior edge with large stridulatory membrane; sides undulate, deeply emarginate near basal 1/4; anterior angles produced, bluntly rounded; posterior angles acutely produced; disc weakly convex; median furrow absent; lateral sulci distinct, linear, extending to 1/3 of pronotal length; basal sulcus weakly sinuate, moderately deep. Prosternal process (Fig. 3A) moderately widely separating procoxae; sides almost parallel, forked apically, not extending beyond front coxae. Mesoventral process (Fig. 3A) nearly pentagonal, distinctly longer than wide; sides curved outwardly; disc with short median ridge near basal 1/4. Elytra 7.3–8.1 mm long, 5.2–5.5 mm wide; 2.8–3.0 times as long as pronotum; 1.4–1.5 times as wide as pronotum; punctations coarser and denser than those on pronotum; sides curved, widest near 1/2 of elytral length; con-

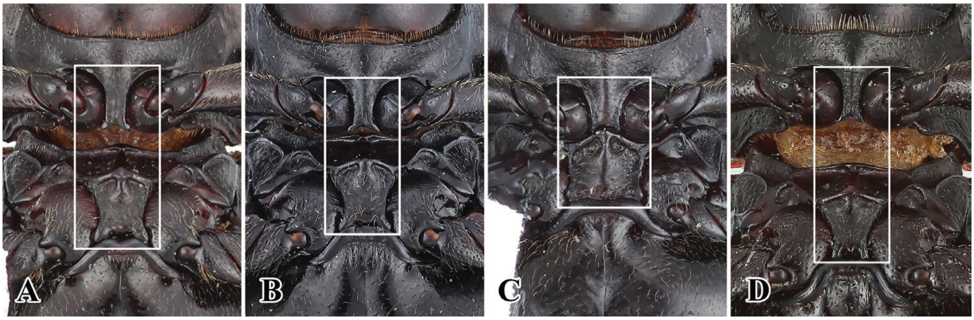

Figure 3. Prosternal and mesoventral process of *Sinocymbachus* spp. nov. **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov.

verging from posterior 1/3 to apex; humeri weakly prominent. Each elytron with two transverse maculae: anterior macula behind humerus, nearly branch-shaped, with outer margin touching lateral margin of elytra, and inner margin distant from elytral suture; posterior macula located at apical 1/3, band-like, with anterior and posterior margins bidentate; outer margin distant from lateral margin of elytra, inner margin distant from elytral suture. Left mesotibia (Fig. 4A-1) in male with small sharp tooth near basal 1/4 on inner edge, then deeply excised to apical 1/3; right mesotibia (Fig. 4A-2) in male with small sharp tooth near apical 1/3 on inner edge. Pro- and metatibiae simple.

Abdomen. Ventrite 1 almost as long as two subsequent ventrites combined; ventrites 2–4 subequal in length. Ventrite 5 with lateral margin gradually converging posteriorly; posterior margin broadly rounded medially in male (Fig. 5A-1); in female lateral margin strongly converging posteriorly; posterior margin acutely rounded medially (Fig. 5A-2). Aedeagus (Fig. 6A) short and stout, heavily sclerotised, curved. Median lobe very short, with wide branches. Tegmen basal, ring-shaped.

Distribution. China: Guizhou.

Sinocymbachus longipennis **Chang & Bi, sp. nov.**

http://zoobank.org/CBB57831-D5E1-4CFF-A122-64FEF26CB4B6
Figures 1B, 2B, 3B, 4B, 5B, 6B

Type material. ***Holotype.*** Male, China: Yunnan Province: male, Gongshan, Dabadi, 2840 m, 14.VI.2015, Wen-Xuan Bi leg. (SHNU); ***Paratypes.*** 1 male, 1 female, same data as holotype (CBWX); 1 female, Gongshan, Sendang-Dabadi, 2840 m, 20.VI.2015, Wen-Xuan Bi leg. (CBWX); 1 male, Diqing, Weixi, Badi, Nanjieluo, 2921 m, 29.VI.2014, Xiao-Dong Yang leg. (CCCC); 5 males, Dayao County, Santai Township, Xiaobaicaoling, 29–30.V.2013, 2980 m Wen-Xuan Bi leg. (CBWX); 1 male, Binchuan County, Jizushan, 2400 m, 18.VII.2010, Liang Tang leg. (CBWX); Sichuan Province: Shimian County, alt. 2580 m, 5.VIII.2016, Ai-Min Shi, Yan-Hong Li leg. (MHBU); 9 males, Puge County, Luobinshan Cableway Station (downhill exit), alt. 2500 m, light

Figure 4. Male mesotibia of *Sinocymbachus* spp. nov. **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov. **1** left **2** right.

trap, 9.VI.2012, Gan-Yan Yang leg. (IZCAS); 9 males, Puge County, Luobinshan, 2616 m, 9–10.VI.2012, Xiao-Dong Yang leg. (CCCC); 2 males, ditto except (CCLX); 1 male, Mianning County, Yele, 2800 m, 11.VIII.2005, Yi Ming leg. (CBWX); 12 males, Liziping, Shoubayan Power Station, alt. 2360 m, light trap, 28.9351N, 102.2468E, 22.VI.2012, Gan-Yan Yang leg. (IZCAS); Xizang Province: 1 female, Chawalong, Mengzhacun, Zhahazu, 2920 m, 3.VIII.2015, Wen-Xuan Bi leg. (CBWX).

Etymology. The name refers to the distinctly elongate elytra, especially in male.

Diagnosis. *Sinocymbachus longipennis* sp. nov. is most similar to *S. angustefasciatus*, *S. fanjingshanensis* sp. nov., *S. quadriundulatus* and *S. wangyinjiei* sp. nov. in external appearance. However, the distinctly more elongate elytra (especially in males) with nearly parallel sides can separate it from all these similar species. In addition, *S. longipennis* sp. nov. differs from *S. angustefasciatus* by having the elytra widest in the middle length (vs. behind middle); left mesotibia in male widely excised (vs. not widely excised); from *S. fanjingshanensis* sp. nov. by the body black and opaque (vs. dark brown, shiny); right mesotibia in male with shallow and weakly undulate excision (vs. not excised); from *S. quadriundulatus* by the body without cupreous sheen (vs. with cupreous sheen); left mesotibia in male widely excised (vs. not widely excised); from *S. wangyinjiei* sp. nov. by the body black and opaque (vs. dark brown, shiny); mesotibia in male with shallow and nearly straight excision (vs. with deeply U-shaped excision).

Description. Length 9.5–10.6 mm. Body long and oval, 1.8 times as long as wide; convex; shiny. Colour black with four orange irregular maculae on elytra, narrow and transverse.

Head. Antenna (Fig. 2B) long, rather stout, extending to ca. 1/2 body length, with antennomeres 1–8 distinctly longer than wide; scape approximately 3.5 times as long

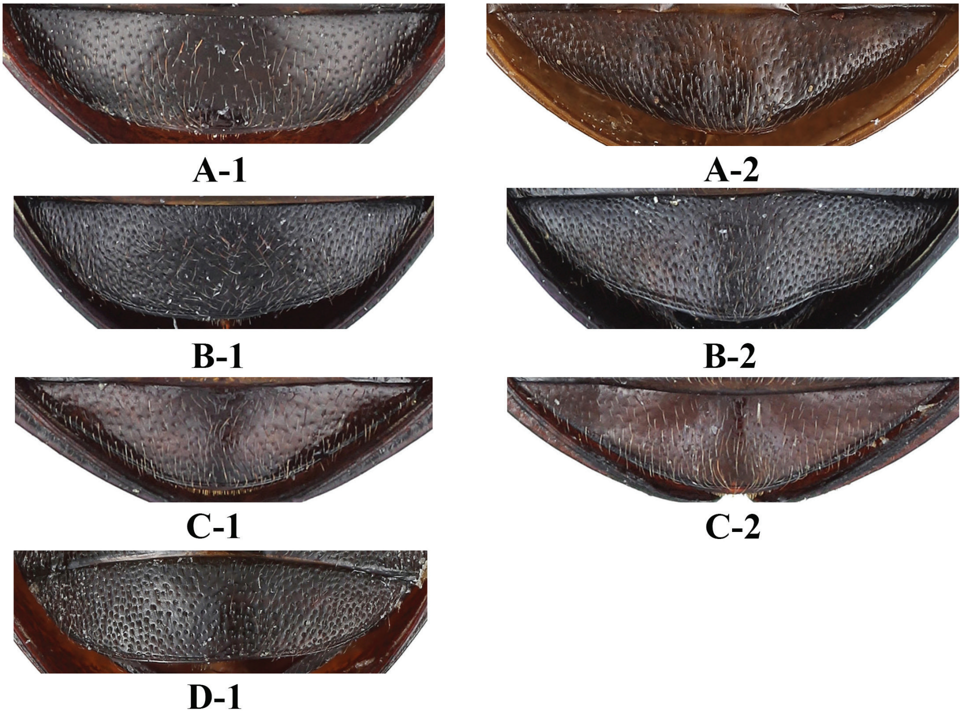

Figure 5. Male ventrite V of abdomen of *Sinocymbachus* spp. nov. **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov. **1** male **2** female.

as pedicel; pedicel wider than long; antennomere 3 longer than 4 and 5 combined; antennomere 4 as long as 5; antennomeres 5–8 gradually shorter; club very broad, approximately 4.0 times as wide as antennomere 8, moderately flat, loose; antennomeres 10 and 11 ventrally with wide concavity.

Thorax. Pronotum 2.3–2.8 mm long, 3.2–3.5 mm wide; widest at base; coarsely and rather densely punctate; lateral and anterior margins narrowly bordered; anterior edge with moderately large stridulatory membrane; sides undulate, deeply emarginate near basal 1/3 length; anterior angles produced, bluntly rounded; posterior angles acutely produced; disc weakly convex; median furrow absent; lateral sulci distinct, linear, extending to 1/3 of pronotal length; basal sulcus weakly sinuate, moderately deep. Prosternal process (Fig. 3B) moderately widely separating procoxae; sides curved outwardly, forked apically, not extending beyond front coxae. Mesoventral process (Fig. 3B) nearly pentagonal, with sides curved outwardly; disc distinctly ridged. Elytra 7.7–8.2 mm long, 5.2–5.8 mm wide; 2.9–3.3 times as long as pronotum; 1.6–1.7 times as wide as pronotum; punctations coarse and denser than those on pronotum; sides weakly curved, widest near 1/2 length of elytron; strongly converging from posterior 1/3 to apex; humeri weakly prominent. Each elytron with two transverse maculae: anterior elytral macula located on humerus, nearly W-shaped, in some specimens separated into two parts; outer margin almost touching lateral margin of elytra, inner margin distant from elytral suture; posterior macula located at apical 1/3, nearly band-shaped; outer margin distant from lateral margin of elytra, inner margin distant from elytral suture. Left mesotibia (Fig. 4B-1) in male with small sharp tooth near basal 1/3 on inner edge, then deeply excised to apical 1/3; right mesotibia (Fig. 4B-2) in male with small sharp tooth near apical 1/3 on inner edge. Pro- and metatibiae simple.

Abdomen. Ventrite 1 almost as long as subsequent two ventrites combined; ventrites 2–4 subequal in length. Ventrite 5 with lateral margin gradually converging posteriorly; posterior margin broadly rounded in male (Fig. 5B-1); in female lateral margin strongly converging posteriorly and acutely rounded (Fig. 5B-2). Aedeagus (Fig. 6B) short and stout, heavily sclerotised, curved. Median lobe very short, with two large finger-like branches. Tegmen basal, ring-shaped.

Distribution. China: Yunnan and Sichuan.

Sinocymbachus sinicus **Chang & Bi, sp. nov.**

http://zoobank.org/CAB67E33-813E-4C10-81A8-92E7A029B91E

Figures 1C, 2C, 3C, 4C, 5C, 6C

Type material. ***Holotype.*** Male, China: Xizang Province: Motuo, Baricun, 1700 m, 7.VIII.2014, Wen-Xuan Bi leg. (SHEM); ***Paratypes.*** 1 male, 1 female same data as holotype (CCLX); 1 male ditto except (CBWX); 1 female, Motuo, 1900 m, 20.VIII.2013, Wen-Xuan Bi leg. (CBWX); 2 females, Xizang, Linzhi, Motuo, 1559 m, 2016.VIII.5, Xiao-Dong Yang leg. (CCCC); 1 male, 1 female, Linzhi, Motuo, 1526 m, 2016. VIII.21, Xiao-Dong Yang leg. (CCCC); 1 male, ditto except 2016.VIII.23 (CCCC); 1 male, Yunnan Province: Gongshan, Dulongjiang, Maku, 1250 m, Wen-Xuan Bi leg. (CBWX).

Etymology. The name is dedicated to our country which has created good research environment for us.

Diagnosis. *Sinocymbachus sinicus* can be separated from all its congeners by having the body short oval and each elytron with two transverse maculae, more regular without distinct projections.

Description. Length 8.9–9.1 mm. Body short oval, approximately 1.3 times as long as wide; moderately convex; smooth. Colour black with four orange irregular transverse maculae on elytra.

Head. Antenna (Fig. 2C) long and slender, extending to approximately 1/2 body length, with antennomeres 1–8 distinctly longer than wide; scape approximately 4.0 times as long as pedicel; antennomere 3 longer than 4–5 combined; antennomere 4 nearly as long as antennomere 5; antennomeres 5–8 gradually shorter; club broad, approximately 2.5 times as wide as antennomere 8, moderately flat, loosely articulated.

Thorax. Pronotum 2.3–2.4 mm long, 3.5–3.9 mm wide; widest near 1/2 of pronotal length; coarsely and rather densely punctate; lateral and anterior margins

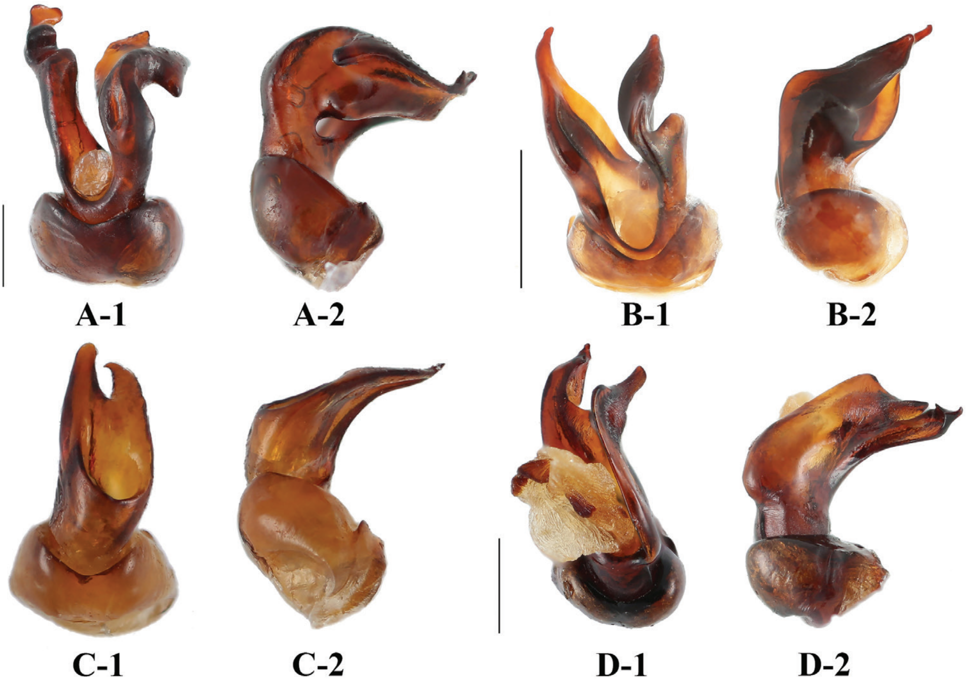

Figure 6. Aedeagus of *Sinocymbachus* spp. nov. **A** *S. fanjingshanensis* sp. nov. **B** *S. longipennis* sp. nov. **C** *S. sinicus* sp. nov. **D** *S. wangyinjiei* sp. nov. **1** ventral view **2** lateral view. Scale bar: 1 mm.

narrowly bordered; anterior edge with moderately large stridulatory membrane; sides nearly parallel; anterior angles produced, bluntly rounded; posterior angles moderately acutely produced; disc weakly convex; two round raised areas laterally; inflexed laterally; median furrow absent; lateral sulci very short and deep, in form of triangular dent; basal sulcus weakly curved, moderately deep. Prosternal process (Fig. 3C) comparatively widely separating procoxae; sides curved outwardly near apex, forked apically, not extending beyond front coxae. Mesoventral process (Fig. 3C) nearly pentagonal, as long as wide, with short median ridge anteriorly. Elytra 6.6–6.8 mm long, 5.0–5.2 mm wide; 2.8–2.9 times as long as pronotum; 1.3–1.4 times as wide as pronotum; punctures as large as the pronotal ones, densely distributed; sides strongly curved, widest near 1/2 length of elytron; humeri weakly prominent. Each elytron with two irregular transverse maculae. Anterior elytral macula located behind humerus, in form of arcuate irregular band; anterior margin deeply emarginate; posterior margin weakly emarginate or nearly straight; outer margin not touching lateral margin of elytra, inner margin distant from elytral suture. Posterior macula located at apical 1/3, in form of nearly straight band; outer and inner margin of macula distant from both elytral lateral margin and suture. Both mesotibiae (Fig. 4C) in male with small sharp tooth near apical 1/4 on inner edge, in female without teeth. Pro- and metatibiae simple.

Abdomen. Ventrite 1 longer than 2 and 3 combined; ventrites 2–4 subequal in length. Ventrite 5 (Fig. 5C) arcuate in both sexes. Aedeagus (Fig. 6C) short and stout, heavily sclerotised, curved. Median lobe with two short branches, acute apically. Tegmen basal, ring-shaped.

Distribution. China: Xizang and Yunnan.

Sinocymbachus wangyinjiei Chang & Bi, sp. nov.

http://zoobank.org/1040CEF1-2A3C-4FD2-A9E5-FF27D3490BA3
Figures 1D, 2D, 3D, 4D, 5D, 6D

Type material. *Holotype.* Male, China: Hubei Province: Shennongjia, 1635 m, 4.X.2007, Yin-Jie Wang leg. (SHNU).

Etymology. The name is dedicated to Mr. Yin-Jie Wang, who collected the holotype of this species for our study.

Diagnosis. *Sinocymbachus wangyinjiei* sp. nov. resembles *S. angustefasciatus*, *S. fanjingshanensis* sp. nov., *S. longipennis* sp. nov., and *S. quadriundulatus*. However, it can be differentiated from *S. angustefasciatus* by the body shiny (vs. opaque); mesotibia in male with deeply U-shaped excision (vs. not excised); from *S. fanjingshanensis* sp. nov. by the anterior margin of mesoventral process much wider than posterior margin (vs. anterior margin as wide as posterior margin); mesotibia in male with deep and narrow excision (vs. with shallow and wide excision); from *S. longipennis* sp. nov. by the body dark brown and shiny (vs. black, opaque); elytra oval with sides distinctly curved (vs. long oval, nearly parallel); mesotibia in male with deep and narrow excision (vs. with shallow and wide excision); from *S. quadriundulatus* by the body without cupreous sheen (vs. with cupreous sheen); mesotibia in male with deeply U-shaped excision (vs. not excised).

Description. Length 9.7 mm. Body oval, approximately 2.1 times as long as wide; convex; shiny. Colour black, shiny, with four orange irregular transverse maculae on elytra.

Head. Antenna (Fig. 2D) long, rather slender, extending to approximately 1/2 body length, with antennomeres 1–8 distinctly longer than wide; scape 5.5 times as long as pedicel; pedicel wider than long; antennomere 3 nearly as long as 4 and 5 combined; antennomeres 4–8 gradually shorter; club moderately broad and flat, loose; antennomeres 10 and 11 with wide concavity ventrally.

Thorax. Pronotum 2.1 mm long, 3.2 mm wide; widest at base; rather coarsely and densely punctate; lateral and anterior margins narrowly bordered; anterior edge with large stridulatory membrane; sides undulate, deeply emarginate near basal 1/4 length; anterior angles bluntly produced; posterior angles acutely produced; disc weakly convex; median furrow absent; lateral sulci short and deep, in form of triangular dent; basal sulcus sinuate, moderately deep. Prosternal process (Fig. 3D) moderately widely separating procoxae; sides curved outwardly toward apex, forked apically, not extending beyond front coxae. Mesoventral process (Fig. 3D) nearly pentagonal, distinctly longer than wide; sides converging to apex; disc with short median ridge anteriorly. Elytra 7.2 mm long, 4.6 mm wide; 3.4 times as long as pronotum; 1.4 times as wide as pronotum; punctation coarse and dense; sides curved, widest near 1/2 length of elytron; converging from here to apex; humeri weakly prominent. Each elytron with two irregular transverse maculae: anterior elytral macula located on humerus, nearly W-shaped; outer margin touching lateral margin of elytra, inner margin distant from elytral suture; posterior macula located at apical 1/3, transverse bands with four distinct projections; outer margin distant from lateral margin of elytra, inner margin distant from elytral suture. Left mesotibia (Fig. 4D-1) in male with small sharp tooth behind 1/2 length on inner edge, then deeply U-shaped excised; right mesotibia (Fig. 4D-2) in male with small sharp tooth near apical 1/3 on inner edge, then deeply U-shaped excised. Pro- and metatibiae simple.

Abdomen. Ventrite 1 almost as long as two subsequent ventrites combined; ventrites 2–4 subequal in length. Ventrite 5 (Fig. 5D) with posterior margin gently rounded. Aedeagus (Fig. 6D) short and stout, heavily sclerotised, straight. Median lobe very short, with two wide, large and rather flat branches. Tegmen basal, ring-shaped.

Distribution. China: Hubei.

Sinocymbachus angustefasciatus **(Pic, 1940)**

Figures 12A, 13A, 14A, 15A, 16A, 17A, 18A

Engonius angustefasciatus Pic, 1940: 11.
Sinocymbachus angustefasciatus: Strohecker and Chûjô 1970: 517.

Diagnosis. *Sinocymbachus angustefasciatus* is most similar to *S. fanjingshanensis* sp. nov., *S. longipennis* sp. nov., *S. quadriundulatus* and *S. wangyinjiei* sp. nov. by having transverse elytral maculae. However, *S. angustefasciatus* differs from *S. fanjingshanensis* sp. nov. by the body opaque (vs. body shiny); left mesotibia in male not excised (vs. widely excised); from *S. longipennis* sp. nov. by the oval elytra with sides distinctly curved (vs. long oval, nearly parallel); left mesotibia in male not excised (vs. widely excised); from *S. quadriundulatus* by the body opaque (vs. body shiny); mesotibial tooth in male symmetric (vs. asymmetric); from *S. wangyinjiei* sp. nov. in having the body opaque (vs. body shiny); mesotibia in male not excised (vs. deeply excised).

Length. 9.2–10.6 mm; width: 4.9 mm.

