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Phylogeography and systematics of the westernmost Italian *Dolichopoda* species (Orthoptera, Rhaphidophoridae)

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Abstract

The genus *Dolichopoda* (Orthoptera; Rhaphidopohoridae) is present in Italy with 9 species distributed from northwestern Italy (Piedmont and Liguria) to the southernmost Apennines (Calabria), occurring also in the Tyrrhenian coastal areas and in Sardinia. Three morphologically very close taxa have been described in Piedmont and Liguria, i.e., *D. ligustica ligustica*, *D. ligustica septentrionalis* and *D. azami azami*.

To investigate the delimitation of the northwestern species of *Dolichopoda*, we performed both morphological and molecular analyses. Morphological analysis was carried out by considering diagnostic characters generally used to distinguish different taxa, as the shape of epiphallus in males and the subgenital plate in females. Molecular analysis was performed by sequencing three mitochondrial genes, 12S rRNA, 16S rRNA, partially sequenced and the entire gene of COI.

Results from both morphological and molecular analyses highlighted a very homogeneous group of populations, although genetically structured. Three haplogroups geographically distributed could be distinguished and based on these results we suggest a new taxonomic arrangement. All populations, due to the priority of description, should be assigned to *D. azami azami* Saulcy, 1893 and to preserve the names *ligustica* and *septentrionalis*, corresponding to different genetic haplogroups, we assign them to *D. azami ligustica* Baccetti & Capra, 1959, **stat. n.** and to *D. azami septentrionalis* Baccetti & Capra, 1959, **stat. n**.

Keywords

Westernmost *Dolichopoda* species, barcoding, systematics

Introduction

Dolichopoda is a Mediterranean genus, consisting of more than fifty species distributed throughout the North Mediterranean regions from the Pyrenees to Transcaucasia and north Iran (Di Russo and Rampini 2014). The highest species diversity is present in insular and peninsular Greece where most of the species have been described (Di Russo et al. 2007). However, many species are present also in Italy. In particular, nine species of *Dolichopoda* occur in Italy, where they range from the Maritime Alps to the southern tip of the Italian peninsula, excluding the oriental Alps, the Liguria Apennines, the Apuane Alps and the southern Apulia. Most species of this genus are strictly dependent upon caves. However, especially in the northern part of the range, several populations inhabit cave-like habitat such as rock-crevices and ravines and individuals can be observed, during the night, outside in moist or mesic woods. In peninsular Italy, *Dolichopoda* populations often live in cellars, catacombs, aqueducts, Etruscan tombs and other similar man-made hypogean environments. Population sizes can be small and constant over long periods, at least in natural caves (Carchini et al. 1983; Sbordoni et al. 1987).

Based on morphology three subgenera have been described in Italy: *Dolichopoda* (*Dolichopoda*), *D.* (*Chopardina*) and *D.* (*Capraiacris*) (Baccetti 1975; Baccetti and Capra 1959, 1970). One of the main morphological differences between these subgenera is presence or absence of spinulation on the legs. The subgenus *Dolichopoda* includes the highest number of species distributed throughout the range of the genus, except for some coastal areas and it is characterized by the presence of spines on the anterior tibiae. Species belonging to *Chopardina* sub-genus are mostly found in insular and peninsular Tuscany and Sardinia in Italy and in Corsica, with two other species found in Greece (Macedonia and Etolia Akarnania). *Chopardina* species are characterized by the presence of several spines also on the hind femurs. The subgenus *Capraiacris* includes only two species, restricted to the Giglio Island and Monte Argentario in the Tuscan archipelago. Its two species (*D. aegilion* and *D. baccettii*) are distinct from all the other species because of the lack of spines on the anterior tibiae and on the hind femur. However, studies based on molecular characters did not support the subdivision in sub-genera, showing that the subgenus *Chopardina* is polyphyletic and the subgenus

Dolichopoda is paraphyletic (Allegrucci et al. 2005). Since the main morphological character defining the subgenera is the presence/absence of spines on the appendages, Allegrucci et al. (2005) concluded that such character is an adaptive character subject to homoplasy. Based on these observations we decided to not consider the subdivision in sub-genera of the species belonging to genus *Dolichopoda*.

Based on molecular phylogenetic reconstruction (Allegrucci et al. 2005; 2009; 2011) the current distribution of *Dolichopoda* species has been essentially shaped by the palaeogeographic and climatic events occurred in the Mediterranean region, starting from Late Miocene. However, also adaptation to cave life seems to have played an important role in this process. In particular, the end of Messinian salinity crisis would mark the geographic separation of the epigean forest populations and the beginning of dispersal toward the west Mediterranean region. The migration and /or the isolation of the different insular populations might have also been favored by marine regressions and transgressions, during the Plio-Pleistocene. This era has been also characterized by climatic shifts during alternating glacial and interglacial periods. The sylvicolous ancestors of *Dolichopoda* might have used caves as refugia during the unfavorable climatic conditions, beginning their adaptation to subterranean habitat. Therefore, the current distribution of *Dolichopoda* can be explained by a combination of both vicariance and dispersal events, with many processes occurring in ancestral epigean populations before the invasion of the subterranean environment.

The most western Italian species are represented by *D. ligustica*, and *D. azami*. Two subspecies are attributed to *D. ligustica*, i.e., *D. ligustica ligustica* and *D. l. septentrionalis*. The first one is widespread in the Southern Piedmont (Maritime Alps) and in the north-western Liguria while the range of *D. l. septentrionalis* is northernmost and limited to a small area in Val di Lanzo valley, close to Turin, and in some easternmost caves, close to Bergamo. *D. azami* Saulcy, 1893 is widespread in the south eastern France and observed also in Piedmont in a cave in Grana Valley (Baccetti and Capra 1959). The systematic position of *D. azami* has long been discussed (Finot 1890; Azam 1893; Chopard 1922, 1951) until Baccetti (1966) reclassified the systematics of the western *Dolichopoda* species, based on the morphology of the epiphallus and of the tergum 10, the most important characters for the systematics of the genus *Dolichopoda*.

D. ligustica and *D. azami* have very similar morphologies with little variation in the characters on which the systematics are based. To better understand the differentiation between these two species and the limits of the ranges occupied by each of them, we carried out a study on several populations of *D. ligustica* and *D. azami*, both at morphological and molecular levels. The main aims of this study are: i) to infer the phylogenetic relationships of these two species, using molecular markers; ii) to compare their differentiation with the differentiation of all other species belonging to genus *Dolichopoda* previously analyzed (Allegrucci et al. 2005, 2009, 2011); iii) to revise the taxonomic arrangement of species and subspecies based on both morphological and molecular characters.

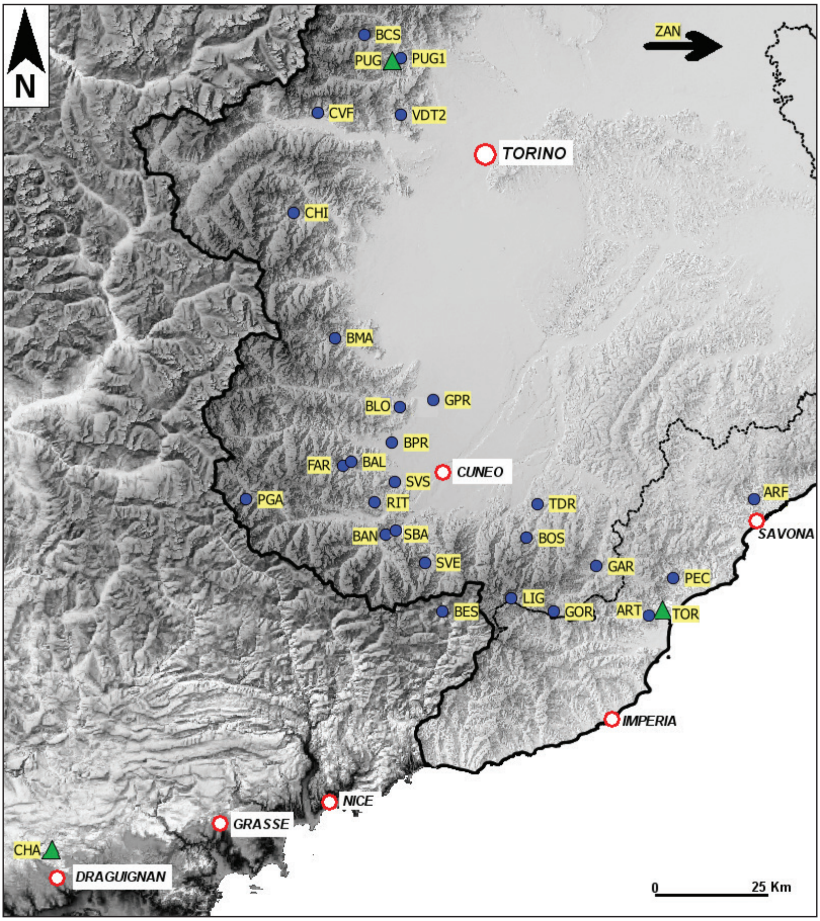


Figure 1. Sampling sites of *Dolichopoda* populations considered in this study (see also Table 1). Triangles indicate the type locality of the three considered taxa (CHA: *D. azami*, TOR: *D. l. ligustica*, PUG: *D. l. septentrionalis*).

Materials and methods

Taxon sampling and laboratory procedures

A total of 26 populations from Piedmont and Liguria (Maritime Alps, and western Liguria Apennines in northwest Italy), were analyzed in this study (Fig. 1, Table 1).

DNA was isolated from leg muscle of each individual, using a GenElute Mammalian Genomic DNA minipreparation Kit (Sigma-Aldrich, St. Louis, MO, USA) resuspended in 200 µl of sterile water and stored at -40 °C.

The entire Cytochrome Oxidase I gene (COI, total of 1500 bp), a 550-bp fragment of the 16S rRNA gene, a 450-bp fragment of the 12S rRNA gene and were amplified through the polymerase chain reaction (PCR) and sequenced from each individual.

Table 1. North Western Italian *Dolichopoda* sampled in this study. All populations were analyzed at molecular level, while only the populations in which adults were present, were analyzed also at morphological level.

Taxon	Localities and sample size	Code	Morphology	GenBank Accession No.
D. azami	Mine close to Chauves-souris Cave, Chateaudouble, Var, France, type locality, 525 m asl; Sampled individuals: 3	CHA	X	12S: KM086460; 16S: KM086485; COI: KM086535; 28S: KM086510
D.l. ligustica	Taragnina Cave, Balestrino, SV, Liguria, close to Santa Lucia Inferiore Cave, 310 m asl; Sampled individuals: 5	ART		12S: KM086464; 16S: KM086489; COI: KM086539; 28S: KM086514
	Santa Lucia Inferiore Cave, Toirano, SV, Liguria, type locality, 194 m asl	TOR	X	
D. l. septentrionalis	Borna Maggiore del Pugnetto Cave, Mezzenile, Lanzo Valley, TO, Piedmont, type locality, 820 m asl; Sampled individuals : 8	PUG	X	12S: KM086474; 16S: KM086499; COI: KM086549; 28S: KM086524
Dolichopoda sp.	Tana del Peccetto Cave, Magliolo, SV	PEC	X	
	Besta Cave, Vievola, Tenda, France, 910 m asl; Sampled individuals: 2	BES	X	12S: KM086459; 16S: KM086484; COI: KM086534; 28S: KM086509
	Falconiere Cave, Garessio,CN, Piedmont, 1000 m asl	GAR	X	
	Orso Cave, Ponte di Nava, Ormea, CN, Piedmont, 808 m asl; Sampled individuals: 3	GOR		12S: KM086472; 16S: KM086497; COI: KM086547; 28S: KM086522
	Viozene, Ormea, upper Tanaro Valley, CN, Piedmont (epigean), 1250 m asl; Sampled individuals: 2	LIG		12S: KM086470; 16S: KM086495; COI: KM086545; 28S: KM086520
	Vernante hypogeum, Vernante, Vermenagna Valley, CN, Piedmont, 800 m asl; Sampled individuals: 5	SVE	X	12S: KM086458; 16S: KM086483; COI: KM086533; 28S: KM086508
	Bossea Cave, Frabosa Soprana, Corsaglia Valley, CN, Piedmont, 836 m asl; Sampled individuals: 2	BOS	X	12S: KM086465; 16S: KM086490; COI: KM086540; 28S: KM086515
	Arma de Faie Cave, Albissola, Sansobbia Valley, SV, Liguria, 624 m asl	ARF	X	
	Bandito Cave, Valdieri, Gesso Valley, CN, Piedmont, 726 m asl; Sampled individuals: 2	BAN	X	12S: KM086471; 16S: KM086496; COI: KM086546; 28S: KM086521
	Bandito hypogeum, Roaschia, Gesso Valley, CN, Piedmont, 730 m asl; Sampled individuals: 7	SBA	X	12S: KM086463; 16S: KM086488; COI: KM086538; 28S: KM086513
	Dronera Cave, Vicoforte Mondovì, Ermetta Valley, CN, Piedmont, 525 m asl; Sampled individuals: 6	TDR	X	12S: KM086468; 16S: KM086493; COI: KM086543; 28S: KM086518
	Rittana Cave, Rittana, Stura di Demonte Valley, CN, Piedmont, 1000 m asl; Sampled individuals: 3	RIT	X	12S: KM086467; 16S: KM086492; COI: KM086542; 28S: KM086517
	Vallone Saben eastern hypogeum, Valdieri, Gesso Valley, CN, Piedmont, 750 m asl; Sampled individuals: 6	SVS	X	12S: KM086462; 16S: KM086487; COI: KM086537; 28S: KM086512
	Gaiola Cave, Gaiola, Stura di Demonte Valley, CN, Piedmont, 1020 m asl; Sampled individuals: 3	PGA	X	12S: KM086457; 16S: KM086482; COI: KM086532; 28S: KM086507

	Farout Cave, Pradleves, Grana Valley, CN, Piedmont, 1050 m asl; Sampled individuals: 3	FAR	X	12S: KM086461; 16S: KM086486; COI: KM086536; 28S: KM086511
	Balmarossa Cave, Pradleves, Grana Valley, CN, Piedmont, 1180 m asl; Sampled individuals: 2	BAL	X	12S: KM086452; 16S: KM086477; COI: KM086527; 28S: KM086502
	Buco del Partigiano Cave, Roccabruna, Maira Valley, CN, Piedmont, 1100 m asl; Sampled individuals: 7	BPR		12S: KM086455; 16S: KM086480; COI: KM086530; 28S: KM086505;
	Partigiani Cave, Rossana, Varaita Valley, CN, Piedmont, 615 m asl; Sampled individuals: 8	GPR	X	12S: KM086469; 16S: KM086494; COI: KM086544; 28S: KM086519
	Buco delle Locuste Cave, Pagliano, Varaita Valley, CN, Piedmont, 595 m asl; Sampled individuals: 2	BLO	X	12S: KM086466; 16S: KM086491; COI: KM086541; 28S: KM086516
	Buco del Maestro Cave, Paesana, Po Valley, CN, Piedmont, 750 m asl; Sampled individuals: 6	BMA		12S: KM086453; 16S: KM086478; COI: KM086528; 28S: KM086503;
	Chiabrano Cave, Perrano, Germanasca Valley, TO, Piedmont, 1080 m asl; Sampled individuals: 6	CHI	X	12S: KM086456; 16S: KM086481; COI: KM086531; 28S: KM086506
	Villar Focchiardo Cave, Villar Focchiardo, Susa Valley, TO, Piedmont, 460 m asl; Sampled individuals: 6	CVF		12S: KM086473; 16S: KM086498; COI: KM086548; 28S: KM086523
	Val della Torre Mine, Val della Torre, Casternone Valley, TO, Piedmont, 840 m asl; Sampled individuals: 5	VDT2		12S: KM086475; 16S: KM086500; COI: KM086550; 28S: KM086525
	Wolf Cave, Mezzenile, Lanzo Valley TO, Piedmont, 813 m asl; Sampled individuals: 4	PUG1	X	Same as PUG
	Borna del Servais Cave, Ala di Stura, Ala Valley, TO, Piedmont, 1440 m asl; Sampled individuals: 2	BCS		12S: KM086454; 16S: KM086479; COI: KM086529; 28S: KM086504;
	Lacca Selva Cave, Zandobbio, BG, Lombardy, 340 m asl; Sampled individuals: 2	ZAN	X	12S: KM086476; 16S: KM086501; COI: KM086551; 28S: KM086526

The large subunit of the nuclear ribosomal DNA (28S rRNA) was also included. The primers used were: LCO1490, HCO 2198 (Folmer et al. 1994), UEA1, UEA5 and UEA10 (Lunt et al. 1996) for the COI gene, 12Sai, 12Sbi (Kocher et al. 1989; Simon et al. 1994) for the 12S rRNA gene and 16Sar, 16Sbr (Simon et al. 1994) for the 16S gene. 28S rRNA was partially amplified and sequenced for a fragment of 580 base pairs, belonging to domains 3-5, using primers from Friedrich and Tautz (1997). Double-stranded amplifications were performed with a Perkin-Elmer-Cetus thermal cycler in 25 µl reaction volume containing genomic DNA (10–100 ng), 1.5 mM MgCl2, 0.2 mM of each dNTP, 0.1 µM primer, 1.5 units EuroTaq (Euroclone, UK) and the buffer supplied by the manufacturer. Optimal cycling parameters varied for each primer pair used. PCR products were purified using the ExoSAP digestion (Amersham Pharmacia Biotech), directly sequenced in both directions using the BigDye terminator ready-reaction kit, and resolved on ABI 3100 Genetic Analyzer (PE Applied Biosystems), following the manufacturer's protocols. Sequence data were edited and compiled using CodonCode Aligner (version 3.7.1). All sequences were submitted to GenBank (Accession Numbers are reported in Table 1).

Each gene fragment (12S, 16S, COI and 28S) was considered separately for the alignment. Sequences of 16S, 12S and 28S were aligned using CLUSTAL_X 1.81 (Thompson et al. 1997) with opening gap = 10 and extending gap = 0.10. Cytochrome oxidase I nucleotide sequences were assembled, aligned, and translated with Codon-Code Aligner 3.7.1.

Data analysis

Genetic differentiation and structure in the westernmost *Dolichopoda* species

Haplotype and nucleotide diversity were calculated using DNASP 5.10 (Rozas et al. 2003). Genetic distances between haplotypes and between groups of haplotypes were calculated using p-distance as implemented in MEGA 5.2 (Tamura et al. 2007). NETWORK 4.502 (Bandelt et al. 1999) was employed to calculate a median joining network representing the genealogical relationships among mtDNA haplotypes.

A Mantel test (Mantel 1967) with 5,000 simulations was used to test for an isolation-by-distance (IBD) signature (a positive correlation between geographic and genetic distances; Wright 1943; Slatkin 1993).

The hierarchical distribution of genetic variation was characterized using analysis of molecular variance (AMOVA). This method apportions genetic variation within and among groups, estimating F-statistics (Weir and Cockerham 1984; Excoffier et al. 1992; Weir 1996) that are analogous to Wright's hierarchical fixation indices under the island model of gene flow (Wright 1951). Three-level AMOVA was conducted in ARLEQUIN 3.5.1.2 (Excoffier et al. 1992; Excoffier et al. 2005) using an F_{ST}-like estimator. Samples were partitioned by geographic regions, populations within geographic regions, and populations. These tests included permutation of inferred haplotypes among groups (F_{CT}); individual haplotypes among populations but within group (F_{SC}); inferred haplotypes among populations (F_{ST}).

Species delimitation and phylogenetic analysis

Species delimitation analysis was carried out with two methods, a) the ”classical” DNA barcoding gap analysis (Hebert et al. 2003) and b) the Automatic Barcode Gap Discovery (ABGD, Puillandre et al. 2012). Both analyses were carried on the present samples and all *Dolichopoda* species previously analyzed (Table 2 and Allegrucci et al. 2005, 2011; Martinsen et al. 2009), considering only COI data set and only the common base pairs consisting of 964 bp.The “classical” DNA barcoding gap analysis was based on the pairwise genetic distances (p-distance). Distribution of genetic distance values was analyzed at different taxonomic levels.

Table 2. Species, populations, localities and accession numbers to GenBank for the *Dolichopoda* sequences included in this study and retrieved from GenBank for phylogenetic reconstruction of the western Mediterranean *Dolichopoda* species (Data from Allegrucci et al. 2005, 2009, 2011 and Martinsen et al. 2009).

Taxon	Localities	GenBank Accession No.
Outgroup		
Euhadenoecus insolitus	Indian Grave Point Cave (IND), De Kalb Co., TN, USA	12S: EF216947; 16S: AY793563; COI: AY793591; 28S: EF217005
Hadenoecus cumberlandicus	Bat Cave (BAT), Carter Cave State Park, Carter Co., KY, USA	12S: EF216948; 16S: AY793562; COI: AY793592; 28S: EF217004
Troglophilus cavicola	Covoli di Velo Cave (TRO), Veneto, Northern Italy	12S: EF216946; 16S: AY793564; COI: AY793624; 28S: EF217003
Ingroup		
D. bolivari	Forat negre Cave, Serra del Llerida, Pyrenees, Spain	16S: AY507579-80, COI: AY507648-49
D. linderi	Sirach Cave (SIR) Eastern Pyrenees, Western-South France	12S: JF826039; 16S: AY793567; COI: AY793598-99; 28S: JF826069
D. laetitiae	Poscola Cave (PSC), Veneto, Northern-East Italy	12S: JF826054; 16S: AY793581; COI: AY793611 and 13; 28S: JF826076
	Piane Cave (GDP), Umbria, Central Italy	12S: JF826053; 16S: AY793582; COI: AY793610 and 12; 28S: JF826075
	Diavolo Cave (DIA), Tuscany, Central Italy	12S: JF826052; 16S: AY793580; COI: AY793614-15; 28S: JF826074
D. geniculata	Valmarino Cave (VAL), Latium, Central-South Italy	12S: JF826055; 16S: AY793583; COI: AY793616-17; 28S: JF826077
	Fontanelle Cave (FON), Campania, Southern-West Italy	12S: JF826057; 16S: AY793584; COI: AY793594; 28S: JF826079
	Ischia cellars (ISC), Ischia Island, Campania, Southern-West Italy	12S: JF826058; 16S: AY793585; COI: AY793595; 28S: JF826080
	Roman Aqueduct (PNZ), Ponza Island, Latium, Southern-West Italy	16S: AY793586; COI: AY793596-97
D. capreensis	San Michele Cave (CPR), Capri Island, Campania, Southern Italy	12S: JF826059; 16S: AY793587; COI: AY793606-7; 28S: JF826081
D. palpata	Tremusa cave (TRE), Calabria, Southern Italy	12S: JF826060; 16S: AY793588; COI: AY793608-9; 28S: JF826082
D. baccettii	Punta degli Stretti Cave (PST), Tuscany, Central-West Italy,	12S: JF826046; 16S: AY793571; COI: AY793639-40; 28S: JF826068
D. aegilion	Campese Mine (CAM), Giglio Island, Tuscany, Central-West Italy	12S: JF826045; 16S: AY793570; COI: AY793600; 28S: JF826067
D. schiavazzii	Pipistrelli Cave (ORS), Tuscany, Central-West Italy	12S: JF826044; 16S: AY793573; COI: AY793633; 28S: JF826066
	Marciana Cave (MRC), Elba Island, Tuscany, Central-West Italy	12S: JF826043; 16S: AY793572; COI: AY793635; 28S: JF826065
	Fichino Cave (FIC), Tuscany, Central-West Italy	12S: JF826042; 16S: AY793574; COI: AY793634-36; 28S: JF826064
D. bormansi	Brando Cave (BRA), Corsica Island, France	12S: JF826047; 16S: AY793578; COI: AY793627 and 31-32; 28S: JF826069
	Sisco Cave (SIS), Corsica Island, France	12S: JF826048; 16S: AY793579; COI: AY793625-26 and 28; 28S: JF826070

D. cyrnensis	Valletto Cave (VLT), Corsica Island, France	12S: JF826050; 16S: AY793577; COI: AY793620-21; 28S: JF826072
	Sabara Cave (SAB), Corsica Island, France	12S: JF826049; 16S: AY793576; COI: AY793618-19; 28S: JF826071
D. muceddai	Limbara Mount, Sardinia Island, Italy	12S: JF826051; 16S: AY793575; COI: AY793629-30; 28S: JF826073

The ABGD method (Puillandre et al. 2012) automatically finds the distance at which a barcode gap occurs and sorts the sequences into putative species based on this distance. The method statistically infers the barcode gap from the data and partitions the data accordingly. Populations belonging to the same species therefore should be grouped in the same partition. This procedure is then recursively applied to the previously obtained groups of sequences. COI alignments were uploaded at http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html and ABGD was run with the default settings (*P*min = 0.001, *P*max = 0.1, Steps = 10, X (relative gap width) = 1.5, Nb bins = 20) and using p-distance.

A phylogenetic analysis was carried out considering the four sequenced genes, by constructing a concatenated matrix, partitioned by genes. Phylogenetic analysis was performed only on the western Mediterranean *Dolichopoda* species, using Bayesian inferences as implemented by the software MrBayes 3.1b4 (Huelsenbeck and Ronquist 2001). Mrmodel test (Nylander 2004) was used to perform hierarchical likelihood ratio test and calculate approximate Akaike Information Criterion (AIC) values of the nucleotide substitution models for each gene fragment.

At least two simultaneous searches were conducted comprising four Markov chains started from a randomly chosen tree and run for 1,000,000 generations, with sampling every 100 generations. The following descriptors were assumed to indicate convergence on a common phylogenetic topology by separate Bayesian searches: similarity in log likelihood scores at stationarity, similarity in consensus tree topologies and PP values for supported nodes, and a final average standard deviation of split frequencies (ASDSF) for simultaneous searches approaching zero. The first 1,000 trees were discarded as burn-in and posterior probabilities (PP) were calculated from post burn-in trees.

Morphological analysis

The most important morphological characters used in the systematics of the genus *Dolichopoda* are the shape of the epiphallus and of the male tergum 10. In this study, the investigation of these characters was integrated by the analysis of other morphological features as male sub-genital plate, female sub-genital plate and shape of ovipositor.

Overall, we have checked 22 populations from the northwestern Italy for a total of 64 adult individuals. All these populations are the same analyzed for the genetic varia-

Table 3. Measures (min and max in mm) of 12 morphological characters in six samples of northwestern Italian *Dolichopoda* taxa.

	CHA		BES		CHI		FAR		TOR		PEC	
	♂ n=4	♀ n=3	♂ n=4	♀ n=2	♂ n=4	♀ n=4	♂ n=4	♀ n=5	♂ n=3	♀ n=4	♂ n=2	♀ n=1
Body	16.0–16.5	17.0–18.0	14.0–16.0	14.0–15.0	15.0–16.0	15.0–17.0	14.0–15.5	15.0–18.0	17.0–21.0	19.0–21.0	16.0–17.0	16.0
Pronotum	4.0–5.0	4.0	3.5–4.0	3.5–4.0	3.8–4.0	4.0	4.0–4.5	4.0–4.5	4.0	4.0–4.5	4.0	4.0
Fore tibia	15.0–17.0	14.5–15.0	14.5–17.0	13.0–14.0	14.5–15.5	13.0–14.0	14.0–16.0	13.5–15	17.0–18.5	15.0–17.0	14.0–15.5	14.5
Fore femur	15.5–16.0	14.0	14.0–15.5	12.0–13.0	14.0–15.0	12.0–13.0	13.0–15.0	12.0–14.0	14.5–17.0	14.0–16.0	14.0–15.0	14.0
Fore tarsum	7.0–7.5	6.0–7.0	6.0–7.0	5.0	6.0–7.0	5.0–6.0	5.0–6.5	5.0–6.0	6.0–7.5	6.0–7.0	5.5–6.5	6.0
Medium tibia	17.0	14.5–16.0	15.0–16.5	13.0–14.0	15.0–16.0	13.0–14.0	13.0–16.0	13.5–15.0	17.0–19.0	16.0–17.0	14.0–16.0	15.0
Medium femur	16.0–16.5	14.0	14.5–15.5	12.0	14.0–15.0	12.0–13.0	13.0–15.0	12.5–14.0	15.0–17.0	14.0–16.0	14.0–15.0	13.0
Medium tarsum	6.0	5.0	5.0–6.0	5.0	5.0–5.5	4.5–5.0	5.0–6.0	4.5–5.0	6.0–6.5	5.0–6.0	5.5–6.0	5.0
Hind tibia	30.0–32.0	30.0–34.0	25.0–29.0	25.0–27.0	23.5–27.0	24.0–25.0	24.5–27.5	25.0–27.5	26.5–34	30.0–32.0	27.0–29.0	28.0
Hind femur	25.5–26.5	25.0–26.5	22.5–24.5	22.0–23.0	21.0–24.0	22.0–22.5	22.0–24.0	22.0–23.5	24.0–27.0	23.5–27.0	22.0–24.0	24.0
Hind tarsum	6.0–7.0	6.0	5.5–6.0	5.0–6.0	4.0–6.0	4.0–5.5	5.5–6.0	5.0	6.0–7.0	5.5–6.0	5.5–6.5	5.5
Ovipositor		13.0–14.0		11.0		12.0–13.0		10.0–13.0		11.0–13.0		12.0

tion (Table 1). Further comparisons were made using three more samples (PEC, ARF, GAR) coming from the collection of Museum of Natural History of Genoa G. Doria. The specimens were studied using a stereomicroscope Leica MZ 12.5. All the measures of the morphological parameters are in mm. Photos were taken with a digital camera, Nikon Coolpix P300. Pictures were processed using a digitiser board WACOM CTH 461 and Adobe Photoshop CS3 Extended Version 10.0.

Table 3 shows the measures of twelve morphological characters in 6 populations where a sufficient number of adults were available. In particular, we considered the total body length, the pronotum length, and the length of tarsum, femur and tibia of the fore, middle and hind legs in both males and females and the ovipositor length in females. Measurements were taken using a digital caliper (accuracy 0.01 mm). Morphometric variables were analyzed by using the non-parametric ANOVA Kruskal-Wallis test. A multiple regression analysis was carried out comparing morphometric variables with the altitude of the caves.

Results

Genetic differentiation and structure in the westernmost *Dolichopoda* species

A total of 2450 mitochondrial base pairs corresponding to the entire *COI* gene, to 450 bp of 12S and 550 bp of 16S were successfully sequenced and aligned in 104 specimens of *Dolichopoda* populations from northwestern Italy. 28S rRNA, consisting of 500 bp was also sequenced in all considered samples. Ribosomal genes were identical in all assayed samples. Therefore, the analysis was limited to the COI mitochondrial gene.

The 104 individual COI sequences comprised a total of 15 haplotypes determined by 13 segregating sites. Global haplotype diversity, *h*, was 0.875 and nucleotide diversity, *p*, was 0.00231.

Dolichopoda haplotypes were organized in three main haplogroups in which haplotypes are ordered geographically (Fig. 2). In particular, haplogroup 1 included samples from the northernmost area, haplogroup 2 samples from the westernmost area and haplogroup 3 consisted of samples from the south-eastern area (Fig.2).

To investigate this further we carried out a genetic distance analysis using COI gene as a barcode and p-distance between all studied *Dolichopoda* species (Allegrucci et al. 2005, 2009, 2011; Martinsen et al. 2009). Genetic distance values at intra- and interspecific levels are compared in Figure 3. In particular, Figure 3 shows the genetic distance values found in intra- and interspecific comparisons of all studied *Dolichopoda* species compared to the interspecific values found in comparisons between the northwestern Italian populations. Intraspecific values between all *Dolichopoda* species ranged from 0 to 0.023, with a mean of 0.001(± 0.0019, standard deviation), while interspecific values ranged from 0.016 to 0.134, with a mean of 0.134 (± 0.020, standard deviation). Pairwise comparisons between the northwestern Italian populations ranged from 0 to 0.007 with a mean of 0.003 (± 0.0015, standard deviation).

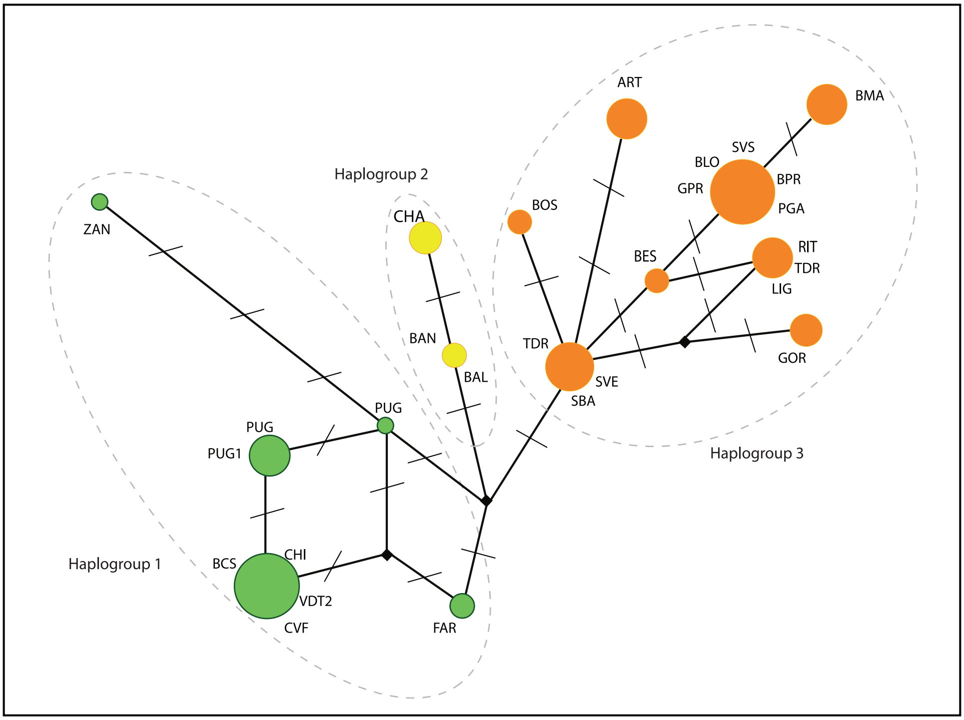


Figure 2. Median-joining network analysis in the populations of *Dolichopoda* considered in this study: circled areas are proportional to the number of individuals sharing the same haplotype; bars, along connections, indicate the number of nucleotide substitutions. Individuals from the same population can show different haplotypes. Based on number of nucleotide substitutions, three haplogroups can be distinguished, each indicated with different color.

ABGD analysis proposed several partitions that varied according to the different a priori thresholds. Apart from the two extreme a priori threshold values ($P = 0.001$ and $P = 0.035$), for which aberrant number of species hypotheses were obtained (almost every haplotype was considered as a different species hypothesis for $P = 0.001$ and, conversely, all the haplotypes were combined in a single species hypothesis for $P = 0.035$), all the tested a priori thresholds lead to the same splitting. The westernmost *Dolichopoda* taxa were grouped together, while the other groups corresponded to the nominal species.

Analysis of molecular variance (AMOVA; Excoffier et al. 1992) used to measure the proportion of genetic variation among subdivided populations, suggested a strong structure within the populations ($F_{ST} = 0.979$, P=0). Genetic variation among different geographic groups and among populations within each group was 52.16 % and 45.8 %, respectively, with $F_{CT} = 0.522$ ($P = 0$) and $F_{SC} = 0.957$ ($P = 0$). Mantel test suggested a clear isolation by distance across the sampled region ($R^2 = 0.623$, $P \leq 0.002$).

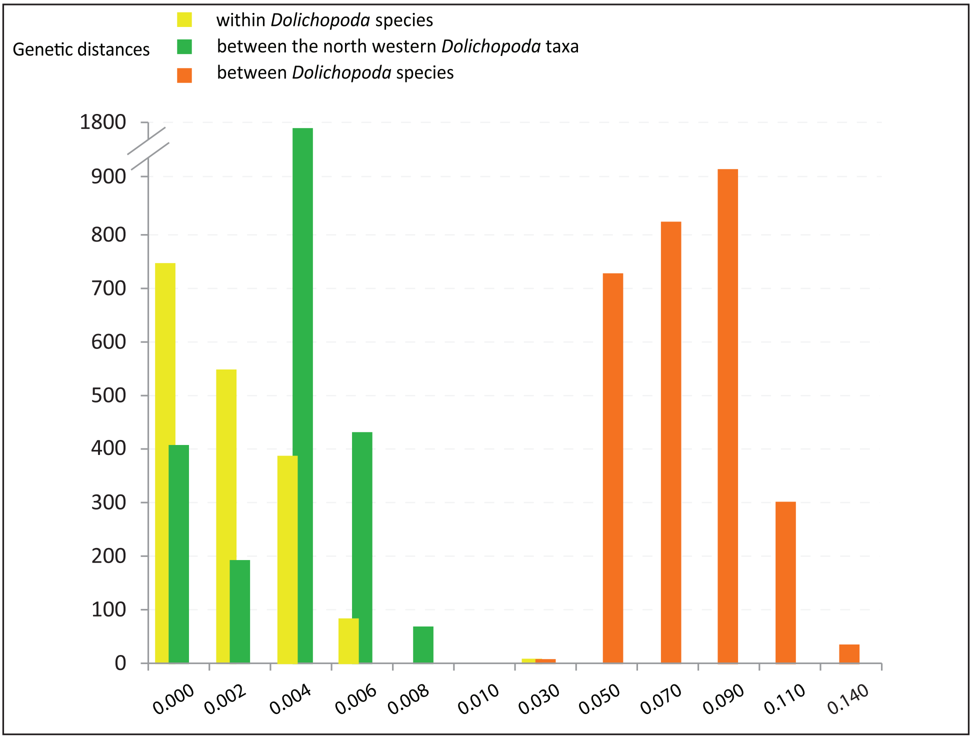


Figure 3. Distribution of genetic distance values (p-distances) at different taxonomic levels. Pairwise comparisons at the intra- and inter-specific level in all *Dolichopoda* species are reported.

Phylogenetic analysis

MRMODELTEST (Nylander 2004) indicated GTR + I + G (Lanave et al. 1984; Gu et al. 1995) and K80 + I (Kimura 1980) as the best models of DNA substitution for the mitochondrial genes and the nuclear one, respectively. The phylogeny in Figure 4 supports the major phylogenetic relationships previously demonstrated (Allegrucci et al. 2005, 2011; Martinsen et al. 2009). The Italian *Dolichopoda* species are separated in two main clusters, as expected. The first group included the continental species from Liguria to southern Italy (*D. ligustica*, *D. l. septentrionalis*, *D. azami*, *D. laetitiae* and *D. geniculata*). Populations from *D. ligustica*, *D. l. septentrionalis*, and *D. azami* constituted a homogeneous clade well differentiated from *D. laetitiae* and *D. geniculata*. The second group was represented by the southernmost species from Tuscany, to Corsica, Campania and Calabria (i.e., *D. aegilion*, *D. baccettii*, *D. schiavazzii*, *D. cyrnensis*, *D. bormansi* and *D. muceddai* and *D. palpata* with its sister taxon *D. capraensis*). Linked to these clusters are *D. linderi* and *D. bolivari*.

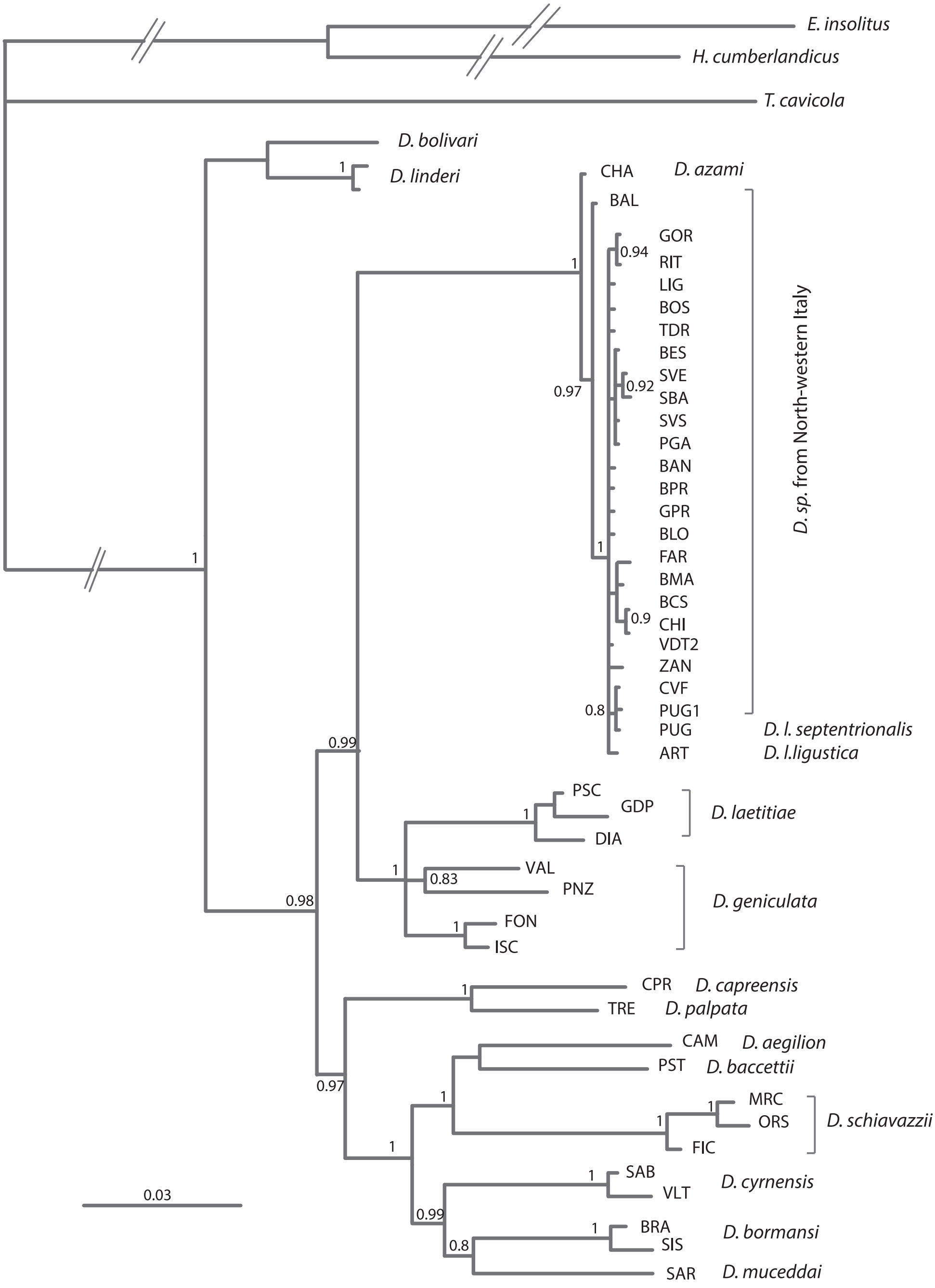
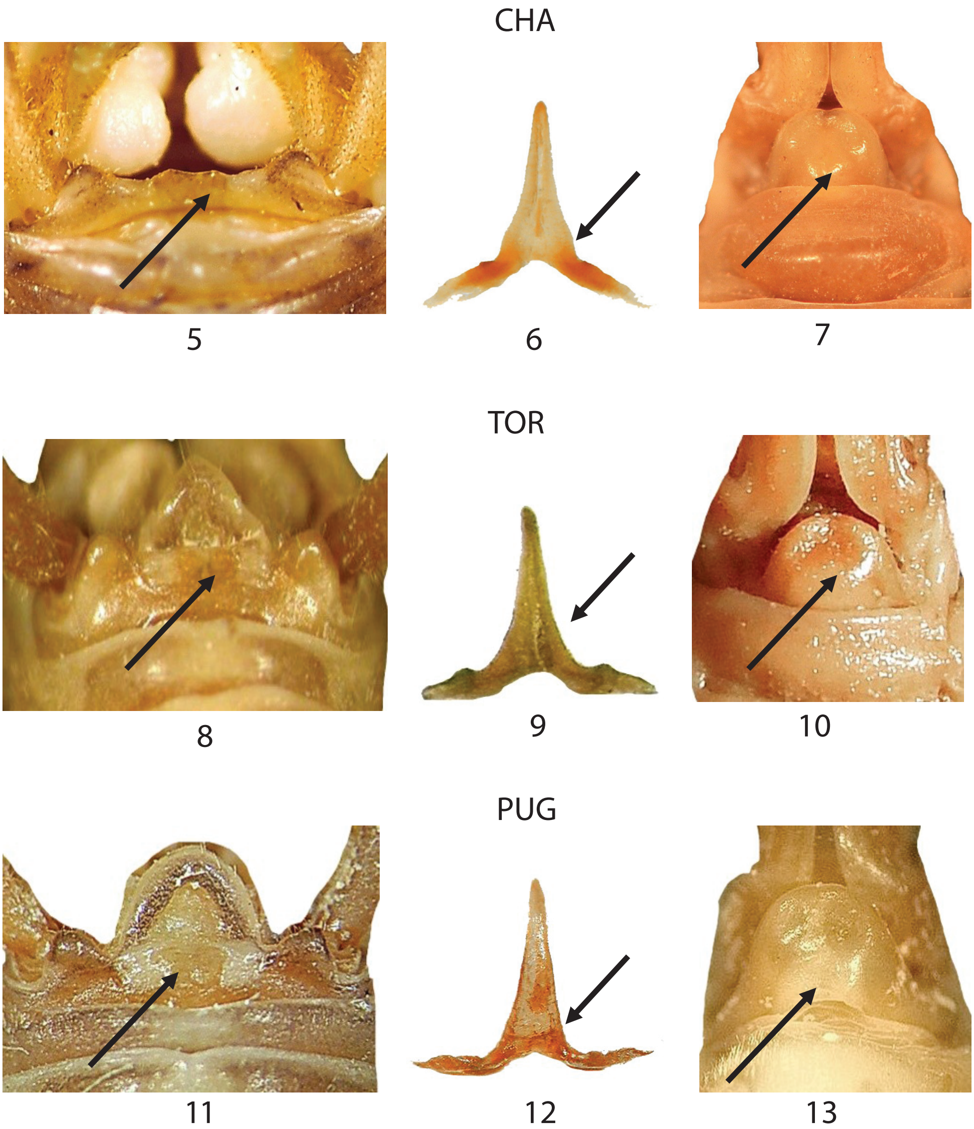


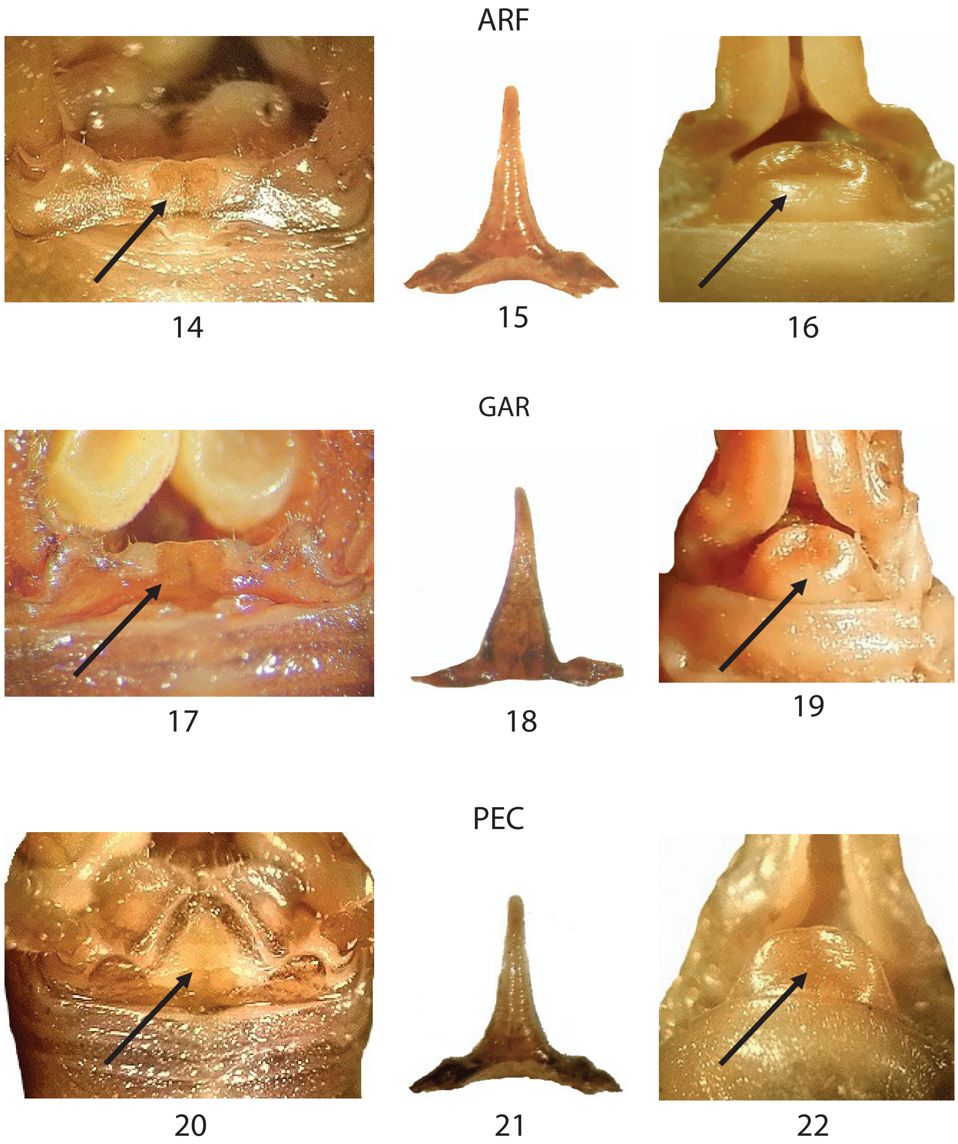
Figure 4. Relationships among Italian species of *Dolichopoda* inferred from Bayesian analysis based on three mitochondrial and one nuclear genes. Values above branches indicate posterior probabilities derived from Bayesian analysis. Scale bars: 0.03 substitutions per site. Only posterior probability (PP) values ≥ 0.80 are shown.



Figures 5–13. Morphological characters of *Dolichopoda azami* (CHA type locality), *Dolichopoda l. ligustica* (TOR type locality) and *Dolichopoda l. septentrionalis* (PUG type locality). Left: dorsal view of tergum 10; centre: epiphallus of the male; right: particular of the female sub-genital plate. Arrows show diagnostic characters.

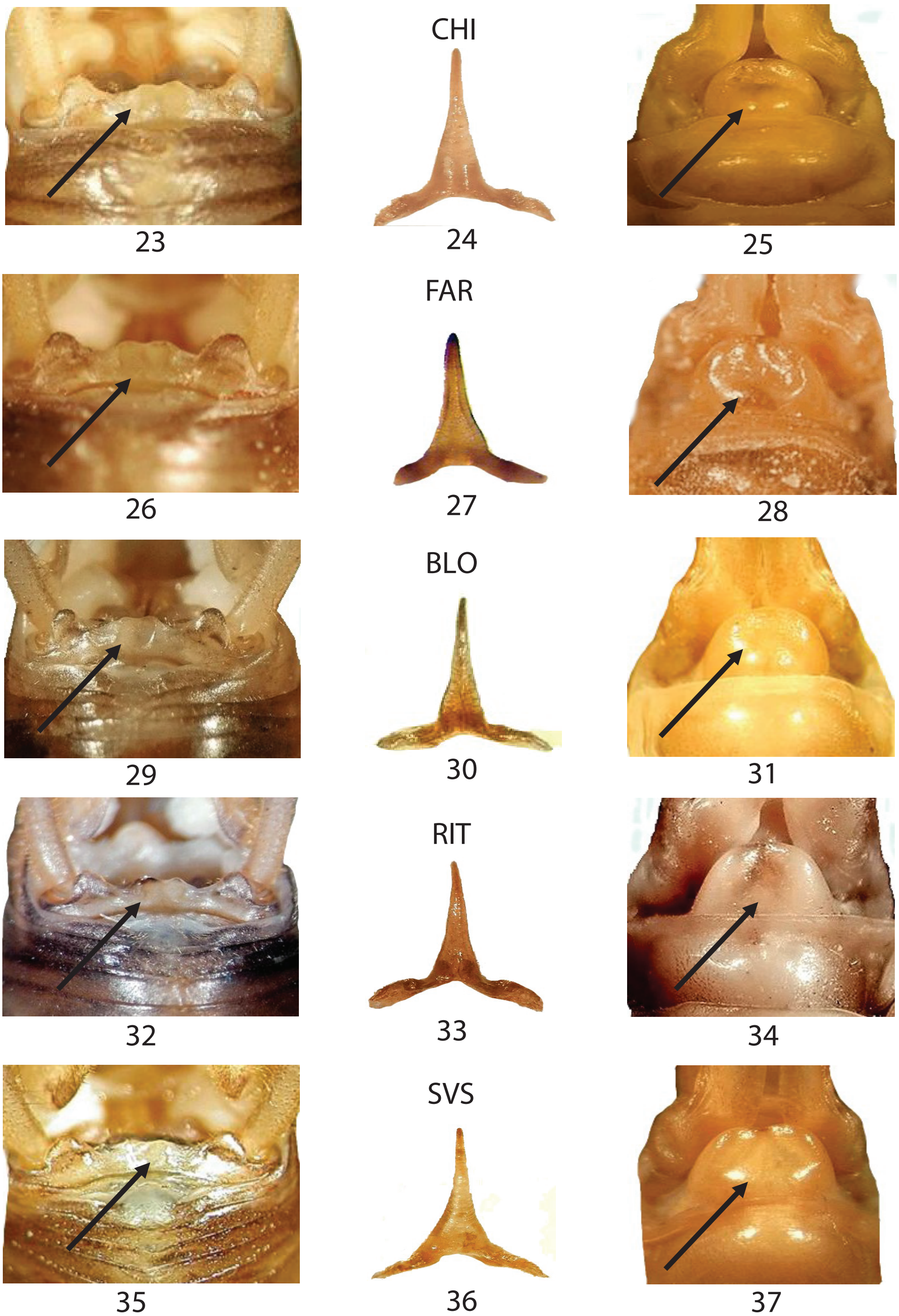
Morphological analysis

In Figures 5–13 morphological comparisons among the three samples from the typical locality of *D. azami* (Chateaudouble, CHA), *D. ligustica* (Toirano, TOR) and *D. l. septentrionalis* (Pugnetto, PUG) are reported. In these figures, the three main characters are compared: male tergum 10, epiphallus and female sub-genital plate. The other two con-



Figures 14–22. Morphological characters of the *Dolichopoda* from Liguria: ARF, GAR and PEC. Left: dorsal view of tergum 10; centre: epiphallus of the male; right: particular of the female sub-genital plate. Arrows show diagnostic characters.

sidered morphological features, male sub-genital plate and ovipositor, are not reported because showed a very uniform pattern. As already evidenced in the taxonomic revision of the genus *Dolichopoda* (Baccetti and Capra 1959), it is possible to distinguish the species *D. azami* through the male tergum 10 that shows two rounded lobes separated by a large concavity with two little acuminate tips (Fig. 5) and median process of the epiphallus enlarged at the basis (Fig. 6). In the female, the sub-genital plate is completely



Figures 23–37. Morphological characters of the *Dolichopoda* from Piedmont: CHI, FAR, BLO, RIT and SVS. Left: dorsal view of tergum 10; centre: epiphallus of the male; right: detail of the female subgenital plate. Arrows show diagnostic characters.

rounded with a narrow apical incision (Fig. 7). On the contrary, *D. ligustica* shows a male tergum 10 with little oval lobes separated by almost straight margin (Fig. 8), and median process of epiphallus pyramidal with lateral margin almost straight (Fig. 9). The female sub-genital plate is very similar to that of *D. azami* (Fig. 10) but the median incision appears less pronounced. Finally, the subspecies *D. l. septentrionalis* is distinguishable only for the more slender median process of the epiphallus (Fig. 12). Based on these observations, it is evident the great similarity of the three taxa here considered and consequently the strong difficulty in their morphological distinction.

In Figures 14–22, we compared three samples from western Liguria (Table 1). The three considered characters appear uniform resembling all to the morphology of TOR (Figs 8–10) the typical *D. ligustica*. On the contrary, the analysis of a series of samples from northern and southern Piedmont (Figs 23–37) highlights a more complex situation with the contemporary presence of characters typical of one or the other species in the same individual. In particular, even if all the specimens analyzed show the tergum 10 very similar to that of *D. azami* (cfr Fig. 5 with Figs 23, 26, 29, 32, 35) the same specimens often show the shape of epiphallus and of the female sub-genital plate more similar to that of *D. ligustica*.

In Table 3, the measures of 12 morphological characters, recorded on 6 populations, where a sufficient number of adults were available, are reported. Mann-Whitney test carried out between males and females morphometric traits revealed significant differences ($P < 0.05$), being the females smaller than males. ANOVA analysis highlighted significant differences between some morphometric measures in specimens coming from caves situated at different altitude both in males and in females. Multiple regression analysis revealed a significant correlation between the morphometric measures and the altitude of the cave ($R^2 = 0.661$, Wilk's lbd = 0.0045; $P << 0.01$). In particular, samples coming from caves at low altitudes resulted bigger than those from caves at higher altitudes.

Discussion

The Northwestern Italian *Dolichopoda* species group comprises a uniform assemblage of populations, both genetically and morphologically. From genetically point of view, the median joining network analysis (Fig. 2) evidenced three main haplogroups geographically distributed, but the resulting scenario is rather homogeneous with a maximum number of mutation events equal to 8. Genetic distance values based on COI gene revealed a very little differentiation between all studied samples. All pairwise comparisons fall in the range of intraspecific comparisons observed in all the other *Dolichopoda* species, with a mean of 0.3% (Fig. 3). These results suggest a level of differentiation usually found between populations belonging to the same species rather than to different species. ABGD analysis confirms these results, grouping together all the northwestern *Dolichopoda* taxa.

However, despite the low variability, these populations show a significant level of genetic structure. Indeed, AMOVA analysis evidenced significant partitioning of variation within and among populations and among regions and a low level of gene flow between the different regions. Isolation by distance was also detected by Mantel test, suggesting that dispersal rates in these *Dolichopoda* populations are very low and limited to the geographically close ones. This result is not surprising for cave dwelling organisms because it reflects the geographic isolation of the different caves and / or groups of caves to which *Dolichopoda* populations are confined (Sbordoni et al. 2012). The Maritime Alps region is characterized by a combination of Mediterranean, Apennine and Alpine flora and this diversity in habitat geography could strongly influence the different degree of isolation of the *Dolichopoda* populations. While the presence of beech and oak forests would account for continuing gene flow among *Dolichopoda* species, the occurrence of Alpine forests and to some extent of the Mediterranean "macchia" could prevent the gene exchange (Allegrucci et al. 1997; Sbordoni et al. 1985, 2012).

The phylogeny illustrated in Figure 4, based on three mitochondrial (COI, 12S and 16S) and one nuclear (28S) genes, supports the major phylogenetic relationships previously demonstrated (Allegrucci et al. 2005, 2011) highlighting that the northwestern Italian populations represent a single, uniform, well supported cluster. With respect to the other Italian species, they are genetically very similar, showing very short branch lengths and forming a single cluster in which the relationships between the different populations are not clearly resolved. Based on previous studies carried out on the 90% of the species belonging to genus *Dolichopoda* (Allegrucci et al. 2005, 2011), we know that divergence time between these populations and their sister taxon, represented by the cluster *D. laetitiae–D. geniculata*, is dated back to about 2 Million years ago, during the late Pliocene. In that time, the western Mediterranean lineages probably arose from a single colonization event from the North of Italy. An ancestral group spread in two directions, colonizing on one hand Piedmont, Liguria and France and, on the other side, the entire inland of Italian Peninsula.

The morphological analysis shows high degree of similarity between all analyzed samples, suggesting that the morphological traits commonly used in the taxonomy of the genus *Dolichopoda* (tergum 10, epiphallus shape in the male and sub-genital plate in the female), are not able to discriminate clearly specimens belonging to *D. azami*, *D. ligustica* and *D. l. septentrionalis*. In particular, although very few morphological differences can be observed between specimens from the typical localities of the three taxa (CHA, typ. loc. of *D. azami*; TOR, typ. loc. of *D. ligustica* and PUG, typ. loc. of *D. l. septentrionalis*), the most of the studied samples show some variability in the diagnostic characters occurring more or less randomly. Often we observed in the same specimen, the contemporary presence of characters typical of one or the other taxon.

Morphometric analysis suggested significant differences both between males and females and between samples from caves situated at different altitudes. Caves situated at high altitude are presumably subjected at lower temperatures and therefore the bioclimatic factors may be the major determinants of the morphometric patterns observed. Morphological traits might be subjected to substantial non-genetic variation and/or might show local short-term adaptations to peculiar environmental conditions.

These differences were already been observed in populations of *D. laetitiae* and *D. geniculata* in the central southern Italy (Allegrucci et al. 1987; Cesaroni et al. 1997). In those studies, we demonstrated that variations in morphometric measures (and in particular in leg elongation) is almost entirely under the control of an environmental gradient, synthetically described by the cave temperature.

In conclusion, the scenario, depicted by both molecular markers and morphological traits, suggests that the northwestern Italian *Dolichopoda* constitute a single species with populations characterized from high similarity between each other and, due to the priority of description, they should be assigned to *D. azami* Saulcy, 1893 which is the older available name at the species rank. However, in order to portrait the geographical partitioning and the related genetic differences we suggest to preserve the names *ligustica* Baccetti & Capra, 1959 and *septentrionalis* Baccetti & Capra, 1959 to indicate groups of populations corresponding to the different COI haplogroups as outlined in the network analysis (Fig. 2).

Therefore, the new taxonomic arrangement here proposed is:

***D. azami azami* Saulcy, 1893**
Type locality. Mine close to Chauves-souris Cave, Chateaudouble, Var, France, 525 m asl;

***D. azami ligustica* Baccetti & Capra, 1959, stat. n.**
Type locality. Santa Lucia Inferiore Cave, Toirano, SV, Liguria, 194 m asl;

***D. azami septentrionalis* Baccetti & Capra, 1959, stat. n.**
Type locality. Borna Maggiore del Pugnetto Cave, Mezzenile, Lanzo Valley, TO, Piedmont, 820 m asl.

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Two new species of the leafhopper subgenus *Empoasca* (*Empoasca*) Walsh (Hemiptera, Cicadellidae, Typhlocybinae, Empoascini) from China

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Abstract

Two new species of the leafhopper subgenus *Empoasca* (*Empoasca*) namely, *E.* (*E.*) *dorsodenticulata* Yu & Yang, **sp. n.** and *E.* (*E.*) *spiculata* Yu & Yang, **sp. n.** from China are described and illustrated and a key provided for Chinese subgenera of *Empoasca*.

Keywords

Subgenera, Key

Introduction

The leafhopper genus *Empoasca* Walsh, 1862 includes 11 subgenera (Oman et al. 1990) of which five occur in China: *Empoasca* (*Empoasca*) Walsh, 1862, *Empoasca* (*Distantasca*) Dworakowska, 1972, *Empoasca* (*Matsumurasca*) Anufriev, 1973, *Empoasca* (*Livasca*) Dworakowska & Viraktamath, 1978 and *Empoasca* (*Okubasca*) Dworakowska, 1982. The subgenus *Empoasca* (*Empoasca*) is very species rich with over

400 known species worldwide of which 53 species are known from China treated by Dworakowska (1972, 1982), Kuoh (1966), Chou and Ma (1981), Cai and Shen (1999), Matsumura (1931), Zhang and Xiao (2000), Zhang, Liu and Qin (2008), Liu, Qin, Fletcher and Zhang (2011a, 2011b) and Yu, Yang and Meng (2012). In the current paper we describe two new species in the subgenus from China and provide a key to the subgenera of *Empoasca* from China.

Material and methods

The methods and terminology follow Zhang (1990) except for the nomenclature of wing, for which we follow Dworakowska (1993). Male specimens were dissected under a MOTIC B1 SMS-168 SERIES microscope. Figures were made using an OLYMPUS CX41 and enhanced using Adobe Illustrator CS4. Pictures were taken with VHX-1000C and dealt with by Adobe Illustrator CS4. The body length is measured from the apex of the head to the apex of the forewing, the specimens examined are deposited in Institute of Entomology, Guizhou University, Guizhou Guiyang, China (GUGC) and The Natural History Museum, England.

Results

Empoasca (*Empoasca*) Walsh, 1862

Empoasca (*Empoasca*) Walsh, 1862: 149

Type species. *Empoasca viridescens* Walsh (a junior synonym of *Tettigonia fabae* Harris, 1841).

Diagnosis. Body color green to yellowish, with variable symmetrical patches on head and thorax; coronal suture not reaching midlength of crown (Figs 18a, 20a, 24a, 26a); forewing with RP and MP' stalked (Fig. 22) or separated (Fig. 28), hindwing with CuA unbranched (Fig. 23, 29); male pygofer, with fine sparse setae distally, macrosetae absent, ventral pygofer appendage present (in some species processes crossed in dorsal view), free from pygofer lobe, at least for halflength of pygofer (Figs 1, 9); subgenital plate broad basally, basal series of setae on outer margin and an oblique series of macrosetae from base to apex bi-seriate basally (Figs 5, 13); paramere elongate, curved, with apical teeth (Figs 6, 14); aedeagus with preatrium present, shaft without processes or occasionally with pair of processes, gonopore apical on ventral surface, dorsal apodeme poorly developed or absent (Figs 7, 8, 15, 16); anal tube processes distinct.

Distribution. Worldwide.

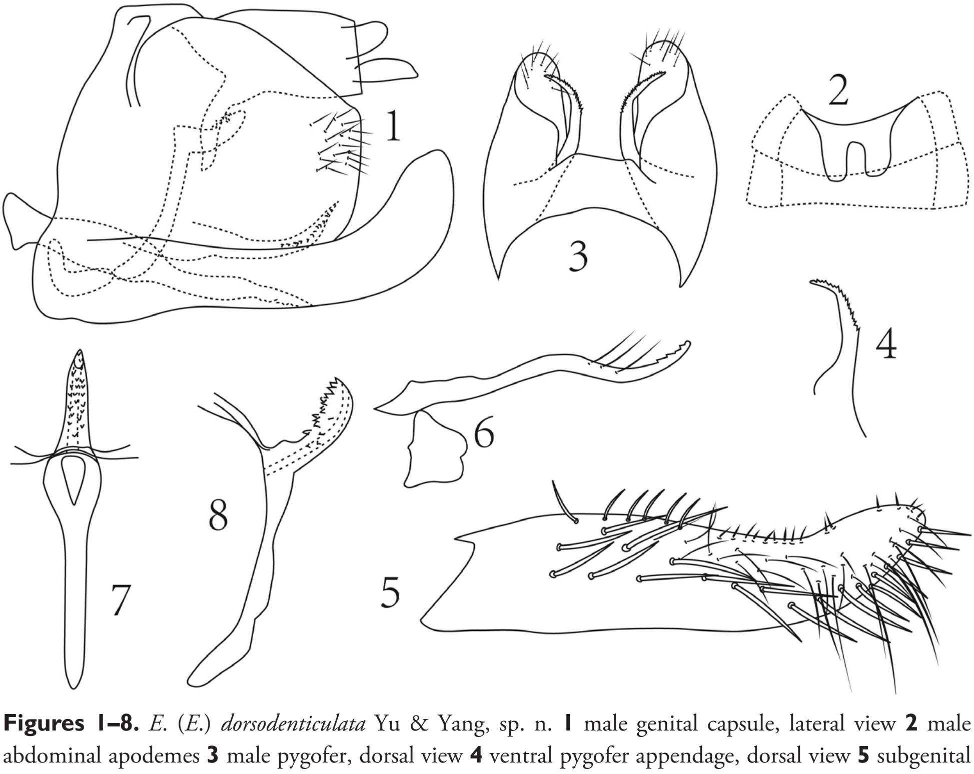
***Empoasca* (*Empoasca*) *dorsodenticulata* Yu & Yang, sp. n.**
http://zoobank.org/D485282D-C23B-4CC4-B628-22179ACC251A
Figs 1–8, 18–23

Type material. Holotype: male, Kuankuoshui, Guizhou Province, 14 August 2010, coll. Xiaofei Yu. Paratypes: 1 male, Shiwandashan, Guangxi Province, 4 May 2011, coll. Rong Huang; 1 male, Liupanshui, Guizhou Province, 2 June 2012, coll. Maofa Yang, Zhijiang Bai and Xiaofei Yu.

Length. Male: 4.0–4.1mm.

Green to yellowish (Fig. 18a). Crown with a green patch each side of coronal suture (Figs 18a, 20a). Face in some species with an off-white longitudinal stripe on anteclypeus (Figs 19b, 21b). Scutellum with a whitish stripe medially (Figs 18a, 20a). Forewing with RP and MP' stalked at base (Fig. 22).

Male ventral abdominal apodemes reaching segment 4 (Fig. 2). Male pygofer lobe with dorsal margin oblique and apical margin straight in lateral view, with fine setae adjacent apical margin; ventral pygofer appendage shorter than pygofer, tapering caudad, subapically denticulate; dorsal bridge about 1/3 length of pygofer (Figs 1, 3, 4). Subgenital plates elongate, with 20 macrosetae arranged obliquely in two basal rows centrally and a



Figures 1–8. *E.* (*E.*) *dorsodenticulata* Yu & Yang, sp. n. **1** male genital capsule, lateral view **2** male abdominal apodemes **3** male pygofer, dorsal view **4** ventral pygofer appendage, dorsal view **5** subgenital plate, ventral view **6** paramere and connective **7** aedeagus, dorsal view **8** aedeagus, lateral view.

single distal row on lateral margin, ca. 25 elongate fine setae and medial margin with 6 basal group macrosetae followed by ca. 16 spine-like setae (Figs 1, 5). Paramere as in Fig. 6. Aedeagus with elongate preatrium; shaft slightly expanded near apex in lateral view, tapered from base to apex in ventral view, apical 1/3 with numerous irregular denticles dorsally (Figs 1, 7, 8). Anal tube process slightly sinuate (Fig. 1). Connective lamellate (Fig. 6).

Etymology. The new species name alludes to the dorsal denticles on the aedeagal shaft.

Remarks. The new species is similar to *Empoasca* (*Empoasca*) *borowikae* Dworakowska, 1976 but differs in having the male ventral abdominal apodemes reaching segment 4, ventral pygofer appendage denticulate near apex and apical 1/3 of aedeagus with dorsal denticles. The new species is also similar to *Empoasca* (*Empoasca*) *gutianensis* Liu, 2011 but differs in the aedeagus without denticles ventrally and anal tube process sinuate.

Empoasca (*Empoasca*) *spiculata* Yu & Yang, sp. n.

http://zoobank.org/4CDD261B-E282-4D5F-9F8F-26BA4CA306B2
Figs 9–17, 24–29

Type material. Holotype. male, Luya mountain, Shanxi Province, 19 August 2011, coll. Hu Li; Paratypes: 5 males, Lvliang mountain, Shanxi Province, 22 August 2011, coll. Hu Li, Zhihua Fan and Xiaofei Yu (1 male, BMNH).

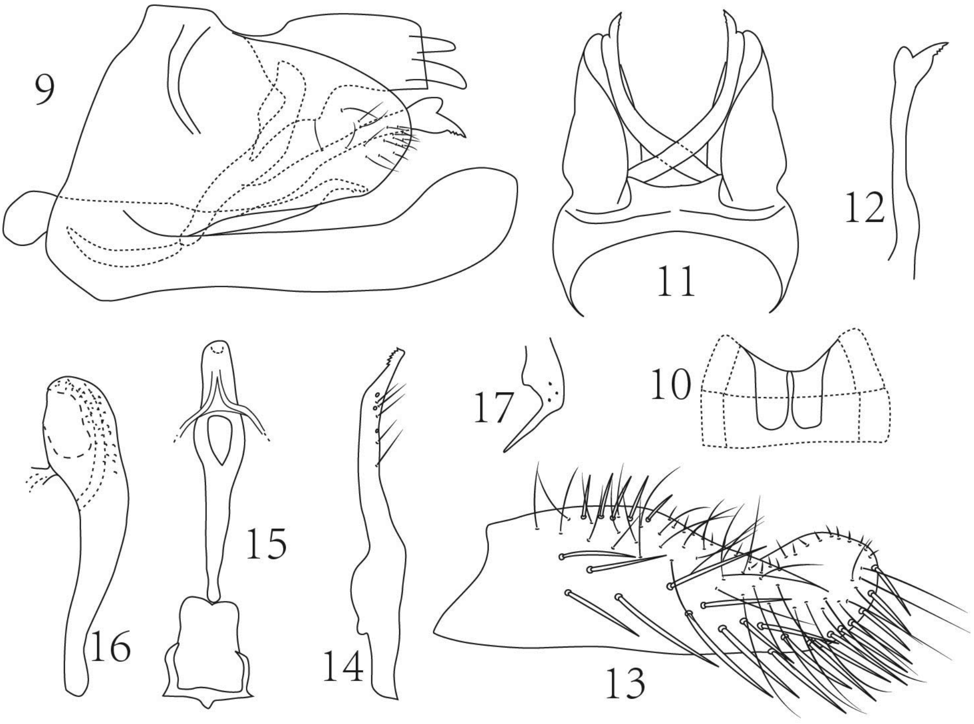
Length. Male 3.9–4.1 mm.

Yellowish (Fig. 24a). A yellow stripe along coronal suture (Figs 24a, 26a). Scutellum with a central whitish streak (Figs 24a, 26a). Forewing with RP and MP' stalked at base or separated (Fig 28).

Male ventral abdominal apodemes reaching segment 4 (Fig. 10). Male pygofer lobe tapered to rounded apex with ca. 15 setae, ventral pygofer appendage extended far beyond pygofer, procceses crossed in dorsal view, apex expanded and forked, lower branch serrate; dorsal bridge about 1/4 length of pygofer (Figs 9, 11, 12). Subgenital plates relatively broad with 20 macrosetae arranged obliquely in two basal rows centrally and a single distal row on lateral margin, and ca. 37 elongate fine setae from base to apex and medial margin with 5 basal group macrosetae followed by ca. 22 spine-like setae (Figs 9, 13). Paramere as Fig. 14. Aedeagus club-shaped in lateral view; shaft dorsally laterally compressed and less sclerotized, ventrally spiculate, with apex broadly rounded in ventral view; (Figs 9, 15, 16). Anal tube process falcate, apex spine-like (Figs 9, 17). Connective lamellate (Fig. 15).

Etymology. The new species name alludes to the ventral spicules on the aedeagal shaft.

Remarks. The new species differs from other members of the subgenus in having the ventral pygofer appendage forked, aedeagal shaft laterally compressed dorsally and ventrally spiculate.



Figures 9–17. *E.* (*E.*) *spiculata* Yu & Yang, sp. n. **9** male genital capsule, lateral view **10** male abdominal apodemes **11** male pygofer, dorsal view **12** ventral pygofer appendage, dorsal view **13** subgenital plate, ventral view **14** paramere **15** aedeagus and connective, dorsal view **16** aedeagus, lateral view **17** anal tube process.

Key of the subgenera of *Empoasca* known from China (males only)

1 Subgenital plates with very long fine setae distally (Fig. 30) ...***E.* (*Distantasca*)**

– Subgenital plates with macrosetae distally (Figs. 31, 32, 33, 34) **2**

2 Pygofer lobe with rigid microsetae at ventral margin and ventral pygofer appendage short; subgenital plates elongate and tapered to narrow apex, with all outer marginal setae short (Fig. 31).......................................***E.* (*Okubasca*)**

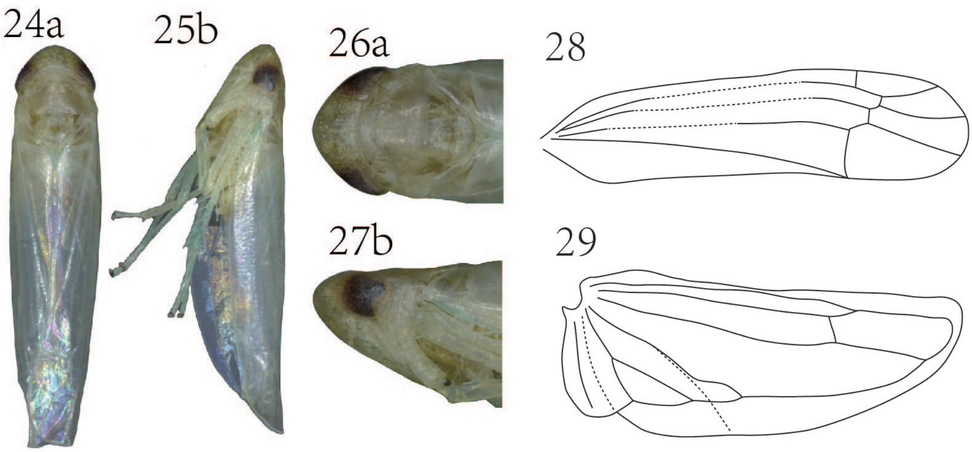
– Pygofer lobe without rigid microsetae at ventral margin and ventral pygofer appendage long (Fig. 1); subgenital plates moderately long and tapered to broadly rounded apex, with outer basal group of long macrosetae and more distal short setae (Figs. 32, 33, 34)..**3**

3 Subgenital plates very short and broad (Fig. 32) ....***E.* (*Livasca*)**

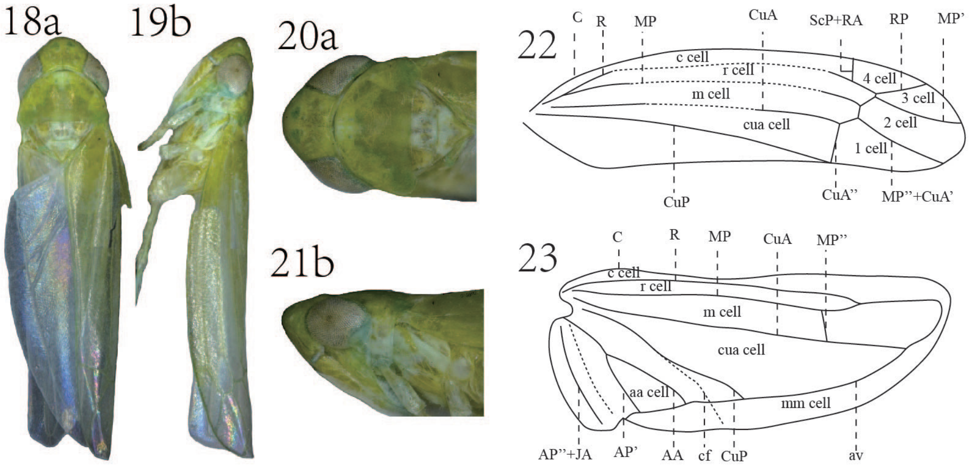
– Subgenital plates elongate...**4**

4 Subgenital plates distinctly broader basally than distally (Fig. 33) ....***E.* (*Matsumurasca*)**

– Subgenital plates slightly broader basally than distally (Fig. 34) ... ***E.* (*Empoasca*)**



Figures 24–29. *E.* (*E.*) *spiculata* Yu & Yang, sp. n., **24–25** whole body **26–27** head and thorax **28** forewing **29** hindwing **a** dorsal view **b** lateral view.