Material examined. China: Sichuan Province. Qingchuan County, 13.VII.2013, Jun-Xia Zhang leg. (1 female, MHBU); Wolong Nature Reserve, 18.VII.2013, Yun-Xia Zhang leg. (1 female, MHBU); Wolong, 6–8.VIII.2004, Xiu-Juan Yang & Hui-Ran Hua leg. (2 males, MHBU); Kangding, Pengta, 28.VIII.2005, Fu-Ming Shi leg. (10 males, MHBU); ditto except 29.VIII.2005 (17 males, MHBU); ditto except 30.VIII.2005 (5 males, MHBU); ditto except 31.VIII.2005 (7 males MHBU); ditto except 1.IX.2005 (24 males, MHBU); Yajiang, Decha, 7.IX.2005, Fu-Ming Shi leg. (2 males, MHBU); Jiulong, Hongba, 23.IX.2008, Fu-Ming Shi leg. (1 male, MHBU); ditto except

25.IX.2008 (1 female, MHBU); Kangding, alt. 2624 m, 31.VII.2010, Fu-Ming Shi & Yong-Sheng Pan leg. (1 male, MHBU); Shimian Conty, Liziping, 13.VIII.2010, Fu-Ming Shi leg. (2 males, MHBU); Baoxing Country, Ganyanggou, 30°24'N, 102°38'E, alt. 2000 m, 28.VI.2012, Huang Hao leg. (1 female, SHNU); Shimian Country, Liziping, 28°55'N, 102°13'E, alt. 2600 m, 15.VII.2012, Peng, Dai & Yin leg. (1 female, SHNU); Shimian Country, Caoke Township, Tuanjie Village, 25.VIII.2016, Jian-Yue Qiu & Hao Xu leg. (1 male, CCLX); Fengtongzhai, Mahuanggou, 30.VII.2016, Cai-Xia Yuan leg. (1 female, MHBU); ditto except 31.VII.2016 (2 males, 2 females, MHBU); Liziping, Zimaping, 31.VII.2016, Cai-Xia Yuan et al. leg. (1 female, MHBU); Kangding, 2500–2700 m, 18.VIII.2014, Wen-Xuan Bi leg. (6 males, 9 females, CBWX); Tianquan County, Labahe, 2060 m, 28–30.VII.2007, Liu, Zhang, Zhou & Bi leg. (2 males, 1 female, CBWX); Emeishan, Huayanding, 1914 m, 15.VIII.2011, Hao Huang leg. (1 male, CCCC); Baoxing, Jiajinshan, Mahuanggou, 27.VI.2012, Xiao-Dong Yang leg. (1 male, CCCC); **Yunnan Province:** Yiliang, Xiaocaoba, 24.VIII.2013, Xun Bian & Guang-Lin Xie leg. (1 male, MHBU); Chongzhou, Jiguanshan, Shaoyaogou, 29.V.2016, Fu-Ming Shi leg. (3 males, 1 female, MHBU); ditto except 31.V.2016 (5 males, MHBU); Shimian, Liziping Protection Station, Gongyihai Station, Liu et al. leg. (1 male, SHEM 24348709); Tianquan County, Labahe, alt. 2100 m, 28–30.VII.2007, Liu et al. leg. (1 female, SHEM24348710); ditto except (1 male, SHEM24348711); ditto except (1 male, SHEM24348712); Shimian Hsien, Liziping N.R., Gongyihai Refuge, 29°01'30.76"N, 102°23'05.11"E, 2056 m, mixed leaf litter, sifted, 25.VII.2016, Zhou, Jiang, Liu & Gao leg. (3 males, 4 females, SHNU); Shimian Hsien, Liziping N.R., Gongyihai-Mamadi, 28°59'24.55"N, 102°24'33.92"E, 2056–2615m, 24.VII.2016, Zhou, Jiang, Liu & Gao leg. (3 males, 2 females, SHNU); Baoxing Hsien, Fengtongzhai N.R., Dashuigou, 30°34'21.95"N, 102°52'54.92"E, 1594 m, 31.VII.2016, Zhou, Jiang, Liu & Gao leg. (1 male, SHNU); **Shaanxi Province:** Ningshan, Pingheliang, 33.479148N, 108.491827E, alt. 2388m, 15.VIII.2013, Xi-Chao Zhu & Ying Tian leg. (2 males, MHBU); Liuba, Caishenmiao, 33°43'27.0"N, 107°12'11.1"E, alt. 1212m, 17.VIII.2013, Xi-Chao Zhu & Ying Tian leg. (1 female, MHBU).

Distribution. China: Sichuan. First records from Yunnan and Shaanxi Provinces of China.

***Sinocymbachus bimaculatus* (Pic, 1927)**

Figures 7A, 8A, C, E, 12B, 13B, 14B, 15B, 16B, 17B, 18B

Amphisternus bimaculatus Pic, 1927: 11.
Cymbachus bimaculatus: Strohecker 1953: 90.
Sinocymbachus bimaculatus: Strohecker and Chûjô 1970: 513.

Diagnosis. *Sinocymbachus bimaculatus* is most similar to *S. humerosus* in appearance, sharing two round maculae on each elytron. However, *S. bimaculatus* differs from *S. humerosus* by the scutellum (Fig. 7) being distinctly longer than wide (vs. nearly as long

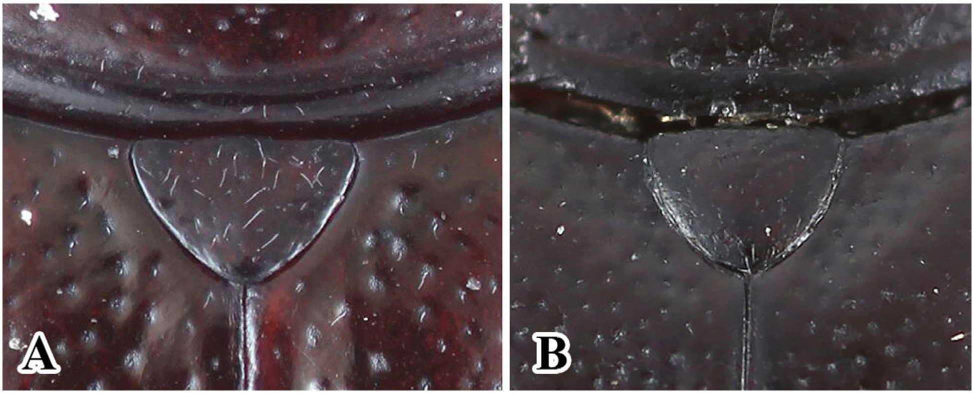

Figure 7. Scutellum. **A** *Sinocymbachus bimaculatus* **B** *Sinocymbachus humerosus*.

as wide); and mesotibial tooth in male placed near apical 1/3 length of tibia (vs. near 1/4 length).

Length. 8.0–9.7 mm; width: 5.1–5.8 mm.

Material examined. China: Guizhou Province: Xishui, Dabaitang, 25–29. IX.2000, Guo-Dong Ren leg. (1 female, MHBU); ditto except 30.IX.2000 (1 female, MHBU); Yanhe County, Mayanghe, Maojia Village, 5–12.VI.2007, Feng-Yan Wang leg. (2 females, MHBU); Fenghuangshan Mt., 27°42'N, 106°55'E, alt. 900 m, 6.III.2012, LI Runyu leg. (1 female, SHNU); Libo Hsien, Maolan N.R., 25°16'38"N, 107°55'29"E, mixed leaf litter, sifted, 800 m, 19.VII.2015, Chen, He, Hu, Wang & Zhao leg. (1 male, 1 female, SHNU); **Guangxi Province:** Shangsi County, Hongqi, 29.XI.2001, Xiu-Juan Yang & Ai-Min Shi leg. (1 female, MHBU); Longsheng County, Huaping, 15.X.2005, Ji-Liang Wang & Chao Gao leg. (1 female, MHBU); Huanjiang County, Yangmeiao Protection Station, 15.VIII.2016, Ling-Xiao Chang leg. (4 males, 1 female, MHBU); Lin'gui Country, Huaping N.R., Anjiangping, alt. 1200 m, 13.VII.2011, He W.-J. & Tang L. leg. (1 female, SHNU); Hechi City, Mulun N.R., 25°8'54"N, 108°2'37"E, mixed leaf litter, sifted, 350–450m, 24.VII.2015, Chen et al. leg. (1 male, 1 female, SHNU); Huanjiang, Jiuwanshan, Yangmeiao, 1200 m, 18.VII.2015, light, Liu & Zhu leg. (1 male, SHEM24344878); Jinxiu, Changtanhe, 860 m, 15.VII.2014, Xiao-Bin Song leg. (1 male, CBWX); Maoershan, Lijiangyuan, 810 m, 28.VII.2014, Xiao-Bin Song leg. (2 females, CBWX); Jinxiu, Houzishan, 960 m, 13.VII.2014, Xiao-Bin Song leg. (1 male, CBWX); **Sichuan Province:** Luzhou, Huangjing, 20.VII.2002, Ming Bai & Jian-Feng Wang leg. (1 female, MHBU); **Hunan Province:** Zhangjiajie, Sangzhi, Guandiping, day, 16.VII.2010, Hao Xu leg. (1 male, MHBU); ditto except 28.VII.2010 (6 females, MHBU); Anhua County, Liubu, 16–17.VII.2004, Ji-Liang Wang leg. (1 male, MHBU); Tongdao County, Mujiao, 25.VII.2004, Jiang-Feng Wang & Ji-Liang Wang leg. (1 male, 1 female MHBU); Yongshun County, Xiaoxi, 8.VIII.2004, Ji-Liang Wang leg. (1 male, 1 female, MHBU); Yueyang City, Pingjiang County, Fushoushan, 28°28'N, 113°46'E. 1079 m, 18-26.VII.2016, Jiang-Jiang Liu & Zhou leg. (1 female, SHNU); Dongan County, Damiaokou Town, Shunhuangshan

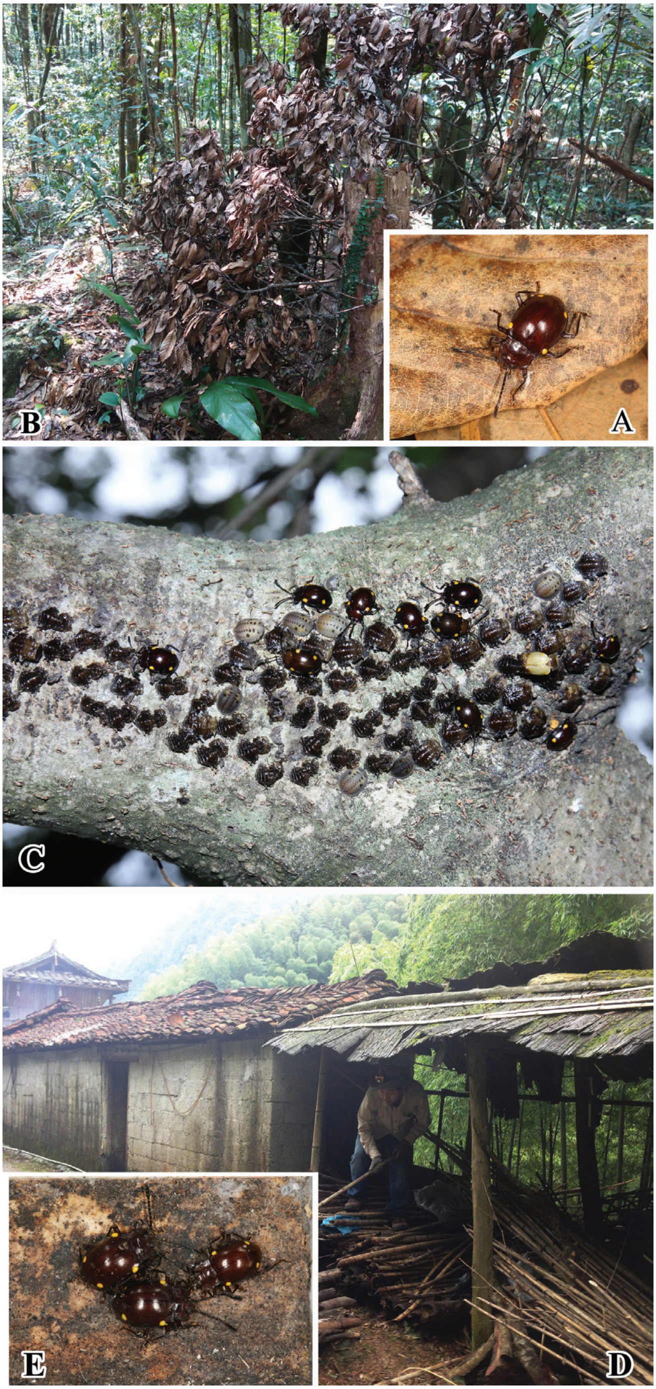

Figure 8. Habitats of *Sinocymbachus bimaculatus* **A, E** adult of *S. bimaculatus* **B** large clump of Fagaceae plants at collection site in Hainan, China **C** clusters of mature larvae, prepupae or pupae of *S. bimaculatus*, with newly emerged adults, beneath the tree trunk **D** search for Endomychidae from large pile of dead bamboos in Guangxi, China.

Park, Ehuangxi, 8.X.2015, Chi Jin leg. (CCLX); **Zhejiang Province:** Quzhou City, Jiangshan County, Shuangxikou, 27°55'02.72"N, 119°11'34.47"E, alt. 496 m, mixed leaf litter, sifted, 12.VIII.2018, Cheng & Miao leg. (1 female, SHNU); Kaihua, Gutianshan, 500–850 m, 21.IV.2013, Xiao-Bin Song leg. (5 males, 5 females, CBWX); **Fujian Province:** Wuyishan, Taohuayu, 9.VI.2013, Chi Jin & Jie Yang leg. (1 male, MHBU); Jianning, Jinraoshan, 12.VI.1956, Gen-Tao Jin & Yang-Ming Lin leg. (1 female, SHEM24295200); ditto except (1 male, SHEM24295201); ditto except (1 female, SHEM24295202); ditto except (1 male, SHEM24295203); ditto except (1 female, SHEM24295204); ditto except (1 male, SHEM24295205); ditto except (1 female, SHEM24295207); ditto except (1 male, SHEM24295208); ditto except (1 female, SHEM24295209); ditto except (1 male, SHEM24295210); ditto except (1 female, SHEM24295211); ditto except (1 female, SHEM24295212); ditto except (1 female, SHEM24295213); ditto except (1 female, SHEM24295214); ditto except (1 female, SHEM24295216); ditto except (1 female, SHEM24295223); ditto except (1 male, SHEM24295226); ditto except (1 female, SHEM24295228); ditto except (1 female, SHEM24295229); ditto except (1 female, SHEM24295199); Nanping City, Mangdangshan Mt., 26°41'51"N, 118°07'00"E, mixed forest, leaf litter, sifted, 400 m, 10.XI.2015, Yan & Tang leg. (1 female, SHNU); **Guangdong Prvince:** Nanling, 8.V.2008, Hong-Liang Shi leg. (2 males, 1 female, MHBU); Lianxian, Dadongshan, 28.V.1997 Chen Hong leg. (1 female, SYSU En-131910); Lianxian, Dadongshan, 3.IX.1994 Chang-Ping Zhao leg. (1 female, SYSU En-131911); Lianzhou City, Dadongshan, 2.VI.1998 Han Zhang leg. (1 female, SYSU En-131912); Lianxian, Dadongshan, 27.V.1997 Xiao-Xin Zhang leg. (1 female, SYSU En-131913); ditto except Ji Zheng leg. (1 female, SYSU En-131915); ditto except, 28.V.1997 Jian-Hua Li leg. (1 male, SYSU En-131916); Fengkai, Heishiding, 3.VII.1986, Zhen-Ao Chen leg. (1 female, SYSU En-131928); **Hainan Province:** Ledong Country, Jianfengling, Mingfenggu, 18°44'N, 108°50'E, alt. 950m, 30.IV.2012, PENG & DAI leg. (1 female, SHNU); Qiongzhong Country, Limushan, 1160 m, 4.IV.2016, Ling-Xiao Chang & Xing-Long Bai leg. (1 female, CCLX).

Distribution. Vietnam: Tonkin. China (new country record): Guizhou, Guangxi, Sichuan, Hunan, Zhejiang, Fujian, Guangdong and Hainan.

Biology and ecology. The adults were collected by shaking the tree from a large clump of dead wood of Fagaceae plants (Mt. Limushan, Qiongzhong, Hainan) (Fig. 8A, B). The adults and larvae were hand collected from a large pile of dead bamboos (Yangmeiao, Huanjiang, Guangxi) (Fig. 8D, E). The adults and larvae apparently feed together (Fig. 8C). *Sinocymbachus bimaculatus* is not only most similar to *S. humerosus*, but both are also sympatric.

Sinocymbachus decorus Strohecker & Chûjô, 1970

Figures 12C, 13C, 14C, 15C, 16C, 17C, 18C

Sinocymbachus decorus Strohecker & Chûjô, 1970: 516.

Diagnosis. *Sinocymbachus decorus* is most similar to *S. luteomaculatus* and *S. politus* in appearance: elytra in both species have two basal spots and one narrow transverse apical band. However, *S. decorus* differs from *S. luteomaculatus* by having a shiny body (vs. body opaque); humeri roundly subcarinate, prominent (vs. weakly prominent); from *S. politus* by the body without cupreous sheen (vs. with cupreous sheen); two basal elytral maculae arranged in oblique line (vs. spots arranged in horizontal line); mesotibial tooth in male asymmetric (vs. symmetric).

Length. 10.4–10.6 mm; width: 5.1–5.5 mm.

Material examined. China: Yunnan Province: Lincang, Wulaoshan Forest Farm, 23°54'36.4"N, 100°11'04.3"E, alt. 2371 m, 8–10.VII.2009, Ji-Shan Xu & Li-Xiang Zhang leg. (2 females, MHBU); Lincang, Wulaoshan Forest Farm, Qingrengu, 25.VIII.2019 D, Ling-Xiao Chang leg. (1 male, 1 female, CCLX); Yun County, Yongbao Town, Pinghe Reservoir, X.2018, Zi-Chun Xiong leg. (1 male, 1 female, CCLX); Jingdong County, Ailaoshan, 7–9.VIII.2009, Ji-Shan Xu & Zhong-Kun Li leg. (1 male, MHBU); Lushui, Yaojiaping, 2700 m, 21.VI.2010, Wen-Xuan Bi leg. (2 males, CBWX); ditto except 2450 m, 4.V.2015 (2 males, 1 female, CBWX); ditto except 13.VIII.2015 (1 male, 1 female, CBWX); ditto except 2450–2700 m, 14.IV.2018 (1 male, 1 female, CBWX); ditto except 2500 m, 15.IX.2018 (1 male, CBWX); Lushui, Pianma, Gangfang, 2100 m, 7.VI.2015, Wen-Xuan Bi leg. (1 male, CBWX); Dayao County, Santai Town, Xiaobaicaoling, 2980 m, 29–30.V.2013, Wen-Xuan Bi leg. (1 female, CBWX); Nanjian Sheyaojing, 2450 m, 11.VII.2017 em VII.21, Wen-Xuan Bi leg. (1 female, CBWX); Tengchong, Houqiao, Heinitang, 11–14.IX.2018, Wen-Xuan Bi leg. (2 females, CBWX); Gongshan, Shaunglawa, 1650 m, 17.VI.2015, Wen-Xuan Bi leg. (1 female, CBWX).

Distribution. China: Yunnan.

Biology and ecology. The adults were collected from dead leaves of Fagaceae plants by shaking the tree (Mt. Wulaoshan, Lincang, Yunnan).

***Sinocymbachus excisipes* (Strohecker, 1943)**

Figures 9, 12D, 13D, 14D, 15D, 16D, 17D, 18D

Engonius excisipes Strohecker, 1943: 383.
Cymbachus excisipes: Strohecker 1953: 90.
Sinocymbachus excisipes: Strohecker and Chûjô 1970: 515.

Diagnosis. *Sinocymbachus excisipes* can be separated from all its congeners by having the intercoxal process of mesoventrite with large tubercle instead of short medina ridge at base; ventrite 5 with posterior margin abruptly projecting medially in male. Furthermore, the basal and apical elytral maculae varied in different specimens - they may be composed of 2–4 small spots, or form transverse bands with strong dentations/projections (Fig. 9).

Length. 9.5–10.9 mm; width：6.0–6.2 mm.

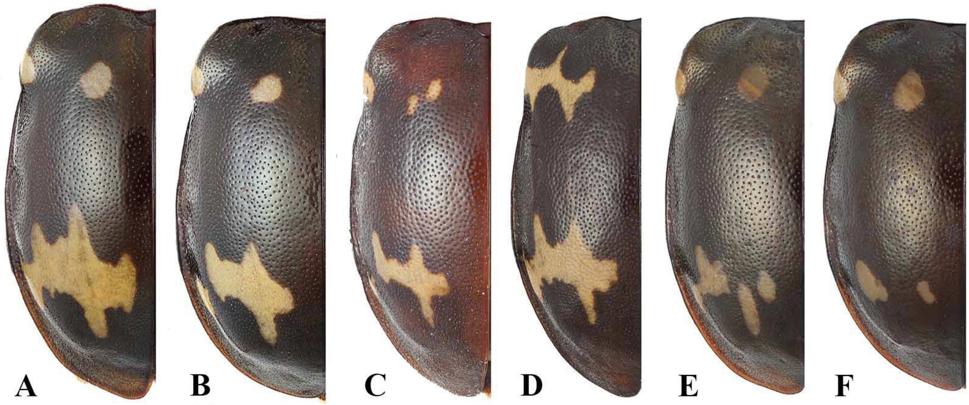

Figure 9. Variation in elytral maculae of *Sinocymbachus excisipes*. **A** general morph **B–F** variants morphs.

Material examined. China: Zhejiang Province. Tianmushan, 370–1100 m, 5.VIII.1962, Gen-Tao Jin leg. (1 female, SHEM 24343460); Longquan, Fengyangshan, 1926 m, 29.VI.2015, Liu et al. leg. (1 male, SHEM 24345681); Tianmushan, 11–14.VIII.1987, Wu Wu leg. (1 female, SYSU En-096206); Linan, Xitianmushan, 1100 m, 1–9.VII.2006, Wen-Xuan Bi leg. (1 male, 1 female, CBWX); ditto except 29.VI–1.VII.2007 (1 male, CBWX); ditto except 1100–1050 m, 14.VII.2016 (3 males, 3 females, CBWX); ditto except 10-16.VII.2018 (48 males, 24 females, CBWX); **Hunan Province:** Sangzhi County, near Tianpingshan Control Station, 15.IX.2015, Chi Jin leg. (1 male, CCLX); Yichang City, Wufeng Hsien, Houhe N. R., 3.VIII.2013, Hao Huang leg. (1 female, SHNU); **Chongqing Province:** Qianjiang District, Shuishicun, 8.VII.2011, Qiang Guo leg. (1 male, MHBU); **Guizhou Province:** Daozhen, Dashahe, 24.VIII.2004, Fu-Ming Shi leg. (1 female, MHBU); **Sichuan Province:** Emeishan, alt. 890 m, 28.VI.2009, Yu-Ting Chen leg. (2 females, MHBU); Emeishan, Leiyinsi, 11.VIII.2011, Fu-Ming Shi & Le-Hong Zhao leg. (1 male, MHBU); Eemeishan, Xixinsuo, 1400 m, 28.VI.2018, Wen-Xuan Bi leg. (1 female, CBWX); Wolong, 6–8.VIII.2004, Xiu-Juan Yang & Hui-Ran Hua leg. (3 males, 3 females, MHBU); Dujiangyan, Qingchengshan, 11–12.VIII.2004, Xiu-Juan Yang & Hui-Ran Hua leg. (1 female, MHBU); **Guangxi Province:** Jinxiu, Dayaoshan, Pingbanshan, 1150 m, 18.VII.2016, Jin-Teng Zhao leg. (2 females, CBWX); **Fujian Province:** Wuyishan, 541 m, VI.2018, leg. Zhu-Qing He (1 male, CBWX).