Figures 18–23. *E.* (*E.*) *dorsodenticulata* Yu & Yang, sp. n. **18–19** whole body **20–21** head and thorax **22** forewing **23** hindwing **a** dorsal view **b** lateral view.

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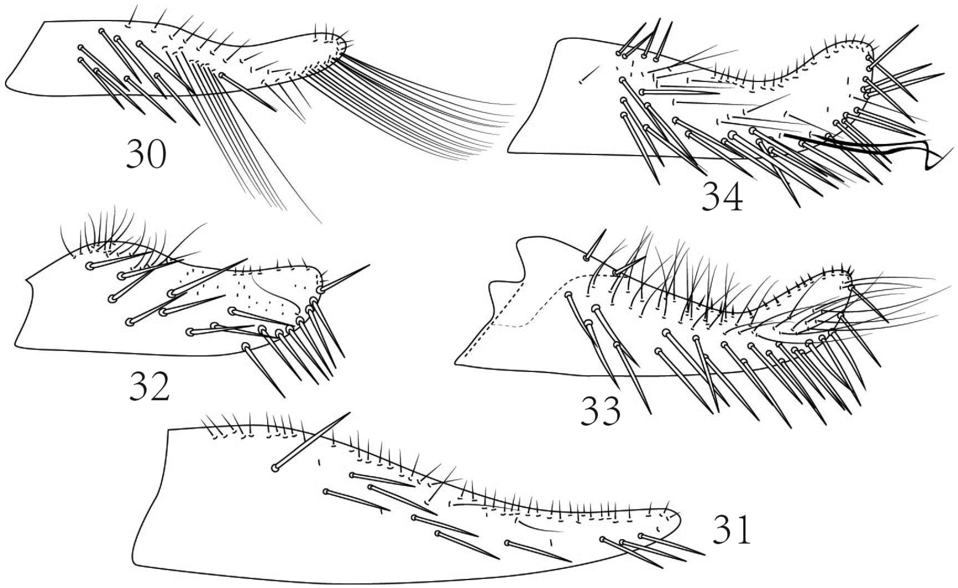

Figures 30–34. *Empoasca* subgenera from China, subgenital plates (type species except 33). **30** *Empoasca* (*Distantasca*) *terminalis* (following Distant 1918) **31** *Empoasca* (*Okubasca*) *okubella* (following Matsumura 1931) **32** *Empoasca* (*Livasca*) *malliki* (from Dworakowska and Viraktamath 1978) **33** *Empoasca* (*Matsumurasca*) *clypealata* (from Qin and Zhang 2008) **34** *Empoasca fabae* (from Harris 1841).

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RESEARCH ARTICLE

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A new opiine (Hymenoptera, Braconidae) from Australia with discussion of *Diachasma* Foerster

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Abstract

A new species of Opiinae, *Diachasma dentatum* Shirley, Restuccia & Ly, is described from Australia. This species is similar to several other Australian opiines previously described or included in the genus *Diachasma*, but the mandibles are unusually broad, nearly exodont. Notable differences between Australian and Palaearctic *Diachasma* are discussed. *Diachasma tasmaniae* Fischer, 1995, originally described from Tasmania and New South Wales, is newly recorded from Victoria. *Diachasma rufipes* Szépligeti, 1905 is transferred to *Notiopambolus*, new combination.

Keywords

Lord Howe Island, New Guinea, *Atoreuteus*, *Notiopambolus*

Introduction

Diachasma Foerster is a morphologically diverse group containing 34 valid, extant species. The geographic range is primarily Holarctic, but the distribution is disjunct, with several species endemic either to eastern Australia or the island of New Guinea. The genus is based on *D. fulgidum* (Haliday), a West Palaearctic species. Basic information on *Diachasma* and its included species can be found in the catalog by Yu et al. (2012). Keys to species are available in Fischer (1972, 1977, 1987, 1988, 1995) and Tobias (1998).

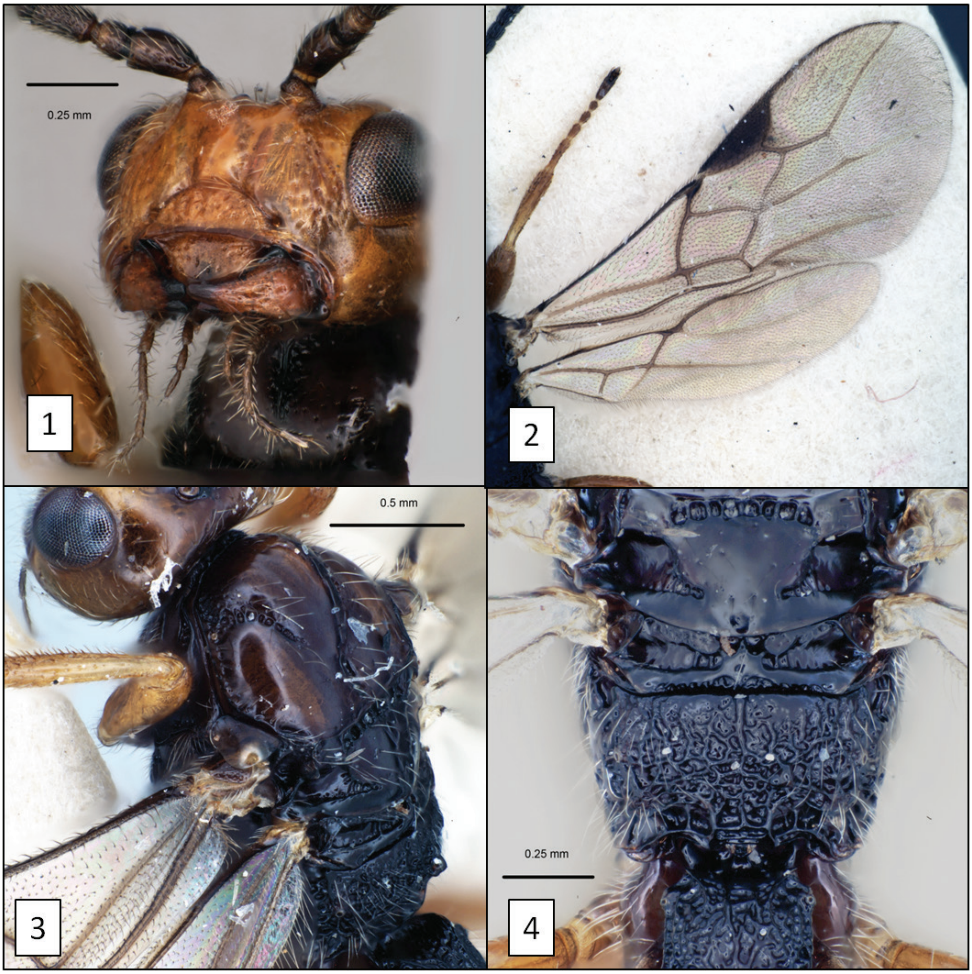
Diachasma has traditionally been characterized by the combination of a short second submarginal cell, short clypeus with broadly exposed labrum, occipital carina that is broadly absent dorsal-medially, and relatively complete fore wing venation. *Diachasma* lacks the carapace-like metasoma and clypeal adornments that characterize the few other opiines with these same features. The genus is not demonstrably monophyletic (Tobias 1977, Wharton 1988, 1997) but resolution of this problem will require dense sampling across the subfamily to uncover relationships of the various, seemingly disparate, elements currently residing within *Diachasma*. As is true of all opiines, members of the genus *Diachasma* are parasitoids of cyclorrhaphous Diptera. Three host groups are known, corresponding to three morphologically distinct groups of species. *Diachasma fulgidum* and two other morphologically similar species are parasitoids of leaf-mining flies in the genus *Pegomya* Robineau-Desvoidy (Anthomyiidae) (Fischer 1972, Jimenez et al. 1992), some of which are notable pests. *Diachasma striatum* (Foerster) and *D. wichmanni* (Fischer) have been reared from species of *Chyliza* Fallén (Psilidae) inhabiting twig galls on trees and shrubs (Fischer 1957, Grijpma and van Achterberg 1991). These two species are sometimes placed in *Atoreuteus* Foerster (Wharton 1988, Grijpma and van Achterberg 1991, Quicke et al. 1997), of which *striatum* is the type species. A further three species from the Nearctic Region are parasitoids of fruit-infesting Tephritidae (Muesebeck 1956, Wharton 1997, Wharton and Yoder 2014). One of these, *D. alloeum* (Muesebeck), shows evidence of sequential sympatric speciation in association with its host *Rhagoletis pomonella* (Walsh) (Forbes et al. 2009). Wharton (1997) suggested that these three species may be more closely related to the Nearctic species of *Diachasmimorpha* Viereck that also attack fruit-infesting Tephritidae than to *D. fulgidum*.

The purpose of the present contribution is to describe a new species with unusual mandibular morphology and contrast the New Guinea/Australian fauna with *D. fulgidum* and similar species from the Palaearctic.

Materials and methods

Specimens. Specimens used in this study, including type material of previously described species, were borrowed from or examined at the following institutions: American Entomological Institute, Gainesville, Florida, USA (AEIC), Australian National Insect Collection, Canberra, ACT, Australia (ANIC), Canadian National Collection, Ottawa, Ontario, Canada (CNC), Museum fuer Naturkunde der Humboldt-Universitaet, Berlin, Germany (ZMHB), Hungarian Natural History Museum, Budapest, Hungary (HNHM), Naturhistorisches Museum Wien, Vienna, Austria (NHMW), Texas A&M University Insect Collection, College Station, Texas, USA (TAMU), The Natural History Museum, London, England (BMNH), and U. S. National Museum of Natural History, Washington, D. C., USA (USNM).

In the material examined section, we record label data for the holotype exactly as they appear on the label.



Figures 1–4. *Diachasma fulgidum* (Haliday) female. **1** Head, frontal view showing exposed labrum and absence of malar sulcus **2** fore and hind wing venation **3** mesosoma, dorsal-lateral view showing notaulus and midpit **4** middle part of body, dorsal view.

Figures. Images were acquired digitally using Syncroscopy's AutoMontage® software, in combination with a ProgRes 3008 digital camera mounted on a Leica MZ APO dissecting microscope. All images were further processed using various minor adjustment levels in Adobe Photoshop® such as image cropping and rotation, adjustment of contrast and brightness levels, color saturation, and background enhancement. Automontage images are available in color and high resolution at http://mx.speciesfile.org/projects/8/public/site/wharton_lab/home.

Database management and digital dissemination. Illustrations and free-text diagnoses for morphospecies were assembled in mx, a web-based content management system that facilitates data management and dissemination for taxonomic and phylogenetic works (e.g. Yoder et al. 2006). The mx project is open source, with code and further documentation available at http://sourceforge.net/projects/mx-database/. Data pertinent to this work, including specimen-level data, images, diagnoses, and descriptions, are available at http://mx.speciesfile.org/projects/8/public/site/wharton_lab/home.

Terminology, ontology reference, and measurements. Terminology follows Wharton et al. (2012), wherein terms are linked to the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010). Wing cells and abbreviations for wing veins are illustrated in Sharkey and Wharton (1997). Quantitative data in the description are based on all four specimens, unless parts were obscured by positioning on the point mounts. Measurements largely follow Wharton et al. (2012) and Wharton and Norrbom (2013).

Results and discussion

Taxonomy

Diachasma

Diachasma Foerster, 1862: 259. Type species: *Opius fulgidus* Haliday, 1837. Monobasic and original designation.

Atoreuteus Foerster, 1862: 241. Type species: *Atoreuteus striatus* Foerster, 1862. Monobasic and original designation. Synonymized by Fischer (1971).

Bathystomus Foerster, 1862: 235. Type species: *Bathystomus xanthopus* Foerster, 1862. Monobasic and original designation. Synonymized by Fischer (1971).

Lytacra Foerster, 1862: 258. Type species: *Lytacra stygia* Foerster, 1862. Monobasic and original designation. Synonymized by Wharton (1987).

Alysopius Tobias, 1976: 76–77. Type species: *Alysopius compressiventris* Tobias, 1976. Monobasic and original designation. Synonymized by Fischer (1986).

Diagnosis. Ventral margin of clypeus even, without teeth or tubercles, truncate to weakly concave; labrum usually flat, always broadly exposed. Occipital carina broadly absent dorsally, present laterally, extending to base of mandible, widely separated from hypostomal carina. Notauli varying from nearly absent to complete and ending in mesoscutal midpit, often sculptured anteriorly; mesoscutal midpit present, varying from punctiform to narrowly elongate. Precoxal sulcus varying from unsculptured and nearly absent to crenulate and extending nearly full length of mesopleuron. Fore wing stigma broad, discrete, with r1 arising from or distad midpoint; second submarginal cell relatively short, with 2RS and 3RSa approximately equal in length; m-cu antefurcal to postfurcal; RS complete to wing margin; 1st subdiscal cell closed (2cu-a present). Hind wing RS poorly developed, often barely indicated distally; m-cu nearly always present, though often weakly developed. First metasomal tergite with or without dorsope. Metasomal tergum 2+3 either smooth or sculptured. Ovipositor sheath varying from barely exserted to extending 0.5 × length of metasoma.

Remarks. Fischer (1971) placed *Atoreuteus* and *Bathystomus* as synonyms of *Diachasma*, but both have been treated separately in subsequent studies (Wharton 1988, Quicke et al. 1997). Belokobylskij et al. (2003) listed them under *Diachasma*, with a note that not all authors agreed with this placement. Yu et al. (2012) also left them in *Diachasma*. Wharton (1988) noted major differences in external morphology between *Atoreuteus* and *Bathystomus*, and these were corroborated by venom gland differences observed by Quicke et al. (1997). Similarly, Wharton (1988) described differences in labral and mandibular morphology that differentiate these two from more typical *Diachasma*. The type species of both *Atoreuteus* and *Bathystomus* also have an exceptionally large pronope. Their placement remains enigmatic, though the shape of the labrum suggests a basal position within Opiinae. They likely merit recognition as separate genera, but we leave them in *Diachasma*, with reluctance, pending a more rigorous analysis of opiine relationships.

The new species described below belongs to an Australian/New Guinea species group that is also morphologically distinct from typical members of *Diachasma* (as represented by species such as *D. fulgidum* and *D. hispanicum* (Fischer)). These austral species include *D. australe* (Fischer), *D. extasis* Fischer, *D. kaltenbachi* Fischer, and *D. tasmaniae* Fischer. This group can be characterized as monophyletic by the distal origin of r1 from the stigma (distinctly beyond the midpoint). The included species can be further recognized by the combination of a postfurcal fore wing m-cu, propodeal sculpture with well-developed median longitudinal carina on anterior half, bordered by relatively unsculptured areas, and T1 with well-developed dorsope. Most species also have fore wing 2CUa shorter than 2cu-a.

The type species, *D. fulgidum*, is unusual in lacking a well-defined malar sulcus and having a relatively flattened scutellum with polished posterior margin.

Species excluded. Specimens of the species newly described below were compared to primary types and other specimens of nominal species of *Diachasma* previously described from Australia and New Guinea. During this examination, we discovered that a specimen in HNHM labeled as the lectotype male of *Diachasma rufipes* Szépligeti, 1905, is a member of the genus *Notiopambolus* van Achterberg & Quicke. The new combination is *Notiopambolus rufipes* (Szépligeti). Several species of *Notiopambolus* have been described from eastern Australia (van Achterberg and Quicke1990, Belokobylskij 1992). It is likely that *rufipes* is a senior synonym of one of these previously described species, but we are unable to place it at this time.

Key to species of *Diachasma* known from Australia and New Guinea

1 Fore wing r1 arising from middle of stigma **2**
1' Fore wing r1 arising distinctly distad middle of stigma **4**
2. (1) Fore wing m-cu postfurcal, entering second submarginal cell........................ .... ***D. obothorax* Fischer**
2' Fore wing m-cu antefurcal, entering first submarginal cell **3**

3. (2’) Mesosoma 1.33 × longer than high. Temples in dorsal view not strongly receding .... ***D. gressitti*** **Fischer**

3' Mesosoma 1.25 × longer than high. Temples in dorsal view strongly receding .... ***D. anguma*** **Fischer**

4. (1’) T1 3 × longer than apical width .... ***D. extasis*** **Fischer**

4' T1 at most 2 × longer than apical width **5**

5. (4’) Eye in lateral view 5 × longer than temple; mesonotum black .... ***D. kaltenbachi*** **Fischer**

5' Eye in lateral view at most 3 × longer than temple; mesonotum predominantly pale: yellow to orange, rarely with one or two weakly infumate spots **6**

6. (5’) Mandible with broad flanges along dorsal and ventral margins basally, abruptly narrowing to apical teeth (Figs 5, 6) .... ***D. dentatum*** **Shirley, Restuccia & Ly, sp. n.**

6' Mandible strongly but evenly narrowing to apical teeth, without obvious flanges (Figs 1, 13) **7**

7. (6’) Notauli weakly developed, largely confined to anterior-lateral corners, absent or nearly so on mesoscutal disc; precoxal sulcus unsculptured .... ***D. australe*** **(Fischer)**

7' Notauli well developed and deep throughout, extending to midpit posteriorly; precoxal sulcus nearly always crenulate for most or all of its length .... ***D. tasmaniae*** **Fischer**

Diachasma dentatum Shirley, Restuccia & Ly, sp. n.

http://zoobank.org/EE48A796-3A5F-49B9-84CC-19587EC17C29

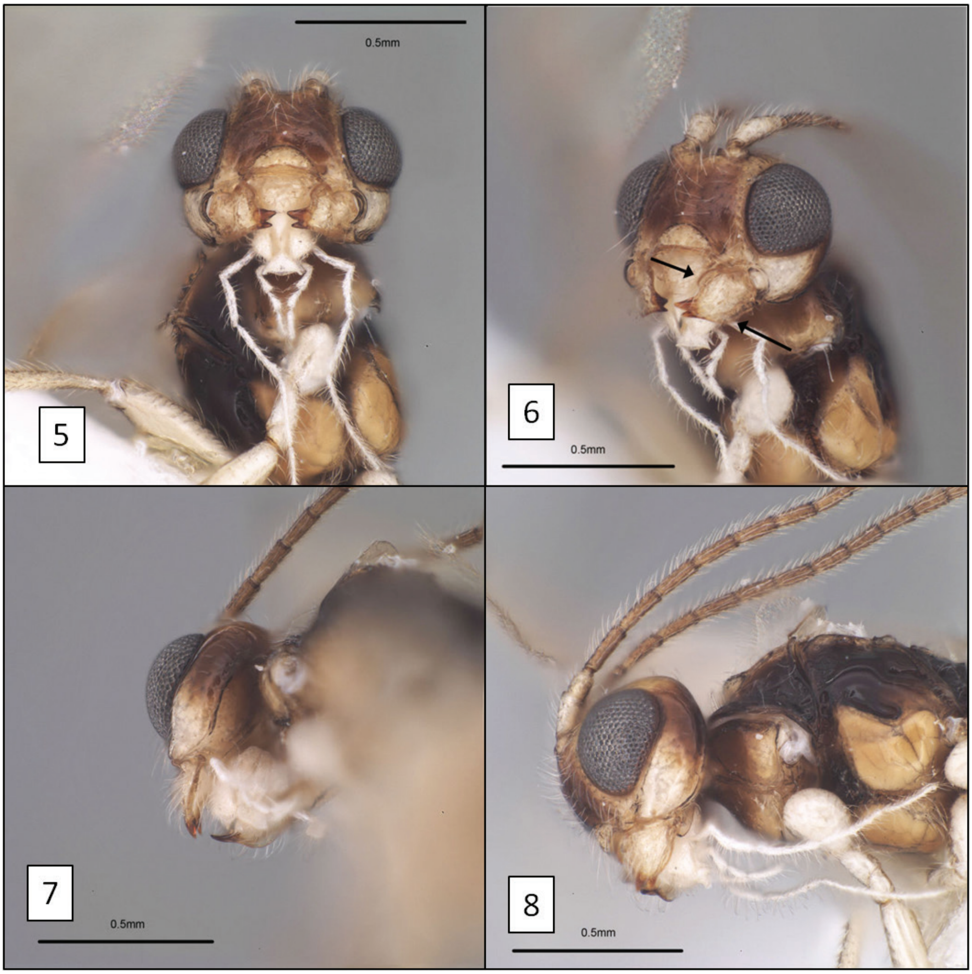
Figs 5–12, 16

Type locality. Australia, New South Wales, Lord Howe Island

Type material. Holotype. Female (ANIC), first and only data label, first line: Aust:NSW second line: Lord Howe Is. third line: 17.31.v.1980 fourth line: S.&J.Peck

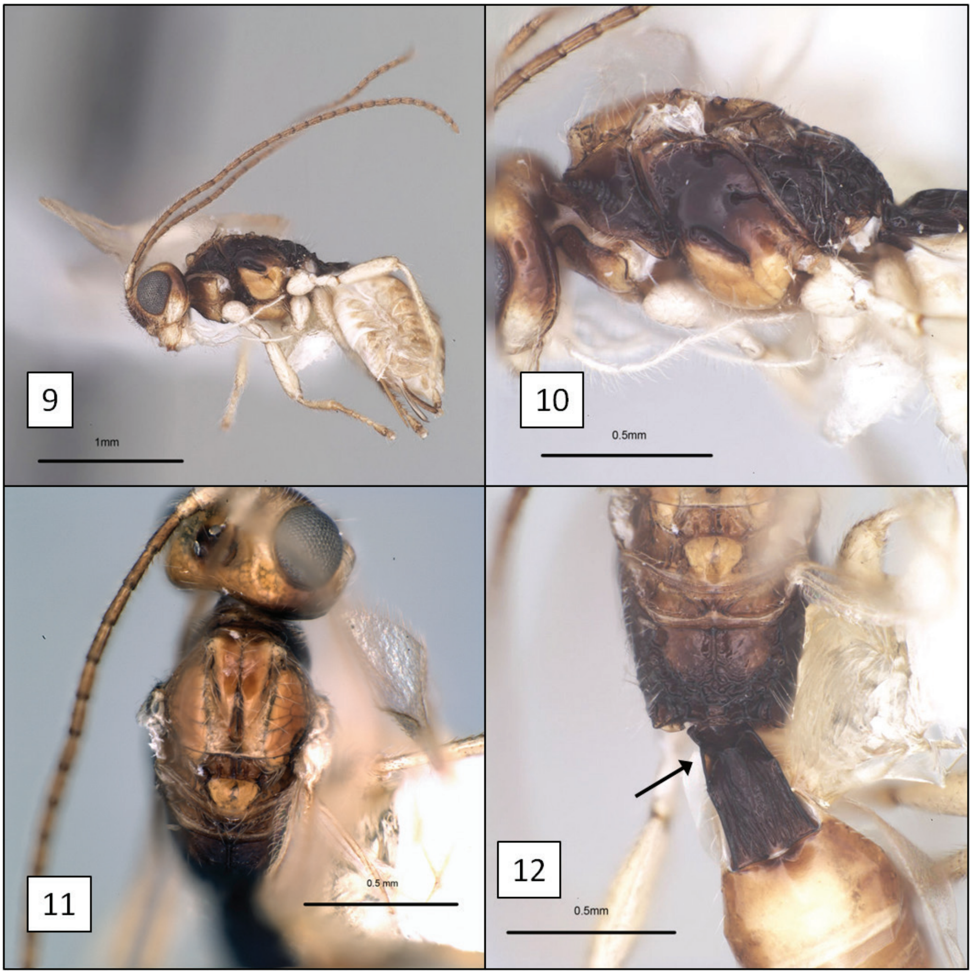
Paratypes. 3 males, same data as holotype (CNC, TAMU).

Description. Face faintly punctate, punctures separated by 5–7 × their diameter, surface weakly shagreened to smooth between punctures. Frons with small, median pit between median ocellus and toruli. Clypeus 2.25–2.65 × wider than high, faintly punctate; ventral margin weakly concave, nearly truncate. Eye moderately large, 2.5–2.75 × longer than temple in lateral view. Malar sulcus distinct, deep throughout; malar space 0.5–0.6 × basal width of mandible. Mandibles deflected ventrally, broadly exposing labrum, apical teeth bent sharply inward relative to base, basal portion as broad as long, with prominent flanges forming dorsal and ventral margins (Figs 5, 6). Antenna with 26 (female) and 30–32 (male) flagellomeres; first flagellomere 3.5–4.0 × longer than wide, 1–1.05 × longer than second. Length of maxillary palps distinctly greater than height of head. Mesosoma 1.5–1.55 × longer than high, 1.85–2.05 × longer than wide. Propleuron smooth, polished, without diagonal sulcus. Pronotum



Figures 5–8. *Diachasma dentatum* Shirley, Restuccia & Ly head, holotype female. **5** Frontal view showing juxtaposition of mandibles **6** mandible, frontal-oblique view, arrows = flanges on dorsal and ventral margins **7** ventral-posterior view showing widely spaced occipital and hypostomal carinae **8** lateral view showing relative size of eye.

dorsally with small median pit; crenulate groove along posterior margin continuing laterally, extending to ventral margin of pronotum laterally; posterior margin of pronotum laterally crenulate. Notauli deeply impressed, extending from anterior margin to narrowly elongate midpit, crenulate anteriorly, unsculptured on most of disc; supramarginal carina distinct throughout, mesoscutal humeral sulcus crenulate; midpit occupying nearly half length of disc (Fig 11); median mesoscutal lobe elevated along edge of anterior declivity in holotype. Scuto-scutellar sulcus broad, twice wider than long. Precoxal sulcus (Fig. 10) deep, broad, nearly extending to anterior margin, widely separated from posterior margin, varying from crenulate to almost completely smooth. Propodeum with smooth anterior-lateral areas separated by median longitu-



Figures 9–12. *Diachasma dentatum* Shirley, Restuccia & Ly, holotype female. **9** Lateral habitus **10** Mesosoma, lateral view **11** Mesoscutum, dorsal view **12** Propodeum and T1, dorsal view, arrow = dorsope.

dinal carina on basal 0.3, carina merging posteriorly with barely discernible median areola largely obscured by fine rugosities covering posterior 0.5 of propodeum. Fore wing stigma discrete, wedge-shaped, gradually widening distally, 4.2–4.5 × longer than wide, r1 arising 0.7 × distance from base, less than half width of stigma at this point; 2RS 1.2 × longer than 3RSa; 3RSb extending to apex of wing; m-cu widely postfurcal; 2CUb arising at or near anterior side of 1st subdiscal cell, 2CUa varying from absent to nearly so. Hind wing RS weak but distinct at base, absent distally; m-cu weakly pigmented and very weakly impressed, long, extending nearly to wing margin, curved basally. Metasoma with T1 1.35–1.45 × longer than apical width, about 1.7 × wider at apex than at base; densely striate, dorsal carinae distinct from base to apex, more nearly parallel-sided and widely separated in male paratypes than female holotype; dorsope large, distinct. T2+3 smooth, very sparsely setose, nearly bare. T2 spiracle on dorsal edge of lateral crease separating median tergite from lateral tergite. Ovipositor sheath about half length of mesosoma, sparsely setose. Color (Figs 9, 10) pale yellow (males) to dark yellow (female) except as follows: pronotum laterally, mesopleuron dorsally, metapleuron, propodeum posteriorly, and T1 dark brown, female more extensively darker than males; ocellar field, most of face, and temple behind eye brown; flagellum and tergal margins light brown; propleuron dorsally and propodeum anteriorly yellow-brown; apical teeth of mandible red; labrum, palps, lower gena, trochanters, and all coxae white, remainder of legs, scape, and pedicel faintly yellow.

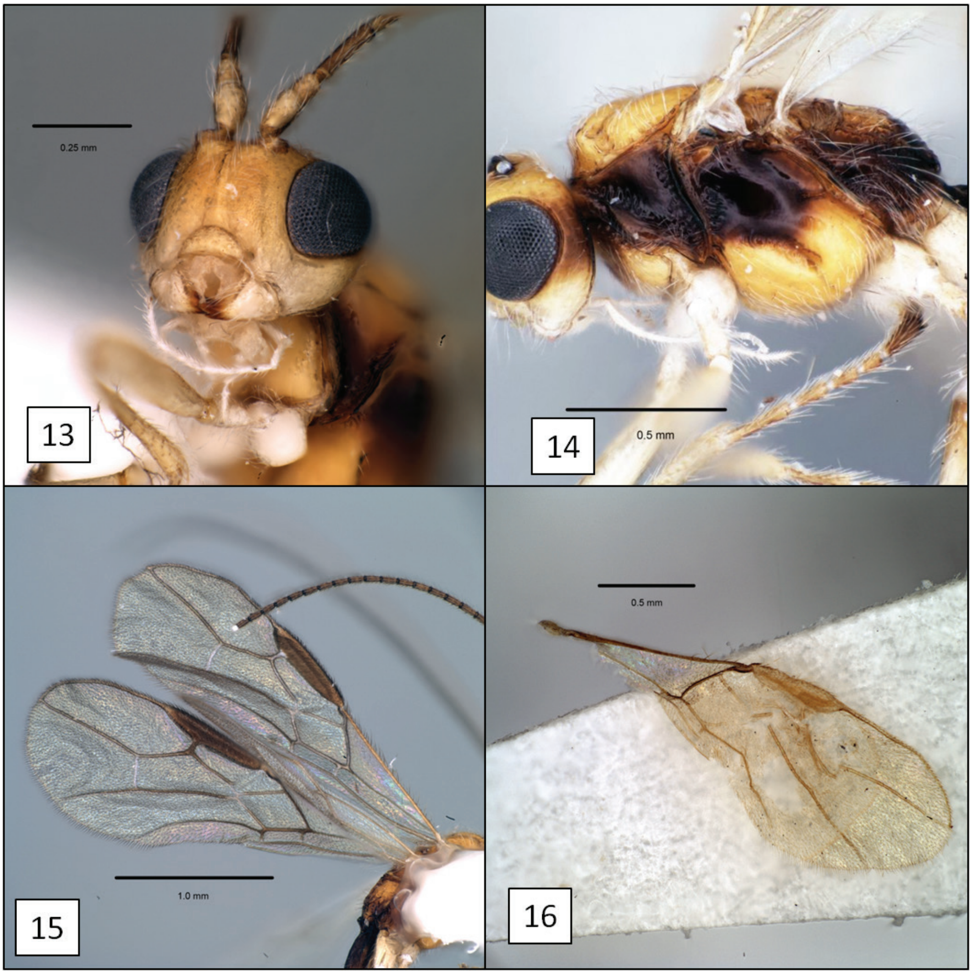
Diagnosis. This new species is almost identical morphologically to *Diachasma tasmaniae*, with very similar wing venation, body sculpture, and coloration (including female darker than male). The mandible, however, is distinctly different. The mandible of *D. tasmaniae* is typical of other members of this species group, lacking the flange-like dorsal and ventral margins of the *D. dentatum* mandible. Both *D. tasmaniae* and *D. dentatum* belong to a group of species readily recognized by the combination of a distinct dorsope, r1 arising from the distal portion of the discrete fore wing stigma, and a relatively short second submarginal cell, with 2RS longer than or less commonly equal in length to 3RSa. All other described species in this group have normal mandibles similar to those of *D. tasmaniae* and are darker in color than *D. tasmaniae* and *D. dentatum*.

Biology. Unknown.

Etymology. The species name is Latin for toothed, calling attention to the unusual form of the mandibles.

Remarks. Intraspecific variation in sculpture and quantitative measurements poses challenges for species delineation in this group. The face is more visibly shagreened in two of the males of *D. dentatum*, for example, but the sculpture is weak in all four specimens compared to most but not all specimens of *D. tasmaniae* available for examination (n = 11). The eye varies in size between sexes and among species of this species group, but in known members of this group, the eye is large compared to that of the relatively small eye of *D. fulgidum*.

The placement of *dentatum* in *Diachasma*, along with *tasmaniae* and the other morphologically similar species noted above, will ultimately need to be re-evaluated. There are compelling morphological differences that strongly suggest that these species are not congeneric with the type species, *D. fulgidum*, nor closely resemble the type species of *Atoreuteus* and *Bathystomus*. There are a large number of available genus group names in the Opiinae, including several for species with a well-developed dorsope (as discussed in detail by Wharton 2006) and we are thus reluctant to create a new generic name since one or more of these may prove applicable with a broader analysis of opiine relationships. The described species from Australia and New Guinea are also morphologically diverse, as exemplified by the key to species presented above, and many new species await description, based on material examined in TAMU and ANIC. As noted above, resolution of relationships will necessitate consideration of many opiines currently placed in other genera and is beyond the scope of this work.



Figures 13–16. *Diachasma* spp. **13** *D. tasmaniae* Fischer, mandible **14** *D. tasmaniae* mesosoma, lateral view **15** *D. tasmaniae* fore wing **16** *D. dentatum* Shirley, Restuccia & Ly, fore wing stigma, female holotype.

Though Lord Howe is an oceanic island well off the coast of New South Wales, this newly described species is remarkably similar in many respects to *D. tasmaniae*. *Diachasma tasmaniae* was originally described from Tasmania and New South Wales (Fischer 1995) and is recorded here for the first time from Victoria (specimens in TAMU and ANIC).

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RESEARCH ARTICLE

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Taxonomic revision of the East Asian genus *Scleropteroides* Colonnelli, 1979 (Coleoptera, Curculionidae, Ceutorhynchinae)

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Abstract

The genus *Scleropteroides* Colonnelli, 1979 (Ceutorhynchinae: Scleropterini) was revised on the basis of detailed morphological observations. The genus was redefined to include three species from East Asia: *S. hypocrita* (Hustache, 1916) is redescribed and recorded from northeastern China and northern Korea for the first time; *S. horridulus* (Voss, 1958) is redescribed with new records from southern Korea; *S. insularis* Voss, 1971 was moved from synonymy with *S. hypocrita* to that with *S. horridulus* (**syn. n.**), and *S. longiprocessus* Huang & Yoshitake, **sp. n.** is described as new, sympatric with *S. hypocrita* in Japan. All the species are associated with woody *Rubus* species (Rosaceae). A key to species, habitus photographs, illustrations of important characters, and distribution maps are provided for each species.

Keywords

Rubus, new record, new species, *Scleropterus*, taxonomy

Introduction

Scleropteroides Colonnelli, 1979 is placed in the tribe Scleropterini, subfamily Ceutorhynchinae, and is characterized mainly by a rostrum expanded from the base to apex, a visible scutellar shield, subtriangular elytra, strongly convex humeri, acute squamate granules on the elytral intervals, a deep rostral channel extending to the metaventrite, and dentate femora (Colonnelli 1979, 2004; Korotyaev 1996). This genus is thought to be related to *Scleropterus* Schoenherr, 1825 (Colonnelli 1979, Korotyaev 1996). The affinity of the two genera was supported by a recent molecular phylogenetic study (Kato et al. 2006).

The genus *Scleropteroides* was established for *Ceuthorrhynchidius hypocrita* Hustache, 1916 from Japan (Colonnelli 1979). After that, Morimoto (1984) treated *Rhytidosomus insulare* Voss, 1971 (an original incorrect spelling of "*insularis*"), which was described from the Ryukyus, as a member of *Scleropteroides*. Kim et al. (1991) and Hong et al. (1999, 2000) recorded *Scleropteroides hypocrita* from South Korea. Later, *R. insularis* was synonymized with *S. hypocrita* by Colonnelli (2004) in his world catalog of Ceutorhynchinae, although Colonnelli did not provide any explanation of this taxonomic treatment. Recently, Korotyaev et al. (2014) combined *Homorosoma horridulum* Voss, 1958 with *Scleropteroides* and recorded it from Taiwan. Thus, until the present paper, *Scleropteroides* comprises *S. hypocrita*, which is known to occur in South Korea and Japan (Morimoto 1984, 1989; Korotyaev and Hong 2004; Yoshitake et al. 2004) and to be associated with *Rubus* species (Rosaceae) (Morimoto 1984, Hong et al. 1999, Korotyaev and Hong 2004), and *S. horridulus*, which is known to occur in Fujian Province of the continental China, Taiwan, and Japan (Korotyaev et al. 2014).

Presently, *Scleropteroides* is in need of revision. Apart from morphological differences associated with hind-wing reduction in *Scleropterus*, the distinction between the two genera is still insufficient because more than half of the defining characteristics of *Scleropteroides* are common to *Scleropterus* or even incorrectly described. Moreover, the taxonomic status of *R. insularis* should be revised because it shows remarkable differences from *S. hypocrita* despite Colonnelli's synonymy. Korotyaev et al. (2014) point out a similarity in general appearance between *S. horridulus* and *S. insularis*. In addition, our preliminary study suggested the presence of a new species in Japan. Finally, fundamental ecological data on *Scleropteroides* weevils are still needed.

In this study, we revise the genus *Scleropteroides* on the basis of detailed examinations of specimens collected from various localities in East Asia. In addition, we provide distributional and ecological information on *Scleropteroides* species. The systematic position of the genus, relationships among species, and the geographic distribution and host plant association of each species are discussed.

Materials and methods

Specimens preserved in the following institutions and private collections were examined for this study: Canadian Museum of Nature, Ottawa/Gatineau (CMN); Entomological

Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (ELKU); Laboratory of Environmental Entomology, Faculty of Agriculture, Ehime University, Matsuyama, Japan (EUMJ); Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS); K. Izawa collection, Tajimi, Japan (KI); Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Institute for Agro-Environmental Sciences, Tsukuba, Japan (NIAES); Natural History Museum Vienna, Wien, Austria (NHMV); S. Miyakawa collection, Kyushu University Museum, Fukuoka, Japan (SM); and Y. Shiozaki collection, Kawasaki, Japan (YS). All the descriptive work in this study was completed by J. Huang and H. Yoshitake.

External structures were observed under a Leica MZ95 stereoscopic microscope. Measurements of body parts are defined and abbreviated as follows: LB = body length, from the apex of the pronotum to the apices of elytra; LR = rostrum length, from a lateral view; WP = maximum width of pronotum; LP = pronotum length, from the base to the apex along the midline; WE = maximum width of elytra; and LE = length of elytra, from the base of humeri to the apex of elytra. All measurements are in millimeters. Habitus photographs were taken using a Nikon Coolpix995 digital camera attached to a Nikon SMZ1500 stereoscopic microscope. To examine terminalia, the specimens were macerated in hot water and dissected under a stereoscopic microscope. The abdomen was removed from the body and then cleaned in hot 10% KOH solution for 5–10 min. Terminalia were extracted from the abdomen and mounted on slides with glycerol (male) or pure water (female), examined using a Nikon Eclipse 55i optical microscope, and illustrated in detail using a camera lucida. Scale bars were calibrated using a Nikon objective micrometer. Details of some external structures were observed with a scanning electron microscope (Hitachi 3000-N). Plant nomenclature follows Yonekura and Kajita (2003). Distribution maps (Figs 133–134) are based on records of *S. hypocrita* from Korea (Hong et al. 1999, 2000, Korotyaev and Hong 2004) and all the specimens examined in this study. Verbatim label data indicated by quotation marks are provided for the holotypes. Label breaks are indicated by a slash (“/”).

Taxonomy

Scleropteroides Colonnelli, 1979

Figs 7–21

Scleropteroides Colonnelli, 1979: 214. – Morimoto 1984: 316; 1989: 514 (in checklist). – Kim et al. 1991: 183 (record from Korea). – Korotyaev 1996: 459 (in key). – Hong et al. 1999: 63. – Hong et al. 2000: 123. – Yoshitake et al. 2004: 105 (in catalog). – Korotyaev and Hong 2004: 146. – Colonnelli 2004: 22, 34 (in catalog). – Korotyaev et al. 2014: 99.

Type species. *Ceuthorrhynchidius hypocrita* Hustache, 1916.

Diagnosis. This genus is very similar to *Scleropterus* in having a six-segmented antennal funicle, elytra bearing acute squamate granules (usually in a row on each interval), and a rostral channel extending to the metaventrite. However, it is easily distinguishable from *Scleropterus* mainly by the bisinuate basal margin of the pronotum (Figs 10, 34, 36, 38), the well-developed scutellar shield (Figs 11, 34–39), prominent elytral humeri (Figs 11, 35, 37, 39), even elytral intervals (Figs 11, 35, 37, 39), dentate femora (Fig. 15), and simple fore tibiae that are not incurved apically (Fig. 15).

Male. Dark brown in general appearance. Head, rostrum, prothorax (except apical part), venter, and pygidium black; antennae, apical part of prothorax, and tarsi paler.

Vestiture. Body surface evenly covered with ochreous pollinosity in life. Head mainly covered with brown clavate scales, mixed with white scales; vertex with scales directed medially; forehead with scales directed basally; basal margin and median carina fringed with white ovate recumbent scales. Rostrum covered with clavate scales on basal 2/3; scales directed basally, gradually becoming smaller toward apex, replaced by hair-like scales on apical 1/3. Prothorax mainly covered with very similar scales as those on head, with longitudinal stripe of white ovate recumbent scales on median and lateral parts; each scale directed basally. Elytra (Fig. 11) bearing row of white and brown clavate scales on each interval; scales directed apically. Legs (Fig. 15) densely covered with white and brown scales; femora mostly covered with clavate semirecumbent scales, mingled with feather-like scales along inner margin; tibiae mainly covered with clavate scales, except semirecumbent hair-like scales along inner margin; corbel of each tibia fringed with brown setae. Lateral pieces of meso- and metathorax mainly covered with white ovate recumbent scales. Sterna mainly covered with white lanceolate to ovate scales; meso- and metaventral receptacles densely covered with white aciculate scales. Venter mainly covered with white lanceolate to ovate recumbent scales, mingled with white and brown clavate scales; ventrites III and IV nearly naked on disc, with only transverse row of clavate scales; ventrite V bearing fine brown scales in median concavity and white ovate scales on sides. Pygidium mainly sparsely covered with short clavate semirecumbent scales, mingled with hair-like recumbent scales; scales brown, directed ventrally.

Head (Figs 7–8) reticulately punctured; each puncture moderate in size; vertex with median carina from base to apex; carina becoming obscure apically; forehead shallowly depressed, with apex slightly broader than base of rostrum and then strongly widened basally; eyes medium-sized, rounded triangular, weakly convex. Rostrum (Figs 7–8) slender, evenly curved; dorsum densely rugosely punctured except apex; punctures moderate in size from base to level between antennal insertions, then becoming smaller, sparser, and shallower toward apex; sides subparallel in basal half, more or less widened before antennal insertions, then subparallel in apical part; antennal scrobes well separated on ventral surface. Antennae (Figs 8–9) inserted before middle of rostrum; scape moderate in length, evidently clavate, round and fringed with 3–4 setae at apex, slightly shorter than funicle; funicle six-segmented; club lanceolate, finely pubescent except basal part.

Pronotum (Figs 10–13) slightly wider than long; dorsum densely coarsely punctured, simple, lacking tubercle or prominence; punctures smaller in apical and basal parts; basal margin bisinuate, smooth, not serrate; apical margin weakly raised, with shallow median incision. Scutellar shield subovate.

Elytra (Figs 11–12) subcordate, nearly as long as wide, widest just behind humeri; suture evidently bent leftward; interval I of right elytron slightly broader than that of left elytron; all intervals subequal in width and height, nearly three times as wide as striae, each with row of more or less small and acute squamate granules; striae less marked, nearly naked, lacking conspicuous scales or hair, finely punctured; each puncture round, separated by distance more than three times as long as its diameter. Hind wings (Fig. 19) well-developed.

Legs (Fig. 15) slender; femora slightly clavate, each armed with small tooth, bearing minute squamate granules; no jumping organ present (Fig. 16); tibiae bearing minute squamate or setiferous granules; protibiae simple, lacking mucro and not curved in at apex; meso- and metatibiae moderately mucronate; corbels short, simple, not dilated outward; tarsi (Figs 17–18) moderate in length; claws free, slender, appendiculate with sharp teeth; each tooth slender, extending from base to middle of each claw.

Underside. Prosternum coarsely and moderately densely punctured; mesoventrite densely and finely punctured; metaventrite with dense medium-sized punctures on disc and with sparser and coarser punctures on sides; lateral pieces of meso- and metasterna sparsely coarsely punctured. Rostral channel (Fig. 13) long, extending far beyond level between posterior margins of mesocoxal cavities, with dense minute punctures; mesoventral receptacle deep, laterally costate; costae short, subparallel; metaventral receptacle very deep, terminating in steep wall and U-shaped margin; lateral walls of meso- and metaventral receptacles interrupted by inner margins of mesocoxae; metaventrite more or less prominent ventrally along apico-lateral margin of metaventral receptacle. Metendosternite as in Fig. 14. Venter coarsely and more or less densely punctured; ventrites III and IV nearly polished on disc, with only transverse row of coarse and sparse punctures; ventrite V with subtriangular median concavity along basal margin; concavity faintly sulcate along midline. Tergum as in Figs 20–21; tergite VII with pair of minute setiferous plectral tubercles near base.

Pygidium transverse-pentagonal, flattened, very coarsely and reticulately punctured; bottom of each puncture opaque due to dense minute punctations; upper flange arcuate downward on each side.

Female. Rostrum (Figs 24–25) slightly more slender. Antennae inserted just behind middle of the rostrum. Tibiae simple, not mucronate on all legs. Ventrites I and II moderately inflated, sparsely punctured, lacking prominence. Ventrite V simple or only with longitudinal median sulcus, lacking concavity. Pygidium smaller, sectorial, mainly covered with hair-like scales. Otherwise as in male.

Distribution. East Asia (China including Taiwan, Korea, and Japan; Figs 133–134).

Scleropteroides hypocrita **(Hustache, 1916)**

Figs 1, 2, 22–25, 34–35, 40–69, 133, 135-138

Ceuthorrhynchidius hypocrita Hustache, 1916: 126 (type locality: "Japon, Mont Takao, près Hachiôji"). – Chûjô 1960: 8 (Tsushima). – Nakane 1963: 374, pl.187, fig. 17 (Honshu).

Ceuthorrhynchidius hypocritus (incorrect subsequent spelling): Dalla Torre and Hustache 1930: 33 (in catalog; "Japon"). – Morimoto 1962: 194 (in checklist; Honshu, Shikoku, Kyushu).

Rhytidosomus (*Rhytidosomus*) *holdhausi* Wagner, 1944: 59 ("Süd-Japan"). – Voss 1971: 55.

Homorosoma horridulum: Chûjô and Voss 1960: 7 (in part; misidentified, not Voss 1958; Shikoku: Ehime, Omogo).

Scleropteroides hypocrita: Colonnelli, 1979: 216. – Morimoto 1985: 316, pl. 62, fig. 15 (Honshu, Shikoku, Kyushu; *Rubus* spp.); Morimoto 1989: 514 (in checklist; Honshu, Izu Islands, Shikoku, Kyushu). – Kim et al. 1991: 183 (record from Korea). – Hong et al. 1999: 63. – Hong et al. 2000: 123. – Yoshitake et al. 2004: 105 (in checklist). – Korotyaev and Hong 2004: 146. – Colonnelli 2004: 34 (in catalog).

Rhytidosomus holdhausi: Morimoto 1983: 54 (= *Scleropteroides hypocrita*).

Scleropteroides hypocritus: Morimoto 1984: 316, pl. 62, fig. 15 (Honshu, Shikoku, Kyushu; *Rubus* spp.).

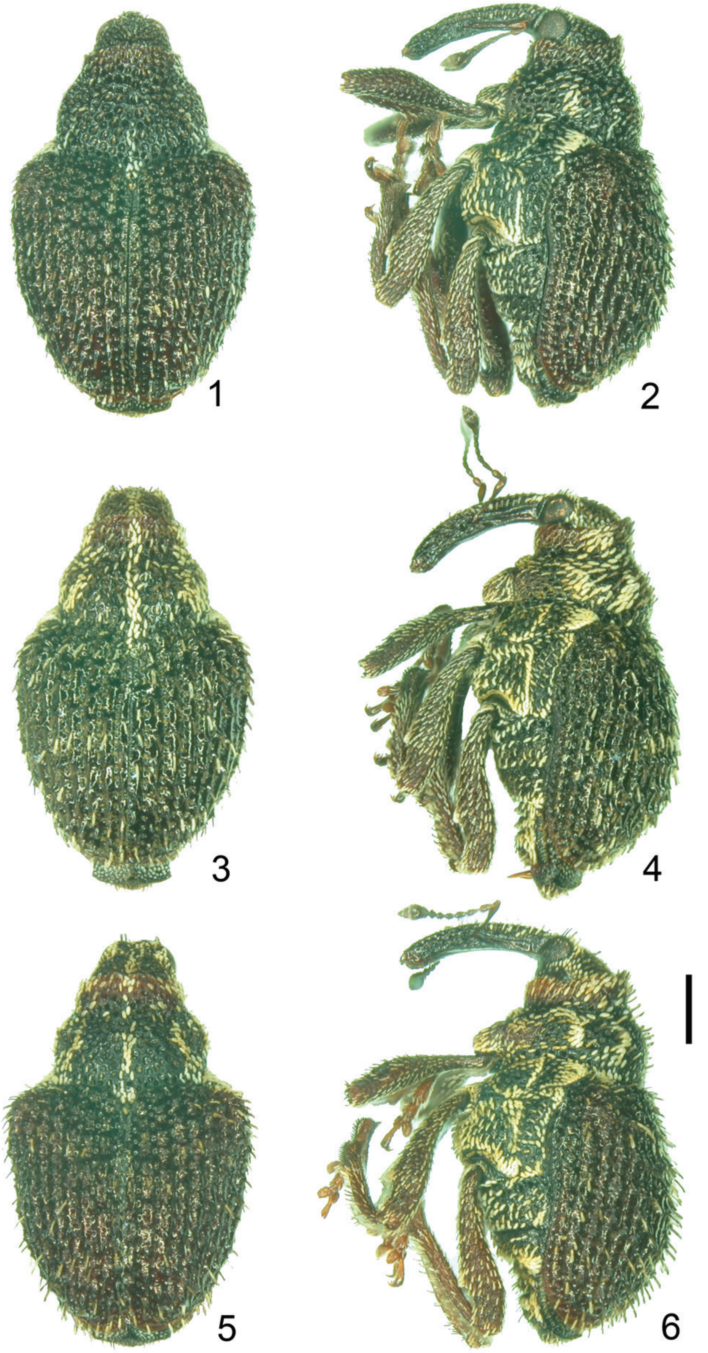
Rhytidosoma (*Rhytidosoma*) *holdhausi*: Colonnelli 1994: 214 (= *Scleropteroides hypocrita*).

Diagnosis. This species is characterized by the following characters: prothorax moderately constricted in the subapical part (Fig. 34); elytra with weakly prominent humeri, gently convergent toward the subapical calli (Fig. 35); scales in a row on elytral intervals, semirecumbent, evidently shorter than width of each interval (Fig. 35); apical half of the male rostrum slightly widened (Fig. 22); male metaventrite weakly prominent ventrally along the apico-lateral margin of the metaventral receptacle; male ventrite I with a median prominence along the apical margin; penis with apical projection blunt, rounded at the apex (Figs 41, 51, 61); basal part of the endophallus with a pair of plate-like sclerites (Figs 40, 50, 60); female sternite VIII with slender arms that are arcuate apically (Figs 47, 57, 67); posterior part of the bursa copulatrix densely covered with minute coniform spicules (Figs 45, 55, 65).

Male. LB: 2.18–2.66 (mean, 2.41). LR: 0.96–1.11 (mean, 1.03). WP: 0.94–1.08 (mean, 1.01). LP: 0.78–0.97 (mean, 0.86). WE: 1.48–1.79 (mean, 1.61). LE: 1.50–1.82 (mean, 1.64). N = 10 for all measurements. Habitus as shown in Figs 1–2.

Vestiture. Clavate scales short and semirecumbent on head, basal 2/3 of rostrum, and pronotum. Hair-like scales fine and semirecumbent on apical 1/3 of rostrum. Scales on elytral intervals (Fig. 35) semirecumbent, short, 0.4–0.8 × as long as interval width. Clavate scales on tibiae semierect.

Rostrum (Figs 22–23) slender, 1.15–1.24 × as long as pronotum; apical part of sides slightly widened and 1.14 × as long as basal part. Antennae (Fig. 23) with length



Figures 1–6. Habitus of *Scleropteroides* spp., males. **1–2** *S. hypocrita* (Hustache) **3–4** *S. longiprocessus* Huang & Yoshitake, sp. n. **5–6** *S. horridulus* (Voss) **1, 3, 5** Dorsal habitus **2, 4, 6** Lateral habitus. Scale: 0.50 mm.

ratio of funicular segments I: II: III: IV: V: VI = 1.89: 1.44: 1.36: 1.00: 1.17: 1.00 and width ratio = 1.71: 1.00: 1.21: 1.29: 1.50: 1.64.

Pronotum (Fig. 34) 1.12–1.21 × as long as wide, 0.51–0.54 × as long as and 0.60–0.66 × as wide as elytra; subapical constriction moderate; sides slightly widened from base to basal 1/3, faintly narrowed to middle, then gradually convergent toward apex.

Elytra 0.98–1.07 × as long as wide, 1.87–1.97 × as long as and 1.51–1.66 × as wide as pronotum, gently convergent toward subapical calli; humeral calli weakly prominent; subapical calli weakly prominent.

Underside. Metaventrite weakly prominent ventrally along apico-lateral margin of metaventral receptacle. Venter coarsely and moderately densely punctured; ventrite I with median prominence along apical margin; prominence weak, semicircular, densely and finely punctured; ventrite V with more or less shallow median concavity; length ratio of ventrites I: II: III: IV: V = 4.18: 2.00: 1.00: 1.14: 1.82 and width ratio = 1.96: 1.75: 1.32: 1.18: 1.00.

Pygidium transverse-pentagonal.

Terminalia and genitalia. Sternite VIII (Figs 44, 54, 64) diminished into pair of eye-shaped sclerites; spiculum gastrale robust, evidently longer than penis or its apodeme, bent leftward. Tegmen (Figs 43, 53, 63) with apodeme more or less stout, nearly 0.8 × as long as the diameter of the tegminal ring, more or less widened toward apex. Penis (Figs 40–42, 50–52, 60–62) broad, relatively thin in profile, more or less moderately curved downward in the basal 2/3, then slightly bent upward in apical 1/3; sides faintly narrowed from base to basal 1/3, slightly broadened from basal 1/3 to apical 1/5, then strongly convergent apically; apical projection blunt, rounded at apex. Basal part of endophallus (Figs 40, 50, 60) with pair of plate-like sclerites, numerous rounded spicules in median part, and moderately dense minute spicules in apical part.

Female. LB: 2.28–2.67 (mean, 2.50). LR: 1.05–1.31 (mean, 1.19). WP: 0.95–1.11 (mean, 1.03). LP: 0.80–0.97 (mean, 0.89). WE: 1.54–1.89 (mean, 1.72). LE: 1.57–1.82 (mean, 1.72). N = 11 for all measurements.

Rostrum (Figs 24–25) slightly more slender, 1.27–1.36 × as long as pronotum.

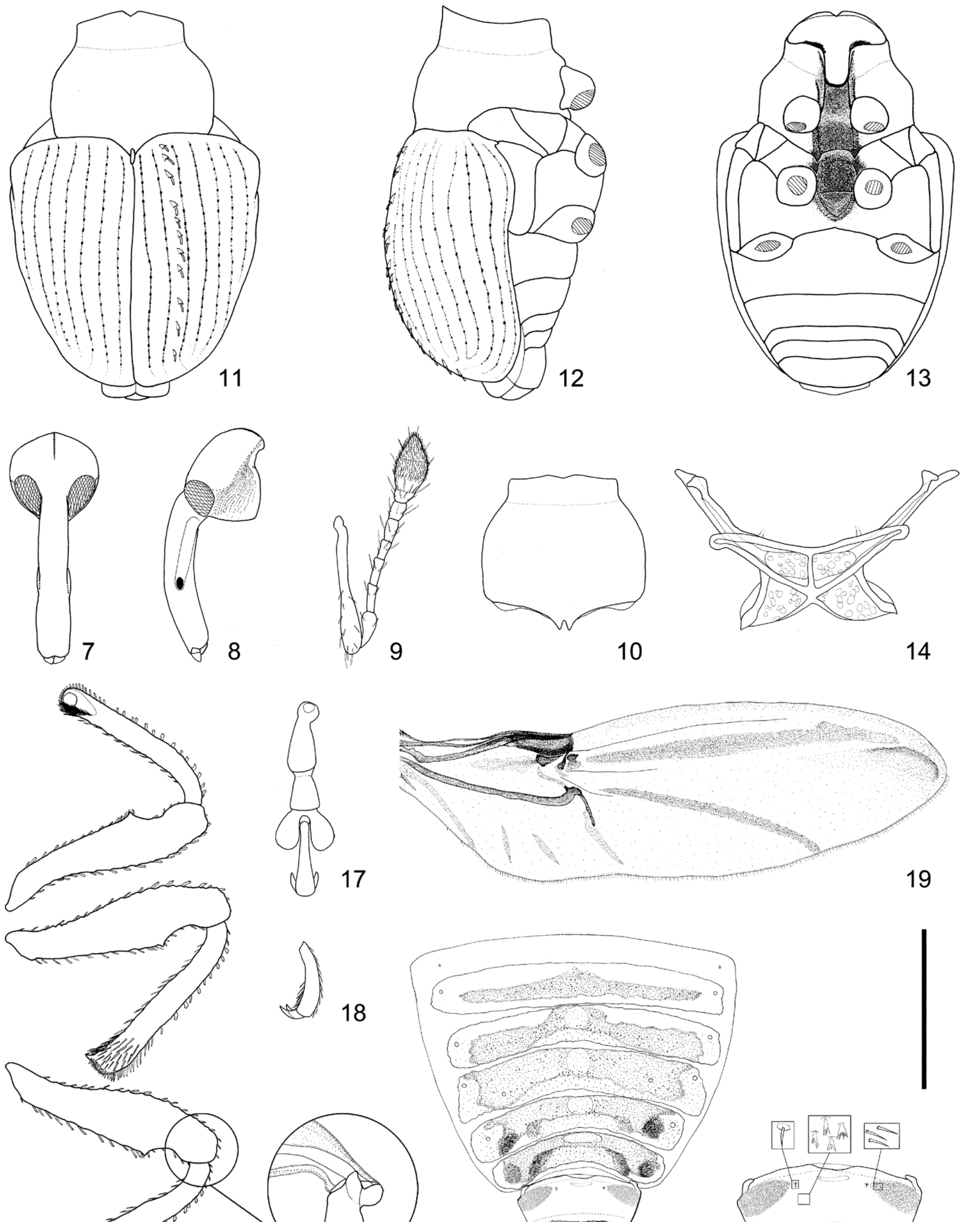
Pronotum 1.11–1.20 × as wide as long.

Elytra 0.97–1.03 × as long as wide.

Underside. Metaventrite more strongly prominent ventrally along apical margin of metaventral receptacle. Ventrites I and II moderately inflated, sparsely punctured, lacking prominence. Ventrite V lacking concavity, with only longitudinal median sulcus that is sometimes obscure.

Pygidium smaller, fan-shaped.

Terminalia and genitalia. Tergite VIII (Figs 46, 56, 66) with pair of combs of dense, long setae along apical margin. Sternite VIII (Figs 47, 57, 67) with pair of patches of several minute setae near apex; arms relatively slender, nearly 0.8 × as long as apodemes, nearly half as long as coxite and stylus combined, slightly basally fused, and apically arcuate; apodemes slender, moderately divergent near apex. Bursa copulatrix (Figs 45, 55, 65) with dense minute coniform spicules in posterior part. Coxites (Figs 48, 58,

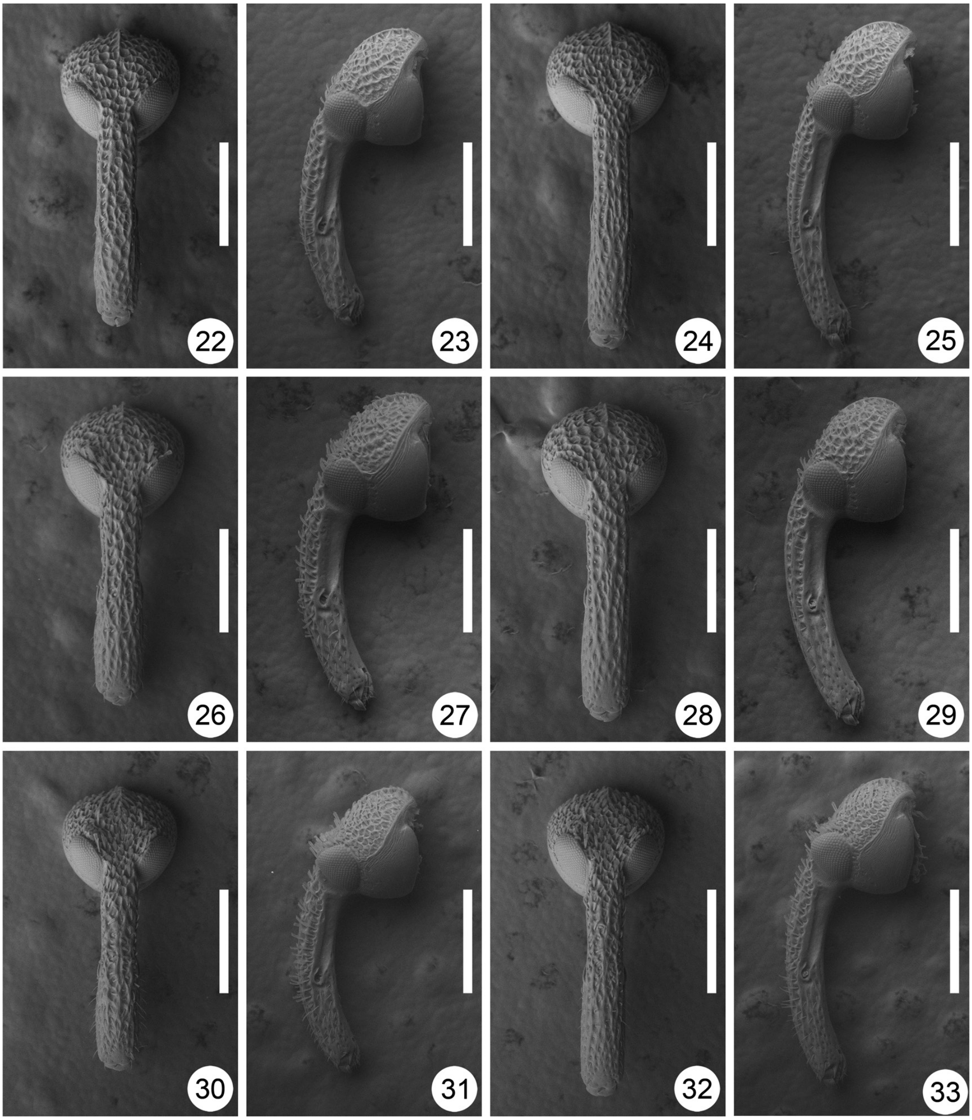


Figures 7–21. Diagnostic characteristics of *Scleropteroides*. **7** Head, dorsal view **8** Head, lateral view **9** Antenna **10** Prothorax **11** Body, dorsal view **12** Body, lateral view **13** Body, ventral view **14** Metendosternite **15** Legs **16** Base of hind-tibia, showing extensor and flexor tendons **17** Tarsus **18** Tarsomere V, lateral view **19** Hind wing **20** Tergites **21** Tergite VII. Scale: 1.00 mm for **7, 8, 10–13, 16, 19–20**; 0.75 mm for **15, 20**; 0.50 mm for **9, 14, 17–18, 21**.

68) robust, subdivided into two pieces, nearly 7.0 × as long as styli; styli apicolaterally inserted, moderate in length, nearly 2.0 × as long as wide. Spermatheca (Figs 49, 59, 69) with cornu slender, strongly curved and slightly attenuate; collum slightly convex; ramus indistinct; insertions of duct and gland close to each other.

Otherwise as in male.

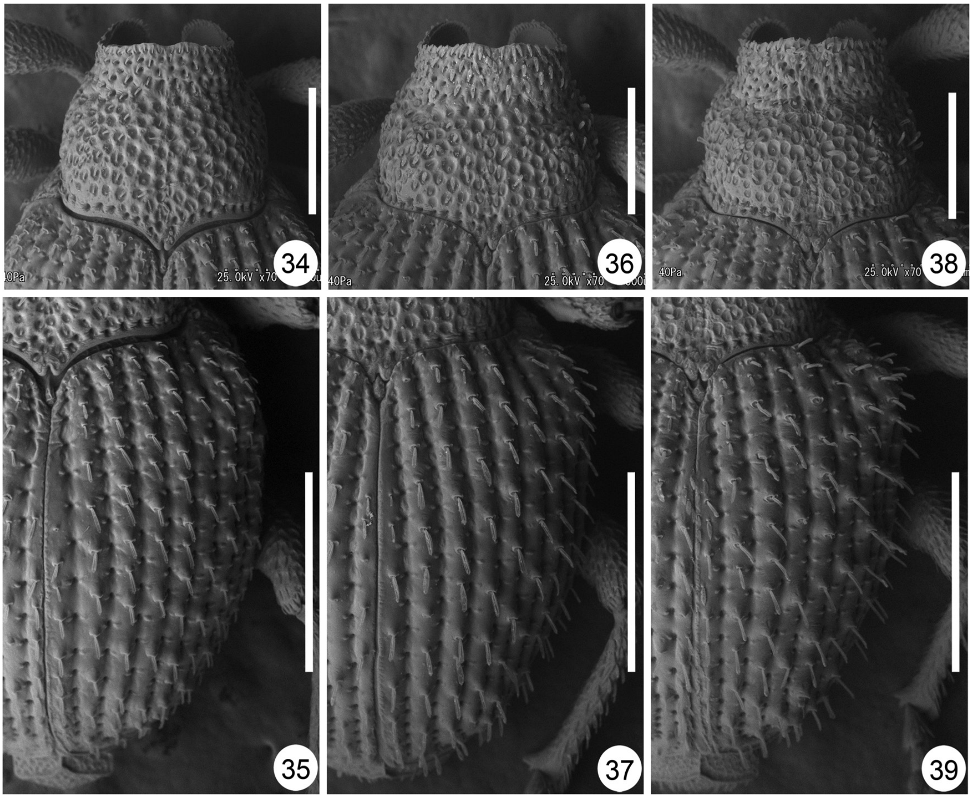
Material examined. HOLOTYPE: 1 female (MNHN), “Mont Takao/près Hachiôji/Japon 30-5-08/Edme Gallois; MUSEUM PARIS/NIPPON MOYEN/E. GALLOIS 1912; *Ceuthorrhynchidius/hypocritus/Hust./type*” (hand written). HOLOTYPE OF RHYTIDOSOMUS (RHYTIDOSOMUS) HOLDHAUSI WAGNER, 1944: 1 male (NHMV), "*Rorelz/1875/Süd/Japan*" (hand-written on grayish card); "♂" (typed on white card); "Typus" (typed on orange card); "*Hÿshichosoma/*det.H.Wagner/ *Holdhausi m./Tÿpe!* ♂" (hand-written in red on white card, partially typed); "TYPUS" (typed on red card); "*Holdhausi/Jap. Wagn.*" (hand-written on grayish card); "*Scleropteroides/hypocrita (Hustache, 1916)*/E. Colonnelli det. 19*91*" (hand-written on white card, partially typed). **CHINA: Liaoning.** 1 male and 1 female, Benxi, 41°17'N, 123°44'E, 3-VI-1963, H. Li (IZCAS, IOZ(E)896779 and 896770). 1 male, Anshan, Qianshan, 41°05'N, 123°06'E, 9-VI-1963, H. Li (IZCAS, IOZ(E)896773). 1 male and 1 female, Fengcheng, Tongyuanpu, 40°17'N, 123°55'E, 30-VI-1963, H. Li (IZCAS, IOZ(E)896771–896772). **Heilongjiang.** 2 males and 2 females, Ercengdianzi, 45°26'N, 127°07'E, 15–22-VI-1941 (IZCAS, IOZ(E)896474–896477). **D.P.R. KOREA: Pyonganbukdo.** 1 female, Mt. Myohyang-San, Around Habiro, 200–550 m, 29-VI- 2009, C. Han (NIAES). **Pyeongyangjikhalsi.** PyongYang-City, around Mt. RyongAk-San, near Suna-river: 1 male and 2 females, 18-V-2012, C. Han (NIAES); 1 female, 19–22-V-2012, C. Han (NIAES). **R. KOREA: Gangwondo.** 3 males and 5 females, Chuncheongun, Dongmyeon, Gamjeongri, 21-V-1992, K. Morimoto (ELKU). 3 males and 1 female, Chuncheongun, 11-VI-1997, K. Morimoto (ELKU). **Gyeonggido.** Pocheongun, Kwangnung: 2 males and 3 females, 16-V-1984, K. Morimoto (ELKU); 1 male and 1 female, 14–19-V-1992, M. T. Chujo (ELKU). **Gyeongsangbukdo.** 1 male and 1 female, Yeonggi, 14-VI-1997, K. Morimoto (ELKU). **Gyeongsangnamdo.** 1 female, Mt. Jirisan, Daesungri, 8-VI-1991, J. D. Bae (ELKU). 1 female, Mt. Jirisan, Bycjum Valley, 9-VI-1983, Lee Lab (ELKU). 1 female, Mt. Jirisan, Yeongsinbong–Samsinbong, 17-VI-1994, H. Kojima (ELKU). 1 female, Mt. Jirisan, Piagol, 30-V-2000, H. Yoshitake (NIAES). 1 male, Mt. Jirisan, Simweon, 31-V-2000, S. Kamitani (NIAES). 1 male, Mt. Jirisan, 31-V-2000, H. Yoshitake (NIAES). Hamyanggun, Macheonmyeon, Samjeongri, Mt. Jirisan: 2 males and 2 females, 9-V-1991, J. D. Bae (ELKU); 1 male, 9-V-1991, K. Morimoto (ELKU); 3 females, 11-V-1991, J. D. Bae (ELKU); 2 males and 3 females, 15-V-1991, J. D. Bae (ELKU); 4 males and 1 female, 6-VI-1991, J. D. Bae (ELKU); 2 males and 2 females, Samjeongrurak, 7-VI-1991, J. D. Bae (ELKU); 1 male, 14-VII-1991, K. Morimoto (ELKU); 13 males and 17 females, 15-V-1991, K. Morimoto (ELKU); 6 males and 6 females, 14-VI-1994, H. Kojima (NIAES); 5 females, 516 m, 35°21'09.2"N, 127°38'58.8"E, 5-V-2005, H. Yoshitake, on *Rubus crataegifolius* (NIAES). **Jeollabukdo.** 1 male and 1 female, Namwongun, Manbok Valley, 1-VI-1991, J. D. Bae (ELKU). 1 male and 5



Figures 22–33. Heads of *Scleropteroides* spp. **22–25** *S. hypocrita* (Hustache) **26–29** *S. longiprocessus* Huang & Yoshitake, sp. n. **30–33** *S. horridulus* (Voss) **22, 23, 26, 27, 30–31** Male **24, 25, 28, 29, 32–33** Female **22, 24, 26, 28, 30, 32** Dorsal view **23, 25, 27, 29, 31, 33** Lateral view. Scale: 0.50 mm.

females, Namwongun, Deongdong Valley, 7-VI-1991, J. D. Bae (ELKU). 1 male, Namwongun, Nogodan, 12-VII-1991, J. D. Bae (ELKU). 3 males and 1 female, Namwongun, Deongdongri, 19-VI-1994, H. Kojima (ELKU). Namwongun, Sannaemyeon, Simwon Valley: 1 female, 10-V-1991, K. Morimoto (ELKU); 1 male and 3 females, 13-V-1991, J. D. Bae (ELKU). Namwongun, Sannaemyeon, Jeonglyongchy: 2 females, 12-V-1991, K. Morimoto (ELKU); 1 male and 1 female, 14-V-1991, K. Morimoto (ELKU); 1 male and 1 female, 5-VI-1991, J. D. Bae; 1 male, 12-VI-1991, J. D.

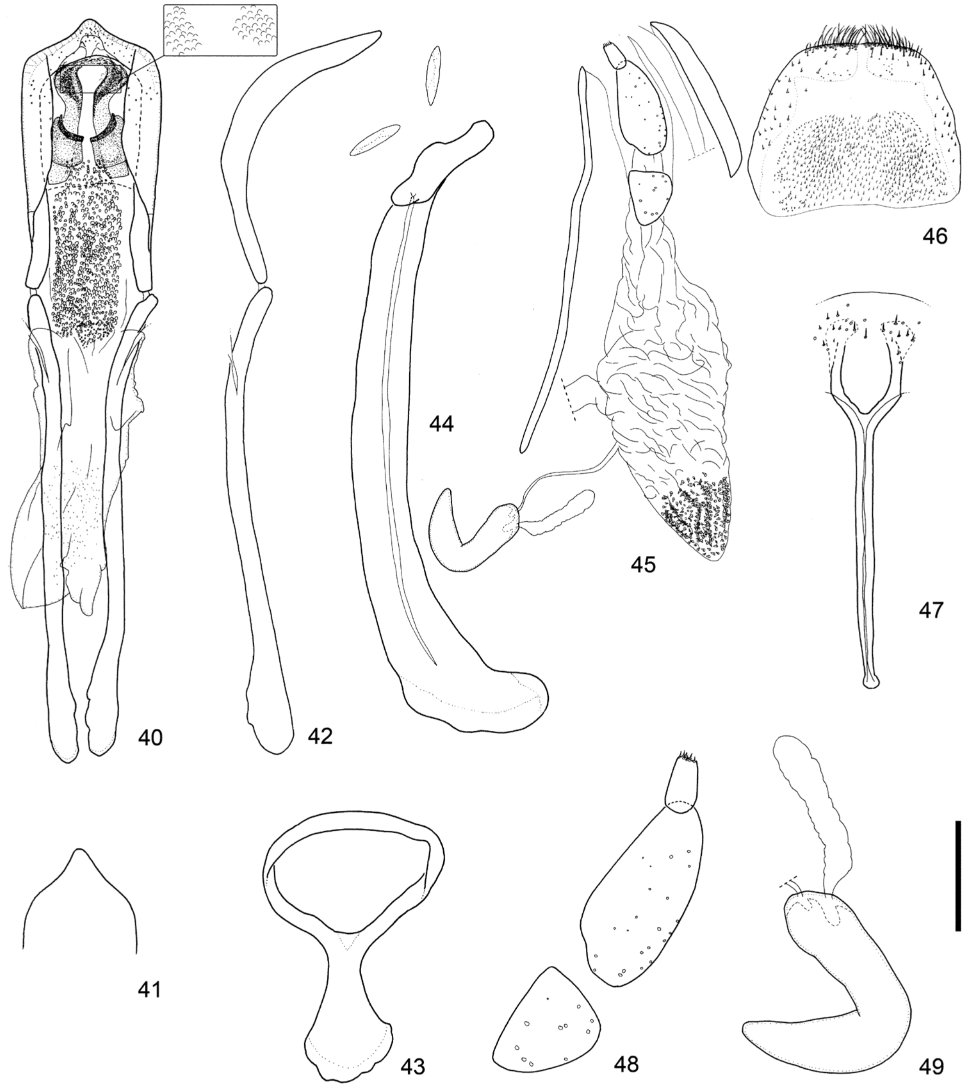
Bae (ELKU). **JAPAN: Hokkaido.** 1 male, Hidaka, 11-VII-83, Y. Shiozaki (YS). 8 males and 4 females, Taisei, Hirahama, 7-VI-2003, T. Miyata (NIAES). 1 male and 1 female, Kamiiso, Tomigawa, Hosokomatazawa, 27-VI-1993, T. Miyata (NIAES). 1 female, Fukushima, Mitake, 13-VI-1998, H. Yoshitake (NIAES). 1 male and 2 females, Assabuchou, Shimizu, 14-VI-1998, H. Yoshitake (NIAES). **Honshu.** AOMORI. Shimokita-hantou Peninsula, Oohata, Yunomata: 1 female, 16-VII-1956, K. Morimoto (ELKU); 1 female, 26-VII-1956, K. Morimoto (ELKU). 1 male and 1 female, Misawa, Yachigashira, 7-VI-2007, K. Morimoto (NIAES). 1 male, Hachinohe, Tanesashi-kaigan, 10-VI-2007, K. Morimoto (NIAES). IWATE. 1 male and 2 females, Miyako, Kamegamori, 15-VI-1986, K. Emoto (NIAES). 2 females, Sawauchi, Yasugasawa, 31-V-1998, H. Yoshitake (NIAES). 2 males and 1 female, Hanamaki, Toyosawa-rindou, 338–313 m, 39°28'36.2"–39°29'08.6"N, 140°56'15.7"–140°56'32.9"E, 8-VI-2007, H. Yoshitake, on *R. crataegifolius* (NIAES). 1 male and 1 female, Kawai, Yoshibezawa, 9-VI-2007, K. Morimoto (NIAES). 1 male, Kuji, Ootsuki-touge Pass, 10-VI-2007, K. Morimoto (NIAES). 1 male and 3 females, Kawai, Tsuchisaka-touge Pass, 12-VI-2007, J. Kantoh (NIAES). 1 male, Matsukusa, 800 m, 21-VI-1989, M. J. Sharkey (CMN). 3 males and 2 females, "Mt. Hyacinthe" (most probably an error in writing Mt. Hayachine), 500 m, 21-VI-1989, M. J. Sharkey (CMN). MIYAGI. 1 male and 3 females, Marumori, Fudou, 5-V-1994, H. Yoshitake (NIAES). 1 female, Shichigashuku, Inago, 20-V-1994, H. Yoshitake (NIAES). 1 female, Shiroishi, Mizubashounomori, 27-VI-1994, H. Yoshitake (NIAES). AKITA. Lake Tazawako: 2 females, 4-VI-1969, S. Miyakawa (SM); 3 males, 12-VI-1971, S. Miyakawa (SM); 1 male and 1 female, 15-VI-1971, S. Miyakawa (SM). 3 males and 2 females, Karabuki-shitsugen, Kuroyu, 12-VI-1974, S. Miyakawa (SM). 2 females, Hiyagata–Kunimi-onsen, 16-VI-1974, S. Miyakawa (SM). 3 males and 2 females, Senboku, Nishiki, Ainai, 10-VI-1983, S. Miyakawa (SM). YAMAGATA. 1 female, Yonezawa, Kariyasu, 15-VI-1975, S. Miyakawa (SM). 5 males and 4 females, Mt. Zaousan, Yoshikari-rindou, 18-VI-1983, S. Miyakawa (SM). 1 male, Oguni, Kotamagawa, 300 m, 6-VI-2005, H. Hirano (NIAES). 1 female, Oguni, Tamagawa, 120–150 m, 6-VI-2005, H. Hirano (NIAES). FUKUSHIMA. 1 female, Kamitoriwata, 20-VI-1976 (NIAES). Iwaki, Eda: 2 males and 1 female, 25-V-1980, Y. Shiozaki (YS). 3 males and 3 females, Minamiaizu, Funamata-rindou, 20-V-1983, S. Miyakawa (SM). 2 males, Namie, 30-IV-1994, H. Yoshitake (NIAES). Haranomachi, Yokokawa, Akane-rindou: 1 male, 15-VI-1984, K. Kinugasa (NIAES); 1 male, 31-V-1987, H. Ebihara (NIAES). Haranomachi, Kozikiishi-rindou: 11 males and 28 females, 4-VI-1988, S. Miyakawa (SM); 1 male, 4-VI-1988, S. Miyakawa (NIAES); 14 males and 9 females, 5-VI-1988, S. Miyakawa (SM). Hinoemata: 1 male, 14-VI-1980, Y. Shiozaki (YS); 1 female, 20-VI-1990, H. Kojima (ELKU); 2 females, Mikawa-rindou, 24-VI-1990, K. Yoshihara (SM). 1 male and 1 female, Nishigou, Yukiuribashi, 3-V-2002, S. Mizunoya (NIAES). 1 female, Nishigou, Daijou, 22-V-2002, S. Mizunoya (NIAES). Nishigou, Mabune: 1 male and 2 females, 650 m, 3-VI-2005 (NIAES), H. Hirano; 1 male and 1 female, 770 m, 3-VI-2005, H. Hirano (NIAES); 6 males and 8 females, 3-VI-2005, H. Yoshitake, on *Rubus* sp. (NIAES). IBARAKI. 3 males and 7 females, Mt. Yamizosan, Shimoki-