Distribution. China: Sichuan, Hubei. First records from Zhejiang, Hunan, Chongqing, Guizhou, and Guangxi Provinces of China.

Sinocymbachus humerosus (Mader, 1938)

Figures 7B, 10, 12E, 13E, 14E, 15E, 16E, 17E, 18E

Cymbachus humerosus Mader, 1938: 40.

Figure 10. Variation in elytral maculae of *Sinocymbachus humerosus*. **A** specimen from mainland China **B** specimen from Taiwan.

Amphisternus quadrinotatus Chûjô, 1938: 396.
Sinocymbachus humerosus: Strohecker and Chûjô 1970: 512.

Diagnosis. *Sinocymbachus humerosus* is most similar to *S. bimaculatus* in sharing two round maculae on each elytron. However, *S. humerosus* differs from *S. bimaculatus* by having the scutellum (Fig. 7) nearly as long as wide (vs. distinctly longer than wide); and mesotibial tooth in male placed near apical 1/4 of tibial length (vs. near 1/3).

Length. 8.4–8.9 mm; width: 4.7–5.3 mm.

Material examined. China: Zhejiang Province: Linan, Dajingwu, 9.VI.2012, Ling-Xiao Chang leg. (1 male, MHBU); Suichang County, Jiulongshan Reserve, Yanping, alt. 700–800 m, 12.X.2008, Jun-Hao Huang leg. (3 males, 3 females, MHBU); Longquan, Fengyangshan, 19.VII.2012, Guang-Lin Xie & Xin Wang leg. (1 male, 4 females MHBU); Tianmushan, Dahenglu, 14.VII.2012, Guang-Lin Xie leg. (1 female, MHBU); Longquan, Fengyangshan, 25.VII–1.VIII.2007, Hao-Yu LIU & Zhen-Hua Gao leg. (1 male, MHBU); Lin'an City, Mt. East Tianmushan, alt. 1050–1150 m, 13.IV.2011, Peng & Zhu leg. (1 female, SHNU); Longquan, Fengyangshan, 1250 m, 17.V.2007, Bao-Feng Zhou & Lei Wang leg. (1 female, SHEM24295628);

Xitianmushan, 300–600 m, 2.VI.2016, Wen-Xuan Bi leg. (1 female, CBWX); ditto except 450 m, 4.VII.2016 (1 male, CBWX); ditto except 1300 m, 26.VII.2016 (10 males, 9 females, CBWX); ditto except 350 m, 11.VIII.2016, (1 female, CBWX); ditto except 450–350 m, 17.VI.2014 (5 males, 6 females, CBWX); ditto except 350 m, 23.VI.2014 (2 females, CBWX); Tianmushan, 1100 m, 2.V.2005, Wen-Xuan Bi leg. (1 female, CBWX); Anji County, Longwangshan, Shenxi, 250–550 m, 22–26. IV.2006, Wen-Xuan Bi leg. (1 female, CBWX); ditto except 350 m, 7–11.VI.2012 (1 male, CBWX); Longquan, Fengyangshan, Fengyanghu, 1560 m, 5.X.2013, Wen-Xuan Bi leg. (1 female, CBWX); Changhua, Qingliangfeng, 950 m, 13–17.VI.2014, Wen-Xuan Bi leg. (1 female, CBWX); Kaihua, Gutianshan, 500–850 m, 21.VI.2013, Wen-Xuan Bi leg. (7 males, 7 females, CBWX); **Jiangxi Province:** Longnan, Jiulianshan, 23.VII.2008, Fu-Ming Shi & Ming Qiu (1 female, MHBU); Ji'an City, Jinggangshan, Longtan, 26°35'47"N, 114°08'25"E, mixed forest, shrub, flower sweeping & beating, 760–920 m, 29.VII.2014, Chen, Hu, Lv & Yu leg. (1 female, SHNU); **Guangxi Province:** Longsheng, Huaping, 6.VI.1963, Si-Kong Liu leg. (1 female, IZCAS); Lingui, Huaping, 500 m, 30.V.2010, Zheng Li leg. (1 male, 3 females, CBWX); Damingshan, 27.V.2011, Qing Zhang & Hai-Ling Wang leg. (1 male, 1 female, MHBU); Jinxiu, 6K, 24°9'19"N, 110°12'22"E, alt. 1155 m, 8.III.2016, Yu-Yang Lei leg. (4 males, 2 females, CCLX); Fangchenggang, Shiwandashan Reserve, 29.VI.2015, Zhi-Lin Chen leg. (5 males, 2 females, MHBU); Rongshui, Jiuwanshan, 24.VII.2015 N, Ling-Xiao Chang leg. (1 male, 1 female, CCLX); Jinxiu, 1155 m, Yu-Yang Lei leg. (4 males, 2 females, CCLX); Jinxiu, Changtanhe, 860 m, 15.VII.2015, Xiao-Bin Song leg. (1 male, 1 female, CBWX); Jinxiu, Houzishan, 960 m, 13.VII.2014, Wen-Xuan Bi leg. (1 male, CBWX); Maoershan, Manjiangyuan, 810 m, 28.VII.2014, Xiao-Bin Song leg. (1 female, CBWX); Shanglin, Xiyan Town, 29.IV.2017, Yan-Quan Lu leg. (1 male, 3 females, CCCC); **Yunnan Province:** Bannan, Menglun, X.2014, Xiao-Yu Zhu leg. (1 female, MHBU); **Hunan Province**: Tongdao County, Mujiao Township, 25.VII.2004, Jian-Feng Wang & Ji-Liang Wang leg. (5 males, MHBU); Dongan County, Shunhuangshan, 3.X.2004, Jian-Hua Huang leg. (1 male, MHBU); Dongan County, Damiaokou Town, Shunhuangshan Park, 9.X.2015, Chi Jin leg. (2 females CCLX); Suining County, Huangsangping Town, Hongjun Road, 22.IX.2015 Chi Jin leg. (1 female, CCLX); Dao County, Qingtang Township, Laozhongping Village, Yueyan Forest Farm, 30.IX.2015, Chi Jin leg. (1 female, MHBU); **Guizhou Province:** Jiangkou, Heiwan, 3.VIII.2011, Guo-Dong Ren leg. (1 male, MHBU); Libo, Maolan, 21.VII.2015, Chi Jin leg. (1 female, CCLX); **Guangdong Province:** Nanling, 8.V.2008, Xiao-Yu Zhu leg. (1 female, MHBU); Nanling, V-VIII.2008, Hong-Liang Shi leg. (2 females, MHBU); Nanling, 18.VIII.2010, Hao-Yu Liu leg. (1 female, MHBU); Fengkai, Heishiding, 12.X.1984, Zhen-Ao Chen leg. (1 female, SYSU En-131937); ditto except 9.X.1984, Zhi-Hong Zhou leg. (1 male, SYSU En-131939); ditto except 17.X.1984, Han-Chuan Hu leg. (1 male, SYSU En-131940); **Hainan Province:** Wanning, Diaoluoshan, 17–18. XI.2006, Guo-Dong Ren leg. (2 males, 2 females, MHBU); Jiangfengling, alt. 950 m, 15.IV.2010, Xiao-Yu Zhu leg. (1 female, MHBU); Yinggeling, Hongxin Village, 11–13.V.2011, Xiao-Qing Yang & Lin-Fei Wang leg. (2 females, MHBU); Ledong, Jianfengling, 16.XI.2006, Li-Zhen Li leg. (1 female, SHNU); Bawangling, 15.XI.1964, Zhen-Yao Chen leg. (1 female, SYSU); Baisha, Yinggezui Protection Station, 678 m, Guo Zheng leg. (1 female, CCLX); Qiongzhong, Limushan, 1160 m, 4.IV.2016, Ling-Xiao Chang & Xing-Long Bai leg. (2 females, CCLX); Jianfengling, Mingfenggu, 983 m, 29.IV.2014, Chao Wu leg. (1 male, 1 fenale, CBWX); Ledong, Jianfengling, 16.XI.2006, Li-Zhen Li leg. (1 female, SHNU); Jianfengling, Mingfenggu, 950–1000 m, Wen-Xuan Bi leg. (2 males, 2 females, CBWX); **Fujian Province:** Jianning, Jinraoshan, 12.VI.1956, Gen-Tao Jin & Yang-Ming Lin leg. (1 female, SHEM24295206); ditto except (1 female, SHEM24295215); ditto except (1 male, SHEM24295220); ditto except (1 female, SHEM24295221); ditto except (1 female, SHEM24295222); ditto except (1 male, SHEM24295227); Daan, 3.VI.1956, Gen-Tao Jin & Yang-Ming Lin leg. (1 male, SHEM24295230); ditto except (1 female, SHEM24295231); Wuyishan, Taoyuanyu, 6.VIII.2016, Hai-Tian Song leg. (1 male, CCLX); **Taiwan Province:** Taoyuan, Tengzhi, 18.III.1997, Wen-Yi Zhou leg. (1 female, MHBU); Pingdong, Wutai Country, alt. 1450 m, 15.IV.2011, Wen-Yi Zhou leg. (1 female, MHBU); Pingdong, Dahanshan, 25.XII.2007, Chang-Chin Chen leg. (1 male, 1 female, MHBU).

Distribution. China: Jiangsu, Jiangxi, Fujian, Guangdong, Hainan and Taiwan. First records from Zhejing, Hunan, Guangxi, Yunnan, and Guizhou Provinces of China.

Remarks. The anterior elytral macula is transverse with anterior margin distinctly emarginate in specimens from Taiwan, China (Fig. 10B).

***Sinocymbachus koreanus* (Chûjô & Lee, 1993), comb. nov.**

Cymbachus koreanus Chûjô & Lee, 1993: 95.

Diagnosis. *Sinocymbachus koreanus* can be separated from all its congeners by having the body very short, nearly circular, strongly converging from 1/2 length of elytron to apex; each elytron with four small round spots, two basal spots located posterior to humerus and arranged in a slightly oblique line, and two apical spots located in apical ¼ length, arranged nearly horizontally.

Length. 7.5–7.9 mm. Width: 5.1–55 mm.

Remarks. This species was originally described in the geuns *Cymbachus* Gerstaecker, 1857. However, the following characters of this species match the definition of *Sinocymbachus* proposed by Strohecker & Chûjô (1970): mesotibiae sexually dimorphic, toothed on inner edge in male, simple in female (Chûjô and Lee 1993); aedeagus complicated, trilobed (Chûjô and Lee 1993; Boo 2013). Therefore, *Cymbachus koreanus* Chûjô & Lee, 1993 is transferred to *Sinocymbachus*.

Distribution. South Korea.

***Sinocymbachus luteomaculatus* (Pic, 1921)**

Figures 12F, 13F, 14F, 15F, 16F, 17F, 18F

Engonius luteomaculatus Pic, 1921: 1.
Cymbachus luteomaculatus: Strohecker 1953: 91.
Sinocymbachus luteomaculatus: Strohecker and Chûjô 1970: 516.

Diagnosis. Based on Strohecker & Chûjô (1970), *Sinocymbachus luteomaculatus* can be separated from all its congeners by having the basal and apical elytral maculae briefly undulately fasciate, but in one specimen examined by the author base of elytron is composed of two spots (Fig. 18F), this elytral pattern is most similar to *S. decorus* and *S. politus* by sharing two basal spots and one narrow transverse apical macula on each elytron. However, *S. luteomaculatus* differs from *S. decorus* by having an opaque body (vs. shiny) and humeri weakly prominent (vs. distinctly prominent); from *S. politus* by the elytra distinctly more elongate (vs. not elongate); two basal elytral maculae arranged in an oblique line (vs. arranged in a horizontal line); mesotibial tooth in male asymmetric (vs. symmetric).

Length. 9.6–10.7 mm; width: 5.2–5.5 mm.

Material examined. China: Yunnan Province: Zhanyi County, Zhujiangyuan, alt. 2100 m, 18.VII.2010, Ji-Shan Xu & Zhong-Kun Li leg. (1 male, 2 females, MHBU).

Distribution. China: Yunnan.

Remarks. Although few specimens only were available for this work, basal elytral maculae briefly undulately fasciate and the shape of the aedeagus were enough to determine they are the same species (Fig. 17F).

***Sinocymbachus parvimaculatus* (Mader, 1938)**

Figures 12G, 13G, 14G, 15G, 16G, 17G, 18G

Cymbachus parvimaculatus Mader, 1938: 40.
Sinocymbachus parvimaculatus: Strohecker and Chûjô 1970: 512.

Diagnosis. *Sinocymbachus parvimaculatus* can be separated from all its congeners by having the body very short, nearly circular and each elytron possessing two small round spots placed on the mid-line of each elytron.

Length. 7.7 mm–8.5 mm; width: 5.6 mm.

Material examined. China: Yunnan Province: Nanjian, Sheyaojing, 2150–2300 m, 11.VII.2017, Wen-Xuan Bi & Yu-Tang Wang leg. (1 male, CBWX); Weishan, Weibaoshan, 2200 m 5.VII.2017, Wen-Xuan Bi leg. (1 female, CBWX); Weishan, Weibaoshan, 2300 m, 9.VII.2017, Wen-Xuan Bi leg. (1 female, CBWX); Eshan Country, alt. 1688 m, 28.VII.2009, Ji-Shan Xu & Li-Xiang Zhang leg. (1 female, MHBU); Shizong Country, Junzishan, 16.VII.2006, Jun-Tong Lang & Yu-Xia Yang leg. (1 female, MHBU); Lincang City, 1900 m, IV. 2016, Zi-Chun Xiong leg. (1 female, CCLX).

Description of male. Length 7.8 mm. Body short oval, approximately 1.5 times as long as wide; strongly convex; smooth. Colour black with four orange round spots on elytra.

Head. Antenna composed of 11 antennomeres, rather stout, extending to ca. 1/2 body length, with antennomeres 1–8 distinctly longer than wide; scape 4.0 times as long as pedicel; antennomere 3 as long as antennomeres 4 and 5 combined; antennomere 4 as long as antennomere 5; antennomeres 5–8 gradually shorter; club composed of three antennomeres, wide, approximately 3.0 times as wide as antennomere 8, moderately flat, rather loose.

Thorax. Pronotum 1.5 mm long, 3.5 mm wide; widest at base; moderately coarsely and rather densely punctate; lateral and anterior margins narrowly bordered; anterior edge with moderately large stridulatory membrane; sides weakly undulate; anterior angles produced, bluntly rounded; posterior angles moderately acutely produced; disc weakly convex; median furrow absent; lateral sulci very short and deep, in form of triangular dent; basal sulcus curved, moderately deep. Prosternal process moderately widely separating procoxae; sides curved outwardly near apex, forked apically, not extending beyond front coxae. Mesoventral process nearly pentagonal, as long as wide, with short median ridge near basal 1/4. Elytra 5.9 mm long, 5.3 mm wide; 3.9 times as long as pronotum; 1.5 times as wide as pronotum; punctures as large as the pronotal ones, more dense; sides strongly curved, widest near 1/2 length of elytron; humeri weakly prominent. Each elytron with two round maculae: anterior macula located near basal 1/5, posterior macula located at apical 1/3, and all these maculae placed in mid-line of elytron; outer and inner margins of macula very distant from elytral lateral margin and suture. Mesotibia with small sharp tooth near apical 1/4 on inner edge, then with deep, small, U-shaped excision. Pro- and metatibiae simple.

Abdomen. Ventrite 1 longer than 2 and 3 combined; ventrites 2–4 subequal in length. Ventrite 5 with lateral margins gradually converging posteriorly; posterior margin broadly rounded medially. Aedeagus (Fig. 18) short and stout, heavily sclerotised, curved. Median lobe with two short branches, simple, acute apically. Tegmen basal, ring-shaped.

Distribution. China: Yunnan.

Sinocymbachus politus **Strohecker & Chûjô, 1970**

Sinocymbachus politus Strohecker & Chûjô, 1970: 515

Diagnosis. Based on Strohecker & Chûjô (1970), *S. politus* is most similar to *S. decorus* and *S. luteomaculatus* in appearance: both species share the elytra with two basal spots and one narrow transverse apical band. However, the body with cupreous sheen, two basal elytral maculae arranged in horizontal line and mesotibial tooth in male symmetric can separate it from all these similar species.

Length. 9.3 mm.

Distribution. China: Taiwan.

Remarks. The diagnosis of *S. politus* is based on its original description of Strohecker & Chûjô (1970) due to a lack of material for study.

Sinocymbachus quadrimaculatus **(Pic, 1927)**

Figures 11, 12H, 13H, 14H, 15H, 16H, 17H, 18H

Amphisternus quadrimaculatus Pic, 1927: 11.
Cymbachus quadrimaculatus: Strohecker 1953: 91.
Sinocymbachus quadrimaculatus: Strohecker and Chûjô 1970: 515.

Diagnosis. *Sinocymbachus quadrimaculatus* differs from all its congeners in having each elytron with four small round spots, two basal spots located posterior to humerus and arranged horizontally, and two apical spots located in apical ¼ length, arranged in oblique line.

Length. 14.0–16.2 mm; width: 8.4–8.5 mm.

Figure 11. Live adult of *Sinocymbachus quadrimaculatus* from Zhejiang, China.

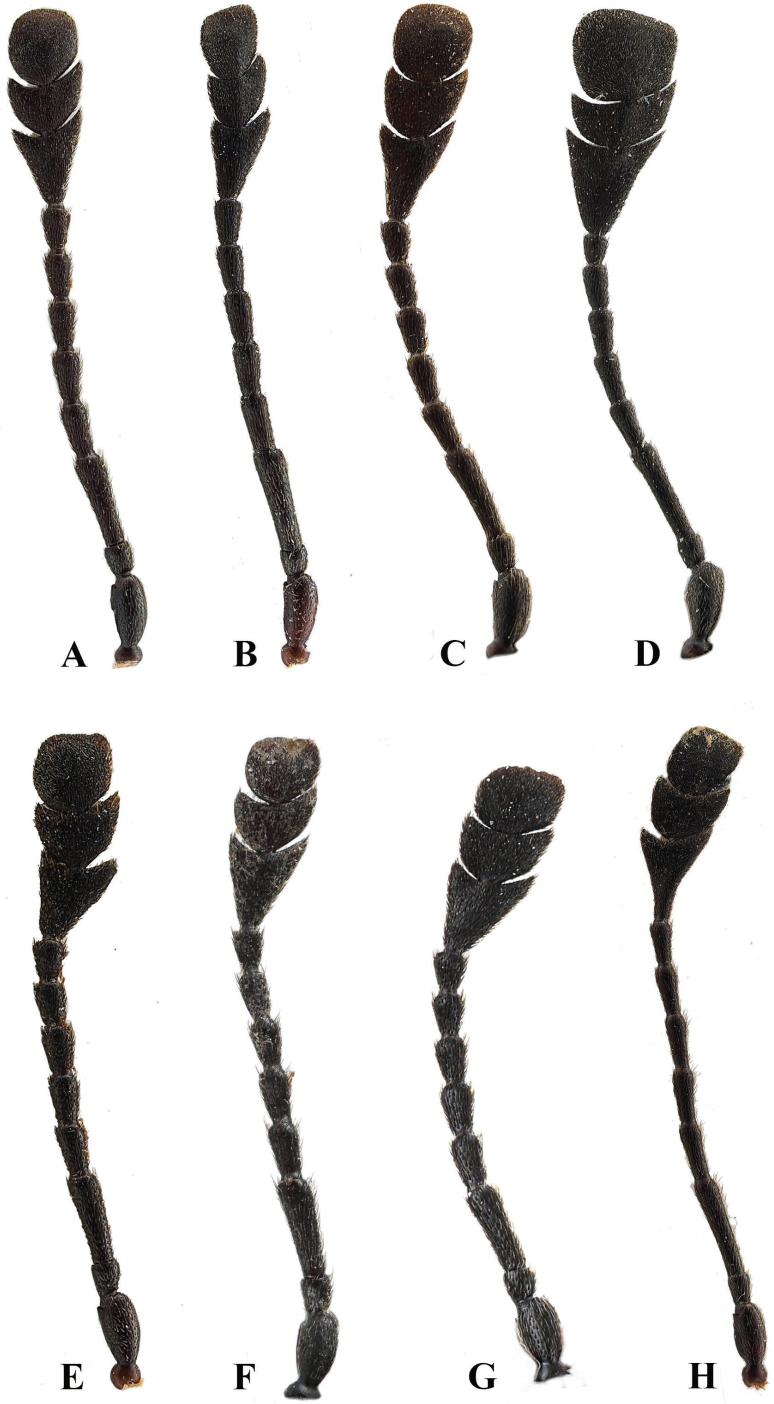

Figure 12. Left antenna of *Sinocymbachus* spp. (dorsal view) **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*.

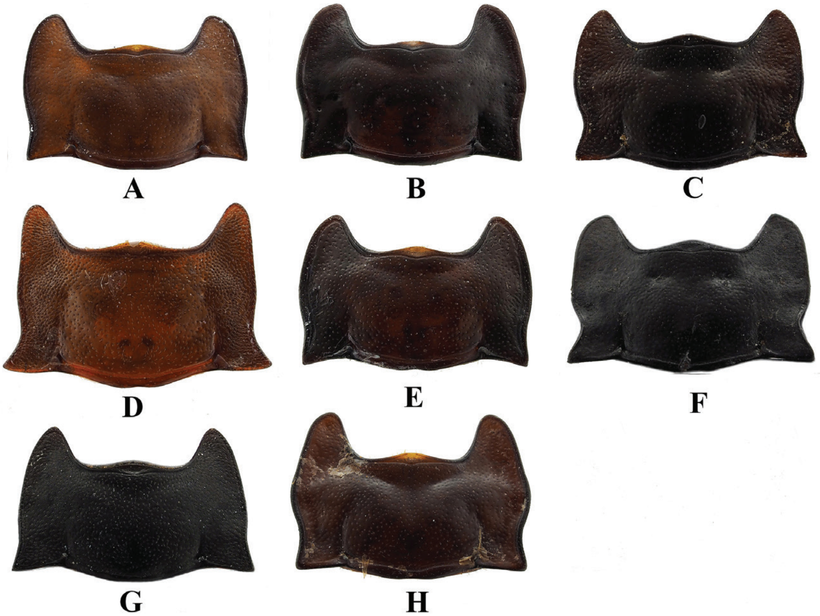

Figure 13. Pronotum of *Sinocymbachus* spp. **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*.

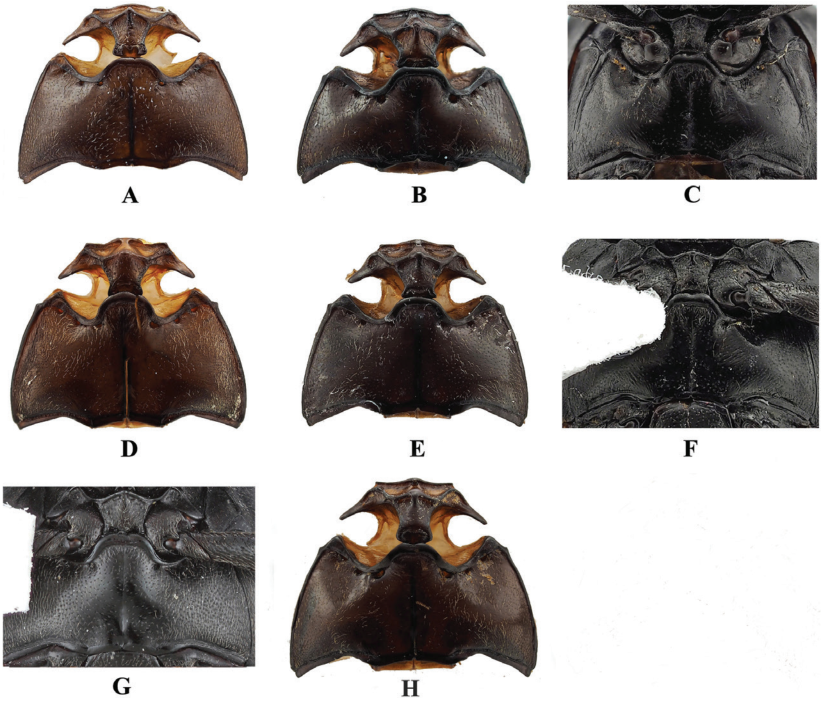

Figure 14. Meso- and metaventrite of *Sinocymbachus* spp **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*.

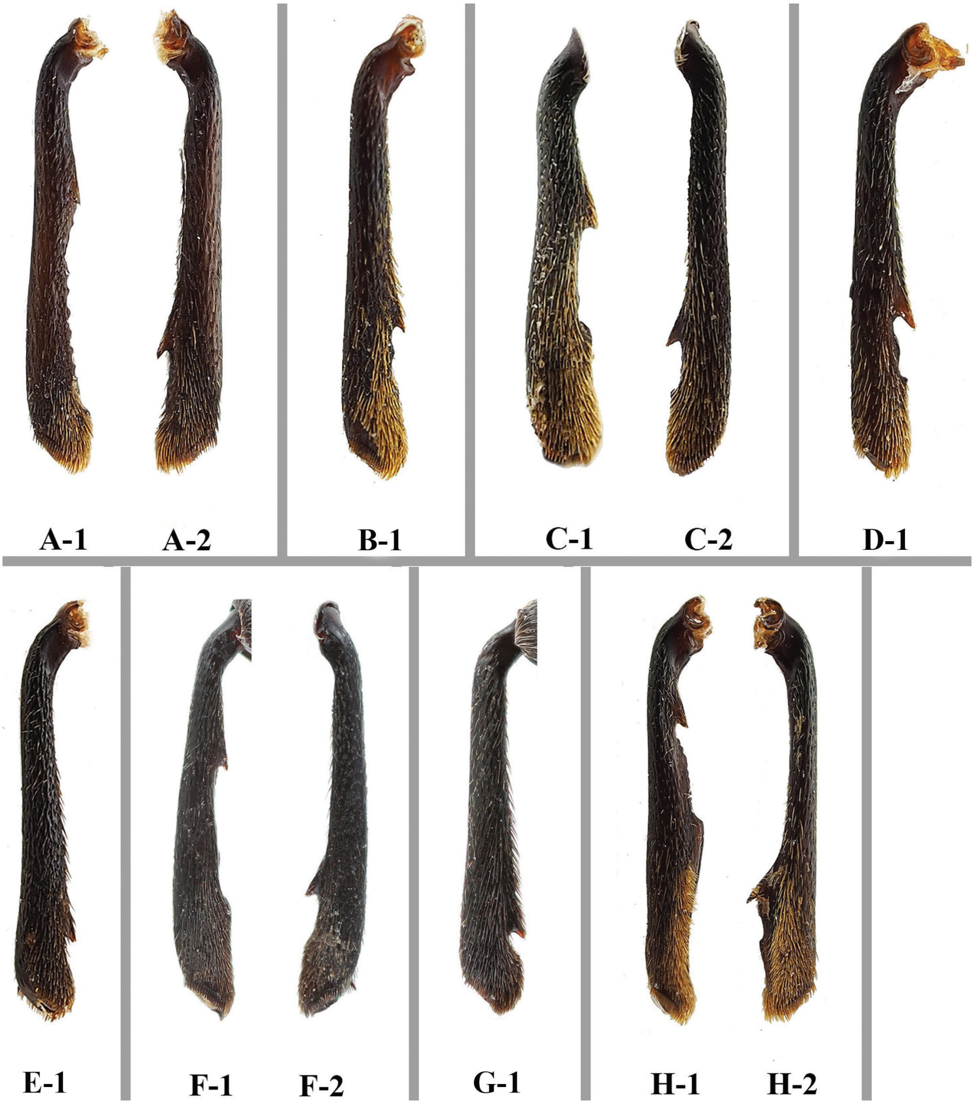

Figure 15. Male mesotibiae of *Sinocymbachus* spp **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*. **1** left **2** right.

Material examined. China. Zhejiang Province: Jiangshan City, Hongyanding, 11.VIII.2016, Yi-Bin Ba & Ling-Xiao Chang leg. (1male, 1 female, MHBU); **Guangxi Province:** Jinxiu, Changtong, Dayaoshan, 23.V.2019, Chun-Fu Feng leg. (4 males, 6 females, CCLX); Xingan, Huanjiang, 5.VII.2006 (1 male, CCLX); Jinxiu, Yinshan Protection Station, 1200 m, 9.VII.2014, Xiao-Bin Song leg. (1 female, CBWX); Laibin, Jinxiu, Dayaoshan, 1017 m, 16.V.2015, Yan-Quan Lu leg. (1 male, 1 female, CCCC); **Hunan Province:** Tongdao County, Mujiao Township, 26.VII.2004, Ji-Liang Wang leg. (2 males, 2 females, MHBU); Sangzhi County, near

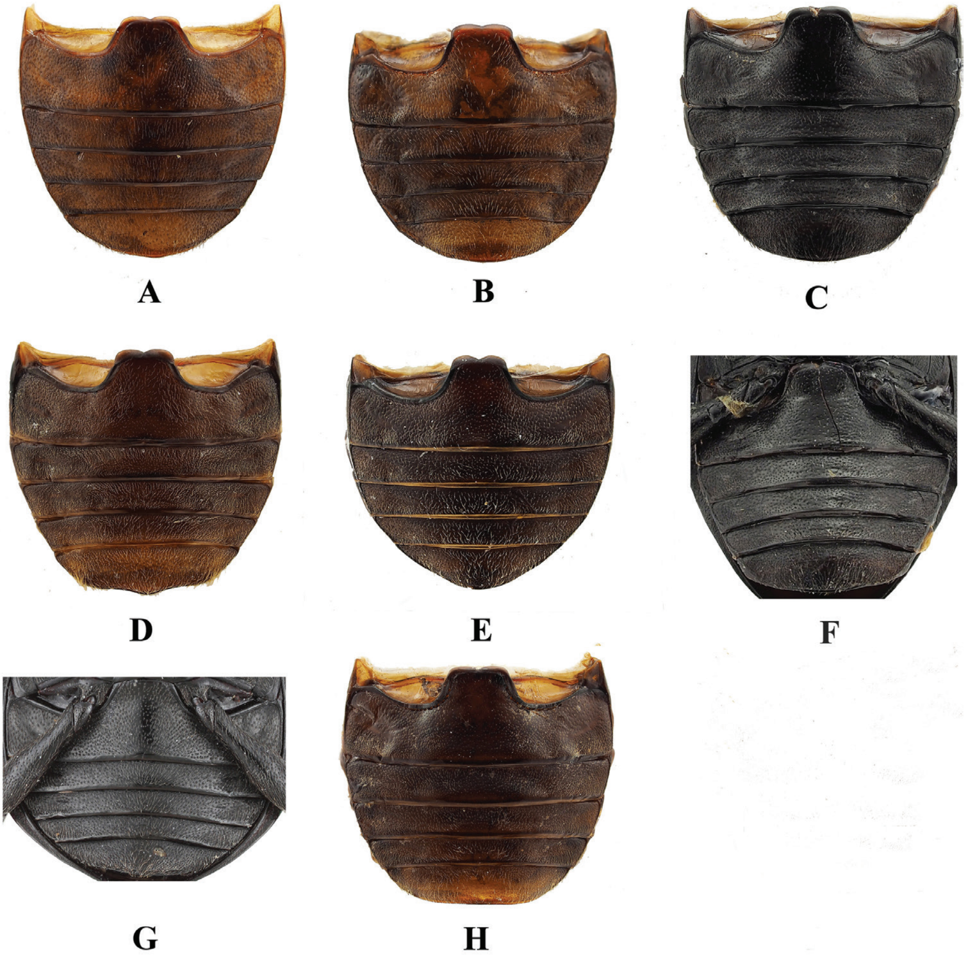

Figure 16. Male abdomen of *Sinocymbachus* spp **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*.

Tianpingshan Control Station, 15.IX.2015, Chi Jin leg. (1 male, CCLX); **Hainan Province:** Bawangling, 9.VII.2006, Ji-Liang Wang & Chao Gao leg. (1 male, 5 females, MHBU); Wuzhishan, 750 m, 15.X.2014, Chao Wu leg. (1 female, CBWX); **Fujian Province:** Ningde, Nanjiao, Houshancun, 200–300 m, 3–5.X.2012, De-Yao Zhou leg. (1 male, 1 female, CBWX).

Distribution. Vietnam: Tonkin; China: Fujian. First records from Zhejiang, Guangxi, Hunan and Hainan Provinces of China.

Remarks. Some live or fresh specimens from Zhejiang or Fujian were observed with the elytral maculae pink in colouration (Fig. 11), which gradually turned yellow after drying. However, elytral maculae in the specimens collected from Hainan are always yellow.

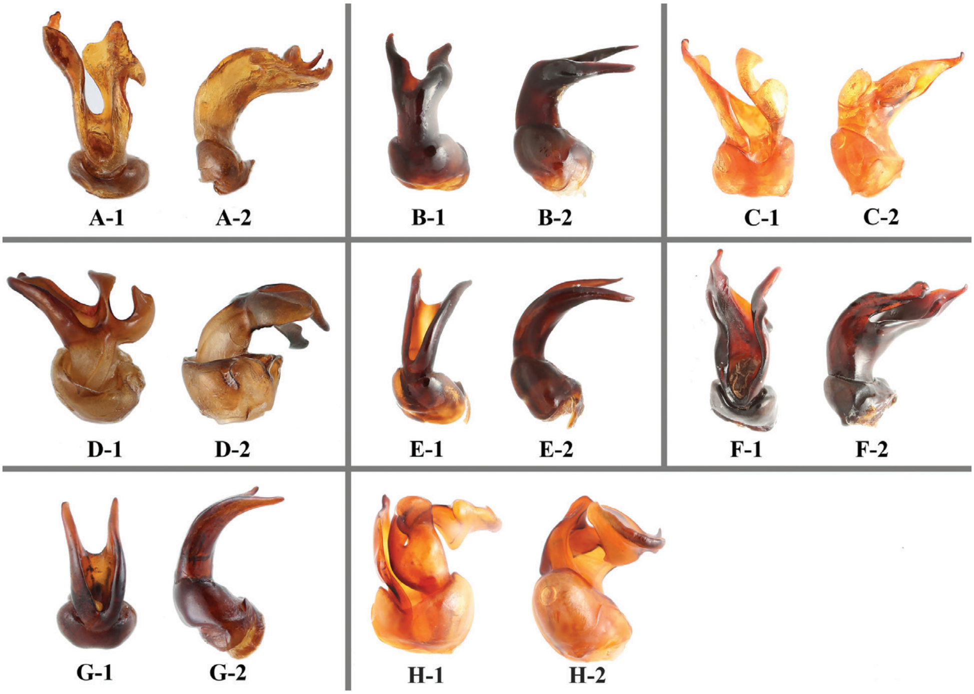

Figure 17. Aedeagus of *Sinocymbachus* spp **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*. 1 ventral view 2 lateral view.

Sinocymbachus quadriundulatus (Chûjô, 1938)

Amphisternus quadriundulatus Chûjô, 1938: 397.
Sinocymbachus quadriundulatus: Strohecker and Chûjô 1970: 515.

Diagnosis. Based on Strohecker and Chûjô (1970), *S. quadriundulatus* close to *S. angustefasciatus*, *S. fanjingshanensis* sp. nov., *S. longipennis* sp. nov. and *S. wangyinjiei* sp. nov. by the similar elytral patterns. But can be readily distinguished from them by the mesotibiae of male with symmetric tooth.

Length. 7.5–8.5 mm.

Distribution. China: Taiwan.

Key to the species of *Sinocymbachus* (modified and updated from Strohecker and Chûjô 1970)

1 Elytra very short, nearly circular..**2**
– Elytra oval or short oval **3**

2 Each elytron with four spots; elytral sides strongly converging from 1/2 length of elytron to apex.......... ***S. koreanus* comb. nov.**

– Each elytron with two spots; elytral sides gradually converging from 1/2 length of elytron to apex (Fig. 18G).......... ***S. parvimaculatus***

3 Intercoxal process of mesoventrite with large tubercle at base (Fig. 14D); ventrite 5 with posterior margin abruptly projecting medially in male (Fig. 16D).......... ***S. excisipes***

– Intercoxal process of mesoventrite with short median ridge at base; ventrite 5 with posterior margin not projecting medially in both sexes **4**

4 Apical elytral maculae composed of round spots **5**

– Apical elytral macula transverse.......... **7**

5 Base of elytron with two spots (Fig. 18H).......... ***S. quadrimaculatus***

– Base of elytron with one spot.......... **6**

6 Scutellum distinctly longer than wide (Fig. 7A); mesotibial tooth in male placed near apical 1/3 length of tibia (Fig. 15B-1) .... ***S. bimaculatus***

– Scutellum as long as wide or slightly longer than wide (Fig. 7B); mesotibial tooth in male placed near apical 1/4 length of tibia (Fig. 15E-1).......... ***S. humerosus***

7 Basal elytral maculae composed of two spots.......... **8**

– Basal elytral macula transverse.......... **10**

8 Body shiny; humeri distinctly prominent.......... **9**

– Body opaque; humeri weakly prominent (Fig. 18F).......... ***S. luteomaculatus***

9 Body with cupreous sheen; basal elytral maculae arranged in horizontal line. .... ***S. politus***

– Body without cupreous sheen; basal elytral maculae arranged in oblique line (Fig. 18C) .... ***S. decorus***

10 Elytra short oval; elytral maculae without distinct projections (Fig. 1C).......... ***S. sinicus* sp. nov.**

– Elytra oval or long oval, elytral maculae with distinct projections.......... **11**

11 Elytra distinctly long oval (especially in males); sides nearly parallel (Fig. 1B) .... ***S. longipennis* sp. nov.**

– Elytra oval; sides curved.......... **12**

12 Body opaque (Fig. 18A).......... ***S. angustefasciatus***

– Body shiny.......... **13**

13 Body with cupreous sheen; mesotibial tooth in male symmetric.......... ***S. quadriundulatus***

– Body without cupreous sheen; mesotibial tooth in male asymmetric.......... **14**

14 Anterior margin of mesoventral process as wide as posterior margin (Fig. 3A) .... ***S. fanjingshanensis* sp. nov.**

– Anterior margin of mesoventral process much wider than posterior margin (Fig. 3D).......... ***S. wangyinjiei* sp. nov.**

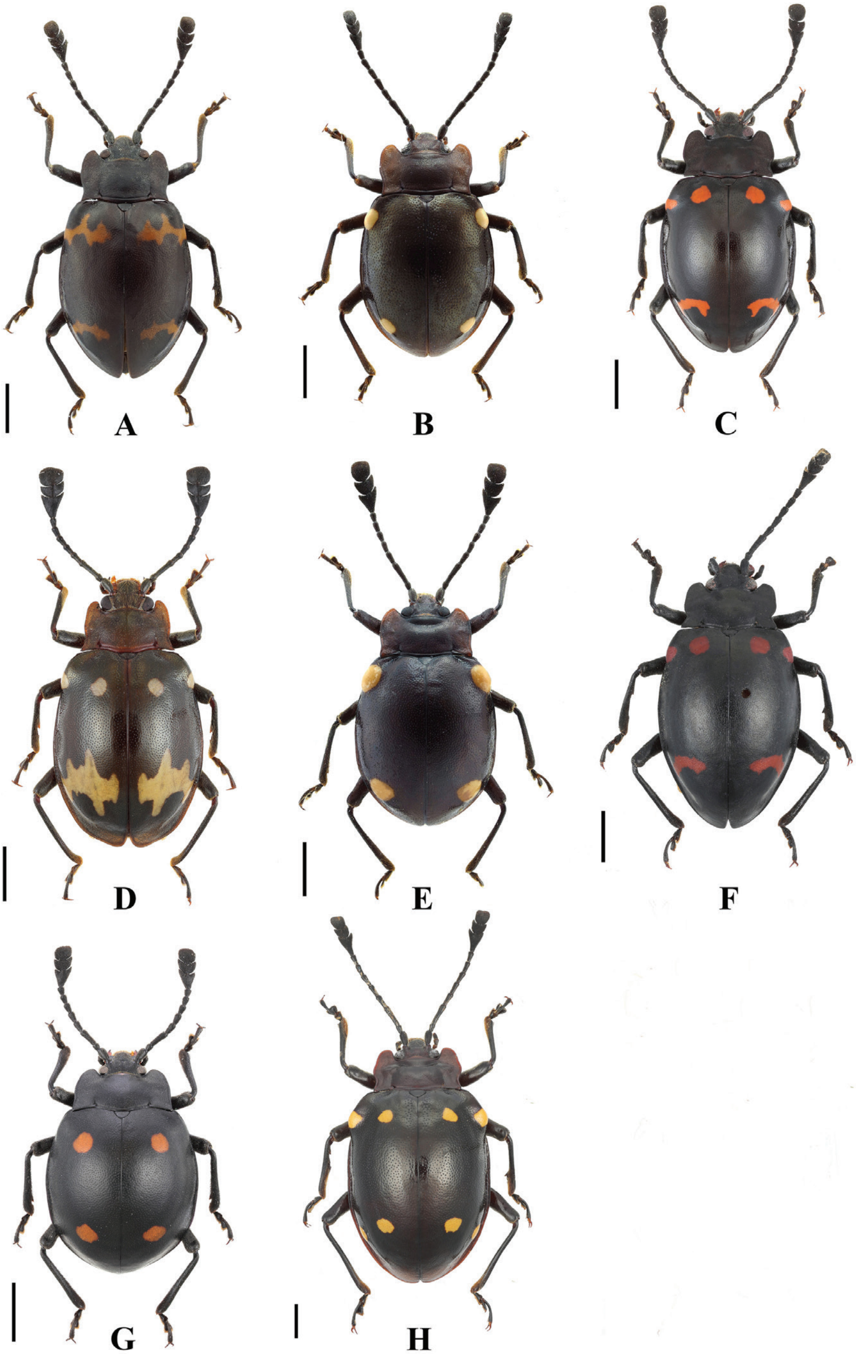

Figure 18. Habitus of *Sinocymbachus* spp. (males) **A** *S. angustefasciatus* **B** *S. bimaculatus* **C** *S. decorus* **D** *S. excisipes* **E** *S. humerosus* **F** *S. luteomaculatus* **G** *S. parvimaculatus* **H** *S. quadrimaculatus*. Scale bar: 2 mm.

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New faunal data on lacewings (Insecta, Neuroptera) collected from Saudi Arabia

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Abstract

This study presents new data on the lacewing fauna of Saudi Arabia based on field work performed between 2014 and 2019. Sixty-one lacewing species from 37 genera and seven Neuroptera families were documented. Additionally, two species belonging to *Dielocroce* and *Pseudomallada* were identified only to genus level. Three of the identified species are new records to Saudi Arabia (*Aspoeckiella gallagheri* Hölzel, 2004, *Bankisus maculosus* Hölzel, 1983, and *Nemoleon secundus* Hölzel, 2002). Another three species are new to the fauna of the Arabian Peninsula (*Mantispa aphavexelte* Aspöck & Aspöck, 1994, *Omoleon jeanneli* Navás, 1936, and *Stylascalaphus krueperi* van der Weele, 1909). The first reports of eight species are provided after their original description from Saudi Arabia; namely, *Creoleon ultimus* Hölzel, 983, *Cueta amseli* Hölzel, 1982, *Cu. asirica* Hölzel, 1982, *Distoleon asiricus* Hölzel, 1983, *Geyria pallida* Hölzel, 1983, *Neuroleon delicatus* Hölzel, 1983, *N. virgineus* Hölzel, 1983 and *Solter buettikeri* Hölzel, 1982 Zoogeographically, most lacewing species documented in the Arabian Peninsula are endemic (26.2%), followed by Afro-syroeremic (23.0%), Afrotropical (18.0%), and Afro-syro-iranoeremic (14.8%) species. Palaearctic species (4.9%) had the lowest contribution.

Keywords

distribution, endemic, new records, Neuroptera, Saudi Arabia

Introduction

The Arabian Peninsula is located on the Arabian tectonic plate in northeast Africa, western Asia. Its fauna has different zoogeographical affinities (Larsen 1984; Hölzel 1998), as it lies at the convergence of three zoogeographical realms: the Palaearctic from the north, the Afrotropical from the southwest, and the Oriental from the east. The Arabian Peninsula covers a surface area of 3.2 million km^2, and encompasses Bahrain, Kuwait, Oman, Qatar, Saudi Arabia, United Arab Emirates, and Yemen (Fig. 1). Saudi Arabia covers approximately two thirds (1,969,000 km^2) of the peninsula and is considered to hold the richest biodiversity in it (Miller 1994; Mallon 2011). The key biological sites in Saudi Arabia include isolated mountain massifs, rawdahs (meadows), wadis (valleys), juniper woodlands, acacia woodlands, freshwater wetlands, salt marshes, mangrove thickets, marine islands, coral reefs, algal beds, and sea grass beds (Abuzinada et al. 2005).