Figures 34–39. Pronotum and right elytron of *Scleropteroides* spp., male. **34–35** *S. hypocrita* (Hustache) **36–37** *S. longiprocessus* Huang & Yoshitake, sp. n. **38–39** *S. horridulus* (Voss) **34, 36, 38** Pronotum **35, 37, 39** Right elytron. Scale: 0.50 mm.

tazawa, 28-V-1988, Y. Kurosawa (SM). 1 female, Takahagi, 29-V-1996, H. Takizawa (NIAES). TOCHIGI. 1 female, Mt. Sukaizan, 4–5-VII-1971, H. Takizawa (NIAES). 1 male and 1 female, Nishinasuno, 8-V-1977, S. Miyakawa (SM). 4 males and 3 females, Nikko, Kashiwagi, 16-V-1982, S. Miyakawa (SM). 1 male, Nikko, Nebazawadani, 19-VII-1940, S. Miyakawa (SM). 1 male, Fujiwara, Midorizawa-rindou, 21-V-1989, S. Miyakawa (SM). 1 female, Nasu, Toyahara, 13-VII-1996, H. Takizawa (NIAES). 1 female, Nasu, Mt. Minamigassan, 20-VII-1996, H. Takizawa (NIAES). 2 males and 1 female, Nasu-kougen, 1200–1500 m, 7-VI-2005, H. Hirano (NIAES). 4 males and 3 females, Nishinasuno, N. G. R. I., 500 m, 10-VIII-1989, M. J. Sharkey (CMN). GUNMA. 1 male and 1 female, Utsunomiya, 6-V-1968, H. Takizawa (NIAES). 2 females, Mt. Hotakayama, 13–15-VII-1975, H. Irie (ELKU). 1 female, Akagi, 21-V-1967 (SM). 1 male, Akagi, Akagi-shizenen, 9–10-V-1988, S. Saito (NIAES). 1 female, Akagi, Mt. Akagisan, 3-VI-1997, T. Ishikawa (NIAES). 1 male, Oku-tone, Lake Fujiwarako, 13-V-1990, S. Tsuyuki (NIAES). 4 males and 5 females, Niiharu, Amemi-rindou, 4-V-1998, S. Arai (NIAES). 5 males and 5 females, near Mt. Aneyama, 19-V-2001, S. Arai (NIAES). Matsuida, Kirizumi-onsen: 1 female, 27-V-1989,

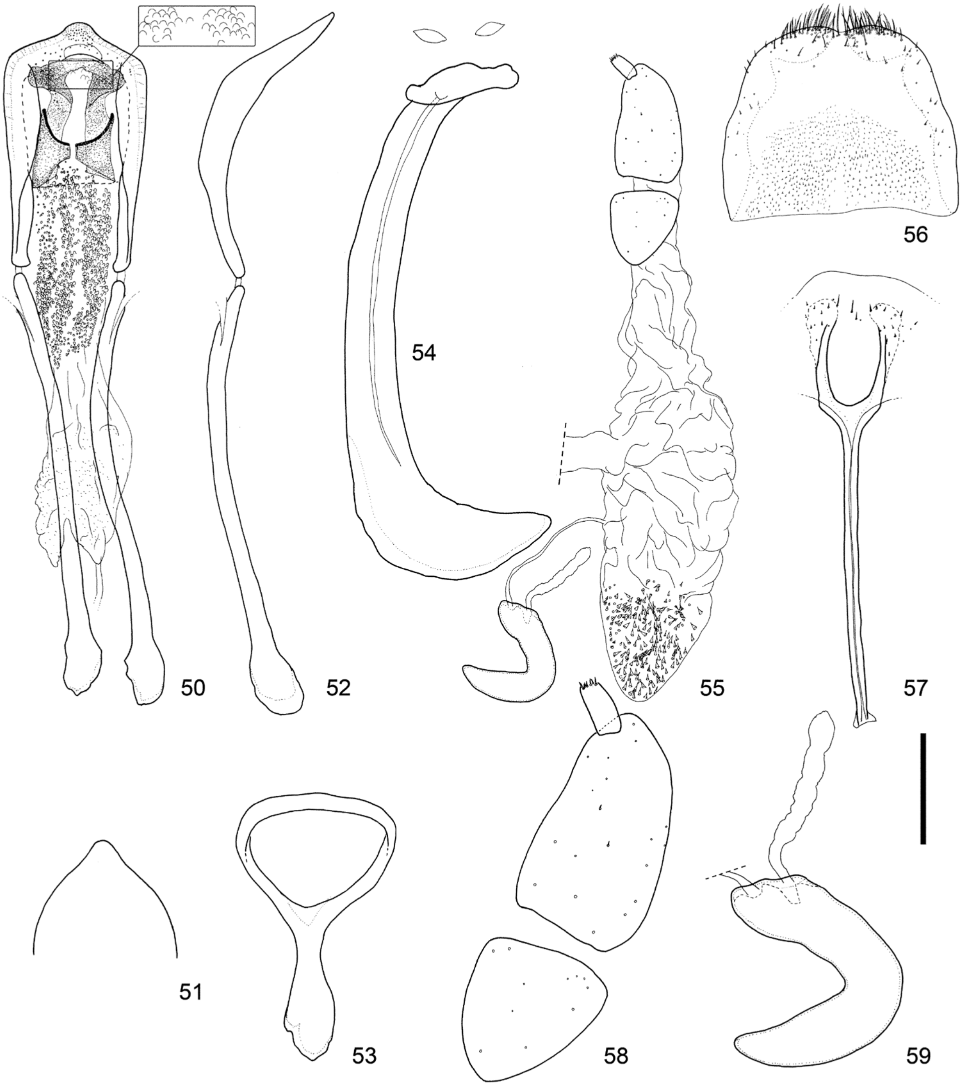
K. Matsumoto (NIAES); 1 male and 1 female, 27-V-1989, H. Kojima (NIAES); 1 male and 1 female, 17-V-1998, S. Arai (NIAES). SAITAMA. 2 males and 2 females, Shoumaru-touge Pass, 9-V-1976, S. Miyakawa (SM). 1 male, Minano, Shimohino-zawa, Sawabe, 1-VI-1984, S. Miyakawa (SM). 1 female, Ootaki, near Taiyouji, 4-VII-1999, S. Arai (NIAES). CHIBA. 4 males and 2 females, Mt. Kiyosumiyama–Kenmin-nomori, 31-III-1979, J. Okuma (SM). 1 female, Bousou-hantou Peninsula, Mt. Kiyosumiyama, 30-IV-1991, S. Tsuyuki (NIAES). TOKYO. 1 male, Mitakadai, 30-V-1941, S. Miyakawa (SM). 1 male and 1 female, Mitaka, 25-V-1948, S. Miyakawa (SM). Mt. Oodakeyama: 1 male and 2 females, 21-V-1942, S. Miyakawa (SM); 4 males and 2 females, 24-V-1942, S. Miyakawa (SM). 1 female, Mt. Mitakesan, 15-V-1966 (SM). 1 female, Itsukaichi, Kariyose, 20-IV-1968, Y. Hasegawa (SM). Mt. Mitousan: 1 female, 4-V-1968, H. Takizawa; 1 male and 1 female, 27-V-1968, H. Takizawa (NIAES). 2 males and 2 females, Mt. Jinbasan, 6-V-1974, S. Miyakawa (SM). 1 male, Hinohara, Yazawa-rindou, 18-V-1997, H. Yoshitake (NIAES). Hachiouji: 3 males and 1 female, 1-V-1938, S. Miyakawa (SM); 1 male and 1 female, 1-V-1966 (SM); 2 males, 1-V-1966, S. Miyakawa (SM). Hachiouji, Uratakao, Kogesawa-rindou: 1 male, 30-IV-1938, S. Miyakawa (SM); 2 males and 2 females, 350–550 m, 35°38'30"–35°39'27" N, 139°11'57"–139°14'30" E, 17-V-2005, H. Yoshitake, on *R. crataegifolius* (NIAES). Okutama: 1 female, 9-V-1968, Hasegawa (SM); 1 male, 29-IV-1980, Y. Shiozaki (YS). 3 males and 4 females, Okutama, Kurasawadani, 6-V-1948, S. Miyakawa (SM). 2 males and 5 females, Okutama, Nippara, 24-V-1970, K. Unno (SM). 1 male and 1 female, Okutama, Unazawa, 7-V-1982, K. Shiozaki (YS). 2 males and 1 female, Okutama, Asamaone, 2-V-1992, K. Matsumoto (NIAES). KANAGAWA. 1 male, Yokohama, Motomachi, 29-VI-1970, S. Miyakawa (SM). 2 females, Hakone, Mt. Daigatake, Kozuka, 24-V-1979, S. Miyakawa (SM). Hadano, Mizunashigawa: 1 male, 29-IV-1983, K. Shiozaki (YS); 1 male, 29-IV-1983, Y. Shiozaki (YS). 1 female, Hadano, Yabitsu-touge Pass, 30-V-1983, K. Shiozaki (YS). 1 male, Yamakita, Mikuni-touge Pass, 23-V-1994, Y. Notsu (NIAES). 1 female, Tsukui, Kaminokawa-rindou, 21-V-1995, Y. Goto (NIAES). NIIGATA. 1 male, Kamikawa, 3-VI-2000, K. Takahashi (NIAES). FUKUI. 2 males and 5 females, Kanazu, Mt. Kariyasuyama, 20-V-1989, S. Inoue (ELKU). YAMAMASHI. 1 female, Mt. Mishotaisan, 17-VII-1940, S. Miyakawa (SM). 1 male and 1 female, Shirosu, 7-VI-1958 (ELKU). 1 female, Uenohara, 17-IV-1968 (SM). 1 male, Kawamura, Akiyama, 4-V-1969, S. Miyakawa (SM). 1 male, Lake Saiko, 27-V-1970, K. Unno (SM). 1 female, Ootsuki, Tomioka, 17-V-1976, S. Miyakawa (SM). 14 males and 19 females, Ootsuki, Koganezawa-rindou, 30-V-1980, J. Okuma (SM). 1 female, Mt. Fujisan, Subaru-line, 2000 m, 3-VI-1977, S. Miyakawa (SM). 1 female, Mt. Yatsugatake, 26-V-1979, A. Seki (NIAES). 16 males and 14 females, Koganezawa, 2-VI-1980, S. Miyakawa (SM). 1 female, Daibosatsu-touge Pass, 8-VI-1968, Y. Hasegawa (SM). Enzan, Hikawa-rindou: 1 male, 1-VII-1982, M. Sawai (SM); 1 male and 1 female, 2-VII-1982, M. Sawai (SM). 1 female, Mt. Kushigatayama, Maruyama-rindou, 23-IV-1984, S. Tsuyuki (NIAES). 2 males, Akeno, Manjuu-touge Pass, 6-VI-1986, S. Miyakawa (SM). 1 male, Kanayama, 1-VII-1989, T. Nonaka (NIAES). Ashiyasu, Hirogawara: 1 male, 24-V-1969, Y.



Figures 40–49. Male and female terminalia of *Scleropteroides hypocrita* (Hustache) from Takaosan, Japan. **40** Aedeagus, dorsal view **41** Apex of the penis, dorsal view **42** Aedeagus, lateral view **43** Tegmen **44** Sternites VIII and IX, male **45** Female terminalia and genitalia, lateral view. **46** Tergite VIII, female **47** Sternite VIII, female **48** Coxite and stylus. **49** Spermatheca. Scale: 0.20 mm for **40–47**, 0.10 mm for **48–49**.

Hasegawa (SM); 1 female, 8-VI-1989, H. Kojima (NIAES); 1 male and 1 female, 1529 m, 17-VI-1990, S. Miyakawa (SM); 1 female, 20-VI-1993, T. Horiguchi (NIAES). 1 male and 1 female, Nirasaki, Mt. Kayagatake, 16-V-1996, S. Miyakawa (SM). 1 female, Tabayama, Sanjounoyu, 20-V-1999 (NIAES). NAGANO. 1 female, Mt. Nyuukasayama, 6-VI-1942, S. Miyakawa (SM). 1 male and 3 females, Nagano, Uematsu, VI-1957, K. Matsuo (SM). 1 male and 1 female, Ina, Onasawa, 6-VI-1962, K. Oshima

(ELKU). 1 male, Shimajimadani, VI-1970, N. Nino (SM). 1 female, Tobira-onsen, 26-VI-1974, H. Hayakawa (SM). 1 female, Kisofukushima, Higashiyama, 19-VII-1986, K. Matsui (SM). 1 female, Kisofukushima, 21-VIII-1988, K. Matsui (SM). 1 female, Kisofukushima, Uyama, 29-VIII-1988, K. Matsui (SM). 1 male, Kisofukushima, Kibio, 18-IX-1988, K. Matsui (SM). 1 male and 1 female, Kisokoma-kougen, Kibio, 21-VIII-1989, K. Matsui (SM). 1 male and 2 females, Nakakawa, 1-V-1998, H. Yoshitake (NIAES). 1 female, Hara, Pension Village, 2–4-VII-1998, H. Yoshitake (NIAES). GIFU. 1 male, Mt. Hakusan, 29-VI-2002, H. Hirano (NIAES). 1 female, Takane, Hiwada-kougen, 1-X-1989, K. Matsui (SM). 6 exs., Toki, 12-V-2010, K. Izawa, on *R. trifidus* (KI). SHIZUOKA. 1 female, Shinfuji, 30-IV-1989, N. Niwa (NIAES). 1 female, Honkawane, Sessokyou, 9–10-V-1992, T. Kishimoto (NIAES). Izu-hantou Peninsula: 2 males and 1 female, Kyuu-amagi-touge Pass, 3-V-1972, S. Miyakawa (SM); 2 males and 3 females, Mt. Nekkodake, 19-V-1974, S. Miyakawa (SM); 21 males and 16 females, Okuhara-rindou, 22-VI-1977, J. Okuma (SM); 2 females, Mt. Toogasayama, 17-V-1980, J. Okuma (SM); 1 male, Izu Okawa, 3-VI-1989, H. Takizawa (NIAES). AICHI. 8 males and 6 females, Kasugai, Hosono, 1-V-1991, H. Kojima (ELKU). Toyota, on *R. trifidus*: 5 exs., Oobora, Nikake-rindou, 3-V-2010, K. Izawa (KI); 6 exs., Nishiichinonochou, 8-V-2013, K. Izawa (KI); 7 exs., Asugawachou, Asugawa-hoan-rindou, 8-V-2013, K. Izawa (KI). MIE. Misugi, Hirakura: 1 male, 2-VI-1985, T. Imamura (NIAES); 3 females, 600–700 m, 15–17-V-2005, H. Hirano, on *R. crataegifolius* (NIAES). 1 male, Fujigawa, Mt. Suzugadake, 600 m, 3-V-2002, S. Arai (NIAES). 4 exs., Komonochou, Komono, 15-V-2013, K. Izawa, on *R. microphyllus* (KI). SHIGA. 1 male and 1 female, Mt. Ibukiyama, 220 m, 3-VI-1990, S. Miyakawa (SM). KYOTO. 1 male, Sugi-touge Pass, 29-V-1977, M. Sawai (SM). HYOGO. 1 male, Haga, Akasai-keikoku, 3-V-1993, S. Tsuyuki (NIAES). NARA. 1 female, Gose, Mt. Kongousan, 1100 m, 4-VII-1998, T. Kishimoto (NIAES). WAKAYAMA. 1 male and 1 female, Mt. Gomadanzan, 7–8-VI-1997, T. Ito (NIAES). 1 female, Nakahechi, Mizukami, 28-IV-2003, H. Hirano (NIAES). 1 male, Arida, Kamiyukawa, 19-V-1973, I. Matoba (ELKU). TOTTORI. 1 male and 1 female, Wakasa, Mt. Hyounosen, 7-VI-1987, K. Yoshihara (SM). SHIMANE. 1 female, Okinoshima I., Mt. Takuhiyama, 13-V-1975, J. Okuma (SM). OKAYAMA. 4 males and 1 female, Yubara, Yubara-onsen, 21-V-1991, H. Nakamura (NIAES). 1 male, Hokubou, Kamimizuta, 8-V-1982, K. Yoshihara (SM). 1 female, Iwayadani, 4-V-1981, K. Yoshihara (SM). 1 male and 1 female, Kawakami, Myouren-keikoku, 27-VI-1982, K. Yoshihara. HIROSHIMA. 1 female, Kouzan, Bessako, 10-V-1996 (ELKU). 1 female, Yoshiwa, 11-V-1976, K. Baba (ELKU). **Shikoku.** TOKUSHIMA. 1 male, Sanuki Mts., Mt. Ryuuousan, 17-VIII-1989, K. Matsumoto (NIAES). EHIME. 5 males and 5 females, Omogokei, 18–19-V-1968, K. Hatta (EUMJ). 1 male, Iyomishima, Tomisato, 3–5-VIII-1974, G. Tokihiro (EUMJ). 4 males and 6 females, Houjou, Kukawa, 22-IV-1977, A. Oda (EUMJ). **Kyushu.** FUKUOKA. Mt. Hikosan: 1 male, 18-VI-1965, K. Takeno (ELKU); 1 female, 12-VI-1965, S. Kimoto (ELKU); 1 female, 17-V-1971, M. T. Chujo (ELKU); 2 males and 1 female, 30-V-1995, K. Morimoto (ELKU). 1 male, Mt. Tachibanayama, 23-IV-1997, H. Kojima



Figures 50–59. Male and female terminalia of *Scleropteroides hypocrita* (Hustache) from Mt. Jirisan, Korea. **50** Aedeagus, dorsal view **51** Apex of the penis, dorsal view **52** Aedeagus, lateral view **53** Tegmen **54** Sternites VIII and IX, male **55** Female genitalia, lateral view **56** Tergite VIII, female **57** Sternite VIII, female **58** Coxite and stylus **59** Spermatheca. Scale: 0.20 mm for **50–57**, 0.10 mm for **58–59**.

(ELKU). SAGA. 1 female, Sefuri Mts., 28-IV-2002, H. Hirano (NIAES). 16 males and 13 females, Mt. Kusenbuyama, Hakotani-rindou, 8-V-2005, H. Yoshitake, on *R. crataegifolius* (NIAES). NAGASAKI. Tsushima I.: 1 female, Mt. Ooboshiyama, 16-VII-1981, Y. Syouno (ELKU); 1 male, Izuhara, Mt. Ariakeyama, 5–9-V-1997, H. Yoshitake (NIAES). 2 males and 1 female, Tashirobaru, 29-IV-1979, S. Imasaka (NIAES). 1 male, Taradake Mts., Mt. Gokaharadake, 12-VI-1979, S. Imasaka (NIAES).

Shimabara, Sanbuki: 1 male and 1 female, 7-V-1976, S. Imasaka (NIAES); 1 male, 10-V-1976, S. Imasaka (NIAES); 6 females, 17-V-1976, S. Imasaka (NIAES); 1 female, 21-V-1976, S. Imasaka (NIAES); 1 male and 2 females, 22-V-1976, S. Imasaka (NIAES). Shimabara, Akamatsudani: 3 females, 24-V-1980, S. Imasaka (NIAES); 1 male, 27-V-1980, S. Imasaka (NIAES). 2 females, Sasebo, Mt. Hattendake, 23-V-1982, S. Miyakawa (SM). 3 males and 2 females, Kawatana, Kobagou, 27-V-1984, J. Okuma (SM). OITA. Kuju Mts., Mt. Kurodake: 1 female, 29-VII-1979, S. Imasaka (NIAES); 1 male, 9-VI-1985, K. Konishi (ELKU); 2 males, Oike-enchi, 7-VI-2002, H. Hirano (NIAES). 1 female, Kuju Mts., Jizoubaru, 28-V-1987, K. Morimoto (ELKU). 1 male, Kuju Mts., Bougatsuru, 27-V-1988, K. Morimoto (ELKU). 1 male and 2 females, Kuju Mts., Choujabaru, 22-V-1999, K. Morimoto (ELKU). MIYAZAKI. 1 male, Ebino, Shiratori-onsen, 30-IV-1991, K. Morimoto (ELKU).

Distribution. China (Liaoning and Heilongjiang – new record), Korea (North – new record, Central, South, and Ulreungdo Island), Japan (Hokkaido, Honshu, Izu Islands, Shikoku, Kyushu, and Tsushima Island) (Fig. 133).

Biological note. Adults of this common species were collected from *Rubus idaeus* L. subsp. *melanolasius* Focke f. *concolor* (Kom.) Ohwi in Korea (Korotyaev and Hong 2004). In addition, we collected a number of adults at several localities in the southern Korean Peninsula, mainly from *R. crataegifolius* Bunge with flower buds and *Rubus pungens* Camb. var. *oldhamii* (Miq.) Maxim. with flowers. In Japan, adults have been collected on many occasions from *Rubus* species, such as *R. crataegifolius*, *R. microphyllus*, and *R. trifidus*. In Toyosawa-rindou, Iwate, Honshu (Fig. 135), a number of adults (Fig. 138) were found on *R. crataegifolius* (Fig. 136) and observed feeding on the leaves and flowers of the plant (Fig. 137).

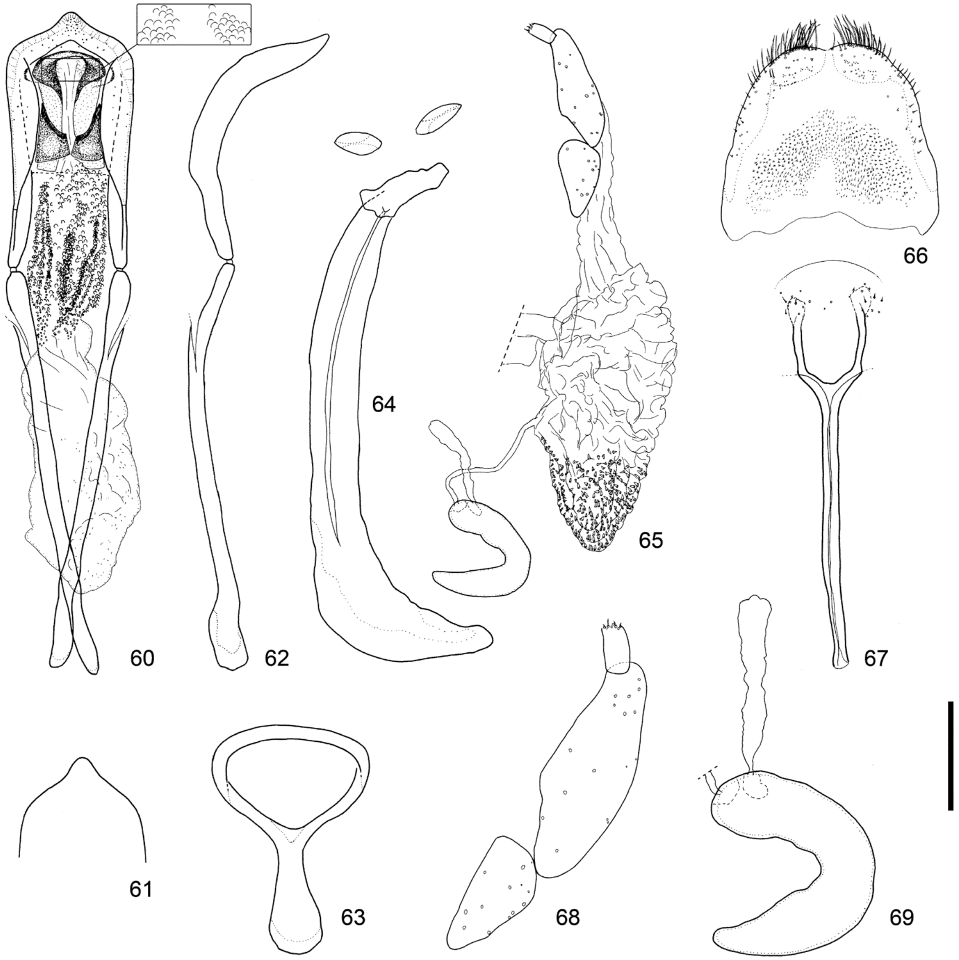
Scleropteroides longiprocessus **Huang & Yoshitake, sp. n.**

http://zoobank.org/C8AC65A6-71E7-4CD0-9387-CFA00B598B09

Figs 3, 4, 26–29, 36–37, 70–89, 134

Diagnosis. The species is very similar to *S. hypocrita* but is distinguished from it by the following characteristics: subapical part of the prothorax strongly constricted (Fig. 36); elytra with strongly prominent humeri, straightly convergent toward the subapical calli, (Fig. 37); scales in a row on elytral intervals semierect, nearly as long as the width of each interval (Fig. 37); apical half of the male rostrum slightly more widened (Fig. 26); male metaventrite more prominent ventrally along the apico-lateral margin of the metaventral receptacle; male ventrite I with no prominence; penis with a longer apical projection (Figs 71, 81); endophallus with a pair of narrow falcate sclerites in the basal part (Figs 70, 80); female sternite VIII with arms that are divergent apically (Figs 77, 87); bursa copulatrix without minute coniform spicules in the posterior part (Figs 75, 85).

Male. LB: 2.27–2.63 (mean, 2.39). LR: 0.97–1.08 (mean, 1.04). WP: 0.95–1.00 (mean, 0.97). LP: 0.76–0.85 (mean, 0.82). WE: 1.49–1.62 (mean, 1.57). LE: 1.53–1.66 (mean, 1.62). N = 10 for all measurements. Habitus as shown in Figs 3–4.



Figures 60–69. Male and female terminalia of *Scleropteroides hypocrita* (Hustache) from Heilongjiang, northeastern China. **60** Aedeagus, dorsal view **61** Apex of the penis, dorsal view **62** Aedeagus, lateral view **63** Tegmen **64** Sternites VIII and IX, male **65** Female genitalia, lateral view **66** Tergite VIII, female **67** Sternite VIII, female **68** Coxite and stylus **69** Spermatheca. Scale: 0.20 mm for **60–67**, 0.10 mm for **68–69**.

Vestiture. Clavate scales slightly longer and semierect on head, basal 2/3 of rostrum, and pronotum. Scales on elytral intervals (Fig. 37) semierect, slightly longer, 0.9–1.2 × as long as interval width.

Rostrum (Figs 26–27) slender, 1.21–1.32 × as long as pronotum; sides more strongly widened in apical part, which is 1.23 × as wide as basal part. Antennae (Fig. 27) with length ratio of funicular segments I: II: III: IV: V: VI = 1.88: 1.54: 1.12: 1.00: 0.96: 0.96 and width ratio = 1.73: 1.00: 1.36: 1.45: 1.45: 1.55.

Pronotum (Fig. 36) 1.13–1.27 × as wide as long, 0.47–0.52 × as long as and 0.59–0.65 × as wide as elytra; subapical constriction stronger; sides subparallel along basal half, then rapidly convergent toward apex.

Elytra 1.01–1.04 × as wide as wide, 1.92–2.14 × as long as and 1.54–1.69 × as wide as pronotum, straightly convergent toward subapical calli; humeral calli slightly more prominent; subapical calli moderately prominent.

Underside. Metaventrite moderately prominent ventrally along apico-lateral margin of metaventral receptacle. Ventrite I weakly flattened on disc, lacking prominence; length ratio of ventrites I: II: III: IV: V = 4.33: 2.00: 1.00: 1.13: 2.22 and width ratio = 1.89: 1.70: 1.23: 1.11: 1.00.

Genitalia. Tegmen (Figs 73, 83) with apodeme strongly widened toward apex. Penis (Figs 70–72, 80–82) thick in profile; sides more or less weakly widened from base to apical 1/5, strongly convergent apically; apical projection more slender. Endophallus (Figs 70, 80) with pair of narrow falcate sclerites in basal part.

Otherwise as in *S. hypocrita*.

Female. LB: 2.08–2.53 (mean, 2.34). LR: 0.97–1.15 (mean, 1.09). WP: 0.90–1.07 (mean, 0.97). LP: 0.74–0.86 (mean, 0.81). WE: 1.43–1.64 (mean, 1.54). LE: 1.46–1.68 (mean, 1.59). N = 10 for all measurements.

Rostrum (Figs 28–29) slightly more slender, 1.30–1.39 × as long as pronotum.

Pronotum 1.14–1.28 × as wide as long.

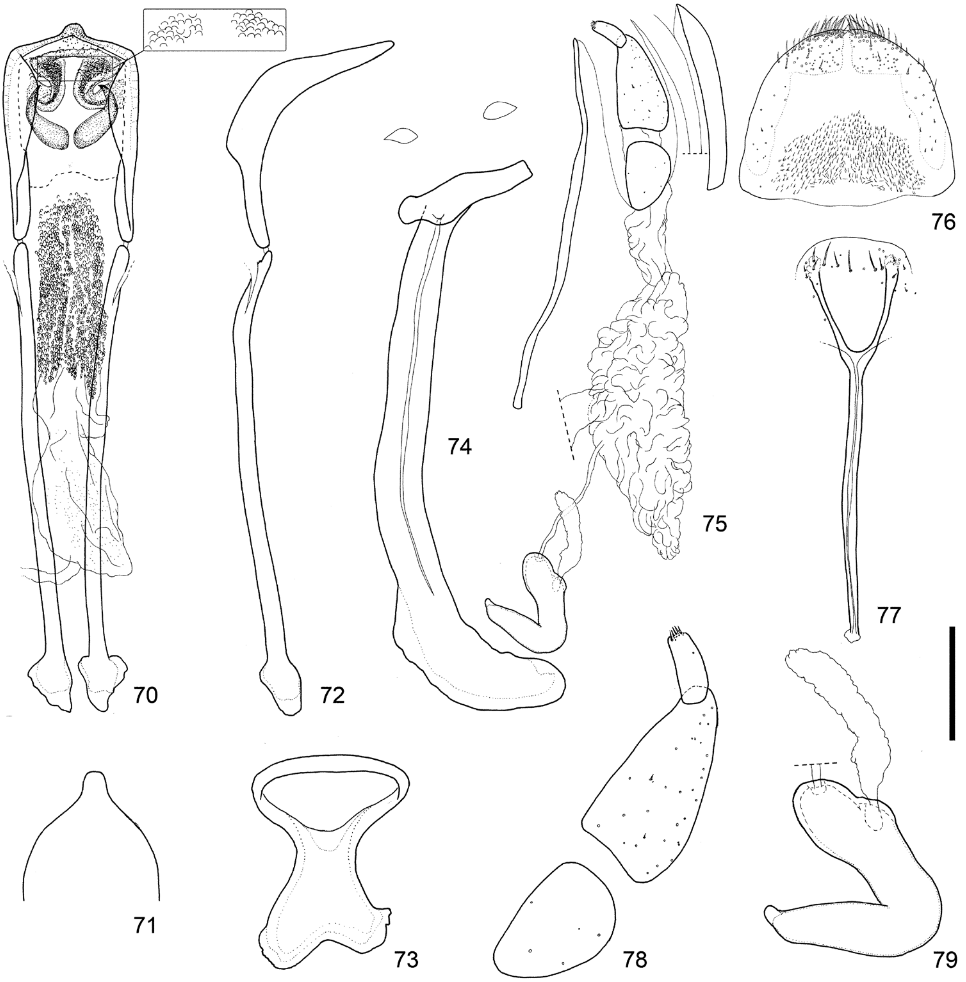
Elytra 1.01–1.08 × as long as wide.

Underside. Ventrite V with small median concavity, which is sometimes obscure. Sternite VIII (Figs 77, 87) with arms slightly more slender and apically divergent.

Genitalia. Bursa copulatrix (Figs 75, 85) lacking spicules. Coxites (Figs 78, 88) nearly 5.0 × as long as styli; styli more slender, nearly three times as long as wide. Spermatheca (Figs 79, 89) with collum more strongly convex; insertions of duct and gland slightly more distant from each other.

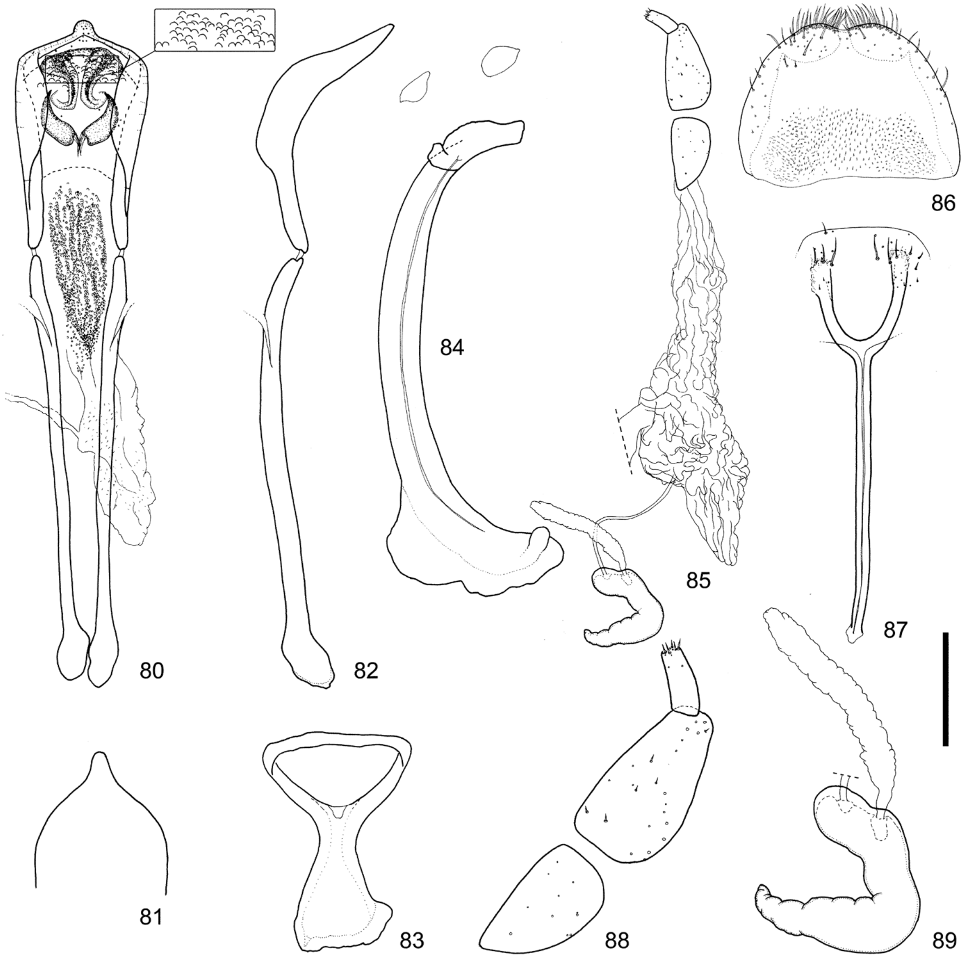
Otherwise showing almost the same sexual dimorphism as in *S. hypocrita*.

Type material. HOLOTYPE: 1 male (NIAES), "[Japan: Kyushu]/Mts. Sefuri-sanchi/Mt. Kusenbu-yama/8-V-2005/Hiraku Yoshitake" (printed on white card); "On *Rubus palmatus* Thunb. (Rosaceae)/[JN: Nagaba-momiji-ichigo] with flowers" (print ed on white card); "[HOLOTYPE] Male/*Scleropteroides*/*longiprocessus*/Huang & Yoshitake, 2008" (typed on red card). PARATYPES. **JAPAN: Honshu.** IWATE. 1 male and 1 female, Miyako, Genbehdaira, 9-VI-2007, K. Morimoto (NIAES). 2 males and 6 females, Tsuchisaka-touge Pass, Kawai, 12-VI-2007, J. Kantoh (NIAES). MIYAGI. 1 male, Naruse, Miyatojima I., V-1995, M. Kodama (NIAES). 1 male and 2 females, Sendai, Mt. Banzan, 20-V-1995, H. Yoshitake (NIAES). AKITA. 1 male and 1 female, Lake Tazawako, 15-VI-1974, S. Miyakawa (SM). YAMAGATA. 2 males and 3 females, Mt. Zaousan, Yoshikari-rindou, 18-VI-1983, S. Miyakawa (SM). FUKUSHIMA. Haranomachi, Kozikiishi-rindou: 1 male, 30-V-1987, H. Ebihara (NIAES); 1 male, 5-VI-1988, S. Miyakawa (SM). 1 female, Haranomachi, Akanesawa-rindou, 5-VI-1988, S. Miyakawa (SM). 1 female, Namie, 30-IV-1994, H. Yoshitake (NIAES). 1 male, Iizaka, Moniwa, Yakematsu, 1-V-1997, S. Saito (NIAES). IBARAKI. Mt. Yamizosan, Shimokitazawa: 7 males and 1 female, 1022 m, 28-V-1988, S. Miyakawa (SM); 1 male and 2 females, 28-V-1988, Y. Kurosawa (SM). TOCHIGI. 1 male and 2 females, Nikko, Kashiwagi, 16-V-1982, S.



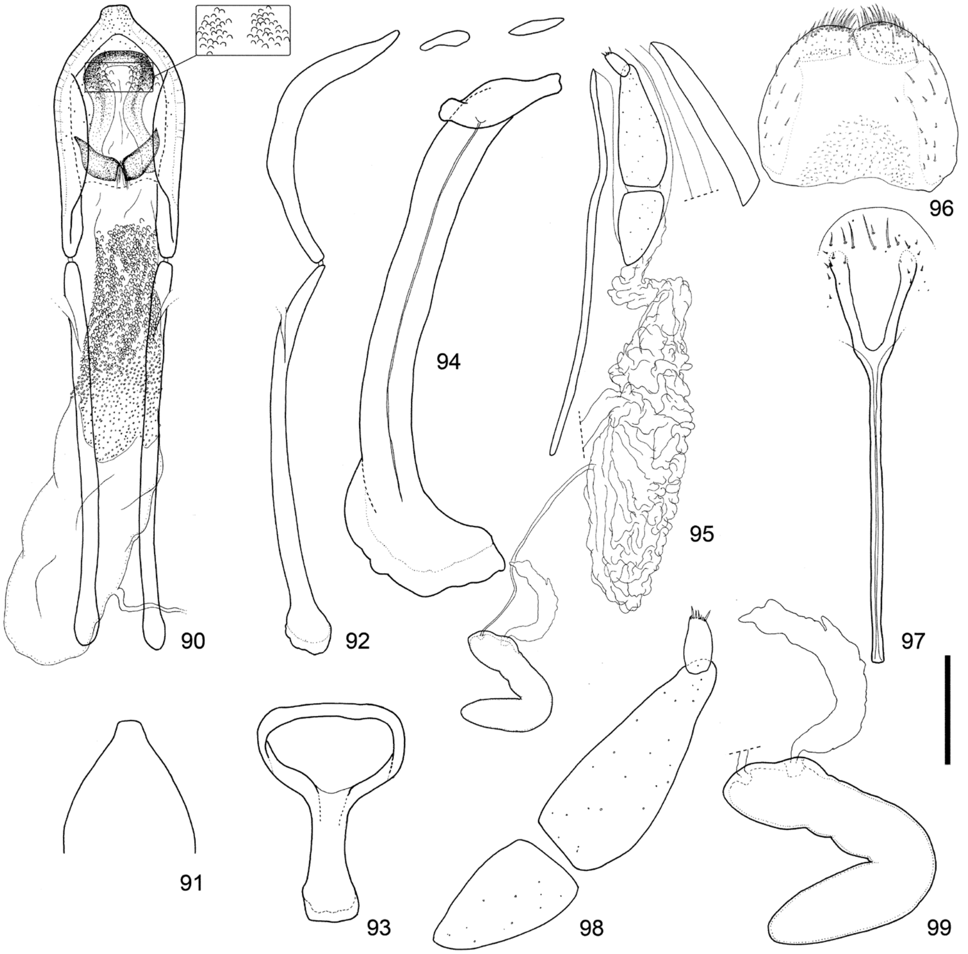
Figures 70–79. Male and female terminalia of *Scleropteroides longiprocessus* Huang & Yoshitake, sp. n. from Mt. Kusenbuyama, Kyushu, Japan. **70** Aedeagus, dorsal view **71** Apex of the penis, dorsal view **72** Aedeagus, lateral view **73** Tegmen **74** Sternites VIII and IX, male **75** Female terminalia and genitalia, lateral view **76** Tergite VIII, female **77** Sternite VIII, female **78** Coxite and stylus **79** Spermatheca. Scale: 0.20 mm for **70**–**77**, 0.10 mm for **78**–**79**.

Miyakawa (SM). 1 male and 1 female, Shiobara, Hikinuma, 19-V-1989, S. Miyakawa (SM). 3 males and 1 female, Mt. Shibakusayama, 18-V-1990, H. Kojima (ELKU). GUNMA. 1 male and 1 female, Matsuida, Kirizumi-onsen, 16-V-1998, S. Arai (NIAES). 2 males and 2 females, Niiharu, Amemi-rindou, 4-V-1998, S. Arai (NIAES). 1 female, Fujiwara, Nakanosawa-rindou, 19-V-1989, S. Miyakawa (SM). 6 males and 4 females, Fujiwara, Midorizawa-rindou, 29-V-1989, S. Miyakawa (SM). NIIGATA. Kurokawa: 1 female, 28-IV-1973, K. Baba (ELKU); 2 females, 26-V-1976, K. Baba (ELKU); 1 female, 24-V-1980, K. Baba (ELKU). 1 male and 1 female, Teradomari, Enjouji, 21–23-V-1996, K. Ishida (NIAES). 1 male, Sadogashima I., Nagaishihama, 22-VII-1970, K. Baba (ELKU). FUKUI. 2 males and 1 female, Obama, Shimonegouri, 6-V-1979, H. Sasaji (ELKU). YAMANASHI. 1 female, Mt. Fujisan, Fuji-rindou, 23-VI-1983, S. Miyakawa (SM). 1 male, Ootsuki, Nanaho, 9-V-1976, S. Miyakawa (SM). 1 female, Ootsuki, Koganezawa-rindou, 30-V-1980, J. Okuma (SM). NAGANO. 1 female, Tobira-onsen, 26-VI-1985, H. Hayakawa (SM). 5 males, Nagiso, 29-IV-1998, H. Yoshitake (NIAES). 2 males and 1 female, Iida, Hatouchi-rindou, 29–30-IV-1998, H. Yoshitake (NIAES). 2 males, Nakakawa, 1-V-1998, H. Yoshitake (NIAES). GIFU. Nakatsugawa, Kamisaka: 1 female, 13-VI-1987, S. Miyakawa (SM); 1 female, 13-VI-1987, K. Morimoto (ELKU). 5 exs., Nakatsugawa, Nenoue-kougen, 6-V-2013, K. Izawa, on *R. palmatus* var. *coptophyllus* (KI). SHIZUOKA. 1 female, Shinfuji, 30-IV-1989, N. Niwa (NIAES). 5 males and 6 females, Nakaizu, Mt. Amagisan, 3-V-1990, H. Kojima (ELKU). 1 male and 4 females, Mt. Ooyama, 5-V-1993, Y. Notsu (NIAES). 3 males and 1 female, Shizuoka, Umegashima, 15-V-1993, T. Kishimoto (NIAES). Izu-hantou Peninsula: 3 males and 1 female, Hacchouike Pond, Amagi-touge Pass, 28-V-1972, S. Miyakawa (SM); 1 female, Kamo, Oogusu, 11-V-1980, J. Okuma (SM); 1 female, Hacchouike Pond–Kantenbashi, 14-V-1980, J. Okuma (SM). 1 male, Umegashima, 15–16-V-1993, H. Sato (NIAES). 1 female, Shizuoka, Nakaizu, Amagi-kougen, 31-V-1987, S. Miyakawa (SM). AICHI. 6 exs., Shitara, Mt. Nishinagura-Iyama, 29-V-2010, K. Izawa, on *R. palmatus* var. *coptophyllus* (KI). Toyota, on *R. palmatus* var. *coptophyllus*: 5 exs., Nishiichinonochou, 8-V-2013, K. Izawa, (KI); 4 exs., Asugawachou, Asugawa-hoan-rindou, 8-V-2013, K. Izawa (KI); 2 exs., Inabuchou, Noirigawa, 22-V-2013, K. Izawa (KI). SAITAMA. 1 female, Mt. Kasayama, 26-V-1967, H. Takizawa (NIAES). 1 male, Saitama Yokote, 28-IV-1974, S. Miyakawa (SM). 1 female, Lake Miyazawako, 11-V-1975, S. Miyakawa (SM). 1 male, Shoumaru-touge Pass, 9-V-1976, S. Miyakawa (SM). CHIBA. 1 female, Mt. Kiyosumiyama–Kenminnomori, 31-V-1979, J. Okuma (SM). TOKYO. 1 female, Okutama, Kurasawadani, 19-VI-1938, S. Miyakawa (SM). Nishitama, Mt. Oodakeyama: 1 male, 21-V-1942, S. Miyakawa (SM); 2 males and 1 female, 15-V-1966, S. Miyakawa (SM). Hachiouji, Mt. Takaosan: 1 female, 30-V-1980, Y. Shiozaki (YS); 1 male and 1 female, 23-VI-1996, H. Yoshitake (NIAES); 5 exs., 22-V-2010, K. Izawa, on *R. palmatus* var. *coptophyllus* (KI). Hachiouji, Mt. Takaosan, Kogesawa-rindou: 3 males, 14-V-1944, S. Miyakawa (SM); 1 male and 1 female, 1–2-V-1999, H. Yoshitake (NIAES). 5 males and 5 females, Hachiouji, Mt. Takaosan, Path 6, 240–599 m, 35°37'30"–35°37'50"N, 139°14'36"–139°15'43"E, 15-V-2005, *R. palmatus* var. *coptophyllus*, H. Yoshitake (NIAES). 1 female, Hachiouji, Kitano, 14-IV-1968, S. Miyakawa (SM). 1 female, Inagi, Yomiuri Land, 17-V-1974, S. Miyakawa (SM). KANAGAWA. 1 male, Mikuni-touge Pass, 7-VI-1970, H. Takizawa (NIAES). 1 female, Mt. Ooyama, 2-VI-1981, S. Miyakawa (SM). 2 males, Yokohama, Nakayama, 3-V-1983, S. Miyakawa (SM). 1 female, Hakone, Oowakudani, 15-VI-1985, S. Tsuyuki (NIAES). Hadano: 1 female, Mt. Koubouyama, 24-IV-1983, Y. Shiozaki (YS); 1 male, 30-IV-1990, H. Takizawa (NIAES). 1 female, Tanzawa Mts., Mizunashigawa, 30-IV-1983, Y. Shiozaki (YS). Hadano, Yabitsu-touge Pass: 1 female, Yabitsu, 1-VII-1983, K. Shiozaki



Figures 80–89. Male and female terminalia of *Scleropteroides longiprocessus* Huang & Yoshitake, sp. n. from Tochigi, Honshu, Japan. **80** Aedeagus, dorsal view **81** Apex of the penis, dorsal view **82** Aedeagus, lateral view **83** Tegmen **84** Sternites VIII and IX, male **85** Female genitalia, lateral view **86** Tergite VIII, female **87** Sternite VIII, female **88** Coxite and stylus **89** Spermatheca. Scale: 0.20 mm for **80–87**, 0.10 mm for **88–89**.

(YS); 1 female, 29-IV, K. Suzuki (ELKU). YAMANASHI. 1 female, Akaishi-sanmyaku Range, Norogawa-rindou, 5-VI-1983, Y. Shiozaki (YS). MIE. 1 female, Ninomata–Owase, 26-VI-1960, H. Ichihashi (NIAES). 1 male, Komono, Unbomine, 28-IV-1985, A. Amagasu (ELKU). 1 female, Shiga, Mt. Ibukiyama, 10-VI-1990, H. Takizawa (NIAES). 1 female, Toba, Mastuno, Mt. Aonomineyama, 19-V-1996, H. Yoshitake (NIAES). 8 males and 6 females, Toba, Toushijima I., 10-IV-1996, K. Ishida (NIAES). 1 male, Misugi, Hirakura, 7–8-VI-1997, H. Yoshitake (NIAES). NARA. 1 female, Kawakami, Mt. Wasamatayama, 8-VII-1995, A. Yoshida (NIAES). 1 male, Mt. Miyama, 7-VII-1989, S. Yamada (NIAES). OKAYAMA. 2 males and 1 female, Kamo, Kurami, 29-VI-1985, K. Watanabe (SM). 2 females, Tetta, Mt. Aratoyama, 16-V-1982, K. Yoshihara (SM). 1 male, Takahashi, Mt. Gagyuusan, 5-V-1984, K. Yoshihara (SM). **Izu Islands.** 1 female, Kouzushima I., Maehama–Tsuzukizawa, 9-V-1979, J. Okuma (SM). **Shikoku.** TOKUSHIMA. 1 female, Haranomachi, 8-VI-1980, K. Shiozaki (YS). 1 male and 1 female, 1-VI-1986, A. Watanabe (YS); 1 female, 5-VI-1986, A. Watanabe (YS). EHIME. 2 females, Imabaru, Mt. Takanawazan, 5-V-1976, S. Inoue (EUMJ). KOCHI. 1 male, Okunanokawa, 4-V-1967, H. Oonishi (EUMJ). Cape Murotomisaki: 1 male and 1 female, 7-VI-1959, M. Miyatake (EUMJ); 1 female, 8-V-1959, S. Hisamatsu (EUMJ); 2 females, 12-VII-1961, M. Miyatake (NIAES). **Kyushu.** FUKUOKA. 1 male, Chikugo, Mt. Kumadoyama, 1-VI-1958, Y. Miyaue (ELKU). 1 female, Munakata, Mt. Jouyama, 6-IV-1975, K. Kido (ELKU). 1 female, Itoshima, Himeshima I., 3-VI-1990, K. Kido (ELKU). 1 female, Shikanoshima I., 29-IV-1994, K. Morimoto (ELKU). 1 female, Fukuoka, Motooka, 2-VII-1994, K. Morimoto (ELKU). 1 male and 1 female, Mt. Sefurisan, 3-VI-2001, H. Hirano (NIAES). 1 male, Yabe, Mt. Shakagatake, 25-IV-2004, H. Hirano (NIAES). 3 males and 1 female, Nokonoshima I., 17-VI-2003, H. Hirano (NIAES). Mt. Hikosan: 2 males and 3 females, 17–19-V-1967, H. Takizawa (NIAES); 1 female, 4-V-1985, Y. Kajida (NIAES); 2 males and 4 females, 30-V-1995, K. Morimoto (ELKU); 1 female, 26-VI-2003, H. Hirano (NIAES). SAGA. 1 male, Okuhiratani, Mt. Taradake, 23-IV-1989, T. Yasunaga (ELKU). 2 males and 3 females, same data as holotype (NIAES). 2 males and 2 females, Mt. Kusenbuyama, Hakotani-rindou, 8-V-2005, H. Yoshitake, on *R. crataegifolius* (NIAES). NAGASAKI. 1 male, Shimabara, Taruki, 16-VII-1976, S. Imasaka (NIAES). 1 female, Shimabara, Akamatsudani Gorge, 8-VI-1979, S. Imasaka (NIAES). Mt. Unzendake: 1 female, 25-V-1976, S. Imasaka (NIAES); 1 female, 21-VII-1976, S. Imasaka (NIAES). 1 male and 2 females, Nomozeki, 13-V-1976, S. Imasaka (NIAES). 1 male, Tashirobaru, 21-IV-1977, S. Imasaka (NIAES). 15 males and 12 females, Sasebo, Mt. Eboshidake, 13-IV-1977, J. Okuma (SM). 4 males, Sasebo, Mt. Hattendake, 23-V-1982, J. Okuma (SM). Sasebo, Mt. Yahirodake: 1 male and 1 female, 18-IV-1977, J. Okuma (SM); 2 males, 6-IV-1981, J. Okuma (SM); 1 female, 21-V-1981, J. Okuma (SM); 1 female, 26-V-1982, J. Okuma (SM); 1 female, 29-III-1983, J. Okuma (SM); 1 female, 30-IV-1983, J. Okuma (SM); 1 male, 2-V-1983, J. Okuma (SM); 2 females, 15-V-1984, J. Okuma (SM). 1 male and 1 female, Hiradoshima I., Mt. Yasumandake, 10-V-1980, S. Imasaka (NIAES). KUMAMOTO. 1 male, Gokanoshou, 26–27-V-1978, K. Ohara (ELKU). Izumi, Mt. Shiratoriyama: 1 female, 1300 m, 6-VI-1980 (ELKU); 1 female, 7–8-VI-1989, T. Yasunaga (ELKU). 1 male and 2 females, Yabe, Naidaijin-rindou, 21-VI-1998, H. Kojima (ELKU). OITA. 1 male and 2 females, Kuju Mts., Bougatsuru, 27-V-1988, K. Morimoto (ELKU). KAGOSHIMA. Oosumi-hantou Peninsula, Cape Satamisaki: 1 male, 25-VI-1957, T. Saigusa (ELKU); 1 female, 8-VI-1958, H. Ueno (ELKU). 5 males and 6 females, Mt. Hoyoshidake, 14–15-IV-2002, H. Yoshitake (NIAES). 1 male, Mt. Kobadake, 28-VI-2003, H. Yoshitake (NIAES).



Figures 90–99. Male and female terminalia of *Scleropteroides horridulus* (Voss) from Amami-Oshima Island, the Ryukyus, Japan. **90** Aedeagus, dorsal view **91** Apex of the penis, dorsal view **92** Aedeagus, lateral view **93** Tegmen **94** Sternites VIII and IX, male **95** Female terminalia and genitalia, lateral view **96** Tergite VIII, female **97** Sternite VIII, female **98** Coxite and stylus **99** Spermatheca. Scale: 0.20 mm for **90–97**, 0.10 mm for **98–99**.

Distribution. Japan (Honshu, Izu Islands, Shikoku, and Kyushu; Fig. 134).

Etymology. The species name refers to the elongate apical projection of the penis, from Latin: *longi-*, from *longus*, *-a*, *-um*, meaning "long", and *processus*, meaning "projection". To be treated as a substantive in apposition.

Biological note. In several localities in Honshu, a number of adults of this species were found on *Rubus palmatus* Thunb. var. *coptophyllus* (A.Gray) Kuntze ex Koidz. In addition, adults of this species were collected mostly from *Rubus palmatus* Thunb. and rarely from *R. crataegifolius* Bunge on Mt. Kusenbuyama, Kyushu.

Scleropteroides horridulus (Voss, 1958)

Figs 5, 6, 30–33, 38–39, 90–132, 134

Homorosoma horridula Voss, 1958: 67 (type locality: China, "Kuatun") (incorrect original spelling). – Chûjô 1971: 34 (Is. Okinawa: Nago).

Homorosoma horridulum (mandatory correction, gender agreement): Chûjô and Voss 1960: 7 (in part; Is. Okinawa: Nago). – Colonnelli 2004: 34 (in catalog; China, Japan).

Rhytidosomus insulare Voss 1971: 54 (type locality: Japan, Is. Amami, Hatsuno) (incorrect original spelling).

Scleropteroides horridulus: Korotyaev et al. 2014: 99 (combination from *Homorosoma*; Taiwan) (mandatory correction, gender agreement).

Scleropteroides insulare: Morimoto 1984: 316 (Amami, Okinawa); 1989: 514 (in checklist; Amami, Okinawa) (incorrect subsequent spelling).

Scleropteroides insularis: Yoshitake et al. 2004: 106 (in checklist).

Scleropteroides hypocrita: Colonnelli 2004: 34 (in part; not Hustache 1916).

Diagnosis. This species differs from *S. hypocrita* on the basis of the following characters: subapical part of the prothorax strongly constricted (Fig. 38); elytra with strongly prominent humeri, straightly convergent toward the subapical calli (Fig. 39); scales in a row on the elytral intervals erect, much longer than the width of each interval (Fig. 39); male metaventrite more strongly prominent ventrally along the apico-lateral margin of the metaventral receptacle; male ventrite I with no prominence; apical projection of the penis truncate at the apex (Figs 91, 101, 111, 114, 117, 120, and 123); basal part of the endophallus with a pair of weakly falcate sclerites (Figs 90, 100); female sternite VIII with apically divergent arms (Figs 97, 107); bursa copulatrix usually without minute coniform spicules (Figs 95, 105).

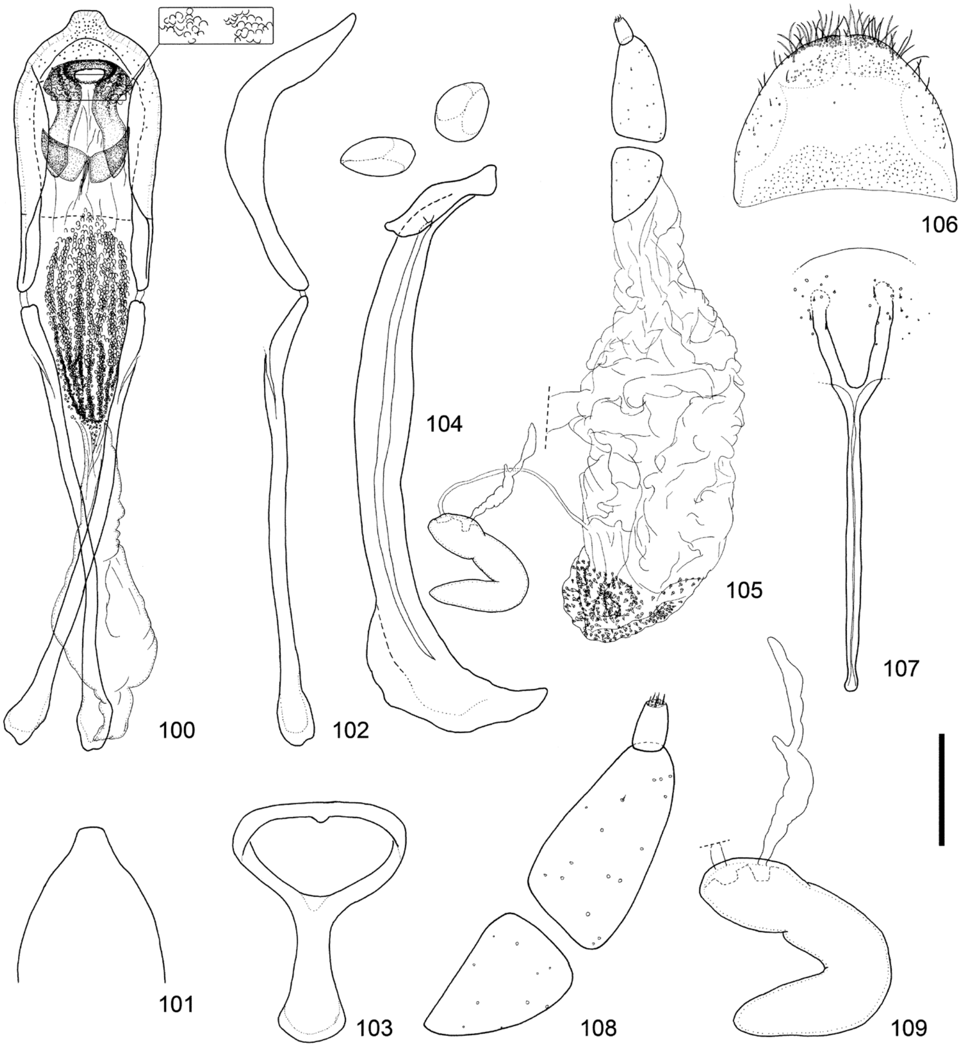
Male. LB: 2.40–2.71 (mean, 2.50). LR: 1.04–1.18 (mean, 1.12). WP: 0.94–1.10 (mean, 1.00). LP: 0.85–0.95 (mean, 0.90). WE: 1.61–1.91 (mean, 1.69). LE: 1.64–1.83 (mean, 1.69). N = 11 for all measurements. Habitus as shown in Figs 5–6.

Vestiture. Clavate scales long and erect on head, basal 2/3 of rostrum, and pronotum. Hair-like scales long and semierect on apical 1/3 of rostrum. Scales on elytral intervals (Fig. 39) erect, long, 1.3–1.5 × as long as interval width. Clavate scales on tibiae erect.

Rostrum (Figs30–31) slender, 1.15–1.27 × as long as pronotum, sides slightly widened in apical part, which is 1.16× as wide as basal part. Antennae (Fig. 31) with length ratio of funicular segments I: II: III: IV: V: VI = 1.86: 1.50: 1.21: 1.00: 1.00: 0.93 and width ratio = 1.60: 1.00: 1.13: 1.20: 1.33: 1.47.

Pronotum (Fig. 38) 1.06–1.19 × as wide as long, 0.50–0.56 × as long as and 0.56–0.65 × as wide as elytra; subapical constriction strong; sides subparallel in basal 2/3, then strongly convergent toward apex.

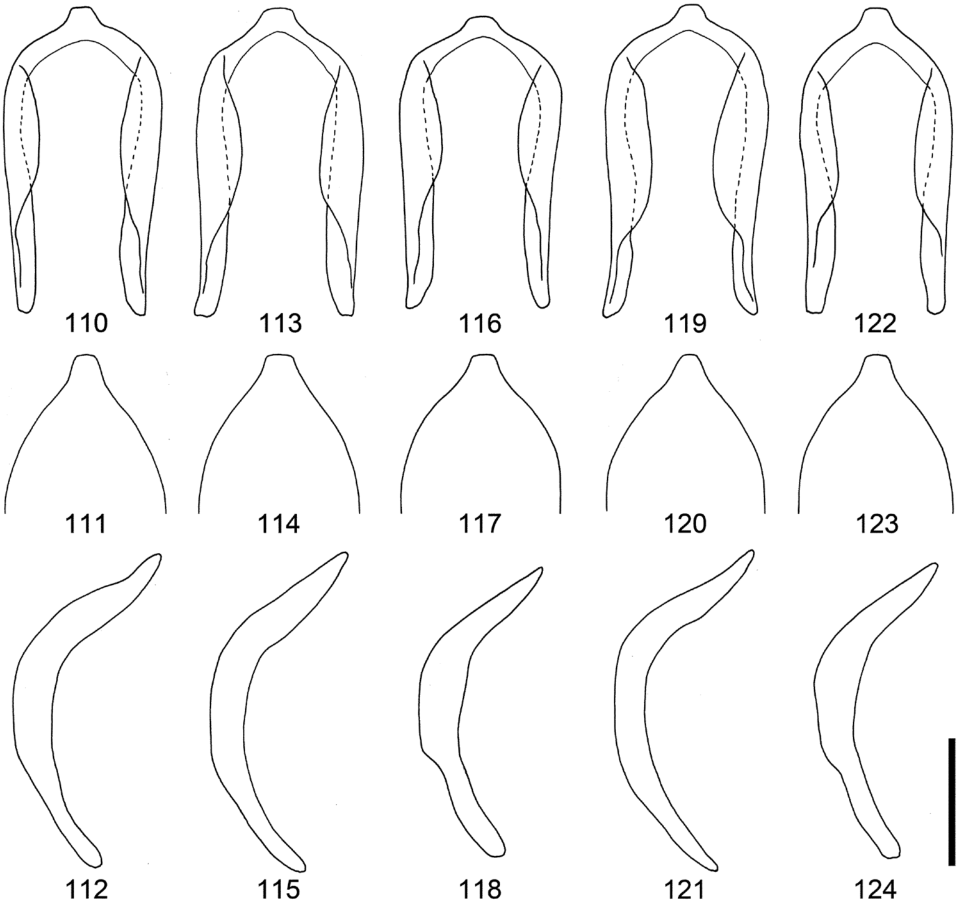
Elytra 0.96–1.04 × as long as wide, 1.79–1.98× as long as and 1.54–1.79× as wide as pronotum, straightly convergent toward subapical calli; humeral calli strongly prominent; subapical calli moderately prominent.



Figures 100–109. Male and female terminalia of *Scleropteroides horridulus* (Voss) from Fujian, southeastern China. **100** Aedeagus, dorsal view **101** Apex of the penis, dorsal view **102** Aedeagus, lateral view **103** Tegmen **104** Sternites VIII and IX, male **105** Female genitalia, lateral view **106** Tergite VIII, female **107** Sternite VIII, female **108** Coxite and stylus **109** Spermatheca. Scale: 0.20 mm for **100–107**, 0.10 mm for **108–109**.

Underside. Metaventrite moderately prominent ventrally along apico-lateral margin of metaventral receptacle. Venter coarsely and very densely punctured; ventrite I weakly flattened on disc, lacking prominence; ventrite V with more or less deeper median concavity; length ratio of ventrites I: II: III: IV: V = 3.56: 2.67: 1.00: 1.00: 2.56 and width ratio = 1.90: 1.76: 1.30: 1.20: 1.00.

Genitalia. Tegmen (Figs 93, 103) with apodeme slightly widened toward apex. Penis (Figs 90–92, 100–102, 110–124) with sides more or less weakly widened toward



Figures 110–124. Male genitalia of *Scleropteroides horridulus* (Voss) from various localities. **110–112** Taiwan, China **113–115** Fujian, southeastern China **116–118** Hunan, central China **119–121** Yakushima Island, Nansei Islands, Japan **122–124** Mt. Jirisan, South Korea **110, 113, 116, 119, 122** Penis, dorsal view **111, 114, 117, 120, 123** Apex of the penis, dorsal view **112, 115, 118, 121, 124** Penis, lateral view. Scale: 0.20 mm.

apical 1/5, then strongly convergent apically; apical projection truncate at apex. Basal part of endophallus (Figs 90, 100) with pair of weakly falcate sclerites.

Otherwise as in *S. hypocrita*.

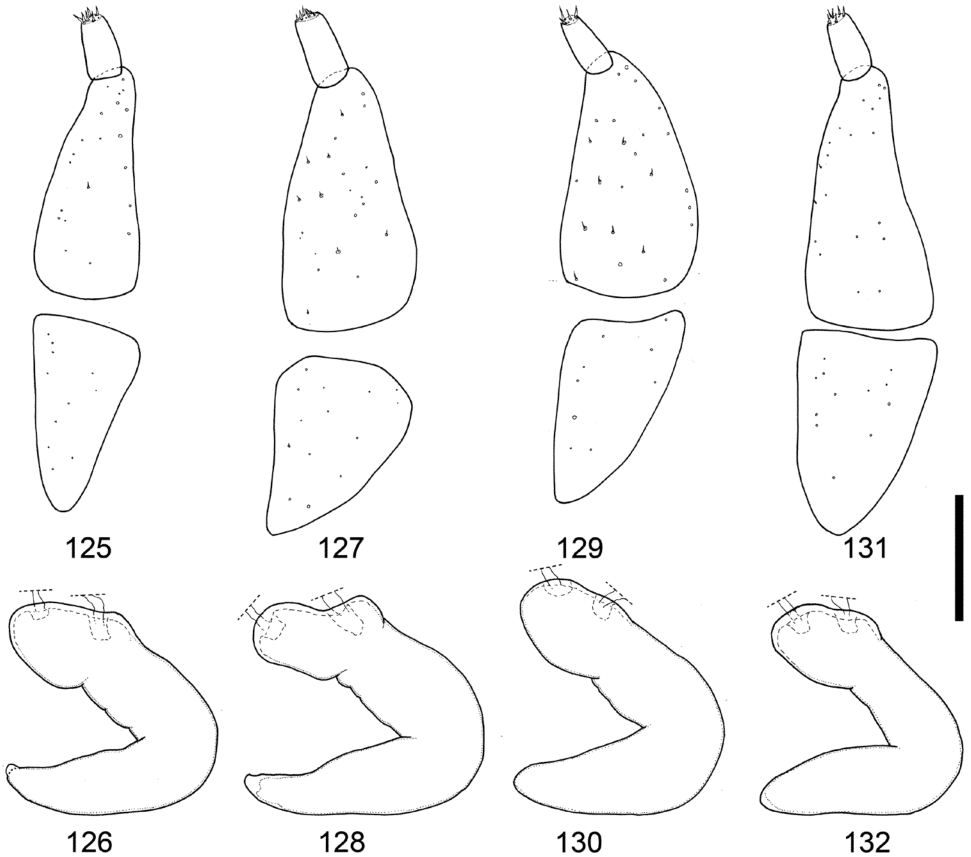
Female. LB: 2.34–2.92 (mean, 2.68). LR: 1.06–1.36 (mean, 1.30). WP: 0.95–1.14 (mean, 1.09). LP: 0.88–1.04 (mean, 0.96). WE: 1.63–1.97 (mean, 1.82). LE: 1.62–2.03 (mean, 1.83). N = 16 for all measurements.

Rostrum (Figs 32–33) slightly more slender, 1.15–1.40 × as long as pronotum.

Pronotum 1.02–1.18 × as wide as long.

Elytra 0.98–1.05 × as long as wide.

Underside. Ventrite V simple, lacking median sulcus or concavity.



Figures 125–132. Female genitalia of *Scleropteroides horridulus* (Voss) from various localities. **125–126** Taiwan, China **127–128** Fujian, southeastern China **129–130** Yakushima Island, Nansei Islands, Japan **131, 132** Namwongun, South Korea. Scale bar: 0.10 mm.

Terminalia and genitalia. Sternite VIII (Figs 97, 107) with arms slender and apically divergent. Bursa copulatrix (Figs 95, 105) usually simple, but sometimes with dense minute coniform spicules in posterior part. Spermatheca (Figs 99, 109, 126, 128, 130, 132) with collum more strongly convex; insertions of duct and gland slightly more distant from each other.

Otherwise showing almost the same sexual dimorphism as in *S. hypocrita*.

Material examined. CHINA: Hunan. 1 male, Pingjiang, Mt. Mupushan, 1600 m, 1–12-VIII-2003, Li et al. (NIAES). **Fujian.** 2 males and 2 females, Jianyang, 27°20'N, 118°06'E, 18-IV-1965 (IZCAS, IOZ(E)896779, 896780, 896781, and 896786); 1 female, Jianyang, Aotou, Sanbanqiao, 27°35'N, 117°39'E, 18-IV-1965 (IZCAS IOZ(E)896788); 1 female, Jianyang, Aotou, Huangbaixi, 27°35'N, 117°39'E, 7-V-1965 (IZCAS IOZ(E)89679); 1 male, Jianyang, Aotou, Daoshui, 27°35'N, 117°39'E, 13-VI-1965 (IZCAS, IOZ(E)897690). 1 female, Shaowu,

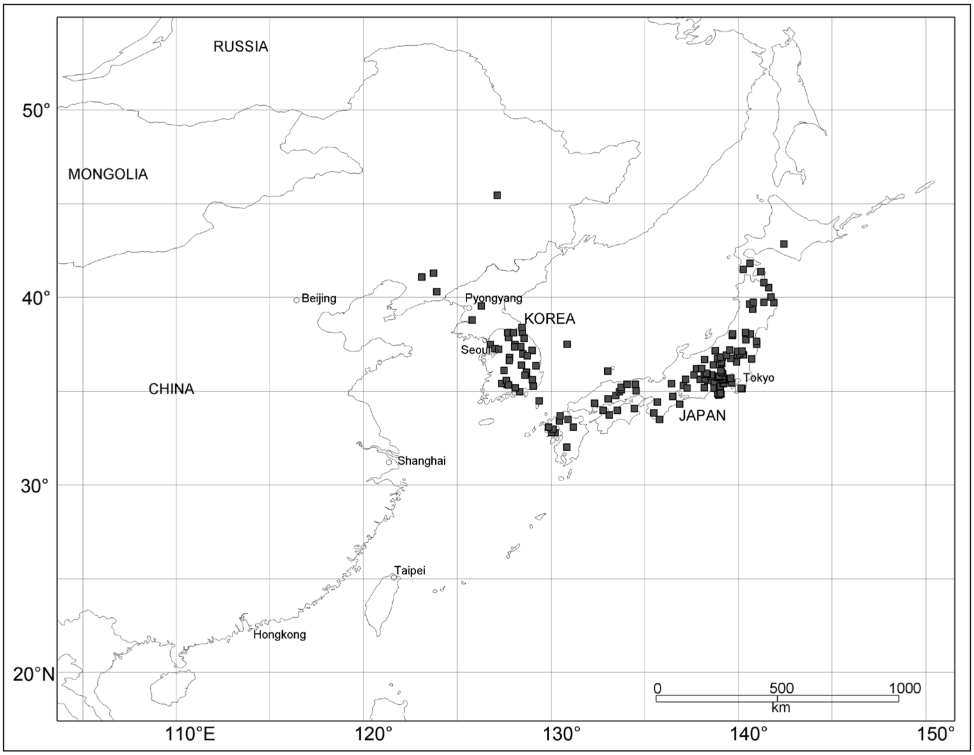


Figure 133. Geographic distribution of *Scleropteroides hypocrita* (Hustache) (■).

Tieyang, 27°10'N, 117°21'E, 15-V-1965 (IZCAS, IOZ(E)896789). 1 male, Wuyishan, Xingcun, Sangang, 752 m, 27°44.804'N 117°40.600'E, 15-IV-2009, J. Huang (ZAFU). 1 female, Wuyishan, Xingcun, Sangang, 752 m, 27°44.804'N 117°40.600'E, 15-IV-2009, S. Zhang (ZAFU). 1 male, Wuyishan, Xingcun, Qili, 899–912 m, 27°43.302'–27°43.042'N 117°39.632'–117°39.334'E, 20-IV-2009, J. Tan (ZAFU). 1 female, Wuyishan, Xingcun, Qili, 899–912 m, 27°43.302'–27°43.042'N 117°39.632'–117°39.334'E, 20-IV-2009, J. Huang (ZAFU). **Chongqing.** 1 female, Nanchuan, Yixiantian, 700 m, 29.05194°N 107.12001°E, 12-VI-2010, R. Nie (IZCAS IOZ(E)1803625). **TAIWAN.** 1 male, Nantou, Sungkan–Meifeng, 25–26-V-1972, M. Sakai (EUMJ). 1 male and 1 female, Nantou, Nanshanchi, 20–23-III-1995, H. Kojima and M. Suehiro (NIAES). 1 male, Mt. Guandaoshan, 16-V-1986, I. Matoba (NIAES). 1 male, Taoyuan, Mt. Daguanshan, 4-IV-1991, H. Kojima (NIAES). **KOREA: Gangwondo.** 1 female, Chuncheongun, Dongmyeon, Gamjeongri, 21-V-1992, K. Morimoto (ELKU). **Kyeongsangnamdo.** 1 female, Mt. Jirisan, Samjeongri, 6-VI-1991, J. D. Bae (ELKU). **Jeollabukdo.** 1 male and 1 female, Namwongun, Nowondan, 5-VI-1991, J. D. Bae (ELKU). 1 female, Namwongun, Deongdongri, 19-VI-1994, H. Kojima (ELKU).