Neuroptera is a small group of insects that currently contains ca. 5,800 species in 19 families (Oswald 2019). Nine families have been reported to occur in the Arabian Peninsula: Chrysopidae, Hemerobiidae, Sisyridae, Coniopterygidae, Mantispidae, Berothidae, Nemopteridae, Myrmeleontidae, and Ascalaphidae (the last two recently fused in a single family, see Machado et al. 2018). Saudi Arabia has an exceptionally rich fauna of aridophilic families, Nemopteridae and Myrmeleontidae, with studies over the last 40 years documenting several new species (Meinander 1980; Hölzel 1982, 1983a, 1988, 1998, 1999, 2001, 2004). For many of these species, the original description represents the only published data. Consequently, despite many studies documenting Neuroptera in the Arabian Peninsula over the last 40 years (Meinander 1979; Hölzel 1980, 1983b; Sziráki 1992, 1997; Aspöck and Aspöck 1998; Sziráki and van Harten 2006; Saji and Whittington 2008), there is still a paucity of faunal surveys focusing on Neuroptera that could provide important distribution and ecological information on this group.

Over the last six years, new faunal unpublished records of lacewings have been gathered in Saudi Arabia. Thus, this study aims to provide new information on this group in Saudi Arabia, with a focus on poorly known and rarely collected species.

Materials and methods

The collection of samples was conducted between 2014 and 2019 at different locations in Saudi Arabia. Adult lacewings were captured mainly with light traps (LT), but also pitfall traps (PT), sugar traps (ST), and sweep nets (SW) were utilized. Specimens were preserved by desiccation or in 70% alcohol. They were then deposited in the collections of King Saud University Museum of Arthropods (**KSMA**) (Riyadh, Saudi Arabia) unless otherwise indicated (AL: Agostino Letardi collection). The species are presented in systematic order, by family and genus, according to Aspöck et al. (2001).

For the examined material, the following information were verified: Saudi Province (in bold) followed by a colon (:), the name of the governorate, locality, geographical co-

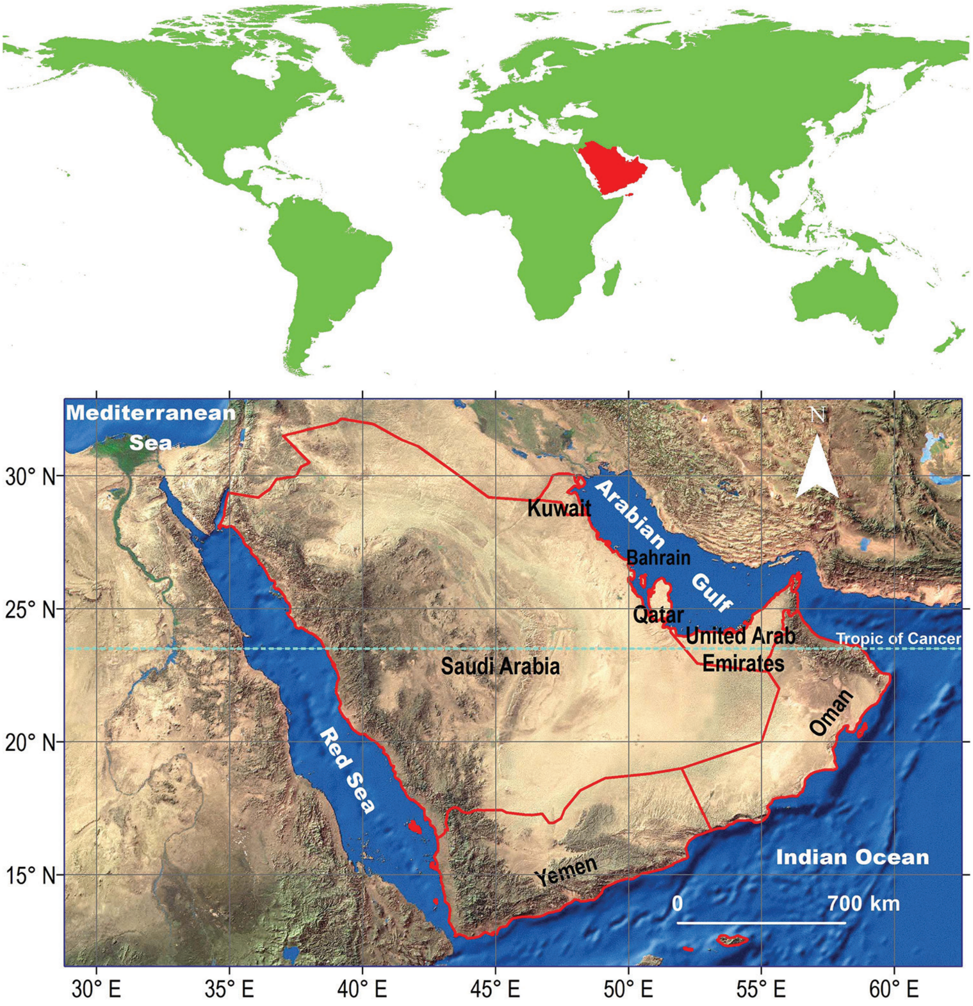

Figure 1. Map of the Arabian Peninsula.

ordinates (latitude, longitude), elevation (m), date of collection, capture technique(s), collector(s), number of examined specimens followed by sex (if determined) or "ex" (if the specimen sex could not be recognized because the abdomen lost or other reasons). The examined material was arranged by province, governorate, and locality name, in alphabetical order. Then, it was presented in ascending order according to altitude, and chronologically based on month of collection. When the records were from different provinces and governorates, a full stop separate them. A semicolon was used to separate different records. The governorate name was only cited at the beginning if the records were from the same governorate. Labels that had the same locality name, except for slight differences (such as elevation, collection date, collector/s), were listed jointly with the second label, specified with "*ibidem*", and followed by a comma and the different data. The global distribution was derived from Oswald (2019) and general range was sourced from Aspöck et al. (2001). A biology entry summarizes previous knowledge on habitat, host, behavior, etc., while a notes entry provides novel information on distribution, habitat, taxonomy, and other relevant data.

Results

Chrysopidae Schneider, 1851

Italochrysa bimaculata Hölzel, 1980

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 15 Oct 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 19°51.762'N, 41°18.089'E, 1225 m, 17 Oct 2014, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 2 Nov 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 19°50.710'N, 41°18.267'E, 1474 m, 3 Nov 2013, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 14 Nov 2015, LT, Al Dhafer et al. leg., 2♂; *ibidem*, 19°50.411'N, 41°18.686'E, 1611 m, 17 Nov 2014, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 19°50.575'N, 41°18.691'E, 1666 m, 3 Apr 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 5 May 2015, LT, Al Dhafer et al. leg., 1♀; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22 ' 34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 5 Sep 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 18 Nov 2015, LT, Al Dhafer et al. leg., 1♂; Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 2♂; *ibidem*, 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ (AL). Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. Africa: Senegal, Tunisia. Asia: Israel, Saudi Arabia, Yemen. A polycentric Afrotropical species.

Notes. This species was previously reported as *I. arabica* in Al Bahah Province (Hölzel 1980). The listed specimens were collected between 1,150 and 1,926 m elevation and seem to be associated with *Acacia* woodlands and rocky areas with Barbary fig shrubs (*Opuntia ficus-indica* (L.) Mill. (Cactaceae)) in the mountainous areas of southwest of Saudi Arabia.

Pseudomallada amseli (Hölzel, 1980)

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 4♀; *ibidem*, 1♀ (AL).

Distribution. Africa: Ethiopia. Asia: Israel, Oman, Saudi Arabia, Yemen. A possible Afrotropical species.

Notes. It was previously reported in the provinces of Al Bahah and Asir (Hölzel 1980). The listed specimens were collected at 1197 m elevation in mountainous *Acacia* woodland areas in southwest Saudi Arabia.

Pseudomallada arabicus (Hölzel, 1995)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 4♀ and 3♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 8♀; *ibidem*, 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 9♀ and 2♂; *ibidem*, 1♀ and 1♂ (AL).

Distribution. Asia: Saudi Arabia, Yemen. A possible Arabian endemic species.

Notes. *Pseudomallada arabicus* was originally described from Fayfa Mountain in Jizan Province (Hölzel 1995). The listed specimens were collected in *Acacia* woodlands in the highlands (1150–1826 m elevation) of southwestern Saudi Arabia.

Pseudomallada spadix (Hölzel, 1988)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 5♀ and 2♂. Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.682'N, 41°18.263'E, 1291 m, 29 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 1♀ (AL). **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂.

Distribution. Africa: Sudan. Asia: Oman, Saudi Arabia, Yemen. A possible Afrotropical species.

Notes. It was originally described from the provinces of Al Bahah and Asir (Hölzel 1988). The listed specimens were collected in *Acacia* woodlands at low and mid elevations (136−1826 m) in southwestern of Saudi Arabia.

Pseudomallada venosus (Rambur, 1838)

Material examined. Asir Province: Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 2♀ and 1♂.

Distribution. Africa: Algeria, Egypt, Morocco, Sudan, Tunisia. Asia: Afghanistan, Iran, Israel, Lebanon, Mongolia, Oman, Pakistan, Saudi Arabia, Turkey, Yemen. Europe: France, Portugal, Spain. It is a Palaearctic species.

Biology. This green lacewing is generally associated with low vegetation in extremely dry-warm biotopes, predominantly in steppes and semidesert-like habitats, and is quite common at light traps (Aspöck et al. 1980; Diaz-Aranda and Monserrat 1990).

Notes. This species was previously reported in several Saudi provinces: Asir, Al Bahah, Eastern Province, Madinah, Makkah, and Riyadh (Hölzel 1988). The listed adult specimens were collected by light traps in sandy areas with *Acacia* woodland at low elevation (451 m) in southwestern Saudi Arabia.

Pseudomallada spp.

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂; *ibidem*, 19°50.329'N, 41°18.604'E, 1563 m, 29 Mar 2017, ST, 1♂; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 3♀, 1♂ and 1ex. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; 18°10.293'N, 42°22.195'E, 1150 m; *ibidem*, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀ and 2♂. Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27'34"N, 42°42'53"E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 2♀. Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 4♀; *ibidem*, 1♀ (AL). **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 21♀ and 12♂, 1♀; *ibidem*, 1♂ (AL).

Notes. *Pseudomallada* Tsukaguchi 1995 is one of the most species-rich genera within the green lacewing family Chrysopidae and is one of the largest in the order Neuroptera (Duelli et al. 2017). Hölzel (1980, 1988, 1995) described several new species of this genus in the Arabian Peninsula; however, a revision of species in this zoogeographic area is not available, with species identification of specimens often being difficult in preserved alcohol (as they are not always in good condition). Specimens were collected at elevations of 136–1926 m in southwestern Saudi Arabia. The listed adult specimens were captured in sugar traps in rocky areas with a Barbary fig shrub community, and by light traps in rocky and sandy areas with *Acacia* woodlands.

Chrysoperla carnea s. l. (Stephens, 1836)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha, near Wadi Mashwas), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 1♀. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 3♀ and 2♂. **Riyadh Province:** Hawtat Bani Tamim, Ibex Reserve Protected Area (W Hotat Bani Tamim), 23°2107'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. This species is widely distributed in the Palaearctic region, extending to Afrotropical (Cape Verde, Oman, United Arab Emirates, Yemen) and Oriental (China, India, Nepal) regions.

Notes. As reported by Hölzel (2002), knowledge about species, as well as the subspecies of *C. phaenon* in the *carnea*-group, of populations in the Arabian Peninsula remains unresolved. Hölzel (1980) recorded this species in the Eastern Province, Madinah, Makkah, and Riyadh provinces of Saudi Arabia. The listed specimens were collected from southwestern and central parts of Saudi Arabia, at elevations up to 1197 m. Most specimens were collected from rocky and sandy areas with *Acacia* woodlands.

Brinckochrysa alfierii (Navás, 1926)

Material examined. Jizan Province: Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂.

Distribution. Africa: Algeria, Egypt, Eritrea, Libya, Sudan, Tunisia. Asia: Israel, Oman, Saudi Arabia, Yemen. A polycentric Afro-syroeremic species.

Biology. Practically unknown. Adults were collected on *Tamarix* sp. in sand dune and coastal dune habitats (Hölzel 2002).

Notes. This species was previously reported in Riyadh Province (Hölzel 1980). The listed single male specimen was attracted to a light trap in sandy areas with *Acacia* woodlands at low elevation of 136 m in southwestern Saudi Arabia.

Brinckochrysa chlorosoma (Navás, 1914)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 1♂. Al Makhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂;

Distribution. Africa: widespread, Cabo Verde. Asia: Israel, Oman, Saudi Arabia, Yemen. Europe: Greece, Italy, Malta. An eremic Afrotropical species.

Notes. This species was previously reported in Makkah Province (Hölzel 1980). The listed specimens were collected in sandy areas with *Acacia* woodlands at elevations of 47–1826 m in southwestern Saudi Arabia.

Chrysemosa andresi (Navás, 1915)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 2♀. Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.682'N, 41°18.263'E, 1291 m, 29 Mar

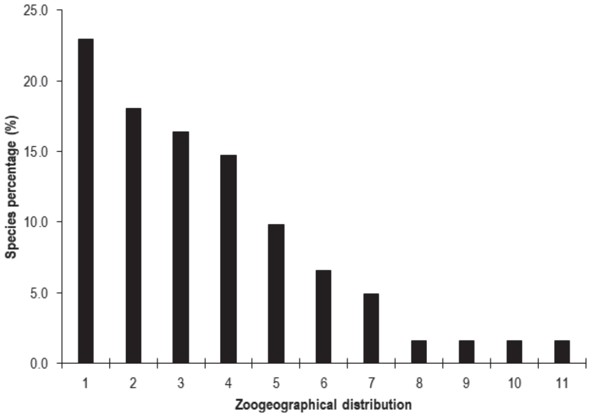

Figure 2. Zoogeographical composition of lacewing fauna in Saudi Arabia **1** afro-syroeremic **2** afrotropical **3** Arabian Endemic **4** afro-syro-iranoeremic **5** Saudi Endemic **6** syro-iranoeremic **7** palaearctic **8** afro-asianeremic **9** asianeremic **10** Palaearctic-Afrotropical-Oriental **11** syroeremic.

2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 4♀ and 2♂; *ibidem*, 19°50.329'N, 41°18.604'E, 1563 m, 29 Mar 2017, ST, 1♂; 10 km NNW of Al Makhwah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 2♂; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 7♀ and 8♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 3♀ and 3♂, 1♀; *ibidem*, 1♂ (AL); *ibidem*, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*,18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 2♀. Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2, Apr 2017, LT, D. Baiocchi leg., 1♀ and 1♂. Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 1♀. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 3♀ and 1♂.

Distribution. Africa: Algeria, Egypt, Senegal, Sudan. Asia: Iran, Oman, Saudi Arabia, Yemen. A polycentric Afro-syro-iranoeremic species.

Notes. *Chrysemosa andresi* was recorded in Asir Province (Hölzel 1988). The specimens were collected at different elevations (136–1926 m) in southwestern Saudi Arabia. The listed specimens were caught by sugar traps set in rocky Barbary fig shrub communities and by light traps set in rocky and sandy areas with *Acacia* woodlands.

Hemerobiidae Latreille, 1802

Micromus sjostedti van der Weele, 1910

Material examined. Jizan Province: Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Africa: sub-Saharan Africa (widespread) to South Africa, Cabo Verde. Asia: Saudi Arabia, Yemen. A possible Afrotropical species.

Notes. The species was previously documented in Asir Province (Hölzel 1988). The listed female specimen was collected at low elevation (136 m) in southwestern Saudi Arabia in a sandy area with *Acacia* woodlands.

Mantispidae Leach in Brewster, 1815

Afromantispa nana (Erichson, 1839)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 6♀ and 5♂. Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50.51'N, 41°18.06'E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 10♀, 11♂ and 1 ex; *ibidem*, 14 Apr 2016, LT, D. Baiocchi leg., 1♀ and 1♂ (AL); Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 6♀, and 24♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 2♀ and 1♂; *ibidem*, 16 Apr 2016, LT, D. Baiocchi leg., 1♀ and 1♂ (AL). Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, LT, 2 Apr 2017, LT, D. Baiocchi leg., 1♀; *ibidem*, 2 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂. Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 1♀; *ibidem*, 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♀; *ibidem*, 18°06'57"N, 42°13'55"E, 462 m, 12 Apr 2019, LT, D. Baiocchi et al. leg., 1♂. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀ and 2♂.

Distribution. Africa: Burkina Faso, Djibouti, Eritrea, Republic of the Congo, South Africa, Sudan. Asia: Saudi Arabia, United Arab Emirates, Yemen. A possible Afrotropical species.

Biology. Unknown.

Notes. This species was previously recorded in the Arabian Peninsula (Yemen: Aden) as *Necyla arabica* (Navás 1914), now a junior synonym. The listed specimens were collected in rocky and sandy areas with *Acacia* woodlands at different elevations (136–1926) in southwestern Saudi Arabia.

Mantispa aphavexelte Aspöck & Aspöck, 1994

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 1♂; *ibidem*, 1♂ (AL); *ibidem*, 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 1♂.

Distribution. Africa: Morocco. Asia: Armenia, China[?], Iran, Kazakhstan, Mongolia, Russia, Turkey. Europe: widespread in southern Europe. It is a Palearctic species.

Biology. *Mantispa aphavexelte* was previously found in ruderal areas and olive groves. The larvae parasitize spiders and feed on spider eggs (Aspöck et al. 1980).

Notes. This study presents the first report for this species in Saudi Arabia. The three males were collected from mountainous *Acacia* woodlands at an elevation of 1197 m in southwestern Saudi Arabia.

Berothidae Handlirsch, 1908

Nodalla eatoni (McLachlan, 1898)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.066'N, 41°18.037'E, 1325 m, 2 Nov 2015, LT, Al Dhafer et al. leg., 2♀; 10 km NNW of Al Makhwah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Africa: widely distributed in northern Africa. Asia: Israel, Oman, Saudi Arabia, Yemen. A polycentric Afro-syroeremic species.

Biology. *Nodalla eatoni* is found in semi-deserts with sparse low vegetation habitats, mainly in the form of isolated spiny dwarf shrubs, surrounded by extensive vegetation-free sandy areas (Aspöck and Aspöck 1983).

Notes. The species was previously documented in several localities (Aspöck and Aspöck 1998). The listed female specimen was collected in foothill *Acacia* woodlands at elevation of 554–1325 m in southwestern Saudi Arabia.

Nodalla saharica (Esben-Petersen, 1920)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.006'N, 41°18.037'E, 1325 m, 5 Mar 2015, LT, Al Dhafer et al. leg., 2♂; *ibidem*, 2 Nov 2015, LT, Al Dhafer et al. leg., 1♀ and 1♂; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂; *ibidem*, 19°50.329'N, 41°18.604'E, 1563 m, 2 Nov 2015, LT, Al Dhafer et al. leg., 2♀. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 7 May 2015, LT, Al Dhafer et al. leg., 2♀ and 1♂; *ibidem*, 18°11.695'N, 42°23.818'E, 1897 m, 5 Nov 2015, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂.

Distribution. Africa: throughout northern Africa. Asia: Afghanistan, Iran, Iraq, Israel, Oman, Saudi Arabia, Yemen. A polycentric Afro-syro-iranoeremic species.

Biology. The biology of *N. saharica* is largely unknown, as with other *Nodalla* species. Adults hide deep inside sparse vegetation or crevices and under stones during the day; at night they are attracted to artificial light sources (Aspöck and Aspöck 1998).

Notes. The species was formerly reported in several localities (Aspöck and Aspöck 1998). The listed specimens were collected in mountainous *Acacia* woodlands, Barbary fig shrublands, and *O. europaea* communities at different elevations (1150–1897 m) in southwestern Saudi Arabia.

Podallea arabica Aspöck & Aspöck, 1981

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 16 Apr 2016, LT, D. Baiocchi leg., 1♂ (AL). **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Endemic to Saudi Arabia.

Notes. The species was previously recorded in Asir Province (Aspöck and Aspöck 1981). The listed adult specimens were collected in sandy and rocky areas with *Acacia* woodlands at elevations of 136–1359 m in southwestern Saudi Arabia.

Nemopteridae Burmeister, 1839

Croce aristata (Klug, 1836)

Material examined. Al Bahah Province: Al Makhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀.

Distribution. Africa: widespread in northern Africa, Ethiopia. Asia: Israel, Oman, Saudi Arabia. Polycentric Afro-syroeremic species.

Biology. This species lives in deserted mines and caves, normally hiding under stones (Hafez and El Moursy 1964).

Notes. It was previously collected in Riyadh Province (Meinander 1980). The listed female specimen was collected in foothill *Acacia* woodlands at low elevation of 473 m in southwestern Saudi Arabia.

Dielocroce berlandi (Navás, 1936)

Material examined. Al Bahah Province: Al Makhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. **Asir Province:** Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06'57"N, 42°13'55"E, 462 m, 12 Apr 2019, LT, D. Baiocchi et al. leg., 5♀.

Distribution. Africa: spread throughout North Africa, Kenya, Sudan. Asia: Israel, Saudi Arabia, Yemen. Polycentric Afro-syroeremic species.

Notes. It was previously collected in Al Madinah Province (Meinander 1980). The listed specimens were found in *Acacia* woodlands at low elevations of 462–473 m in southwestern Saudi Arabia.

Dielocroce chobauti (McLachlan, 1898)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al Asfal, Al-Hamadah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Africa: widespread in North Africa, Sudan, Somalia. Asia: Israel, Oman, Saudi Arabia, Yemen. A possible polycentric Afro-syroeremic species.

Notes. It was previously collected in Asir, Hail and Makkah provinces (Meinander 1980). The listed female specimen was collected in foothill *Acacia* woodlands at an elevation of 554 m in southwestern Saudi Arabia.

Dielocroce elegans (Alexandrov-Martynov, 1930)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al Asfal, Al-Hamadah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♂; 10 km NNW of Al Makhwah, 19°50.47'N, 41°22.40'E, 630 m, 31 Mar 2017, LT, D. Baiocchi leg., 5♀ and 4♂. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 33♀ and 26♂; *ibidem*, 1♀ and 1♂ (AL). Riyadh, NW Al Uyaynah, 24°53.33'N, 46°17.40'E, 761 m, 10 Apr 2016, LT, D. Baiocchi leg., 2♀; *ibidem*, 1♀ (AL).

Distribution. Asia: Afghanistan, Iran, Israel, Oman, Pakistan, Saudi Arabia, Syria, United Arab Emirates, Yemen. A Syro-iranoeremic species.

Notes. This species was formerly reported in Asir, Makkah and Riyadh provinces (Meinander 1980). The listed specimens were collected in sandy areas with *Acacia* woodlands at low elevation (554–6761 m) in southwestern and central Saudi Arabia.

Dielocroce sp.

Material examined. ♀. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♀.

Notes. This listed female specimen was collected at an elevation of 709 m among a huge number of *D. elegans* in sandy *Acacia* woodlands at low elevation in central Saudi Arabia. It might be *D. berlandi* (Navás 1936), but the poor condition of the specimen preserved in alcohol resulted in our identification only to the genus level.