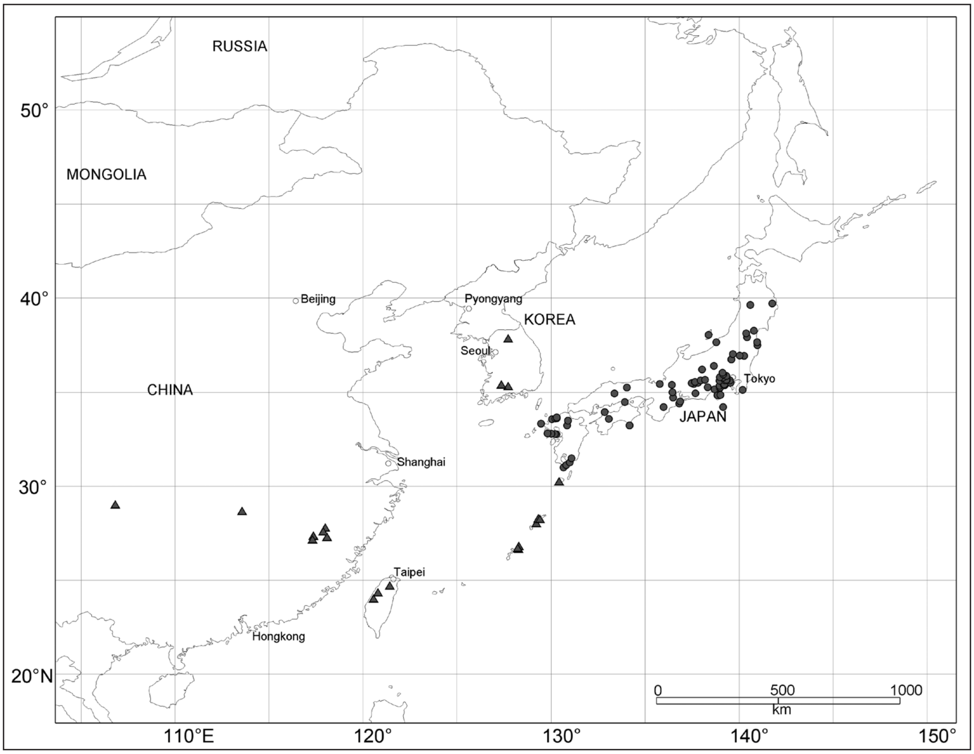
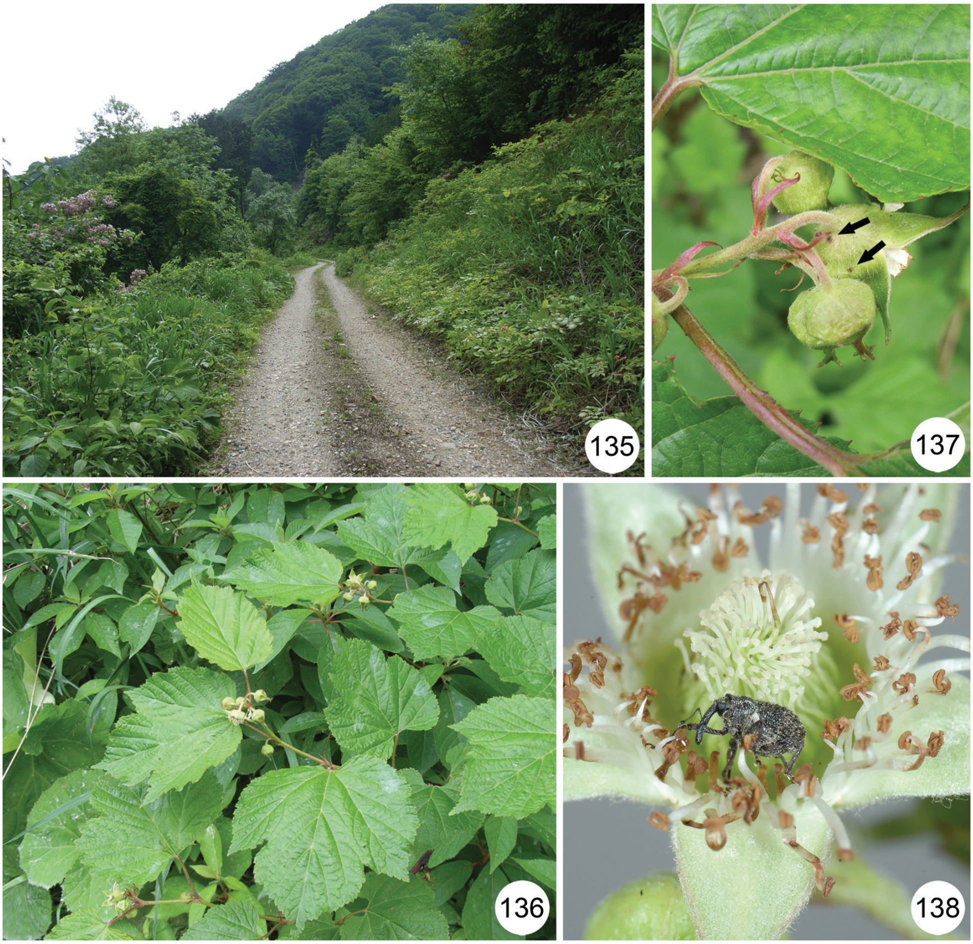


Figure 134. Geographic distributions of *Scleropteroides longiprocessus* Huang & Yoshitake, sp. n. (●) and *S. horridulus* (Voss) (▲).

JAPAN: Nansei Islands. YAKUSHIMA I. Nakama: 1 male, 1-IV-1985, A. Yoshida (NIAES); 1 male and 2 females, 25-III-1991, H. Kojima (ELKU); 4 males and 6 females, 30-III-2005, Y. Kubota (NIAES). AMAMI-OSHIMA I. 1 male, Sutaru-touge Pass, 23-III-1954, T. Mohri (EUMJ). Nishinakama: 1 female, 25-III-1954, T. Edashige (EUMJ); 1 female, 31-III-1968, M. Tomokuni (EUMJ); 1 male, 22-III-1990, T. Ueno (NIAES). Hatsuno: 1 male and 1 female, 24-III-1965, S. Fukuda (SM); 1 female, 12-IV-1971, M. Sakai (EUMJ); 1 female, 11-V-1976, J. Okuma (SM). 1 male, Daikuma, 10-IV-1971, M. Sakai (EUMJ). 1 female, Shinmura, 11-IV-1971, M. Sakai (EUMJ). Mt. Yuwandake: 1 male, 19-IV-1971, M. Sakai (EUMJ); 25 males and 18 females, 25–28-III-2003, H. Yoshitake, on *Rubus croceacanthus* (NIAES). 9 males and 8 females, Chuo-rindou, 18-III-1991, H. Kojima (ELKU). 2 males, Nangawa-rindou, 20-III-1991, H. Kojima (ELKU); 1 male and 2 females, 22-III-1991, H. Kojima (ELKU). 2 males and 5 females, Mt. Akatsuchiyama, 21-III-1991, H. Kojima (ELKU). UKEJIMA I. 1 male, 22-III-2004, K. Takahashi (NIAES). OKINAWAJIMA I. 1 female, Yona, 10-IV-1975, S. Imasaka (NIAES). 1 male, Oku, 15–18-V-1978, T. Tsutsumi (ELKU). 2 males and 1 female, Mt. Yonahadake, 16-IV-1991, H. Kojima (ELKU).



Figures. 135–138. *Scleropteroides hypocrita* (Hustache). **135** Habitat in Toyosawa-rindou, Iwate, Honshu, Japan **136** Adult food plant, *Rubus crataegifolius* **137** Feeding traces of adults on a flower bud of *R. crataegifolius* (indicated with arrows) **138** Adult on a flower of *R. crataegifolius*.

Distribution. China (Chongqing and Fujian – new record, and Taiwan), Korea (Central and South – new record), Japan (Nansei Islands: Yakushima, Amami-Oshima, and Okinawajima Islands; Fig. 134).

Biological note. A number of adults were collected from *Rubus croceacanthus* H.Lév. growing along the edge of an evergreen broad-leaved forest at the foot of Mt. Yuwandake, Amami-Oshima Island.

Comment. In the study, we could not examine the holotype of *Rhytidosomus insularis* Voss, which should be preserved in ELKU, but K. Morimoto (pers. comm., 2005) had examined it and confirmed its taxonomic identity. Also, our examination of a long series of *Scleropteroides* specimens from the type locality, Amami-Oshima Island, revealed that only one species of this genus occurs on the island.

Discussion

Systematic position and definition of the genus

Scleropteroides was established as a genus allied to *Scleropterus* in the tribe Scleropterini (Colonnelli 1979). This placement was followed by subsequent authors (Alonso-Zarazaga and Lyal 1999, Hong et al.1999, Yoshitake et al. 2004, Colonnelli 2004, Korotyaev and Hong 2004), except by Morimoto (1989) who placed it in the tribe Ceutorhynchini. This is not unexpected as Scleropterini has never been clearly defined (Schultze 1902, Reitter 1913, Wagner 1937) and the morphological distinction between Scleropterini and Ceutorhynchini is still unclear because of inconsistencies in character states defining the two tribes (Colonnelli 1984, 2004). In addition, a recent molecular phylogenetic study (Kato et al. 2006) did not support the monophyly of either Ceutorhynchini or Scleropterini, although it supported a close relationship between *Scleropteroides* and *Scleropterus*. Here we follow the recent tribal classification by Colonnelli (2004) for convenience, although we acknowledge it is in need of revision.

Previously, *Scleropteroides* was defined by Colonnelli (1979, 2004) and Korotyaev (1996) as follows: 1) rostrum conspicuously expanded from the base to apex, wider than the profemur; 2) prothorax with large and extremely coarse punctures; 3) scutellar shield visible; 4) elytral humeri prominent; 5) all elytral intervals subequal in width and height; 6) each interval bearing acute squamate granules; 7) striae catenulate, very deep, at least as wide as intervals; 8) rostral channel extending to metaventrite; 9) femora dentate; and 10) claws dentate. However, this definition of *Scleropteroides* is inappropriate because it contained incorrectly described structures (1 and 7), as well as characteristics common to *Scleropterus* (2, 6, 8, and 10). Therefore, the diagnostic differences between the two genera must be clarified.

Morphologically, *Scleropteroides* is close to *Scleropterus* in sharing a rounded apex of the antennal scape, a six-segmented antennal funicle, a pronotum with neither tubercules nor prominences, elytral intervals bearing small and acute squamate granules usually in a row, a rostral channel extending to the metaventrite, and appendiculate claws. In addition, the close affinity between the two genera is emphasized by similarities in structures of the male and female genitalia.

On the basis of detailed morphological observations, we redefined *Scleropteroides* in this study as follows: 1) eyes convex (Figs 22–33); 2) antennal scape fringed with 3–4 linear scales at the apex, in addition to a few minute hairs; 3) basal margin of the pronotum bisinuate (Figs 10, 34, 36, 38); 4) pronotum lacking a sulcus (Figs 10, 34, 36, 38); 5) apical margin of the pronotum raised (Fig. 12); 6) scutellar shield well-developed, visible from above (Figs 11, 34–39); 7) hind wings well-developed (Fig. 19); 8) elytral humeri well-developed (Figs 11, 35, 37, 39); 9) elytral intervals subequal in width and height (Figs 11, 35, 37, 39); 10) femora dentate (Fig. 15); 11) protibiae simple, not incurved apically (Fig. 15); and 12) meso- and metatibiae mucronate only in males.

In contrast, *Scleropterus* has the following defining characteristics: 1) eyes flattened; 2) antennal scape fringed with 3–4 minute hairs at the apex; 3) basal margin of the pronotum nearly straight; 4) basal half of the pronotum with a weak longitudinal median sulcus; 5) apical margin of the pronotum slightly descending; 6) scutellar shield vestigial, usually invisible from above; 7) hind wings vestigial; 8) elytral humeri vestigial; 9) odd numbered intervals of the elytra wider and more prominent than even numbered intervals; 10) femora edentate; 11) protibiae incurved apically; and 12) meso- and metatibiae mucronate in both sexes.

The most apparent differences between the two genera are the structure of the hind wings (character 7) and associated characters (3, 6, and 8). Apart from these differences associated with hind-wing reduction in *Scleropterus*, however, *Scleropteroides* clearly differs from *Scleropterus* in having a pronotum lacking a sulcus, even elytral intervals, dentate femora, and simple protibiae. Additionally, *Scleropteroides* can also be distinguished from *Scleropterus* by the meso- and metatibiae lacking mucrones in females.

Relationships among species

Our extensive and detailed examination of a large number of specimens revealed that *Scleropteroides* comprises three East Asian species – *S. hypocrita*, *S. horridulus*, and *S. longiprocessus*. They are very similar in general appearance, as well as in general structures of male and female terminalia, but can be distinguished clearly by several consistent, taxonomically important morphological differences as shown in the following lines.

Scleropteroides hypocrita is characterized mainly by a moderately constricted prothorax in the subapical part (Fig. 34), gently convergent elytra toward the subapical calli (Fig. 35), moderately prominent humeri (Fig. 35), and elytral intervals with a row of semirecumbent scales that are evidently shorter than the interval width (Fig. 35). In addition, the species is also distinguished by sexual structures in males, such as a slightly widened rostrum in the apical half (Fig. 22), metaventrite that is weakly prominent along the apico-lateral margin of the metaventral receptacle, ventrite I bearing a median prominence along the apical margin, the penis with a blunt apical projection that is rounded at the apex (Figs 41, 51, 61), and a pair of plate-like sclerites on the basal part of the endophallus (Figs 40, 50, 60). In females, the arms of sternite VIII are apically arcuate (Figs 47, 57, 67) and the posterior part of the bursa copulatrix is densely covered with minute coniform spicules (Figs 45, 55, 65). The length of scales in a row on the elytral intervals is variable, from 0.4 to 0.8 times as long as the interval width, mostly ranging from 0.5 to 0.6 times as long. We examined specimens from various localities in detail, but no significant geographical variation was observed in the external or genital structures of either sex.

Colonnelli (2004) synonymized *S. insularis* with *S. hypocrita* in his world catalog of the subfamily Ceutorhynchinae; however, he gave no explanation for this taxonomic treatment. Our study revealed that *S. insularis* is actually identical with *S. horridulus*. *Scleropteroides horridulus* shows remarkable morphological differences from *S. hypocrita* in the strongly constricted subapical part of the prothorax (Fig. 38), straightly convergent elytra toward the subapical calli (Fig. 39), strongly prominent humeri (Fig. 39), erect scales on elytral intervals that are much longer than the interval width

(Fig. 39), and ventrite I lacking a median prominence. In addition, *S. horridulus* clearly differs from *S. hypocrita* in having the following male sexual traits: metaventrite more strongly prominent ventrally along the apico-lateral margin of the metaventral receptacle, apical projection of the penis truncate at the apex (Figs 91, 101, 111, 114, 117, 120, 123), and paired sclerites in the basal part of the endophallus weakly falcate (Figs 95, 105). Furthermore, *S. horridulus* has apically divergent arms on sternite VIII in females (Figs 97, 107). We consider *S. horridulus* a valid species despite of Colonnelli's (2004) synonymy of *S. insularis* with *S. hypocrita*. This species shows geographical variation in female genital structure. In specimens from continental China and Korea, the bursa copulatrix is densely armed with minute spicules in the posterior part (Fig. 105), whereas it is unarmed in specimens from Taiwan and the Nansei Islands (Fig. 95). This may suggest the presence of a cryptic species because structures of the bursa copulatrix are usually conservative and not variable within a species.

Scleropteroides longiprocessus shows character states intermediate between *S. hypocrita* and *S. horridulus* in having a strong constriction in the subapical part of the prothorax (Fig. 36), strongly prominent humeral calli (Fig. 37), and elytral intervals with semierect scales, each of which is nearly as long as the interval width (Fig. 37). This species was previously confused with *S. hypocrita* due to their close resemblance in general appearance and the lack of a detailed morphological examination. However, *S. longiprocessus* differs from *S. hypocrita* by having a stouter rostrum (Fig. 26), more rapidly convergent elytra toward the subapical calli (Fig. 37), and ventrite I lacking a median prominence. Moreover, *S. longiprocessus* is distinguished by male sexual traits, such as a metaventrite that is more prominent ventrally along the apico-lateral margin of the metaventral receptacle, an elongate projection at the apex of the penis (Figs 71, 81), and the paired falcate sclerites in the basal part of the endophallus (Figs 70, 80). With regard to female sexual traits in *S. longiprocessus*, the arms of sternite VIII are apically divergent (Figs 77, 87) and the bursa copulatrix lacks spicules (Figs 75, 85). This species shows non-geographical intraspecific variation in the length of scales on the elytral intervals. Most specimens examined had scales slightly longer than the interval width, but some specimens bore stouter scales that were slightly shorter than the interval width.

Additionally, *S. longiprocessus* resembles *S. horridulus* in having straightly convergent elytra toward the subapical calli (Figs 37, 39), a metaventrite that is moderately prominent ventrally along the apico-lateral margin of the metaventral receptacle in males, ventrite I lacking a median prominence in both sexes, and the apically divergent arms of female sternite VIII (Figs 77, 87, 97, 107). However, *S. longiprocessus* is easily distinguished from *S. horridulus* by the more strongly widened rostrum in males (Fig. 26), the pronotum with subparallel sides in the basal half and a weaker subapical constriction, less-developed elytral humeri, less erect and shorter scales on the elytral intervals (Fig. 37), a penis with a slender apical projection that is rounded at the apex (Figs 71, 81), narrower sclerites in the basal part of the endophallus (Figs 70, 80), and an unarmed bursa copulatrix (Figs 75, 85).

The affinity of the three *Scleropteroides* species is still uncertain and a phylogenetic analysis of the genus is necessary to clarify their relationships.

Host plant associations

Rubus is a cosmopolitan genus and contains an estimated 900–1000 species worldwide (Thompson 1997). *Rubus* are shrubs or subshrubs, deciduous, rarely evergreen or semievergreen, and sometimes perennial creeping dwarf herbs (Lu and Boufford 2003). To date, 249 *Rubus* species have been recorded from China (including Taiwan), Korea, and Japan (Lu and Boufford 2003, KPNI 2008, Yonekura and Kajita 2003). In East Asia, *Rubus* species constitute the understory of open woodlands, especially in and around clearings and margins. They also occur in more open, sunny locations along forest roads and along rivers.

Presently, ecological information on *Scleropteroides* weevils is limited and their host plant associations are not clear (Table 2). However, the available data indicate that *Scleropteroides* weevils are associated with woody *Rubus* species belonging to the subgenus *Idaeobatus* and growing in and around woodlands at least in the adult stage because adults were collected from *Rubus* shrubs and observed feeding on leaves and flowers of the plants on many occasions. With regard to adult feeding habits, *S. hypocrita* widely utilizes at least four *Rubus* species (*R. crataegifolius*, *R. idaeus* subsp. *melanolasius* f. *concolor*, *R. microphyllus*, and *R. trifidus*) in Korea and Japan, whereas *S. longiprocessus* was observed feeding on *R. palmatus* in Honshu and Kyushu, and *S. horridulus* on *R. croceacanthus* in the Ryukyus. In two localities in Toyota City, Honshu, Japan, adults of *S. hypocrita* and *S. longiprocessus* were found separately on *R. microphyllus* and *R. palmatus* var. *coptophyllus*, respectively (K. Izawa, pers. comm., 2014). Similarly, on Mt. Kusenbuyama, Kyushu, Japan, adults of *S. hypocrita* and *S. longiprocessus* were collected separately on *R. crataegifolius* and *R. palmatus*, respectively, except a few individuals of *S. longiprocessus* collected simultaneously with *S. hypocrita* on *R. crataegifolius*. These observations suggest that *Scleropteroides* species might show some differences in host use in localities where they occur sympatrically. As mentioned above, *S. hypocrita* is sympatric with *S. longiprocessus* in Japan and with *S. horridulus* in South Korea (Table 1). Further studies are needed to explore the host plant range of each *Scleropteroides* species, especially in sympatric localities.

Generally, each species in the subfamily Ceutorhynchinae utilizes the same host plant in the adult and larval stages (e.g., Hoffmann 1954, Jordheuil 1963, Dieckmann 1972). Therefore, *Scleropteroides* weevils would be suspected to be associated with *Rubus* species in their larval stage. *Scleropteroides* adults appear before and during the flowering season of *Rubus* and were frequently found on reproductive organs of the plants. Further surveys focusing on larval food sources are necessary to elucidate the host plant associations of *Scleropteroides* weevils.

Distribution and biogeography

The distribution of *Scleropteroides* is limited to East Asia (Figs 133–134), in contrast to *Scleropterus*, which is widely distributed from Central Europe through Central Asia to East Asia (Colonnelli 2004).

Table 1. Localities where *Scleropteroides* species occur sympatrically.

Species	Locality
S. hypocrita and *S. horridulus*	IN THE KOREAN PENINSULA:
	GANGWONDO: Chuncheongun, Dongmyeon, Gamjeongri
	KYEONGSANGNAMDO: Mt. Jirisan, Samjeongri
	JEOLLABUKDO: Namwongun, Deongdongri
S. hypocrita and *S. longiprocessus*	IN THE JAPANESE ARCHIPELAGO:
	IWATE: Kawai, Tsuchisaka-touge
	AKITA: Lake Tazawako
	YAMAGATA: Mt. Zaousan, Yoshikari-rindou
	FUKUSHIMA: Haranomachi, Kozikiishi-rindou; Namie
	IBARAKI: Yamizosan, Shimokitazawa
	TOCHIGI: Fujiwara, Midorizawa-rindou
	GUMMA: Matsuida, Kirizumi-onsen
	SAITAMA: Shoumaru-touge Pass
	TOKYO: Okutama, Kurasawadani; Mt. Oodakeyama; Mt. Takaosan
	KANAGAWA: Tanzawa Mts., Yabitsu-touge Pass; Tanzawa Mts., Mizunashigawa; Yamakita, Mikuni-touge Pass
	CHIBA: Mt. Kiyosumiyama–Kenminnomori
	NAGANO: Nakakawa; Tobira-onsen
	SHIZUOKA: Shinfuji
	AICHI: Toyota, Nishiichinonochou; Toyota, Asugawachou,_Asugawa-hoan-rindou
	MIE: Misugi, Hirakura
	SHIGA: Mt. Ibukiyama
	FUKUOKA: Mt. Hikosan
	NAGASAKI: Tashirobaru; Sasebo, Mt. Hattendake

Scleropteroides hypocrita is distributed in northeast China, North and South Korea, and Japan (Fig. 133), whereas *S. longiprocessus* is restricted to Japan (Fig. 134). The two species occur sympatrically in many localities in Japan (Table 1). Further, *S. horridulus* is distributed from Fujian through Taiwan to the Nansei Islands and in South Korea (Figs 133–134). This species is sympatric with *S. hypocrita* at least in the Korean Peninsula (Table 1), but the distributional boundary of the two species is still unclear in continental China.

Currently, a considerable gap still remains in the distribution of *Scleropteroides*, especially in continental China and the Korean Peninsula. In addition, this genus has never been recorded from the southern part of the Russian Far East. Since the distribution of *Scleropteroides* strongly suggests its occurrence in these regions, further surveys are necessary to elucidate the range of the genus and that of each species.

Table 2. Summary of plant association data for *Scleropteroides*.

Species	Host plant	Observation*	Locality	Author
S. hypocrita	*Rubus* spp.	A	Japan	Morimoto (1984)
S. hypocrita	*R. crataegifolius*	A	Japan, Honshu: Mt. Takaosan	This study
S. hypocrita	*R. crataegifolius*	A	Japan, Honshu: Iwate	This study
S. hypocrita	*R. crataegifolius*	A	Japan, Kyushu: Mt. Kusenbuyama	This study
S. hypocrita	*R.* sp.	A	Japan, Honshu: Fukushima	This study
S. hypocrita	*R. trifidus*	A	Japan, Honshu: Gifu, Toki	This study
S. hypocrita	*R. trifidus*	A	Japan, Honshu: Aichi, Toyota, Oobora, Nikake-rindou	This study
S. hypocrita	*R. microphyllus*	A	Japan, Honshu: Aichi, Asugawachou, Asugawa-hoan-rindou	This study
S. hypocrita	*R. microphyllus*	A	Japan, Honshu: Mie, Komonochou, Komono	This study
S. hypocrita	*R. idaeus* subsp. *melanolasius* f. *concolor*	A	Korea	Hong et al. (1999), Korotyaev and Hong (2004)
S. hypocrita	*R. crataegifolius*	A	Korea, South: Mt. Jirisan	This study
S. longiprocessus	*R. palmatus*	A	Japan, Kyushu: Mt. Kusenbuyama	This study
S. longiprocessus	*R. palmatus* var. *coptophyllus*	A	Japan, Honshu: Tokyo, Hachiouji, Mt. Takaosan	This study
S. longiprocessus	*R. palmatus* var. *coptophyllus*	A	Japan, Honshu: Gifu, Nakatsugawa, Nenoue-kougen	This study
S. longiprocessus	*R. palmatus* var. *coptophyllus*	A	Japan, Honshu, Aichi: Shitara, Mt. Nishinagura-Iyama	This study
S. longiprocessus	*R. palmatus* var. *coptophyllus*	A	Japan, Honshu, Aichi, Toyota: Nishiichinonochou; Asugawachou, Asugawa-hoan-rindou; Inabuchou, Noirigawa	This study
S. horridulus	*R. croceacanthus*	A	Japan, Ryukyus: Amami-Oshima I.	This study

* A: Adults, feeding behavior was confirmed.

Key to species

1 Subapical part of the prothorax moderately constricted (Fig. 34). Elytra gently convergent toward the subapical calli, with weakly prominent humeri. Scales on the elytral intervals semirecumbent, evidently shorter than the interval width (Fig. 35). Metaventrite weakly prominent ventrally along the apico-lateral margin of the metaventral receptacle in males. Ventrite I with a median prominence along the apical margin in males. Female sternite VIII with apically arcuate arms (Figs 47, 57, 67). [Rostrum slightly widened in the apical half in males. Male genitalia with a blunt projection at the apex of the penis (Figs 41, 51, 61) and a pair of plate-like sclerites in the basal part of the endophallus (Figs 40, 50, 60). Female genitalia with the bursa copulatrix bearing dense, minute, coniform spicules in the posterior part (Figs 45, 55, 65).] ....***S. hypocrita***

– Subapical part of the prothorax strongly constricted (Figs 36, 38). Elytra straightly convergent toward the subapical calli, with strongly prominent humeri. Scales on elytral intervals more or less erect, evidently longer than or nearly as long as the interval width (Figs 37, 39). Metaventrite more strongly prominent ventrally along the apico-lateral margin of the metaventral receptacle in males. Ventrite I simple, lacking a median prominence in both sexes. Female sternite VIII with arms divergent apically (Figs 77, 87, 97, 107)..... **2**

2 Apical half of the rostrum slightly widened in males (Fig. 30). Pronotum subparallel-sided in the basal 2/3, with a strong subapical constriction. Elytral humeri strongly prominent. Scales on elytral intervals erect, much longer than the width of each interval (Fig. 39). Apical projection of the penis blunt, truncate at the apex (Figs 91, 101, 111, 114, 117, 120, 123). Basal part of the endophallus with a pair of weakly falcate sclerites. Bursa copulatrix simple (Fig. 95) or with minute coniform spicules in the posterior part (Fig. 105)... .... ***S. horridulus***

– Rostrum more strongly widened in the apical half in males (Fig. 26). Basal half of the pronotum subparallel-sided, with a weaker subapical constriction. Elytral humeri slightly less prominent. Scales on elytral intervals semierect, nearly as long as the interval width (Fig. 37). Apical projection of the penis sharp, rounded at the apex (Figs 71, 81). Basal part of the endophallus with a pair of narrow falcate sclerites (Figs 70, 80). Bursa copulatrix simple, lacking spicules (Figs 75, 85) .... ***S. longiprocessus***

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RESEARCH ARTICLE

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Kymachrysa, a new genus of Nearctic Green Lacewings (Neuroptera, Chrysopidae, Chrysopini)

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Abstract

Two North American species of green lacewings have undergone a number of changes in their generic assignments and are currently classified as *incertae sedis*. Here we demonstrate that adults (both sexes) and larvae of these species share a set of features that distinguishes them from currently described genera. Thus, to promote nomenclatural stability in Chrysopidae, we describe *Kymachrysa*, a **gen. n.** that contains the two species – *Kymachrysa intacta* (Navás), **comb. n.** and *Kymachrysa placita* (Banks), **comb. n.**. Also, we present modifications for the current generic-level key, illustrations, as well as biological information for identifying the genus and its known species.

Keywords

New genus, adult, larva, biology

Introduction

The green lacewing tribe Chrysopini (Neuroptera: Chrysopidae) includes seventeen genera in the New World; ten of these occur in the Nearctic. These New World genera are distinguished from each other on the basis of both adult (male and female), as well as larval, characters (e.g., see Brooks and Barnard 1990; Tauber 1974, 1975, 2003;

Adams and Garland 1982; Brooks 1994; Penny et al. 2000; Tauber and de Leon 2001; Tauber et al. 2000, 2014; Freitas and Penny 2001). However, the adult and larval characteristics of two Nearctic species were shown to be inconsistent with the genera to which the species had been assigned (*Ceraeochrysa* and *Chrysopodes*), nor could they be assigned to any other known chrysopine genus (Tauber and Flint 2010: 64). Most recently, they were retained temporarily in *Ceraeochrysa* (with the caveat of *incertae sedis*) (Tauber and Flint 2010: 64). Here, to foster nomenclatural stability, we describe a new genus to accommodate these two species (original names: *Chrysopa placita* Banks and *Chrysopa intacta* Navás), and we provide information for their identification.

Specimens and methods

Our procedures were those used in previous publications (e.g., Tauber et al 2012, Silva et al. 2013). We examined specimens from the following collections: BMNH, The Natural History Museum (formerly British Museum of Natural History), London, England; CAS, California Academy of Sciences, San Francisco, CA; CMNH, Carnegie Museum of Natural History, Pittsburgh, PA; CNC, Canadian National Collection, Ottawa, Canada; CPG, C. P. Gilette Museum of Arthropod Diversity, Colorado State University, Fort Collins, CO; CUIC, Cornell University Insect Collection, Ithaca, NY; EMEC, Essig Museum of Entomology, University of California, Berkeley, CA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; ROM, Royal Ontario Museum, Toronto, ON, Canada; SDNHM, San Diego Natural History Museum, San Diego, CA; TRC, M. J. & C. A. Tauber Research Collection, Davis, CA; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.

Systematics

Genus *Kymachrysa* gen. n.

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Type-species. *Chrysopa placita* Banks, 1908: 259.

Distinguishing adult features. *Kymachrysa* adults appear to be typical chrysopine lacewings of medium size and green coloration. Their most distinctive adult features occur in the male and female terminalia; in addition, a few external features are diagnostic of the genus:

External features. (i) The longitudinal (radial) veins between the first and second rows of gradate veins of the fore and hind wings are sinuous (Fig. 1A, B), whereas in most other chrysopid genera they are relatively straight. (ii) In both males and females, the fused ninth tergite and ectoproct is completely divided by a dorsal invagination, and each

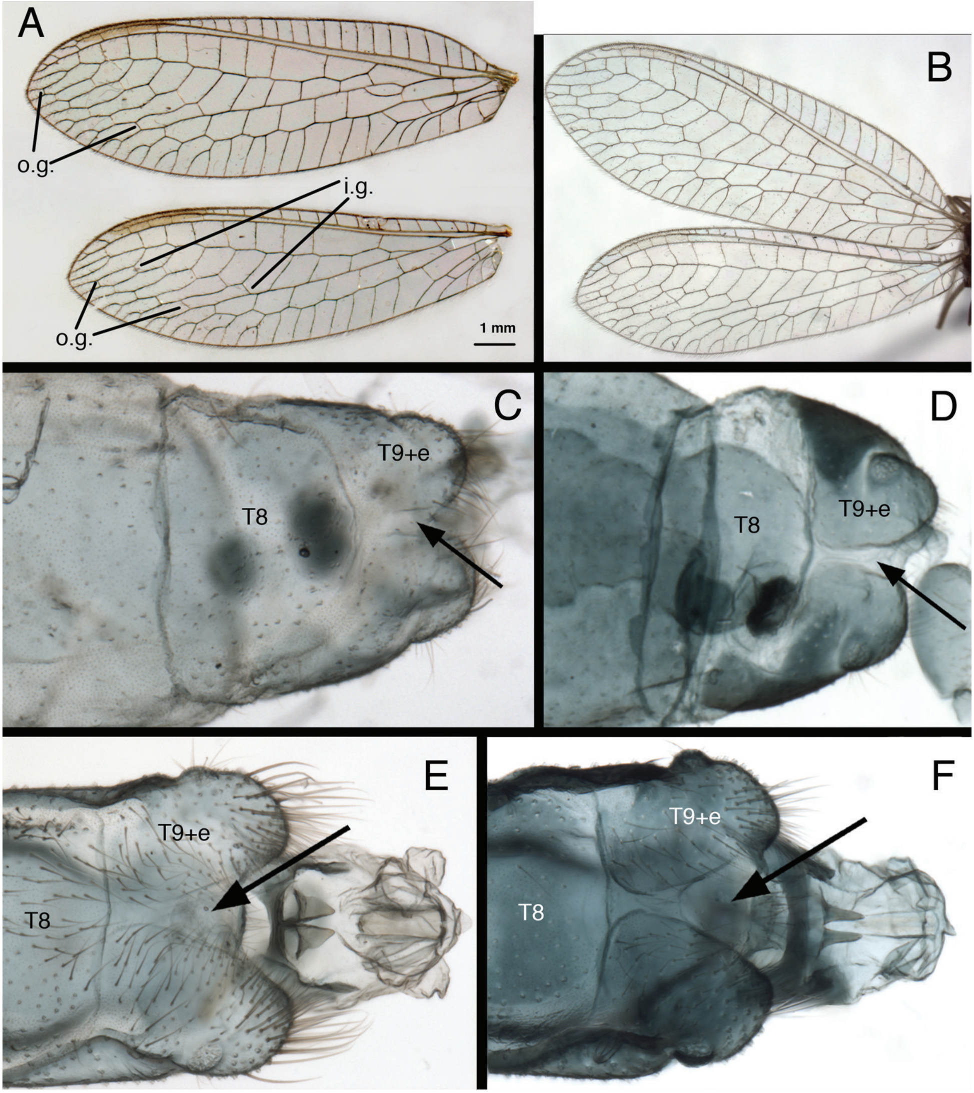

Figure 1. Two external features that characterize *Kymachrysa* adults. **A, B** Fore and hind wings with sinuate longitudinal veins between the first and second gradate series of crossveins **C–F** Terminal segments (dorsal) with Tergite 9+ectoproct separated dorsally **C, D** Female **E, F** Male **A, C, E**. *K. placita* **A, C** Colorado, USNM **E** Type, Colorado, MCZ **B, D, F** *K. intacta* **B** Neotype, Quebec, CNC **D** New York, TRC **F** New York, TRC [Males: gonarcal complex not removed]. *Abbreviations:* **i.g.** inner gradate veins **o.g.** outer gradate veins **T8** eighth tergite **T9+e** fused ninth tergite and ectoproct.

side of the terminal abdominal segment is rounded posterolaterally (especially in males) (Fig. 1C–F). Among other New World genera, a complete dorsal invagination of the T9+ect is reported only for *Chrysopiella* and *Parachrysopiella* (Brooks and Barnard 1990).

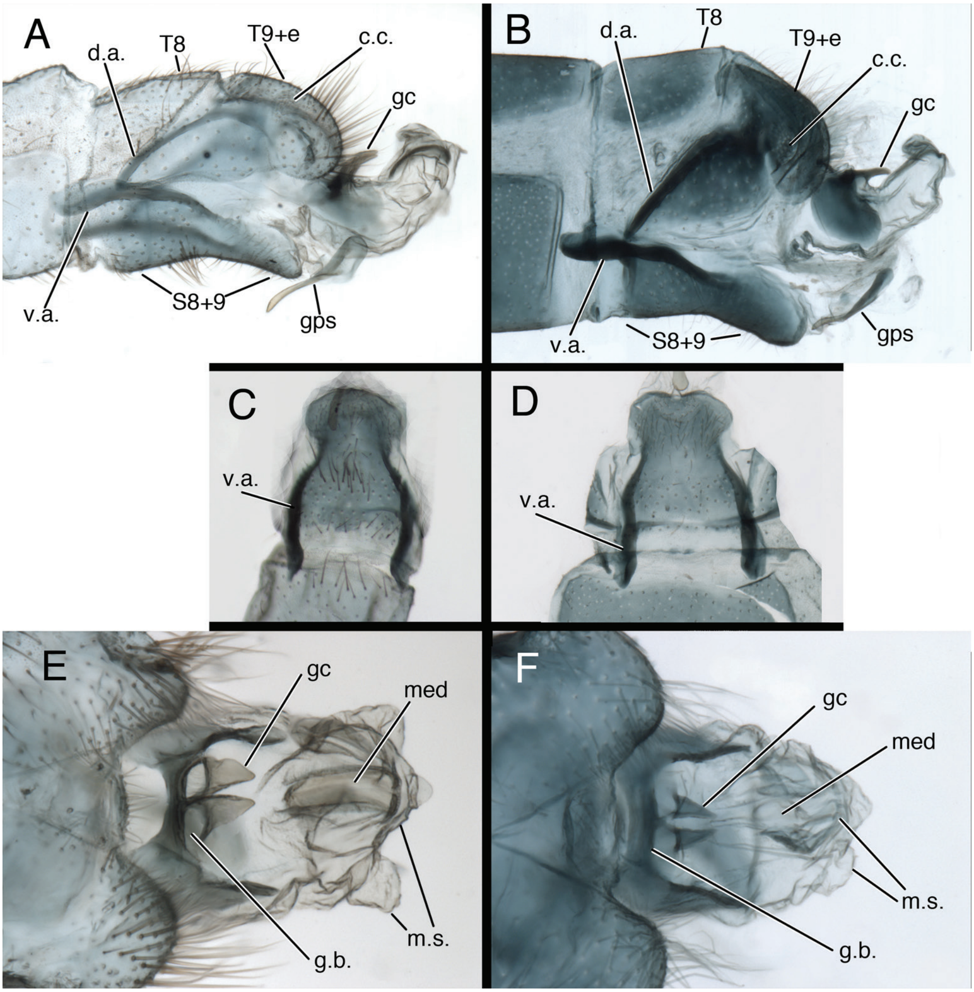

Figure 2. *Kymachrysa* male terminalia. **A, B** Abdominal segments 8 and 9 (lateral), with genitalia everted **C, D** Sternite 8+9 (ventral) **E, F** Genitalia (everted, dorsal) **A, C, E** *K. placita* Type, Colorado, MCZ **B, D, F** *K. intacta*, California, TRC. *Abbreviations:* **c.c.** callus cerci **d.a.** dorsal apodeme (on ninth tergite and ectoproct) **gc** gonocornu **gps** gonapsis **g.b.** gonarcal bridge **med** mediuncus **m.s.** membranous sac **S8+9** fused eighth and ninth sternites **T8** eighth tergite **T9+e** fused ninth tergite and ectoproct **v.a.** ventral apodeme (on sternite 8+9).

Male terminalia. One of the most striking aspects of the *Kymachrysa* male terminalia is the S8+9, which is entirely fused and well sclerotized as in most chrysopine genera. However, in lateral view, the *Kymachrysa* S8+9 has an unusual ventral bend, and the ventral apodeme is heavy and elongate – extending anteriorly well beyond the proximal margin of S8 (Fig. 2A, B). In ventral view, S8+9 is constricted mesally and rounded both anteriorly and posteriorly (Fig. 2C, D). These features are unique among New World chrysopids.

Gonocornua are present on the gonarcal bridge, as in *Ceraeochrysa*. In *Ceraeochrysa*, the gonocornua are usually rounded and unarticulated, and they arise laterally from the gonarcal bridge (see Freitas et al. 2009). But, the gonocornua of *Kymachrysa* are unusual in that they appear at least partially articulated or separated from the gonarcal bridge, and at the base they are juxtaposed and located mesally on the distal margin of the gonarcal bridge (Fig. 2E, F). Furthermore, the dorsum of the mediuncus has a distinct, trough-like shape not found in other genera; the terminus has a weak, lightly sclerotized or membranous beak mesally and expanded membranous sacs laterally.

Female terminalia. Two notable features distinguish the female genitalia. (i) This chrysopid genus is the only one outside of the tribe Belonopterygini (see Tjeder 1966: 235, 324, 337) in which the female is reported to have a praegenitale. [Note: the recording of a praegenitale for *Leucochrysa* (data matrix of Brooks and Barnard 1990: Table 1) appears to be an error – the description of the genus, p. 248, states that the structure is absent.] Moreover, the structure appears unique among chrysopids, in that it is asymmetrical (a condition not reported for Belonopterygini) (Fig. 3C, D). (ii) The spermatheca is shaped like a pillbox with a shallow invagination and a sail-shaped velum that opens via a slit to the bursal duct (Fig. 3F–H). By comparison, in *Ceraeochrysa* the spermatheca is cylindrical, with an elongate invagination and a U-shaped or J-shaped bend that opens via a slit directly to the bursa copulatrix (e.g., Adams and Penny 1985, Freitas and Penny 2001, Sosa and Freitas 2010, 2012). And, in *Chrysopodes* the spermatheca is cylindrical or tubular, with a very deep invagination and an elongate bursal duct (e.g., Adams and Penny 1985, Freitas and Penny 2001, Tauber 2010, Tauber et al. 2012). (iii) Finally, the *Kymachrysa* spermathecal duct (mature specimens) is hairy for almost its entire length; the terminal bristles are long and fine, and their length decreases proximally; at the base of the duct the bristles are very short and stubby, or granular in appearance (Fig. 3E, F).