Halter halteratus (Forskål, 1775)

Material examined. Riyadh Province: Al Aflag, Farshet Sheaal (NW Al Naifiyah), 22°25.496'N, 46°34.544'E, 606 m, LT, 10 Apr 2015, LT, Al Dhafer et al. leg., 1♀;

ibidem, 22°24.381'N, 46°35.594'E, 596 m, LT, 12 Apr 2015, LT, Al Dhafer et al. leg., 1♂; Wadi Ghaihab (33 km N Layla), 22°19.601'N, 46°24.808'E, 460 m, LT, 10 Apr 2015, LT, Al Dhafer et al. leg., 1♂. Al Zulfi, Rawdhat Al Sabalah, 26°21.522'N, 44°59.011'E, 664 m, LT, 19 May 2015, LT, Al Dhafer et al. leg., 2♂. Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 2♀ and 9♂; *ibidem*, 1♀ and 1♂ (AL). Ramah, Rawdat Khuraim (100 km NE Riyadh), 25°25.943'N, 47°13.863'E, 572 m, 15 May 2012, LT, M.S. Abdel-Dayem leg., 1♀ and 1♂; *ibidem*, 25°22.986'N, 47°16.712'E, 559 m, 28 Apr 2012, LT, M.S. Abdel-Dayem leg., 3♂. Riyadh, Wadi Hanifa, 24°54.422'N, 46°10.903'E, 809 m, LT, 22 Apr 2017, M. Abdel-Dayem et al. leg., 3♂.

Distribution. Africa: widespread in North Africa, Mauritania, Sudan. Asia: Afghanistan, India, Iran, Iraq, Israel, Kuwait, Oman, Pakistan, Saudi Arabia, Syria, Yemen. A polycentric Afro-syro-iranoeremic species.

Notes. This species was previously collected in Hail, Madinah, Makkah, and Riyadh provinces (Meinander 1980). The listed specimens were collected at low elevations (460–809 m) in central Saudi Arabia in sandy areas dominated with *Acacia* woodlands or *Calotropis procera* (Aiton) W.T. Aiton (Apocynaceae), or areas cultivated with wheat. Also, two males were collected from *Acacia gerrardii* Benth. (Fabaceae), in a gravelly area at Wadi Ghaihab, Al Aflag.

Myrmeleontidae Latreille, 1802

Goniocercus walkeri (McLachlan, 1894) (Fig. 3A)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.596'N, 41°18.672'E, 892 m, 21 Apr 2014, LT, Al Dhafer et al., 1♀; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂. **Riyadh Province:** Al Aflag, Farshet Sheaal (NW Al Naifiyah), 22°25.543'N, 46°34.543'E, 589 m, 15 Oct 2015, LT, Al Dhafer et al. leg., 1♀. Ramah, Rawdat Khuraim (100 km NE Riyadh), 25°25.943'N, 47°13.863'E, 572 m, 28 Aug 2012, LT, M.S. Abdel-Dayem et al. leg., 1♂.

Distribution. Arica: Kenya, Sudan. Asia: Iran, Israel, Saudi Arabia, Yemen. A polycentric Afro-syro-iranoeremic species.

Notes. This species was previously reported in Al Bahah Province (Hölzel 1982). The listed specimens were collected in sandy *Acacia* woodlands at elevations of 473–892 m in southwestern Saudi Arabia, and from communities of *Acacia ehrenbergiana* Heyne and *Rhazya stricta* Decne. (Apocynaceae) at elevations of 572–589 m in the sandy areas of central Saudi Arabia.

Stenares irroratus Navás, 1912 (Fig. 3B)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.596'N, 41°18.672'E, 892 m, 23 Aug 2014, LT, Al Dhafer et al. leg. 2♂.

Asir Province: Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°07.12'N, 42°13.55'E, 467 m, 5 Apr 2017, LT, 1♀ and 1♂. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Africa: Egypt. Asia: Israel, Oman, Saudi Arabia, Yemen. A Syroeremic species.

Notes. This species was previously reported in Makkah Province (Hölzel 1988). The listed specimens were collected in sandy areas with *Acacia* woodlands at low elevations (16–892 m) in southwestern Saudi Arabia.

Fadrina formosa (Hölzel, 1981)

Material examined. Al Bahah Province: Al Mekhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀.

Distribution. Africa: Egypt, Sudan. Asia: Israel, Oman, Saudi Arabia, Yemen. An Afro-syroeremic species.

Notes. This species was previously reported in Asir Province (Hölzel 1982). The listed female specimen was collected in sandy areas with *Acacia* woodlands at low elevation of 473 m in southwestern Saudi Arabia.

Centroclisis speciosa Hölzel, 1983 (Fig. 3C)

Material examined. Asir Province: Abha, Garf Raydah Nature Reserve, 18°11.695'N, 42°23.818'E, 1897 m, 28 Apr 2014, LT, Al Dhafer et al. leg., 1♀.

Distribution. Asia: Oman, Saudi Arabia, United Arab Emirates, Yemen. Endemic to the Arabian Peninsula.

Notes. *C. speciosa* has been widely reported in Saudi Arabia (Saji and Whittington 2008) and was documented in Asir Province (Hölzel 1983). The listed female specimen was collected at an elevation of 1897 m in an *Olea europaea* (Wall. ex G. Don) Cifferi community.

Myrmecaelurus lepidus (Klug in Ehrenberg, 1834)

Material examined. Riyadh Province: Hotat Bani Tamim, Ibex Reserve Protected Area, (W of Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 2♀ and 2♂; *ibidem*, 1♀ and 2♂ (AL).

Distribution. Africa: Algeria, Egypt, Libya, Tunisia. Asia: Oman, Saudi Arabia. A polycentric Afro-syroeremic species.

Biology. This species is poorly known and is usually reported in savannah habitats (Güsten 2002).

Notes. Hölzel (1982) reported this species for the Riyadh Province. The listed adult specimens were collected at an elevation of 709 m in sandy areas with *Acacia* woodlands in central Saudi Arabia.

Iranoleon arabicus Hölzel, 1982

Material examined. Riyadh Province: Hotat Bani Tamim, Ibex Reserve Protected Area, (W of Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 8♀ and 14♂; *ibidem*, 2♀ and 2♂ (AL).

Distribution. Saudi Arabia, United Arab Emirates. An endemic species to the Arabian Peninsula.

Notes. This record is one of the five published localities where this species was collected in Riyadh Province (Hölzel 1982), with large numbers of specimens being preserved in collections. The listed adult specimens were collected at an elevation of 709 m in sandy areas with *Acacia* woodlands in central Saudi Arabia.

Lopezus fedtschenkoi (McLachlan in Fedchenko, 1875)

Material examined. Riyadh Province: Al Quwaiiyah, Rawdhat Al Harmaliyah, 24°17.433'N, 45°08.493'E, 796 m, 17 Apr 2015, LT, M.S. Abdel-Dayem et al. leg. 1♂; 24°17.864'N, 45°08.746'E, 786 m, 19 Apr 2015, PT, M.S. Abdel-Dayem et al. leg. 1♂.

Distribution. Widespread in southern Palearctic region. Africa: Algeria, Tunisia. Asia: Saudi Arabia. An Afro-syroeremic species.

Biology. *Lopezus fedtschenkoi* is associated with desert biotopes.

Notes. It was reported in Riyadh Province (Hölzel 1982). These specimens were collected from sandy areas with *Acacia* (*Acacia gerrardii* and *A. ehrenbergiana*) woodlands at elevations of 786–796 m in central Saudi Arabia.

Gepus invisus Navás, 1912 (Fig. 3E)

Material examined. Riyadh Province: Al Quwaiiyah, Rawdhat Al Harmaliyah, 24°17.433'N, 45°08.493'E, 796 m, 25 Aug 2015, SW, M.S. Abdel-Dayem et al. leg. 1♂. Al Zulfi, Rawdhat Al-Sabalah, 26°22.056'N, 44°59.136'E, 671 m, 29 Aug 2015, PT, M.S. Abdel-Dayem et al. leg. 1♂.

Distribution. Africa: Algeria, Egypt, Libya, Mauritania, Morocco, Sudan, Tunisia. Asia: Israel, Iran, Iraq, Oman, Saudi Arabia, United Arab Emirates, Yemen. A polycentric Afro-syro-iranoeremic species.

Biology. This species is associated with desert biotopes.

Notes. This species was reported in the Eastern, Madinah, and Riyadh provinces (Hölzel 1982). The listed male specimens were collected at elevations of 671−796 m in sandy areas with milkweed trees, *Calotropis procera*, and sandy areas with *Acacia* woodlands, *Acacia ehrenbergiana*, and *A. gerrardii* Benth. (Fabaceae), in central Saudi Arabia.

Solter buettikeri Hölzel, 1982

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50.329'N, 41°18.604'E, 1563 m, 29 Mar 2017, ST, 1♂; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 9♀ and 7♂; *ibidem*, 1♀ and 1♂ (AL).

Distribution. An endemic species to Saudi Arabia.

Notes. This study presents the first report of this species after the original description from Riyadh Province, based on two males (Hölzel 1982). The listed specimens were collected by light traps in a sandy area with *Acacia* woodlands at low elevation (473 m) and by sugar traps in a rocky area with a Barbary fig shrub community at high elevation (1563 m) in southwestern Saudi Arabia.

Solter propheticus Hölzel, 1981

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♂.

Distribution. Africa: Egypt, Sudan. Asia: Israel, Saudi Arabia. An Afro-syroeremic species.

Notes. The species was previously reported in several localities (Hölzel 1998). The listed male specimen was collected with light trap at an elevation of 1358 m in a rocky area with *Acacia* woodlands in southwestern Saudi Arabia.

Cueta amseli Hölzel, 1982

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 23 Aug 2014, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 14 Nov 2015, LT, Al Dhafer et al. leg., 2♀; 19°51.762'N, 41°18.089'E, 1225 m, 23 Oct 2014, LT, Al Dhafer et al. leg., 3♀ and 2♂; *ibidem*, 2 Sep 2015, LT, Al Dhafer et al. leg., 1♀ and 2♂; *ibidem*, 17 Oct 2014, LT, Al Dhafer et al. leg., 4♀ and 3♂; *ibidem*, 15 Nov 2015, LT, Al Dhafer et al. leg., 3♂; *ibidem*, 19°51.066'N, 41°18.037'E, 1325, 23 Aug 2014, LT, Al Dhafer et al. leg., 5♀ and 11♂; *ibidem*, 2 Sep 2015, LT, Al Dhafer et al. leg., 3♀ and 4♂; *ibidem*, 17 Oct 2014, LT, Al Dhafer et al. leg., 1♀ and 1♂; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♂; *ibidem*, 19°50.710'N, 41°18.267'E, 1474 m, 23 Aug 2014, LT,

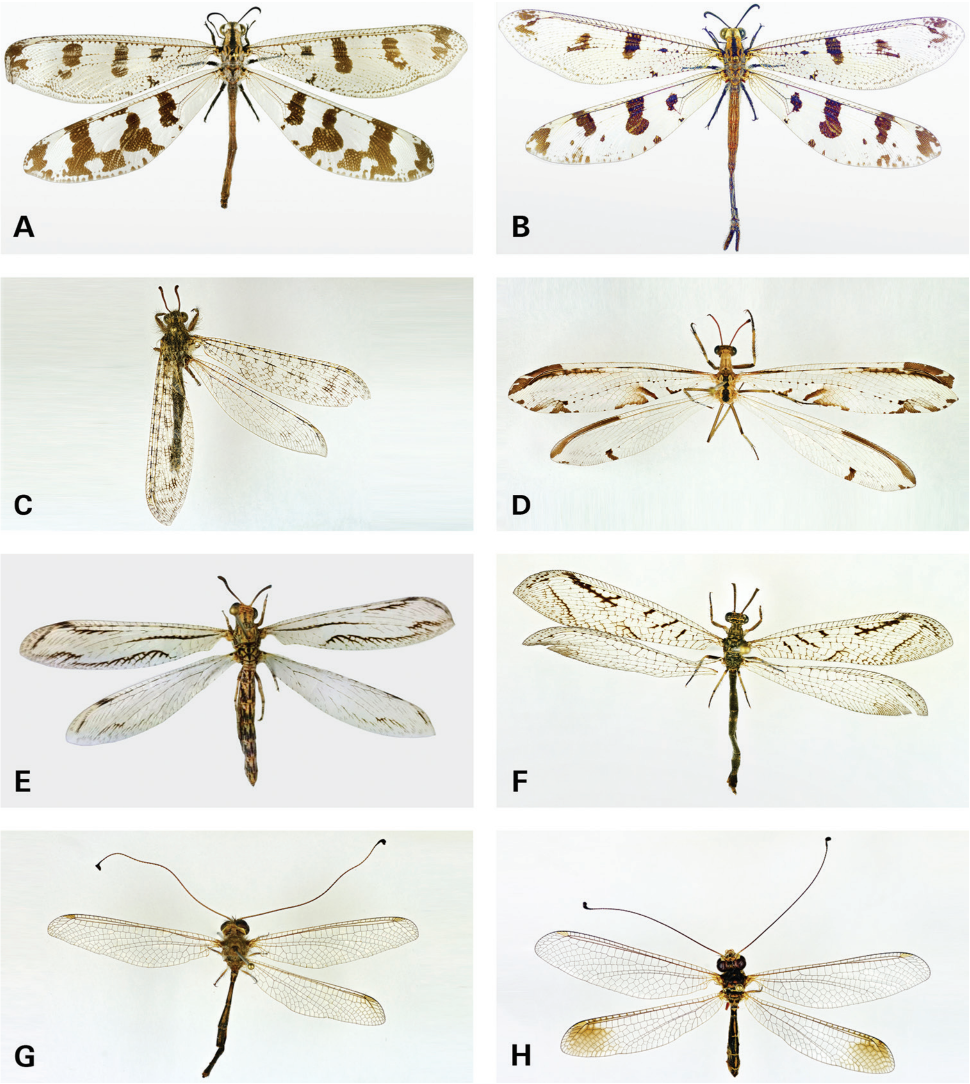

Figure 3. Habitus of lacewing species in Saudi Arabia **A** *Goniocercus walkeri* **B** *Stenares irroratus* **C** *Centroclisis speciosa* **D** *Omoleon jeanneli* **E** *Gepus invisus* **F** *Neuroleon pardalice* **G** *Stylascalaphus kruepери* **H** *Aspoeckiella gallagheri*.

Al Dhafer et al. leg., 9♀ and 7♂; *ibidem*, 2 Sep 2015, LT, Al Dhafer et al. leg., 3♀ and 2♂; *ibidem*, 17 Oct 2014, LT, Al Dhafer et al. leg., 1♀ and 2♂; *ibidem*, 19°50.411'N, 41°18.686'E, 1611 m, 23 Aug 2014, LT, Al Dhafer et al. leg., 5♀ and 9♂; *ibidem*, 2 Sep 2015, LT, Al Dhafer et al. leg., 1♀ and 1♂. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 24 Feb 2014, LT, Al Dhafer et al. leg., 1♀ and 2♂; *ibidem*, 5 Sep 2015, LT, Al Dhafer et al. leg., 2♀ and 2♂; *ibidem*, 18°11.766'N, 42°24.315'E, 2285 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 5♀ and 1♂; *ibidem*, 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 1♂.

Distribution. Oman, Saudi Arabia, Yemen. An endemic species to the Arabian Peninsula.

Biology. Unknown, possibly a pit builder in arid biotopes, like congeners.

Notes. This record is the second locality published for Saudi Arabia, with it being previously collected in Asir Province (Hölzel 1982), with a large number of specimens being preserved in collections. The specimens were collected from mountainous *Acacia* woodlands, Barbary fig shrubland, and *O. europaea* communities at different elevations (892−2285 m) in southwestern Saudi Arabia.

Cueta asirica Hölzel, 1982

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 26 Jan 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 19°50.575'N, 41°18.691'E, 1666 m, 27 Jul 2015, LT, Al Dhafer et al. leg., 1♀. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀ and 2♂; *ibidem*, 18°11.884'N, 42°24.435'E, 2387 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, M.S. Abdel-Dayem leg., LT, 2♀ and 4♂; *ibidem*, 1♀ and 1♂ (AL); *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 7♀ and 8♂. Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♀.

Distribution. This species is endemic to Saudi Arabia.

Biology. Unknown, possibly a pit builder in arid biotopes, like congeners.

Notes. These records represent new localities, with this species previously being collected in Al Bahah Province (Hölzel 1982), with a large number of specimens being preserved in collections. The listed specimens were collected by light traps in *Acacia* woodlands growing on both sandy and rocky soils, and from Barbary fig shrublands and *O. europaea* communities, at different elevations (489−2387 m) in southwestern Saudi Arabia.

Cueta lineosa (Rambur, 1842)

Material examined. Al Bahah Province: Al Mekhwah, 10 km NNW of Al Makhwah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, S.A. El-Sonbati leg., 2♀ and 1♂; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♂. **Jizan Province:** Al Darb, Wadi Reem, 17°51.56'N, 42°16.21'E, 139 m, 3 Apr 2017, LT, D. Baiocchi leg., 2♀ and 3♂. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 2♀ and 5♂. Ramah, Rawdat

Khuraim (100 km NE Riyadh), 25°23.13'N, 47°16.45'E, 550 m, 9 Apr 2016, LT, D. Baiocchi leg., 1♂ (AL).

Distribution. Africa: Egypt, Djibouti, Morocco, Sudan, Tunisia; Asia: Afghanistan, Cyprus, Israel, Iraq, Iran, Lebanon, Oman, Pakistan, Saudi Arabia, Turkey, Turkmenistan, Uzbekistan, Yemen. Europe: Albania, Bulgaria, Greece, Italy, North Macedonia. It is a Palaearctic species.

Biology. This antlion species is common in deserts and steppe-like habitats on the southern edge of the Western Palaearctic. *C. lineosa* larvae construct pits by digging traps in exposed conditions (Badano et al. 2018).

Notes. This species was previously documented in various Saudi provinces, including Asir, Al Bahah, Eastern Province, Jizan, Madinah, and Riyadh (Hölzel 1982). The listed adult specimens were collected in sandy areas with *Acacia* woodlands at low elevations (139−554 m) in southwestern Saudi Arabia and *Rhazya stricta* communities at elevations of 550−709 m in central Saudi Arabia.

Cueta pallens (Klug in Ehrenberg, 1834)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al Asfal, Al Hamadah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♀; 10 km NNW of Al Makhwah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, S.A. El-Sonbati leg., 1♂. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 6♀ and 5♂; *ibidem*, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀ and 2♂; *ibidem*, 1♀ and 1♂ (AL); *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 26♀ and 5♂. Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 1♀; *ibidem*, 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 5♀. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 2♀ and 1♂.

Distribution. Africa. North Africa (widespread), sub-Saharan Africa, Niger, Madagascar. Asia: Israel, Saudi Arabia, Yemen. A polycentric Afro-syroeremic species.

Biology. *Cueta pallens* is possibly a pit builder in arid biotopes, like congeners.

Notes. This species was previously reported in Makkah and Riyadh provinces (Hölzel 1982). The listed specimens were collected from sandy and rocky areas with *Acacia* woodlands at elevations of 136–1150 m in southwestern and central Saudi Arabia.

Myrmeleon caliginosus Hölzel & Ohm, 1983

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 1♀.

Distribution. Africa: North Africa (widespread), Cabo Verde (islands: widespread). Asia: Oman, Saudi Arabia, Yemen. An Afrotropical species.

Biology. The larvae are pit-builders that are associated with sandy shorelines and wide, dry sand-covered habitats (Hölzel and Ohm 1983).

Notes. This species was previously collected in Asir and Al Bahah provinces (Hölzel 1988). The listed female specimen was collected from a rocky area with *Acacia* woodlands in the highlands (1197 m elevation) of southwestern Saudi Arabia.

Myrmeleon fasciatus (Navás, 1912)

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. Africa: northern Africa (widespread). Asia: Israel, Saudi Arabia, Yemen. Europe: Greece. A polycentric Afro-syroeremic species.

Biology. *Myrmeleon fasciatus* inhabits very warm and xeric biotopes, including deserts. The larva builds pits in sheltered areas, such as beneath overhangs and cavities of sedimentary rocks, in very fine detritus or sand (Badano and Pantaleoni 2014).

Notes. This species was previously reported in Al Bahah, Madinah, and Riyadh provinces (Hölzel 1982). The listed specimens were collected from mountainous *Acacia* woodlands at elevations of 1197−1926 m in southwestern Saudi Arabia.

Bankisus maculosus Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.762'N, 41°18.089'E, 1225 m, 17 Oct 2014, LT, Al Dhafer et al. leg., 2♀; *ibidem*, 19°50.411'N, 41°18.686'E, 1611 m, 20 Apr 2014, LT, Al Dhafer et al. leg., 1♀; **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 7 May 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.618'N, 42°23.420'E, 1772 m, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.679'N, 42°23.691'E, 1851 m, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 26 Aug 2014, LT, Al Dhafer et al. leg., 1♀, 1♂; 18°11.695'N, 42°23.818'E, 1897 m, 31 Jul 2015, LT, Al Dhafer et al. leg., 2♂; *ibidem*, 18°11.884'N, 42°24.435'E, 2387 m, 31 Jul 2015, LT, Al Dhafer et al. leg., 2♀; Wadi Marabah (WSW Abha, near Wadi Mashwas), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 4 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 3♀; 11–13 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂; *ibidem*, 16 Apr 2016, LT, D. Baiocchi leg., 2♂ (AL).

Distribution. Asia: Oman, Yemen. An endemic species of the Arabian Peninsula.

Notes. This study presents the first report of the species in Saudi Arabia. The specimens were collected from rocky areas with *Acacia* woodlands, Barbary fig shrublands, and *O. europaea* communities at different elevations (1150–2387 m) in the mountains of southwestern Saudi Arabia.

Omoleon jeanneli Navás, 1936 (Fig. 3D)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.596'N, 41°18.672'E, 892 m, 21 Apr 2014, LT, H. Al Dhafer et al. leg. 1ex.

Distribution. Africa: Ethiopia, Kenya. An Afrotropical species.

Notes. This study presents the first report of the species in Saudi Arabia and Arabian Peninsula. The listed specimen was collected in mountainous *Acacia* woodlands at an elevation of 892 m in southwestern Saudi Arabia.

Geyria lepidula (Navás, 1912)

Material examined. Riyadh Province: Ramah, Rawdat Khuraim (100 km NE Riyadh), 25°25.943'N, 47°13.863'E, 572 m, 28 Aug 2012, LT, M.S. Abdel-Dayem leg., 1ex; *ibidem*, 28 Aug 2012, SW (on *Rhazya stricta*), M.S. Abdel-Dayem leg., 1ex; *ibidem*, 24 Sept 2012, LT, M.S. Abdel-Dayem leg., 1ex; *ibidem*, 25°22.986'N, 47°16.712'E, 559 m, 28 Aug 2012, LT, M.S. Abdel-Dayem leg., 1ex; *ibidem*, 9 Sep 2012, LT, M.S. Abdel-Dayem leg., 2ex.

Distribution. Africa: Egypt (including Sinai), Sudan. Asia: India, Iran, Israel, Saudi Arabia, United Arab Emirates. It is an Afro-syro-iranoeremic species.

Notes. This species was previously recorded in Baha, Makkah, and Riyadh provinces (Hölzel, 1982). The listed specimens were collected from sandy areas dominated with *Rhazya stricta* and *Acacia ehrenbergiana* at elevations of 572–559 m in central Saudi Arabia.

Geyria pallida Hölzel, 1983

Material examined. Riyadh Province: Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♀; *ibidem*, 1♀ (AL).

Distribution. Saudi Arabia, United Arab Emirates. An Arabian endemic species.

Notes. This species was originally described from Eastern Province (Hölzel 1983). The new locality listed here represents a distributional extension for this species. The specimens were collected in sandy areas with *Acacia* woodlands at an elevation of 709 m in central Saudi Arabia.

Neuroleon asirensis Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 2♀ and 2♂. **Asir Province:** Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 1926 m, 18°27.34'N, 42°42.53'E, 2 Apr 2017, LT, D. Baiocchi leg., 1ex. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀.

Distribution. Iran, Oman, Saudi Arabia, United Arab Emirates. A possible Syro-iranoeremic species.

Notes. This species was previously recorded in Asir, Al Bahah, and Makkah provinces (Hölzel 1983). The listed specimens were collected from *Acacia* woodlands in the lowlands and highlands (136–1926 m elevation) of southwestern Saudi Arabia.

Neuroleon delicatus Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50.411'N, 41°18.686'E, 1611 m, 17 Nov 2014, LT, Al Dhafer et al. leg., 4♀; Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 2♀ and 3♂. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 20 Oct 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.679'N, 42°23.691'E, 1851 m, 20 Oct 2014, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 1♀ and 1♂. Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♀ and 1♂; *ibidem*, 1♀ (AL). **Jizan Province:** Al Darb, Wadi Reem, 17°51.56'N, 42°16.21'E, 139 m, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 3 Apr 2017, LT, D. Baiocchi leg., 1♀.

Distribution. Asia: An endemic species to Saudi Arabia.

Notes. This is the first report of this species since it was first described from Asir and Jizan Provinces (Hölzel 1983). The specimens were collected in sandy and rocky areas with *Acacia* woodlands and Barbary fig shrublands at different elevations (136–1614 m) in southwestern Saudi Arabia.

Neuroleon leptaleus (Navás, 1912)

Material examined. Riyadh Province: Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. Africa: Algeria, Libya, Morocco, Tunisia. Asia: Iran, Iraq, Israel, Oman, Saudi Arabia. A polycentric Afro-syro-iranoeremic species.

Notes. It was previously reported in Eastern, Madinah, and Riyadh provinces (Hölzel 1982). The listed specimen was collected from sandy areas with *Acacia* woodlands at an elevation of 709 m in central Saudi Arabia.

Neuroleon lugubris (Navás, 1926)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 3 Mar 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 19°51.762'N, 41°18.089'E, 1225 m, 21 Apr 2014, LT, Al Dhafer et al. leg., 2♀; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 2♀; *ibidem*, 19°50.575'N, 41°18.691'E, 1666 m, 20 Apr 2014, LT, Al Dhafer et al. leg., 1♀. **Asir Province:** Abha, Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 2♀ and 1♂; *ibidem*, 1♀ (AL). Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 1♀. Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 1♀ and 1♂; *ibidem*, 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 5♀ and 1♂. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 2♀ and 2♂. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 5♀.

Distribution. Africa: Egypt, Sudan. Asia: Israel, Oman, Saudi Arabia, Yemen. A polycentric Afro-syroeremic species.

Notes. This species was previously reported in the provinces of Asir, Al Bahah, Jizan, and Makkah (Hölzel 1982). They were collected from sandy and rocky areas with *Acacia* woodlands and Barbary fig shrubs at elevations of 136–1926 m in southwestern and central Saudi Arabia.

Neuroleon modestus (Navás, 1912)

Material examined. Al Bahah Province: Al Makhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. **Asir Province:** Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♀.

Distribution. Africa: Benin, Burkina Faso, Cabo Verde, Cote d'Ivoire, Mali. Asia: Saudi Arabia, Yemen. An Afrotropical species.

Biology. *Neuroleon modestus* occurs in grass savannas and grassy vegetation in cultivated areas (Michel and Akoudjin 2012).

Notes. This species was reported by Hölzel (1988) as *Neuroleon sociorum* Hölzel and Ohm in Asir Province. The listed female specimens were collected with light trap in sandy areas with *Acacia* woodlands at low elevations of 473–489 m in southwestern Saudi Arabia.

Neuroleon pardalice (Banks, 1911) (Fig. 3F)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 3 Mar 2015, LT, M. Mostafa et al. leg., 1♀; *ibidem*, 19°51.762'N, 41°18.089'E, 1225 m, 21 Apr 2014, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 2♀.

Distribution. Africa: Burkina Faso, Eritrea, Ethiopia, Nigeria, Sudan. Asia: Saudi Arabia, Yemen. An Afrotropical species.

Notes. This species was previously reported in Al Bahah and Asir provinces (Hölzel 1982). The specimens were collected with light traps in sandy areas with *Acacia* woodlands at 892–1358 m in southwestern Saudi Arabia.

Neuroleon tenellus (Klug in Ehrenberg, 1834)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.682'N, 41°18.263'E, 1291 m, 29 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♂. **Asir Province:** Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 5♀ and 1♂; *ibidem*, 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 17♀ and 1♂; *ibidem*, 1♀ and 1♂ (AL). **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂; *ibidem*, 17°51.56'N, 42°16.21'E, 139 m, 3 Apr 2017, LT, D. Baiocchi leg., 1♂. **Riyadh Province:** Riyadh, NW Al Uyaynah, 24°53.33'N, 46°17.40'E, 761 m, 10 Apr 2016, LT, D. Baiocchi leg., 2♀ and 1♂ (AL).

Distribution. Africa: Algeria, Egypt, Eritrea, Ethiopia, Libya, Morocco, Mauritania, Sudan, Tunisia. Asia: Afghanistan, Azerbaijan, Cyprus, Israel, Iran, Iraq, Kyrgyzstan, Lebanon, Oman, Saudi Arabia, Turkey, Tajikistan, Turkmenistan, Uzbekistan. Europe: Greece, North Macedonia. A polycentric Afro-asianeremic species.

Biology. *Neuroleon tenellus* is not well known and is usually documented in arid habitats. The larvae have not been documented (Aspöck et al. 1980; Badano et al. 2018).

Notes. The species was previously documented in Eastern Province and Riyadh provinces (Hölzel 1982). The specimens were collected in *Acacia* woodlands on both rocky and sandy soils at elevations of 136–1291 m in southwestern and central Saudi Arabia.

Neuroleon virgineus Hölzel, 1983

Material examined. Al Bahah Province: Al Makhwah, Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 4♀ and 1♂; *ibidem*, 1♀ and 1♂ (AL).

Distribution. Asia: An endemic species to Saudi Arabia.

Notes. This study presents the first record of this species after the original description from Makka Province (Hölzel 1983). The listed specimens were collected from sandy areas with *Acacia* woodlands at low elevation of 473 m in southwestern Saudi Arabia.

Distoleon asiricus Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°51.066'N, 41°18.037'E, 1325, 20 Apr 2014, LT, Al Dhafer et al. leg., 1♂. **Asir Province:** Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 20 Oct 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.618'N, 42°23.420'E, 1772 m, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.679'N, 42°23.691'E, 1851 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀ and 3♂; *ibidem*, 20 Oct 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.766'N, 42°24.315'E, 2285 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 31 Jul 2015, LT, Al Dhafer et al. leg., 1♂; *ibidem*, 18°11.884'N, 42°24.435'E, 2387 m, 28 Apr 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 6 Jun 2014, LT, Al Dhafer et al. leg., 2♀ and 1♂; *ibidem*, 18°12.095'N, 42°24.536'E, 2578 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 20 Oct 2014, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 16 Apr 2016, LT, D. Baiocchi leg., 1♂; *ibidem*, 1♀ (AL). **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♀ and 2♂.

Distribution. Asia: Saudi Arabia, United Arab Emirates, Yemen. An endemic species to the Arabian Peninsula.

Biology. The listed records present further localities in Saudi Arabia from where this species has been recently described.

Notes. It was previously reported in Asir and Al Bahah provinces in southwestern Saudi Arabia (Hölzel 1983). The listed specimens were collected from rocky areas with *Acacia* woodlands, Barbary fig shrublands, and juniper forest at high elevations (1150–2387 m) in southwestern Saudi Arabia, and in sandy areas with *Acacia* woodlands at an elevation of 709 m in the central regions of Saudi Arabia.

Distoleon laticollis (Navás, 1913)

Material examined. Al Bahah Province: Al Mandaq, Wadi Tourabah (E of An Na'Amah), 20°11'01"N, 41°18'42"E, 1826 m, 6 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 2 Mar 2015, LT, A. Mostafa leg., 1♂; *ibidem*, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♀. **Asir Province:** Abha, WSW of Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 5 Nov 2015, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 18°11.679'N, 42°23.691'E, 1851 m, 6 Jun 2014, LT, Al Dhafer et al. leg., 1♀. Wadi Marabah (WSW Abha), 18°10.293'N, 42°22.195'E, 1150 m, 1 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂; *ibidem*, 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 2♀ and 3♂; *ibidem*, 16 Apr 2016, LT, D. Baiocchi leg., 1♂; *ibidem*, 1♂ (AL). Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♂. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area, (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 1♀ and 1♂.

Distribution. Africa: Ethiopia, Sudan. Asia: Cyprus, Israel, Lebanon, Oman, Saudi Arabia, Syria, Turkey. A polycentric Afro-syroeremic species.

Biology. Mainly unknown, associated with arid environments (Badano et al. 2018).

Notes. This species was previously recorded in the mountains of southwestern Saudi Arabia, from Al Bahah and Makkah provinces (Hölzel 1982). The listed specimens were collected in *Acacia* woodlands in rocky and sandy soils and in rocky areas with Barbary fig shrub communities at different elevations (489–1851 m) in southwestern and central Saudi Arabia.

Nemoleon secundus (Hölzel, 2002)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al Asfal, Al-Hamadah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 5♀ and 1♂; *ibidem*, 1♀ and 1♂ (AL); Wadi Reyam (NE Al Makhwah), 19°50'28"N, 41°22'34"E, 473 m, 7 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 4♂.

Distribution. Asia: Oman, Yemen. An endemic species to the Arabian Peninsula.

Notes. This study presents the first report in Saudi Arabia, with this species recently being described from Oman and Yemen (Hölzel, 2002). The listed specimens were collected from foothill *Acacia* woodlands at elevations of 473–554 m in southwestern Saudi Arabia.

Pseudoformicaleo gracilis (Klug in Ehrenberg, 1834)

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 16 Apr 2016, LT, D. Baiocchi leg., 1ex. (AL).

Distribution. Africa: Algeria, Egypt, Libya, Morocco, Tunisia. Asia: Iran, Israel, Lebanon, Oman, Russia, Saudi Arabia, Syria, Turkey, United Arab Emirates, Yemen. A polycentric Afro-syro-iranoeremic species.

Notes. This species was previously recorded in east and southwest Saudi Arabia, in Eastern Province and Makkah provinces, respectively (Hölzel 1982). The listed specimen was collected from mountainous *Acacia* woodlands at an elevation of 1197 m in southwestern Saudi Arabia.

Creoleon elegans Hölzel, 1968

Material examined. Asir Province: Abha, Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 1 Apr 2017, LT, D. Baiocchi leg., 2♀.

Distribution. Asia: Israel, Iran, Iraq, Pakistan, Saudi Arabia, Syria. Syro-iranoeremic species.

Biology. The larvae possibly inhabit sandy soils, like congeners.

Notes. This species was previously reported in central (Riyadh Province) and southwestern (Makkah Province) Saudi Arabia (Hölzel 1982). The listed specimens were collected from rocky areas with *Acacia* woodlands at an elevation of 1197 m in the highlands of southwestern Saudi Arabia.

Creoleon griseus (Klug in Ehrenberg, 1834)

Material examined. Asir Province: Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. Africa: Egypt, Senegal, Sudan, Tunisia. Asia: Afghanistan, India, Iran, Iraq, Israel, Oman, Pakistan, Saudi Arabia, Syria, Yemen. Europe: Spain. A widespread polycentric Afro-syro-iranoeremic species.

Biology. The larva possibly inhabits sandy soils, like congeners.

Notes. It was previously recorded in central Saudi Arabia, in Riyadh Province (Hölzel 1982). The listed male specimen was collected from sandy areas with *Acacia* woodlands at an elevation of 192 m in southwestern Saudi Arabia.

Creoleon persicus Hölzel, 1972

Material examined. Al Bahah Province: Al Mekhwah, Shada Al Asfal, Al-Hamadah, 20°10.750'N, 41°19.072'E, 554 m, 30 Mar 2017, LT, M.S. Abdel-Dayem leg., 1♀. **Asir Province:** Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.34'N, 42°42.53'E, 1926 m, 2 Apr 2017, LT, D. Baiocchi leg., 1♀.

Distribution. Asia: Afghanistan, Iran, Israel, Saudi Arabia. A Syro-iranoeremic species.

Biology. The larva possibly inhabits sandy soils, like congeners.

Notes. It was documented in northern and southwestern Saudi Arabia, in Tabouk, Asir and Riyadh provinces (Hölzel 1982). The listed specimens were attracted to light traps in sandy areas with *Acacia* woodlands at elevations between 554–1926 m in southwestern Saudi Arabia.

Creoleon ultimus Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50'51"N, 41°18'06"E, 1358 m, 9 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ and 1♂. **Asir Province:** Khamis Mushait, Wadi Ibn Hashbal (14 km N Khamis Mushait), 18°27.558'N, 42°42.876'E, 1926 m, 2 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♂.

Distribution. Asia: An endemic species to Saudi Arabia.

Biology. The larva possibly inhabits sandy soils, like congeners.

Notes. This study presents the first report of this species after the original description, based on one male and one female collected in Al Bahah Province in southwestern Saudi Arabia (Hölzel 1983). The listed male specimens were collected in sandy and rocky areas with *Acacia* woodlands at elevations of 1358–1926 m in the highlands of southwestern Saudi Arabia.

Ascalaphidae Lefèbvre, 1842

Ascalaphus festivus (Rambur, 1842)

Material examined. Al Bahah Province: Al Mandaq, Wadi Turubah, 20°14.369'N, 41°15.234'E, 1757 m, 3 Jun 2012, H. Al Dhafer et al. leg., 3♀. **Asir Province:** Al Magardah, Wadi Al Talalie, 18°59.840'N, 41°43.910'E, 242 m, 1 Jun 2012, B. Kondratiff and H. Al Dahfer leg., SW, 1♀. Rijal Almaa, Wadi Kasan (3 km N Al Hubail), 18°06.981'N, 42°13.939'E, 451 m, 3 Apr 2017, LT, M.S. Abdel-Dayem and I. Rasool leg., 1♂; *ibidem*, 18°06'57"N, 42°13'55"E, 462 m, 12 Apr 2019, LT, D. Baiocchi et al. leg., 1♀ (AL); *ibidem*, 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 3♂. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Africa: widespread, including Cabo Verde and Madagascar. Asia: Israel, Oman, Saudi Arabia, United Arab Emirates, Yemen. Europe: Italy. An Afrotropical species.

Biology. It is commonly collected with light traps in open savannah areas that are sometimes cultivated or grazed by cattle (Tjeder 1980).

Notes. This species was previously reported in Eastern Province, Jizan, and Riyadh provinces (Hölzel 1983). The specimens were collected in sandy areas with *Acacia* woodlands at elevations of 136–1757 m in southwestern Saudi Arabia.

Stylascalaphus krueperi (van der Weele, 1909) (Fig. 3G)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°52.598'N, 41°18.672'E, 892 m, 24 Apr 2014, LT, Al Dhafer et al. leg., 1♀; *ibidem*, 23 Aug 2014, LT, Al Dhafer et al. leg., 1♀.

Distribution. Africa: Algeria, Morocco (Ábrahám 2017), Egypt. Asia: Jordan, Syria. An Afro-syroeremic species.

Notes. This species is a new listing for fauna in the Arabian Peninsula. The listed female specimens were collected in sandy areas with *Acacia* woodlands at an elevation of 892 m in southwestern Saudi Arabia.

Aspoeckiella gallagheri Hölzel, 2004 (Fig. 3H)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°57.686'N, 41°18.262'E, 607 m, 9 Apr 2019, LT, D. Baiocchi leg., 1♀. **Jizan Province:** Al Darb, Wadi Reem, 17°51.56'N, 42°16.21'E, 139 m, 3 Apr 2017, LT, D. Baiocchi leg., 1♂.

Distribution. Asia: Oman, United Arab Emirates. An endemic species to the Arabian Peninsula.

Notes. This study presents the first report of this species in Saudi Arabia, which was originally described from Oman and the United Arab Emirates (Hölzel 2004). The listed specimens were collected at low elevations (139–607 m) in sandy areas with *Acacia* woodlands in southwestern Saudi Arabia.

Bubopsis hamata (Klug in Ehrenberg, 1834)

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature Reserve, 19°50.51'N, 41°18.06'E, 1358 m, 14 Apr 2016, LT, D. Baiocchi leg., 1♀. **Riyadh Province:** Hotat Bani Tamim, Ibex Reserve Protected Area (W Hotat Bani Tamim), 23°21.07'N, 46°21.36'E, 709 m, 11 Apr 2017, LT, D. Baiocchi leg., 2♂ (AL). Riyadh, Wadi Hanifa, 24°54.422'N, 46°10.903'E, 809 m, LT, 22 Apr 2017, M. Abdel-Dayem et al. leg., 1♀ and 2♂.

Distribution. Africa: Egypt. Asia: Azerbaijan, Georgia, Iran, Iraq, Israel, Jordan, Kyrgyzstan, Lebanon, Saudi Arabia, Syria, Turkey, Turkmenistan, United Arab Emirates. Europe: Greece. An Asianeremic species.

Biology. It is frequently collected by light traps; adults tend to inhabit steppe-like habitats, and rocky grasslands with long stalks (Dobosz and Ábrahám 2007).

Notes. The species was previously reported in Asir, Madinah, and Riyadh provinces (Hölzel 1983). The listed specimens were collected with light traps in mountainous areas and sandy areas with *Acacia* woodlands at elevations of 709–1358 m in southwestern and central Saudi Arabia, respectively.

Tmesibasis larseni Hölzel, 1983

Material examined. Al Bahah Province: Al Mekhwah, Shada Al-A'Ala Nature, 19°51.066'N, 41°18.037'E, 1325 m, 24 Feb 2014, Al Dhafer et al. leg., 1♂; *ibidem*, 19°50.51'N, 41°18.06'E, 1358 m, 14 Apr 2016, LT, D. Baiocchi leg., 1♀ (AL). **Asir Province:** Abha, WSW of Abha, Garf Raydah Nature Reserve, 18°11.749'N, 42°23.345'E, 1614 m, 24 Mar 2014, LT, S.A. El-Sonbati leg., 1♀; *ibidem*, 5 Sep 2015, LT, Al Dhafer et al. leg., 1♀; Wadi Marabah (WSW Abha), 18°10.18'N, 42°22.12'E, 1197 m, 16 Apr 2016, LT, D. Baiocchi leg., 1♂ (AL). Rijal Almaa, Wadi Kasan (2 km N Al Hubail), 18°07.12'N, 42°13.55'E, 489 m, 5 Apr 2017, LT, D. Baiocchi leg., 1♀. **Jizan Province:** Al Darb, Wadi Reem, 17°52.551'N, 42°16.664'E, 136 m, 5 Apr 2017, LT, M.S. Abdel-Dayem leg., 1♀.

Distribution. Asia: Oman, Saudi Arabia, Yemen. An endemic species to the Arabian Peninsula.

Notes. The listed records for this species extend existing published Saudi Arabian localities from Gizan, based on a single female specimen (Hölzel 1983). The listed specimens were collected in rocky and sandy areas with *Acacia* woodlands and rocky areas with Barbary fig shrub communities at elevations of 136–1358 m in southwestern Saudi Arabia.

Discussion

Between 2014 and 2019, specimens of 61 lacewing species belonging to seven families were collected in Saudi Arabia. Also, two species belonging to *Dielocroce* and *Pseudomallada* were identified only to genus level. The families included are: Ascalaphidae (5 species), Berothidae (3 species), Chrysopidae (10 species), Hemerobiidae (1 species), Mantispidae (2 species), Myrmeleontidae (36 species), and Nemopteridae (6 species). This list includes six new species records for the country. Of these, three species are new records to the Arabian Peninsula: *Mantispa aphavexelte* Aspöck & Aspöck, *Omoleon jeanneli* Navás, and *Stylascalaphus krueperi* (van der Weele). The other three are new records to Saudi Arabia only: *Aspoeckiella gallagheri* Hölzel, *Bankisus maculosus* Hölzel and *Nemoleon secundus* (Hölzel). Notably, *Mantispa aphavexelte* was recorded close to the southern boundary of its distributional range. This study also provides the first record for eight species since their original description: *Creoleon ultimus* Hölzel, *Cueta amseli* Hölzel, *C. asirica* Hölzel, *Distoleon asiricus* Hölzel, *Geyria pallida* Hölzel, *Neuroleon delicatus* Hölzel, *Neuroleon virgineus* Hölzel, and *Solter buettikeri* Hölzel.

Many of the lacewing species documented in this study are characteristic of fauna from eremial bioregions (47.5%; Fig. 2), particularly Afro-syroeremic species (14 spp., 23.0%), followed by Afro-syro-iranoeremic species (9 spp., 14.8) and Afrotropical species (11 spp., 18.0%). Three species were representatives of Palaearctic species (4.9%):

Cueta lineosa (Rambur), *Mantispa aphavexelte* Aspöck & Aspöck and *Pseudomallada venosus* (Rambur). *Chrysoperla carnea* (Stephens) was the only species that had a wide distributional range (Afrotropical, Oriental and Palaearctic regions). These findings confirm that the lacewing species recorded in Saudi Arabia have strong relationships with the eremic fauna of North Africa (Afroeremic) and Asia (Syroeremic, Iranoeremic, and Turanoeremic), as well as the Afrotropical fauna. The high percentage of eremic (Saharo-Arabian and Saharo-Sindian) components in the fauna of Saudi Arabia has been previously documented (Larsen 1984; Penati and Vienan 2006; Abel-Dayem et al. 2017, 2018, 2019).

A large number of species are endemic to Saudi Arabia and the Arabian Peninsula (16 spp., 26.2%). *Creoleon ultimus* Hölzel, *Cueta asirica* Hölzel, *Neuroleon delicatus* Hölzel, *N. virgineus* Hölzel, *Podallea arabica* Aspöck & Aspöck, and *Solter buettikeri* Hölzel, are known as endemic to Saudi Arabia. Ten species are endemic to the Arabian Peninsula, being distributed in Oman, Saudi Arabia, the United Arab Emirates, and Yemen: *Aspoeckiella gallagheri* Hölzel, *Bankisus maculosus* Hölzel, *Centroclisis speciosa* Hölzel, *Cueta amseli* Hölzel, *Distoleon asiricus* Hölzel, *Geyria pallida* Hölzel, *Iranoleon arabicus* Hölzel, *Nemoleon secundus* (Hölzel), *Pseudomallada arabicus* (Hölzel), and *Tmesibasis larseni* Hölzel. The southwestern region of Saudi Arabia is particularly rich in insect species (Larsen 1984; Abuzinada et al. 2001; Ziani et al. 2019), reflecting the high number of endemic lacewing species that are mostly syroeremic species (Hölzel 1998). A high percentage of endemic species to Saudi Arabia are emerging partly because current knowledge on Afrotropical and Oriental fauna is limited and partly because the Arabian Peninsula is in the transitional zone between Palaearctic and Afrotropical regions, as well as being close to Oriental regions.

According to Oswald (2019), 170 lacewing taxa are known from Saudi Arabia in addition to six new country records from our study (Appendix I). We listed 61 species of the (now) 176 taxa known from Saudi Arabia, so we sampled and reported a little more than one third (34.7%) of the total known Neuropterida fauna of Saudi Arabia. The most prominent in our survey, is the absence of Coniopterygidae (Appendix I) which are very hardly to detect (a very small insects) without specific researches. The huge differences of knowledge of this family in Yemen (57 spp.) and Saudi Arabia (10 spp.) is due only to the lack of a specific research of Coniopterygidae in Saudi Arabia.

Despite a large number of studies existing on the lacewing fauna of the Arabian Peninsula (Meinander 1979, 1980; Hölzel 1980, 1982, 1983, 1988, 1995, 1998; Sziráki and van Harten 2006; Sziráki 2010), including the current study, there is still a paucity of knowledge about the lacewing fauna in the Arabian Peninsula. This issue is reflected by the rate of discovery of lacewing species in the Arabian Peninsula has not yet reached a plateau. The addition of lacewing species after more thorough sampling efforts is expected to provide more reliable biogeographical patterns on this group. Further studies on the lacewing fauna of Saudi Arabia should also focus on the biology and ecology of this group.

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Appendix I

List of known lacewings from Saudi Arabia.

Family	Species	This study
Ascalaphidae	*Ascalaphus dicax* Walker, 1853	
Ascalaphidae	*Ascalaphus festivus* (Rambur, 1842)	+
Ascalaphidae	*Aspoeckiella gallagheri* Hölzel, 2004	+
Ascalaphidae	*Bubopsis hamata* (Klug in Ehrenberg, 1834)	+
Ascalaphidae	*Stylascalaphus krueperi* (van der Weele, 1909)	+
Ascalaphidae	*Tmesibasis larseni* Hölzel, 1983	+
Berothidae	*Nodalla eatoni* (McLachlan, 1898)	+
Berothidae	*Nodalla saharica* (Esben-Petersen, 1920)	+
Berothidae	*Podallea arabica* Aspöck & Aspöck, 1981	+
Chrysopidae	*Brinckochrysa alfierii* (Navás, 1926)	+
Chrysopidae	*Brinckochrysa chlorosoma* (Navás, 1914)	+
Chrysopidae	*Brinckochrysa plagata* (Navás, 1929)	
Chrysopidae	*Chrysemosa andresi* (Navás, 1915)	+
Chrysopidae	*Chrysemosa mosconica* (Navás, 1931)	
Chrysopidae	*Chrysemosa sodomensis* (Hölzel, 1982)	
Chrysopidae	*Chrysopa sogdianica* McLachlan in Fedchenko, 1875	
Chrysopidae	*Chrysoperla carnea* (Stephens, 1836)	+
Chrysopidae	*Chrysoperla mutata* (McLachlan, 1898)	
Chrysopidae	*Italochrysa asirensis* Hölzel, 1980	
Chrysopidae	*Italochrysa bimaculata* Hölzel, 1980	+
Chrysopidae	*Italochrysa pittawayi* Hölzel, 1988	
Chrysopidae	*Italochrysa stigmatica* (Rambur, 1838)	
Chrysopidae	*Pseudomallada amseli* (Hölzel, 1980)	+
Chrysopidae	*Pseudomallada arabicus* (Hölzel, 1995)	+
Chrysopidae	*Pseudomallada healdi* (Navás, 1926)	
Chrysopidae	*Pseudomallada nicolainus* (Navás, 1929)	
Chrysopidae	*Pseudomallada phlebius* (Navas, 1927)	
Chrysopidae	*Pseudomallada spadix* (Hölzel, 1988)	+
Chrysopidae	*Pseudomallada venosus* (Rambur, 1838)	+
Chrysopidae	*Suarius alisteri* (Navás, 1914)	
Chrysopidae	*Suarius caviceps* (McLachlan, 1898)	

Family	Species	This study
Chrysopidae	*Suarius gobiensis* (Tjeder, 1936)	
Chrysopidae	*Suarius mongolica* (Tjeder, 1936)	
Chrysopidae	*Suarius walsinghami walsinghami* Navás, 1914	
Coniopterygidae	*Aleuropteryx arabica* Meinander, 1977	
Coniopterygidae	*Aleuropteryx vartianorum* Aspöck & Aspöck, 1967	
Coniopterygidae	*Coniopteryx deserta* Meinander, 1979	
Coniopterygidae	*Coniopteryx mucrogonarcuata* Meinander, 1979	
Coniopterygidae	*Coniopteryx ressli* Rausch & Aspöck, 1978	
Coniopterygidae	*Coniopteryx venustula* Rausch & Aspöck, 1978	
Coniopterygidae	*Coniopteryx wittmeri* Meinander, 1979	
Coniopterygidae	*Cryptoscenea serrata* (Meinander, 1979)	
Coniopterygidae	*Hemisemidalis pallida* (Withycombe, 1924)	
Coniopterygidae	*Nimboa macroptera* Aspöck & Aspöck, 1965	
Hemerobiidae	*Hemerobius reconditus* Navás, 1914	
Hemerobiidae	*Micromus sjostedti* van der Weele, 1910	+
Hemerobiidae	*Sympherobius fallax* Navás, 1908	
Hemerobiidae	*Wesmaelius navasi* (Andréu, 1911)	
Hemerobiidae	*Wesmaelius saudiarabicus* Hölzel, 1988	
Mantispidae	*Afromantispa nana* (Erichson, 1839)	+
Mantispidae	*Mantispa aphavexelte* Aspöck & Aspöck, 1994	+
Mantispidae	*Mantispa scabricollis* McLachlan in Fedchenko, 1875	
Myrmeleontidae	*Acanthaclisis mesopotamica* Hölzel, 1972	
Myrmeleontidae	*Bankisus maculosus* Hölzel, 1983	+
Myrmeleontidae	*Centroclisis cervina* (Gerstaecker, 1863)	
Myrmeleontidae	*Centroclisis distincta* (Rambur, 1842)	
Myrmeleontidae	*Centroclisis speciosa* Hölzel, 1983	+
Myrmeleontidae	*Creoleon cervinus* Hölzel, 1983	
Myrmeleontidae	*Creoleon cinerascens* (Navás, 1912)	
Myrmeleontidae	*Creoleon desertus* Hölzel, 1982	
Myrmeleontidae	*Creoleon elegans* Hölzel, 1968	+
Myrmeleontidae	*Creoleon griseus* (Klug in Ehrenberg, 1834)	+
Myrmeleontidae	*Creoleon neftanus* Navás, 1930	
Myrmeleontidae	*Creoleon neurasthenicus* (Navás, 1913)	
Myrmeleontidae	*Creoleon parvulus* Hölzel, 1983	
Myrmeleontidae	*Creoleon persicus* Hölzel, 1972	+
Myrmeleontidae	*Creoleon pullus* Hölzel, 1983	
Myrmeleontidae	*Creoleon ultimus* Hölzel, 1983	+
Myrmeleontidae	*Cueta amseli* Hölzel, 1982	+
Myrmeleontidae	*Cueta asirica* Hölzel, 1982	+
Myrmeleontidae	*Cueta clara* Hölzel, 1981	
Myrmeleontidae	*Cueta divisa* (Navás, 1912)	
Myrmeleontidae	*Cueta genialis* Hölzel, 1988	
Myrmeleontidae	*Cueta lineosa* (Rambur, 1842)	+
Myrmeleontidae	*Cueta modesta* Hölzel, 1972	
Myrmeleontidae	*Cueta pallens* (Klug in Ehrenberg, 1834)	+
Myrmeleontidae	*Cueta paula* Hölzel, 1983	
Myrmeleontidae	*Cueta pusilla* Hölzel, 1983	
Myrmeleontidae	*Cueta striata* Kimmins, 1943	
Myrmeleontidae	*Cueta virgata* (Klug in Ehrenberg, 1834)	
Myrmeleontidae	*Distoleon asiricus* Hölzel, 1983	+
Myrmeleontidae	*Distoleon laticollis* (Navás, 1913)	+
Myrmeleontidae	*Fadrina formosa* (Hölzel, 1981)	+
Myrmeleontidae	*Ganguilus flavipennis* (Navás, 1932)	
Myrmeleontidae	*Ganguilus oblitus* (Navás, 1914)	
Myrmeleontidae	*Ganguilus pallescens* Navás, 1912	
Myrmeleontidae	*Ganguilus pulchellus* (Banks, 1911)	
Myrmeleontidae	*Gepella modesta* Hölzel, 1968	

Family	Species	This study
Myrmeleontidae	*Gepus cunctatus* Hölzel, 1982	
Myrmeleontidae	*Gepus invisus* Navás, 1912	+
Myrmeleontidae	*Geyria arabica* Hölzel, 1983	
Myrmeleontidae	*Geyria lepidula* (Navás, 1912)	+
Myrmeleontidae	*Geyria pallida* Hölzel, 1983	+
Myrmeleontidae	*Geyria saharica* Esben-Petersen, 1920	
Myrmeleontidae	*Goniocercus klugi* (Kolbe, 1898)	
Myrmeleontidae	*Goniocercus walkeri* (McLachlan, 1894)	+
Myrmeleontidae	*Iranoleon arabicus* Hölzel, 1982	+
Myrmeleontidae	*Iranoleon darius* Hölzel, 1972	
Myrmeleontidae	*Isoleon arabicus* Hölzel, 1972	
Myrmeleontidae	*Lopezus arabicus* Hölzel, 1972	
Myrmeleontidae	*Lopezus fedtschenkoi* (McLachlan in Fedchenko, 1875)	+
Myrmeleontidae	*Macronemurus delicatulus* Morton, 1926	
Myrmeleontidae	*Mesonemurus harterti* Navás, 1919	
Myrmeleontidae	*Myrmecaelurus acerbus* (Walker, 1853)	
Myrmeleontidae	*Myrmecaelurus laetus* (Klug in Ehrenberg, 1834)	
Myrmeleontidae	*Myrmecaelurus lepidus* (Klug in Ehrenberg, 1834)	+
Myrmeleontidae	*Myrmecaelurus lobatus* Navás, 1912	
Myrmeleontidae	*Myrmecaelurus luridus* Hölzel, 1983	
Myrmeleontidae	*Myrmecaelurus obscurus* Hölzel, 1983	
Myrmeleontidae	*Myrmecaelurus parvulus* Hölzel, 1982	
Myrmeleontidae	*Myrmecaelurus peterseni* Kimmins, 1943	
Myrmeleontidae	*Myrmecaelurus philbyi* Kimmins, 1943	
Myrmeleontidae	*Myrmecaelurus pittawayi* Hölzel, 1983	
Myrmeleontidae	*Myrmecaelurus saudiarabicus* Hölzel, 1982	
Myrmeleontidae	*Myrmeleon alternans* Brullé in Webb & Berthelot, 1839	
Myrmeleontidae	*Myrmeleon caliginosus* Hölzel & Ohm, 1983	+
Myrmeleontidae	*Myrmeleon fasciatus* (Navás, 1912)	+
Myrmeleontidae	*Myrmeleon hyalinus* Olivier, 1811	
Myrmeleontidae	*Myrmeleon pellucidus* Hölzel, 1988	
Myrmeleontidae	*Myrmeleon vittatus* Olivier, 1811	
Myrmeleontidae	*Myrmeleon wismanni* (Navás, 1936)	
Myrmeleontidae	*Naya palpalis* (Klapálek, 1914)	
Myrmeleontidae	*Nemoleon secundus* (Hölzel, 2002)	+
Myrmeleontidae	*Neuroleon amseli* Hölzel, 1983	
Myrmeleontidae	*Neuroleon asirensis* Hölzel, 1983	+
Myrmeleontidae	*Neuroleon delicatus* Hölzel, 1983	+
Myrmeleontidae	*Neuroleon erato* Hölzel, 1972	
Myrmeleontidae	*Neuroleon gracilis* (Navás, 1926)	
Myrmeleontidae	*Neuroleon leptaleus* (Navás, 1912)	+
Myrmeleontidae	*Neuroleon lugubris* (Navás, 1926)	+
Myrmeleontidae	*Neuroleon modestus* (Navás, 1912)	+
Myrmeleontidae	*Neuroleon nubilatus* (Navás, 1912)	
Myrmeleontidae	*Neuroleon pardalice* (Banks, 1911)	+
Myrmeleontidae	*Neuroleon parvus* Kimmins, 1943	
Myrmeleontidae	*Neuroleon taifensis* Kimmins, 1943	
Myrmeleontidae	*Neuroleon tenellus* (Klug in Ehrenberg, 1834)	+
Myrmeleontidae	*Neuroleon virgineus* Hölzel, 1983	+
Myrmeleontidae	*Noaleon limbatellus* (Navás, 1913)	
Myrmeleontidae	*Nophis flava* Hölzel, 1972	
Myrmeleontidae	*Nophis luteus* Hölzel, 1972	
Myrmeleontidae	*Nophis teillardi* Navás, 1912	
Myrmeleontidae	*Omoleon jeanneli* Navás, 1936	+
Myrmeleontidae	*Palpares angustus* McLachlan, 1898	
Myrmeleontidae	*Palpares cephalotes* (Klug in Ehrenberg, 1834)	
Myrmeleontidae	*Palpares papilionoides* (Klug in Ehrenberg, 1834)	

Family	Species	This study
Myrmeleontidae	*Palpares venustus* Hölzel, 1988	
Myrmeleontidae	*Parapalpares dispar* (Navás, 1912)	
Myrmeleontidae	*Phanoclisis longicollis* (Rambur, 1842)	
Myrmeleontidae	*Pseudoformicaleo gracilis* (Klug in Ehrenberg, 1834)	+
Myrmeleontidae	*Quinemurus cinereus* Kimmins, 1943	
Myrmeleontidae	*Solter buettikeri* Hölzel, 1982	+
Myrmeleontidae	*Solter hardei* Hölzel, 1968	
Myrmeleontidae	*Solter pallidus* Hölzel, 1982	
Myrmeleontidae	*Solter parvulus* Hölzel, 1988	
Myrmeleontidae	*Solter propheticus* Hölzel, 1980	+
Myrmeleontidae	*Solter tenellus* Hölzel, 1988	
Myrmeleontidae	*Solter vartianae* Hölzel, 1967	
Myrmeleontidae	*Solter virgilii* Navás, 1931	
Myrmeleontidae	*Solter wittmeri* Hölzel, 1982	
Myrmeleontidae	*Stenares irroratus* Navás, 1912	+
Myrmeleontidae	*Subgulina lineata* (Navás, 1913)	
Myrmeleontidae	*Syngenes arabicus* Kimmins, 1943	
Myrmeleontidae	*Tomatarella markli* Kimmins, 1952	
Nemopteridae	*Afghanocroce vartianorum* Hölzel, 1968	
Nemopteridae	*Croce aristata* (Klug, 1838)	+
Nemopteridae	*Croce schmidti* (Navas, 1927)	
Nemopteridae	*Dielocroce baudii* (Griffini, 1895)	
Nemopteridae	*Dielocroce berlandi* (Navás, 1936)	+
Nemopteridae	*Dielocroce chobauti* (McLachlan, 1898)	+
Nemopteridae	*Dielocroce elegans* (Alexandrov-Martynov, 1930)	+
Nemopteridae	*Dielocroce necrosia* (Navás, 1913)	
Nemopteridae	*Halter halteratus* (Forskål, 1775)	+
Nemopteridae	*Halter nutans* Navás, 1910	
Nemopteridae	*Necrophylus arenarius* Roux, 1833	
Sisyridae	*Sisyra nigra* (Retzius, 1783)	
Sisyridae	*Sisyra nilotica* Tjeder, 1957	

Key: + species is recorded in the current study.

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IN MEMORIAM

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Memories of a Beloved Friend. *In Memoriam* of Terry Lee Erwin (1 December 1940 – 11 May 2020)

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Terry Erwin and I first met in 1966 at San Jose State University while he was completing his Master's degree under the supervision of J. Gordon Edwards, a noted coleopterist and a great mentor, and I was an undergraduate pre-med student. Terry was the assistant curator of the entomology collection and one day invited me in to see the collection there. In subsequent visits, he soon got me interested in carabid beetles and taught me how to identify them to genus using the key to carabid genera in Arnett's *Beetles of the United States*. Only later did I learn that the key had been written by George Eugene Ball, a man who was to impact both our lives greatly. When I showed special interest in these beetles, Terry gave me a workspace in the museum and taught me how to make use of the collection.

I remember Terry telling me early on that his parents had named him after Terry Lee, the lead character in a very popular comic strip, *Terry and the Pirates*, which ran in broad syndication from the mid-1930's through the mid-1970's. Terry Lee was a man of action, charismatic and fearless, adventurous, and so was Terry Lee Erwin. I always wondered how his parents had been so insightful about the son that he would grow up to be. He was simply a superb field man—tireless, eager, always enthusiastic and upbeat and always ready to try some new technique or tackle a new challenge.

Terry took me on my first collecting trip looking specifically for carabids. We collected along Coyote Creek above Anderson Reservoir just south of San Jose, a place he had visited many times for his thesis project on the *Brachinus* species of California. I remember being so excited at finding a single brilliant green elytron and wondering what beetle it was. Terry simply smiled and said that it was a *Chlaenius* species, probably *C. sericeus*. He didn't laugh at my naive excitement, a fact that I would come to appreciate after I'd found perhaps my thousandth specimen of that species. Many times over the years, I've seen him show other novices the same kind of gentle support and respect.

In late summer of 1966, Terry was off to Edmonton, Alberta to work for his PhD with George Ball at the University of Alberta. We kept in contact by mail, which, before email or texting, was a frustratingly slow process, usually involving many days or even weeks for a turnaround of exchanges. He encouraged me from afar through completion of my bachelor's degree and then during my first two years in medical school at the University Colorado in Denver. I kept collecting carabids as a hobby in my spare time and Terry generously identified the many specimens I sent him. Among them were specimens of a new species of *Brachinus*, the group he continued to study for his PhD dissertation project. He ended up naming it *Brachinus kavanaughi*. Terry knew how to encourage and support students and colleagues in many different ways.

Terry didn't like cold climates at all and this, I think, along with his typical demonically hard work, helped him to complete his dissertation project in less than three years, a record time for a George Ball student. With PhD in hand, he went home to California to pick up items he had left with his parents in Vallejo, loaded up his car, jammed full to the ceiling inside and until the springs were fully compressed, and headed east to begin his postdoc with Philip Darlington, Jr. at the Museum of Comparative Zoology at Harvard. We had arranged to meet at Capitol Reef National Monument (now a national park) at around dinnertime. I was so eager to see Terry again after three years of long-distance correspondence that I left Denver heading west at about 3:00 am. When I realized that I would be way too early if I proceeded straight to Capitol Reef, I decided to make a detour south along the north side of the Colorado River toward Bullfrog. The detour led me to a place called Indian Gulch, just on the southeast edge of the Boulder Mountains in Garfield County, Utah. I stopped to collect briefly and found specimens that would turn out to be a new species, which I later named *Nebria desolata* for the forsaken place in which I had found them. Unfortunately, I had car trouble and didn't arrive in Capital Reef until almost midnight. When I got there, I found Terry still waiting for me, sitting at a camp table sorting specimens by Coleman lantern. We shared our experiences of the day, which for him included collecting specimens of *Nebria zioni* Van Dyke, a species at that time known only from the type series. After we swapped a few specimens of each of our *Nebria* species, Terry got up, went into his tent and came out with a bound copy of his massive PhD dissertation on brachinines that he gave me. It was a wonderfully thoughtful, generous and unexpected gesture on his part. This eventful day would lead me to leave medical school and pursue a PhD with George Ball in Edmonton, and also it initiated my career-long passion for nebriine carabid beetles.

Terry Erwin (left) and Dave Kavanaugh (right) in Petaluma, California, mid 1980's.

Eventually, Terry and I were to hold very comparable positions as curators of beetles in two of the greatest entomological collections in the world. Over 54 years, we remained close friends and confidants. We co-authored ten scientific papers, one published abstract, and two electronic publications together and had several other projects planned or in progress. We also co-supervised three graduate students. In September, 1984, Terry brought me with him to his beloved Amazon rainforest, to Tambopata Reserve in Madre de Dios, Peru, where I helped him with his canopy fogging project there. Keeping up with Terry in that heat and humidity and at the break-neck pace of his work schedule was hard, but I enjoyed it thoroughly. Without experiencing the work first-hand, I could never have appreciated fully the monumental effort that Terry's fogging work at various tropical rainforest sites over the years represents. He persevered in these ambitious projects over decades and, in the process, generated literally millions of forest canopy specimens that otherwise might never have been seen and which have formed the material basis for dozens of research projects by students and colleagues in addition to his own. Sadly, that trip in 1984 was our only extended time together in the field…my research interests were in much colder places than Terry's.

Terry was in innovator at heart, always trying new things. When he encountered a problem, he tried to find a simple way around it. For example, his fogging program was his solution to finding out just what lived up in the tropical rainforest canopy, completely out of reach for earth-bound collectors. It was simple, relatively inexpensive and mobile, all attributes that rainforest canopy ziplines, walkways and other fixed structures do not share and certainly much safer than climbing the trees. Another example is Terry's initial and continued involvement in *ZooKeys*. He saw this as a solution to the taxonomic publication bottleneck that had challenged him and all of us throughout our careers. That solution has worked out pretty well too. See https://zookeys.pensoft.net/article/7316 for a biography of Terry, written in celebration of his 75th birthday and his role as Editor-in-Chief of *ZooKeys*.

Our relationship was much more than just professional. We got to know each other's families well but had all too infrequent home visits due to our bi-coastal disjunct distribution. Terry honored me by asking me to be best man at his wedding to Grace Servat, his loving and accomplished spouse. Although Terry and I had very different habitat preferences, working styles, family lives and strengths, together we covered a lot of ground, complemented each other and made a great team. No other person influenced my career in so many pivotal ways. Although my history with Terry Erwin is unique in many ways, I'm sure it is just one of many such stories those fortunate enough to have met and engaged with him could tell. I mourn his sudden and unexpected passing and I will miss him always.