Description. Adult (Figs 4, 5, 8C, D). Delicate, slender, medium sized (forewing length, *K. placita*: 11–13 mm; *K. intacta* 11–15 mm), predominantly green with yellow longitudinal stripe, mesally. **Head** (Figs 4, 5). Vertex with pair of crescent-shaped, red or brown sublateral marks (sometimes absent or faint), usually with lateral red or brown stripe near margin of eye; frons with or without markings; gena with red or brown longitudinal markings. Distal segments of labial, maxillary palpi with elongate, lateral, black marks. Antenna cream colored, without markings. **Thorax** (Figs 4E–H, 5F–J, 8C, D). Prothorax variable in length and shape (probably developmental variation), usually long, tapered distally; dorsum without lateral stripes, but usually with irregular, red or brownish, sublateral markings (especially western, southern specimens); mesothorax, metathorax with or without markings. Legs mostly light green, without markings, with numerous dark brown to black setae; tarsal claws with deep U-shaped to V-shaped cleft.

Wings (Fig. 1A, B) with costal area slightly enlarged basally; radius straight; im3 cell triangular; forewing, hindwing with two, regular, slightly converging rows of gradate veins; longitudinal veins between inner and outer gradates sinuate; three icu cells, distal one open.

Abdomen (Figs 1C–F, 2A, B, 3A, B, 6A, 7A, 8A, B) with spiracles simple; callus cerci round, located dorsally on T9+ect, with trichobothria stemming from closely

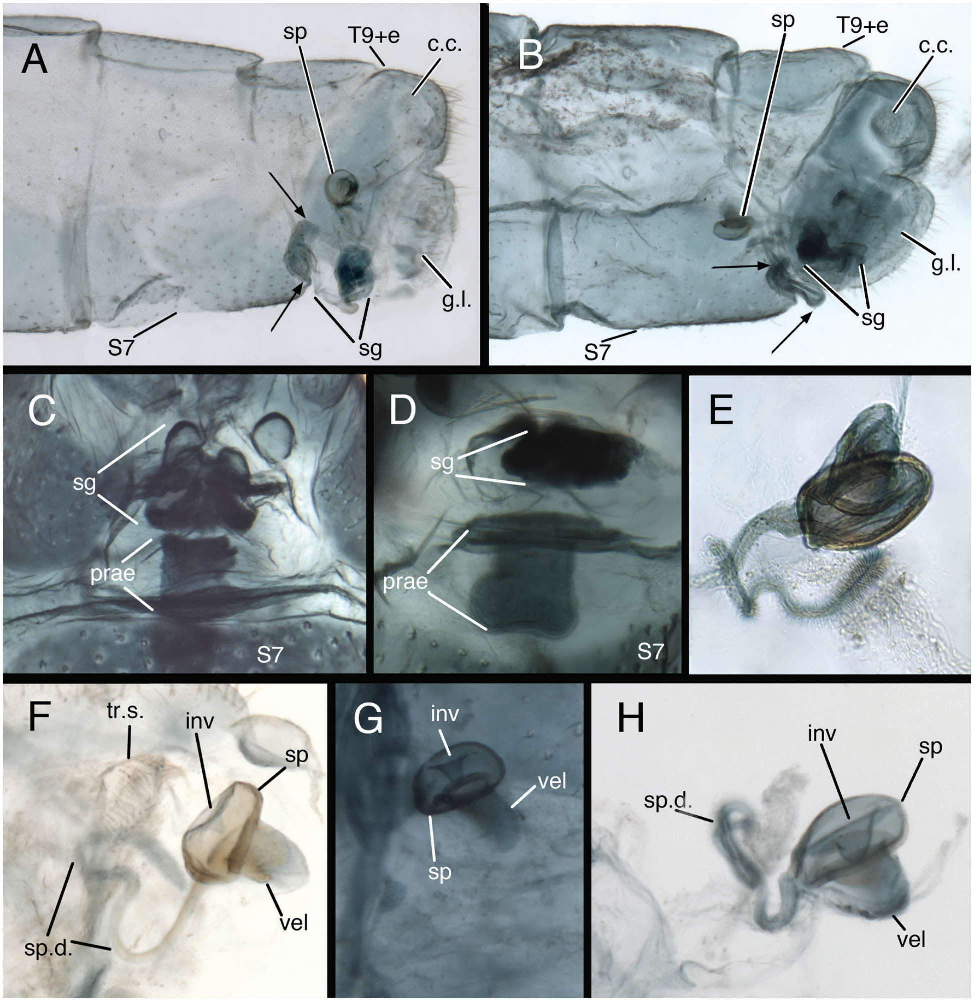

Figure 3. *Kymachrysa* female terminalia. **A, B** Abdominal segments 7 and 9 (lateral) [Arrows delineate the praegenitale] **C, D** Praegenitale at distal margin of S7 (ventral) **E–H** Spermatheca **A, C, F** *K. placita* **A, F** Colorado, USNM **C** New Mexico, USNM **B, D, E, G, H** *K. intacta* **B, D, E** New York, TRC **G** Colorado, CPG **H** California, TRC. *Abbreviations:* **c.c.** callus cerci **g.l.** gonapophysis lateralis **inv** spermathecal invagination **prae** praegenitale **sg** subgenitale **sp** spermatheca **sp.d.** spermathecal duct **S7** seventh sternite **tr.s.** transverse sclerite **T9+e** fused ninth tergite and ectoproct **vel** velum.

spaced sockets; ninth tergite (T9) and ectoproct fused, forming T9+ect; T9+ect completely divided dorsally.

Male abdomen (Figs 2, 6–8) slender, with sternites tall (~0.7× length), with or without microtholi; spiracles simple; terminal segments (A8–A9) compact; ectoproct with heavy apodeme along entire dorsal margin, terminus reaching proximal edge of eighth sternite (S8); eighth and ninth sternites fused; S8+9 shallow, with dorsal surface undulating, anterior section of S8+9 with heavy ventral apodeme extending

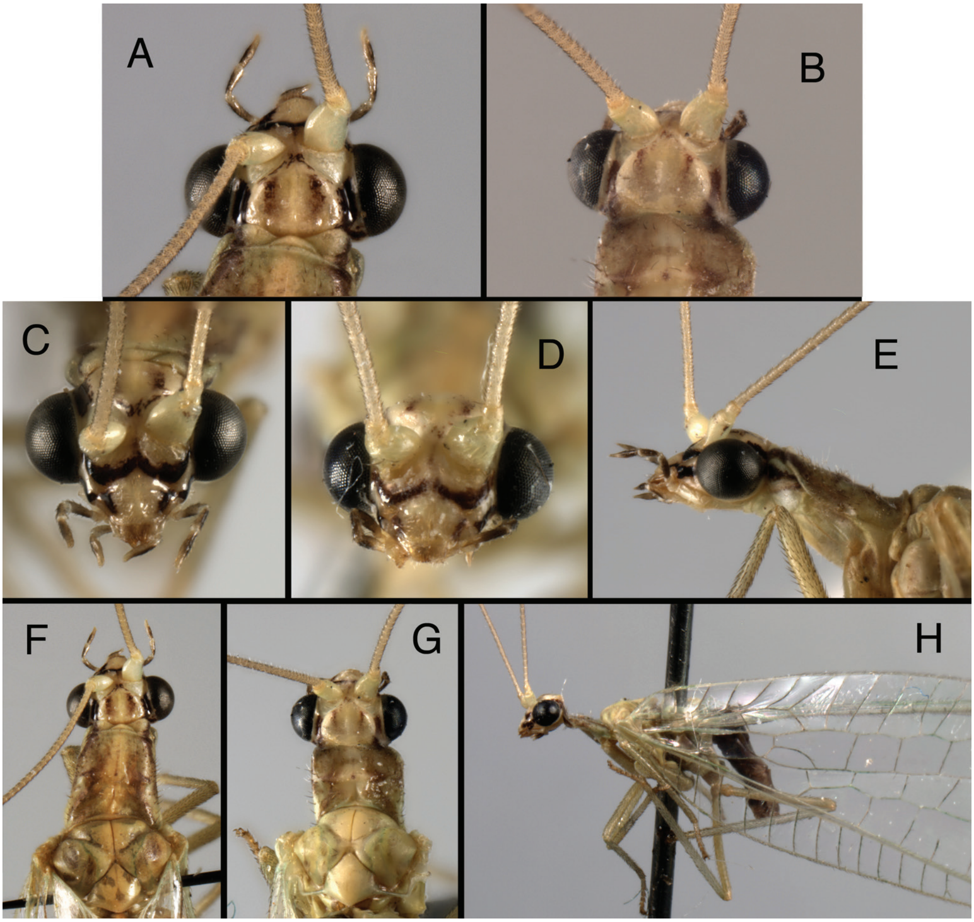

Figure 4. *Kymachrysa placita* external adult features. Note variation in darkness and size of head markings, prothoracic size and shape. **A, B** Head (dorsal) **C, D** Head (frontal) **E** Head, prothorax (lateral) **F, G** Head, prothorax, mesothorax (dorsal) **H** Head, thorax (lateral) [Background with small piece of abdomen visible]. **A, C, E, F** Wyoming, SDNHM; **B, D, G, H** Colorado, CPG.

proximally well beyond margin of segment, into S7; ventral surface indented mesally (hour-glass shaped). Gonapsis, hypandrium internum attached to membrane at tip of S9; gonapsis elongate, with basal margin rounded, toothed, distal margin expanded, curved; gonocristae absent. Gonarcus arcuate, with stout bridge, rounded, expanded lateral apodemes; gonocornua triangular, articulated on laterodistal margin of gonarcal bridge; base of gonocornua clear, tip dark, heavy, tapering to angulate terminus; entoprocessus absent. Mediuncus weak, comprising very lightly sclerotized, curved, mesal band distal to gonocornua, with trough-shaped dorsal surface, small, rounded, membranous terminus. Gonosaccus large, expanded dorsally as pair of large, eversible, distal sacs, expanded ventrally with a second pair of large, eversible sacs; gonosetae absent.

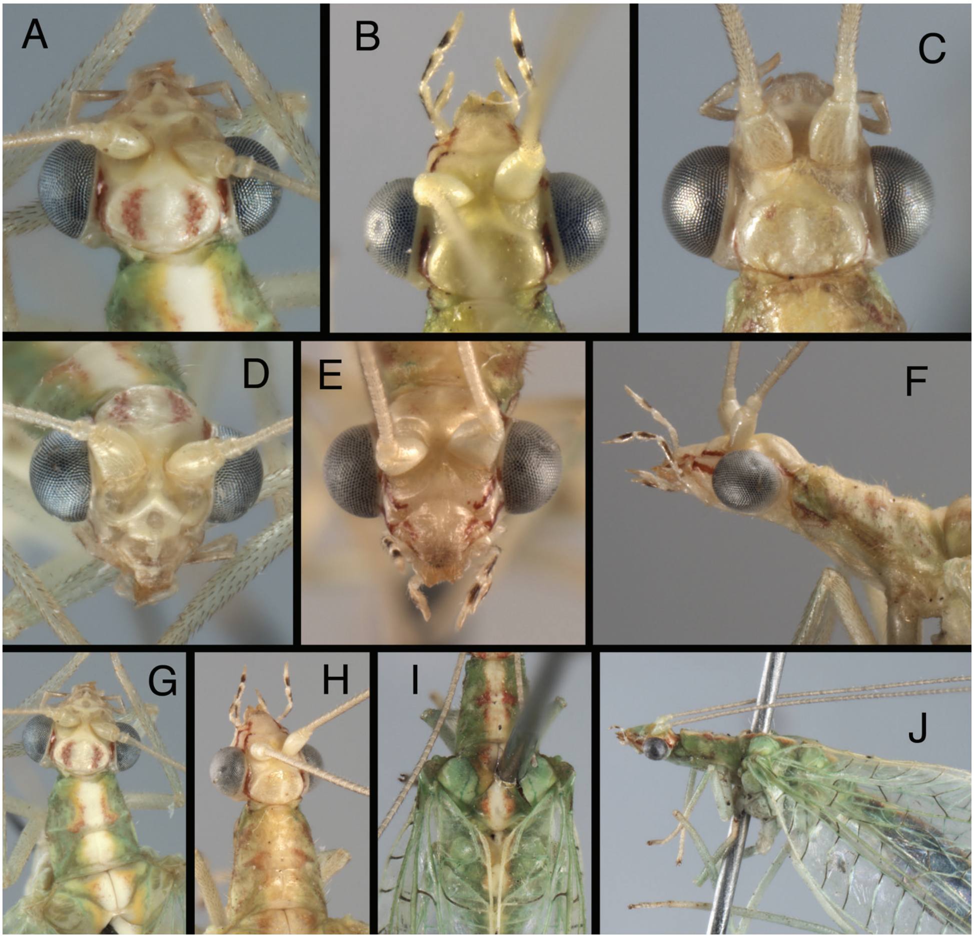

Figure 5. *Kymachrysa intacta* external adult features. Note variation in the presence, darkness, and size of head and thoracic markings. **A–C** Head (dorsal) **D, E** Head (frontal) **F** Head, prothorax (lateral) **G, H** Head, prothorax, mesothorax (dorsal) **I** Thorax (dorsal) **J** Head, thorax (lateral) **A, D, G, I, J** California, TRC **B, E, F, H** Colorado, TRC; **C** New York, TRC.

Female abdomen (Fig. 3) robust, not slender; terminalia compact. Praegenitale present, extending as truncated lobe from distal margin of S7, with distal, asymmetrical lobe, comb-shaped, with single long seta; lobe extending distally beyond S7 or curving internally. Colleterial gland, reservoir membranous, very delicate, extending proximally well into A7; transverse sclerite relatively large, broad, comb-shaped, with elongate teeth. Spermathecal complex simple; spermatheca small, pillbox shaped with small to moderate, U-shaped invagination, sail-like velum, opening to bursa copulatrix via elongate slit and small, membranous bursal duct; spermathecal duct elongate (>3× width of spermatheca), curvy, covered with fine hairs throughout (mature specimens), most dense, long distally, becoming short, stubby basally; immature specimens with basal ~10–20% of spermathecal duct smooth. Bursa copulatrix small, delicate, membranous, sac-like;

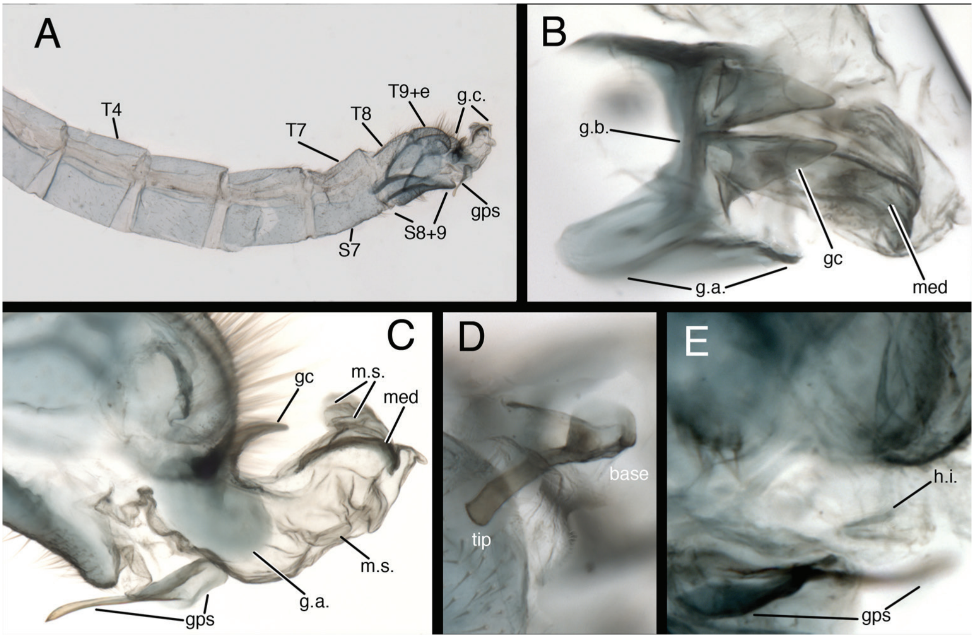

Figure 6. *Kymachrysa placita* male abdomen. **A** Abdominal segments 3 to terminus (lateral), with genitalia everted **B** Gonarcal complex (dorsal) **C** Genitalia (everted–including gonapsis, lateral) **D** Gonapsis (ventral) **E** Hypandrium internum nestled within membrane [Gonapsis not in focus, shown for relative scale]. All Types, Colorado, MCZ *Abbreviations:* **gc** gonocornu **gps** gonapsis **g.a.** gonarcal apodeme **g.b.** gonarcal bridge **g.c.** gonarcal complex **h.i.** V-shaped hypandrium internum **med** mediuncus **m.s.** membranous sac **S7** seventh sternite **S8+9** fused eighth and ninth sternites **Tx** tergite, number **T9+e** fused ninth tergite and ectoproct.

bursal glands either absent or very small. Subgenitale large, robust, triangular in ventral view, with pair of distal lobes, extending outward or concealed beneath ectoprocts.

Etymology. The prefix "*Kyma-*" comes from the Greek word *kýma* (*κύμα*), meaning wave, and refers to the wavy, or sinuate, longitudinal veins between the gradate veins of the forewings that distinguish the two species currently assigned to the genus. The suffix follows the traditional series of chrysopid names ending in "*-chrysa*" – Greek, feminine, "χρυσα" meaning golden.

Geographic distribution. The genus, which currently includes only two species, appears to be restricted to North America (Canada, United States and Mexico, as far south as Mexico City) (Adams 1982, Penny et al. 1997, Tauber 2003, Valencia Luna et al. 2006, Garland and Kevan 2007, Freitas et al. 2009, Tauber and Flint 2010, all as *Ceraeochrysa* or *Chrysopodes*).

Characteristics of *Kymachrysa* larvae. The larvae of only one of the *Kymachrysa* species (*K. intacta*) were described (Tauber et al. 1998, as *Ceraeochrysa placita*). Later they were shown to share a large number of distinctive characteristics with the larvae of several species of *Chrysopodes*, and as a result the species was transferred to *Chrysopodes* (Tauber 2003, as *C. placita*).

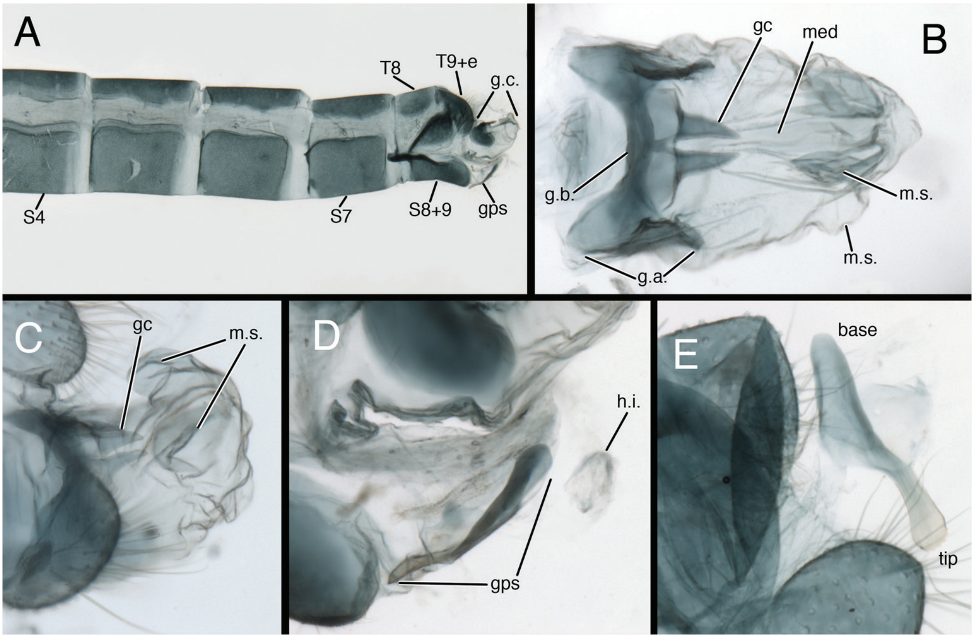

Figure 7. *Kymachrysa intacta* male abdomen. **A** Abdominal segments 4 to terminus (lateral), with genitalia everted **B** Gonarcal complex (dorsal) **C** Everted genitalia (dorsolateral), showing dorsal membranous sacs **D** Gonapsis (lateral), hypandrium internum (dorsal) **E** Gonapsis (ventral). **A, D** California, TRC **B, E** New York, TRC; **C** Colorado, CPG. *Abbreviations:* **gc** gonocornu **gps** gonapsis **g.a.** gonarcal apodeme **g.b.** gonarcal bridge **g.c.** gonarcal complex **h.i.** V-shaped hypandrium internum **med** mediuncus **m.s.** membranous sac **Sx** sternite, number **S8+9** fused eighth and ninth sternites **T8** eighth tergite **T9+e** fused ninth tergite and ectoproct.

Recently, larvae from additional species of *Chrysopodes* were described in sufficient detail for more robust comparisons than were possible earlier. Now, detailed larval descriptions are available for six of the 47 currently recognized species of *Chrysopodes* [Tauber 2003: *Chrysopodes* (*Neosuarius*) *collaris* (Schneider); Silva et al. 2013: *Chrysopodes* (*Chrysopodes*) *divisus* (Walker), *Chrysopodes* (*C.*) *fumosus* Tauber & Albuquerque, *Chrysopodes* (*C.*) *geayi* (Navás), *Chrysopodes* (*C.*) *linaefrons* Adams & Penny; *Chrysopodes* (*C.*) *spinellus* Adams & Penny]. Comparisons with these species confirm that *K. intacta* larvae differ only slightly from those of *Chrysopodes*. And, given the large percentage of species in both *Kymachrysa* and *Chrysopodes* with undescribed larvae, it is not clear at this time, which, if any, of these differences will be informative at the generic level.

Nevertheless, the following features appear most noteworthy:

(a) *Setae*: Previously, certain setae on the *K. intacta* Semaphorant B were reported to be “serrated” or “thorny”, similar to those on *Chrysopodes*; these setae include the LS of the thorax and A4-A8, the large LDS on A6 and A7, and some dorsal thoracic setae (“serrated”: Tauber et al. 2000, as *Ceraeochrysa placita*; “thorny”:

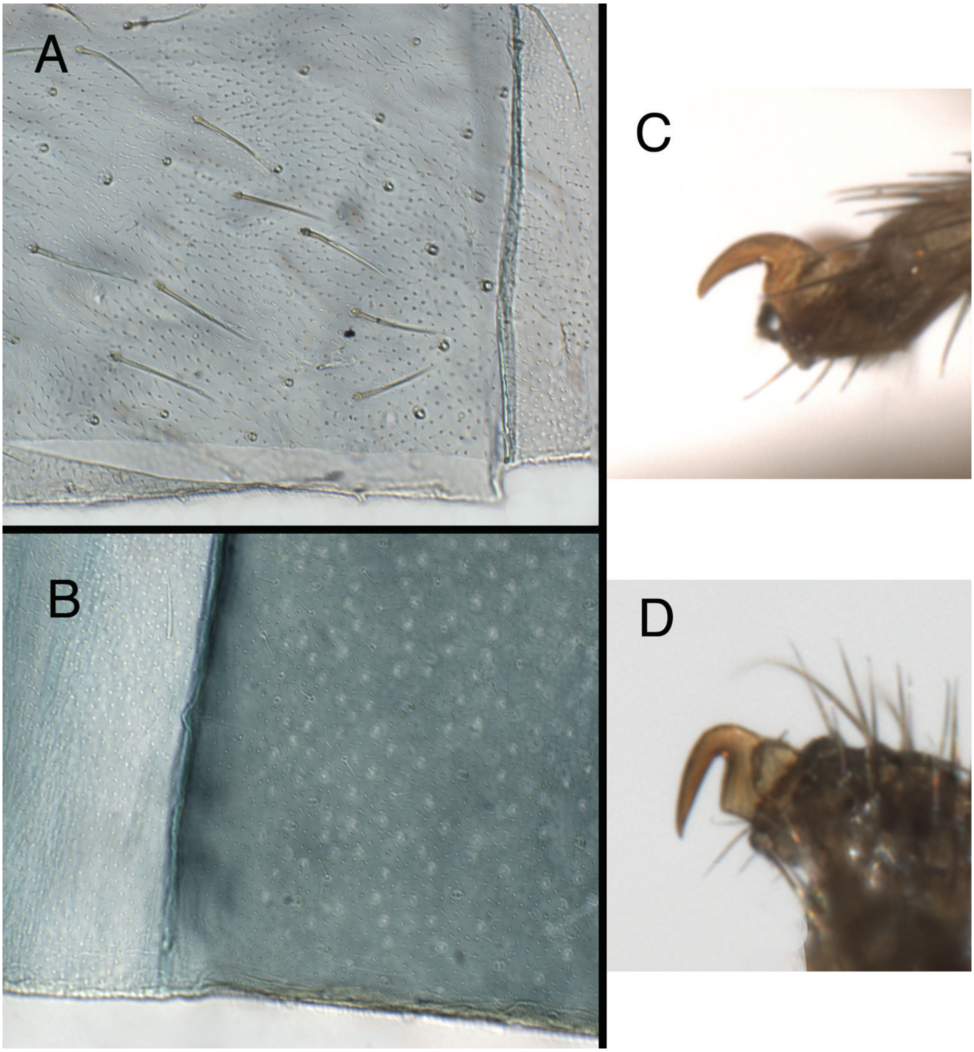

Figure 8. A, B Integument of fifth abdominal sternite. **A** *K. placita*, without microtholi [typical of *K. placita* and some *K. intacta* populations (see text)] **B** *K. intacta*, with microtholi (typical of some populations). **C, D** Prothoracic tarsal claw. **C** *K. placita* **D** *K. intacta*. **A** Type, Colorado, MCZ; **B** California, TRC; **C** Wyoming, SDNHM; **D** Minnesota, CMNH.

Tauber 2003, as *Chrysopodes placita*). Subsequent comparison of these setae with those of the six described *Chrysopodes* species (under higher magnification) indicates that the setal surface of *K. intacta* (Semaphorant B) falls outside the range of variation exhibited by *Chrysopodes* (*Chrysopodes*) and *Chrysopodes* (*Neosuarius*). Rather than serrated or thorny, the *K. intacta* setae have a more sabulose (sandy) or granular surface (Fig. 9C–F). [Note: the same setae on Semaphorant A are thorny on both *Chrysopodes* and *K. intacta*.]

(b) *Metathoracic fold*: One of the primary reasons for transferring *K. intacta* to *Chrysopodes* (Tauber 2003, as *C. placita*) was the shared characteristic of an unusual posterior fold on the larval metathorax. In both taxa, the fold rises well above the anterior part of the metathorax, and it bears a transverse row (R1) of robust setae that stem from enlarged chalazae and that are usually slightly longer than the submedian setae (SMS) on abdominal segments A1 through A6. However, subsequent comparisons indicated that aspects of this feature present some small, but significant differences between *K. intacta* and *Chrysopodes*.

First, as discussed above, the surface of the R1 setae on *K. intacta* Semaphorant B is distinctive. It is sabulose (sandy), not thorny as in *Chrysopodes*.

Second, although the body dimensions of the L3 larvae of *Chrysopodes* (*Chrysopodes*) and *K. intacta* that we studied are similar, the length, robustness, and stiffness of the setae differ between the two taxa (Table 1, Fig. 9). For example, in *Chrysopodes* (*Chrysopodes*), the R1 setae range in length between 0.28–0.42 mm, and they are thick and erect throughout their entire lengths. In comparison, the *K. intacta* R1 setae range between 0.48–0.62 mm; they are slender throughout, and only the basal section stands erect – the distal section tends to curve. [Note: In the large bodied *Chrysopodes* (*Neosuarius*) *collaris* (Schneider), both the R1 setae and SMS are slightly longer and more slender and flexible than those of *Chrysopodes* (*Chrysopodes*) species (Table 1).]

Third, the larvae of *Chrysopodes* spp. (all instars, including the first) have dark brown markings on the frontal surface of the chalazae in metathoracic R1; these markings are elliptical to ovate and at least as broad as the setal base. In *K. intacta* (second and third instars) they are light brown in color, elongate, and narrower than the setal base (Fig. 9A, B); they are either absent or very light in first instars.

Biological features of *Kymachrysa*. Adult specimens of *K. placita* are not common; those that we have seen were collected during July and August. No larval specimens are reported. *K. intacta* appears to be more abundant; we have seen adult specimens collected from June through mid-October (mostly August), and we have collected larvae during March and April (overwintering second instars) and in September and October (prehibernal first instars).

Biological features have been investigated only for *K. intacta* (Tauber et al. 1998). In populations from both eastern and western USA (NY and CA), eggs are laid and larvae occur on the trunks of medium-sized to large-sized deciduous and evergreen

Table 1. Larval setal lengths (range): comparison between *Kymachrysa intacta* and *Chrysopodes* species.

Species	T3-R1	SMS
Kymachrysa intacta	0.48–0.62 mm	0.28–0.43 mm
Chrysopodes (*Chrysopodes*) *divisus*	0.28–0.36 mm	0.24–0.36 mm
Chrysopodes (*Chrysopodes*) *geayi*	0.39–0.42 mm	0.21–0.36 mm
Chrysopodes (*Neosuarius*) *collaris*	0.43–0.51 mm	0.31–0.47 mm

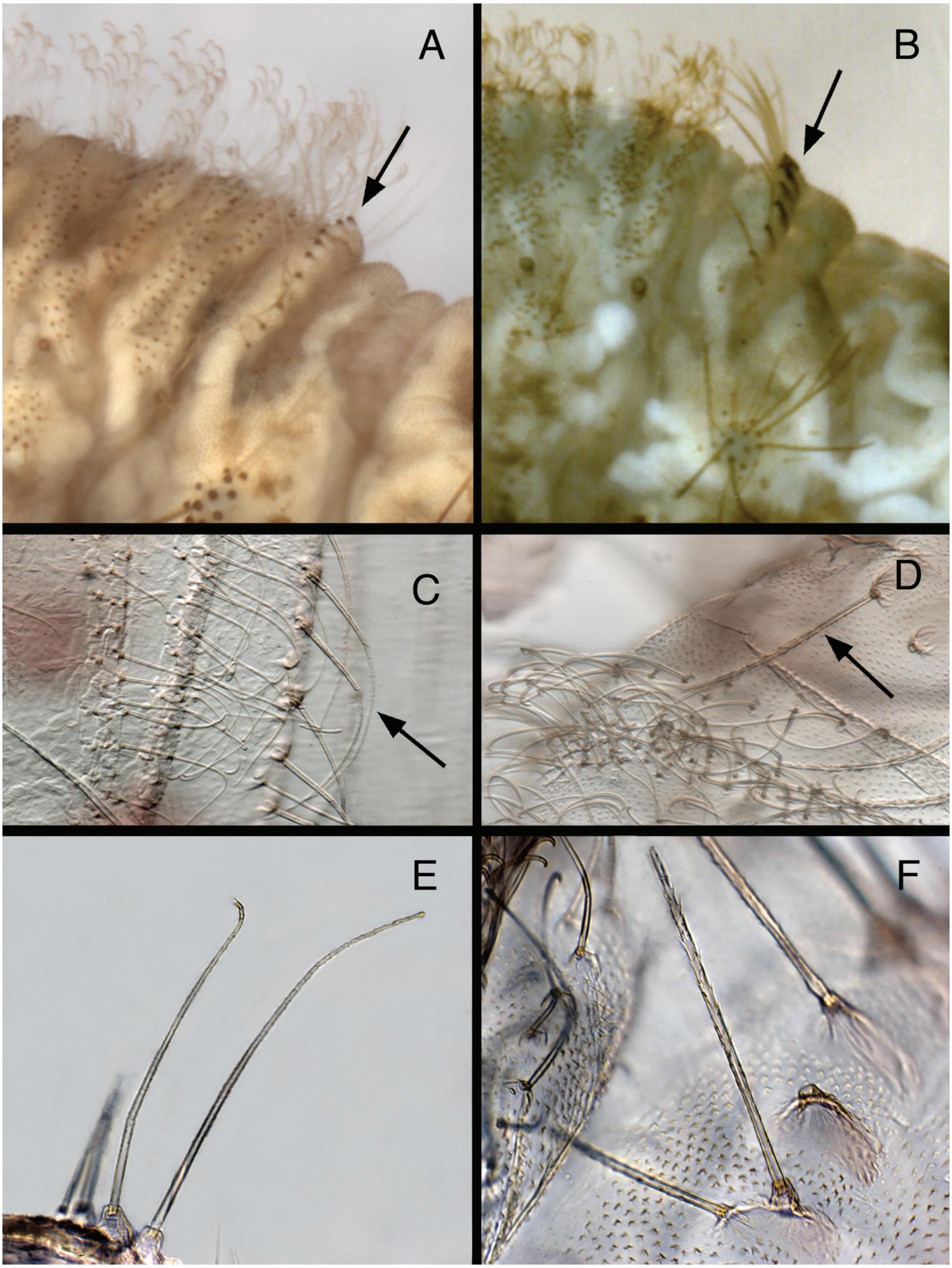

Figure 9. Larval characteristics that distinguish *Kymachrysa* from *Chrysopodes*. **A, B** Raised metathoracic posterior fold [Arrows indicate dark setal bases with distinctive anterior markings] **C–F** Setae on raised metathoracic fold [Note slender, curved structure, granular surface (*Kymachrysa*) vs robust, erect structure, thorny surface (*Chrysopodes*)] **A, C, E** *K. intacta* (Californa, TRC) **B, D, F** *Chrysopodes geayi* (Rio de Janeiro, TRC).

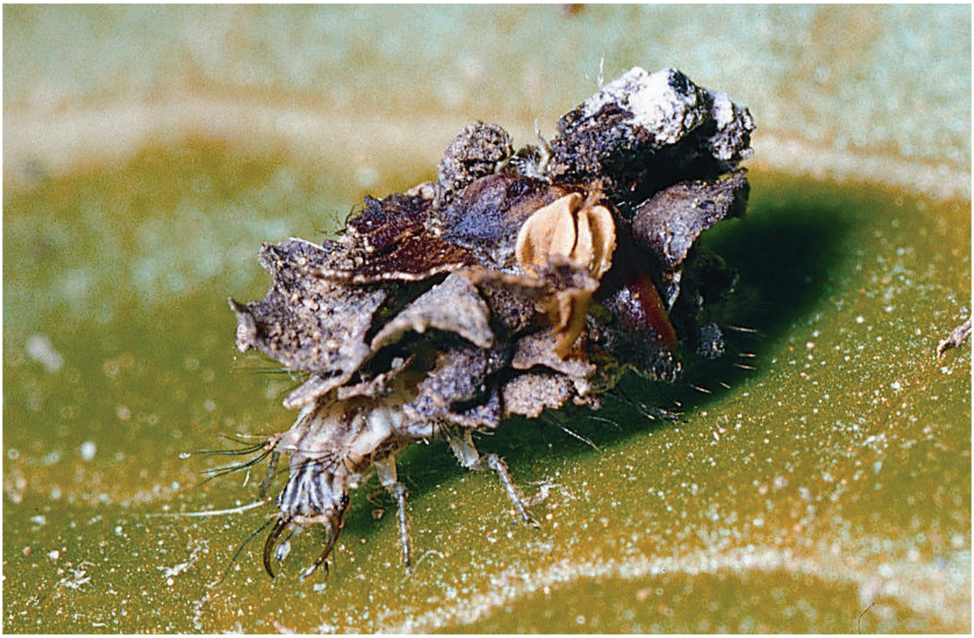

Figure 10. *Kymachrysa intacta* third instar (darkly marked). Note head markings, debris packet containing woody and dried plant material. (Photo: Stephen A. Marshall).

trees. The larvae are debris-carriers; typically they carry pieces of bark or other woody or plant material that blends with their typical substrate (Fig. 10).

Developmental stages are relatively prolonged, and they are strongly influenced by photoperiod (Tauber et al. 1998). The life cycle appears to be univoltine. Larvae overwinter as diapausing second instars. Short daylengths decelerate development during the first instar, and they induce and maintain hibernal diapause in second instars. Daylength also may be important during the postdiapause developmental period. Under field conditions (Tompkins and Schyler Counties, NY), adults emerge in June, and eggs occur from July through late September or early October. Such a life cycle is unusual, but not unknown, for other chrysopids. For example, free-living second and third instars of *Pseudomallada* species also overwinter in a photoperiodically induced diapause (Principi and Sgobba 1987, 1993, Canard et al. 1990).

Kymachrysa**'s generic relationships.** With the addition of *Kymachrysa*, a total of 17 genera of Chrysopini are now known from the New World. Table 2 lists the eleven that are reported from North America, including Mexico, and it provides references to their distributions.

Above, we showed that *Kymachrysa* adults (males and females) express a number of characteristics that provide strong morphological support for a distinct genus. However, its relationship with other chrysopine genera remains perplexing. In general, the male genital structures resemble those of *Ceraeochrysa*, whereas the female genitalia (apart from the presence of a praegenitale in *Kymachrysa*) appear similar to those of

Table 2. Genera in the tribe Chrysopini reported from North America, including the new genus, *Kymachrysa*.

Ceraeochrysa Adams, 1982 – New World, largely Neotropical; 15 species in North America (Valencia Luna et al. 2006, Garland and Kevan 2007, Freitas et al. 2009, Tauber and Flint 2010)
Chrysopa Leach in Brewster, 1815 – Holartic; eleven confirmed species in North America (Penny et al. 1997, Garland and Kevan 2007, Valencia Luna et al. 2006)
Chrysoperla Steinmann, 1964 – Worldwide; ten species from North America (Brooks 1994, Valencia Luna et al. 2006, Henry et al. 2012)
Chrysopodes (*Neosuarius*) Adams & Penny, 1985 – Neotropical; largely Central and South America; one species from North America (Adams and Penny 1985, Tauber 2003, Valencia Luna et al. 2006, Garland and Kevan 2007)
Eremochrysa Banks, 1903 – Nearctic, West Indies; largely southwestern USA & northern Mexico: *Eremochrysa* (*Chrysopiella*) Banks, 1911, four species; *Eremochrysa* (*Eremochrysa*) Banks 1903, thirteen species (Penny et al. 1997, Valencia Luna et al. 2006, Garland and Kevan 2007, Oswald 2013)
Kymachrysa gen. n. – Nearctic (Canada, USA, and montane Mexico), two species
Meleoma Fitch, 1855 – Nearctic, Neotropical, largely USA and Mexico; 28 species (Tauber 1969, Brooks and Barnard 1990, Penny 2006, Garland and Kevan 2007)
Nineta Navás, 1912 – Holarctic; two species from North America (USA, Canada) (Penny et al. 1997, Garland and Kevan 2007)
Plesiochrysa Adams, 1982 – Neotropical, Oriental, Australasia; ~25 species with two from North America (southern USA & Mexico) (Penny et al. 1997, Valencia Luna et al. 2006)
Pseudomallada Tsukaguchi, 1995 – Holarctic; large genus (~165 species) with five species from North America (Adams and Garland 1982)
Yumachrysa Banks, 1950 – Western USA, Mexico; four species (Penny et al. 1997, Oswald et al. 2002)

several other genera (e.g., *Ungla*, *Pseudomallada*). Finally, its larval morphology is very close to that of *Chrysopodes*, and its biological traits (larval habitat, overwintering stage, photoperiodically controlled diapause) resemble those of *Pseudomallada*. Resolution of the dilemma posed by the above mixture of similarities awaits a broadly based phylogenetic analysis of chysopid genera.

Modifications for Brooks and Barnard's (1990) key to adults of chrysopid genera

In the most recent taxonomic key for chrysopid genera (Brooks and Barnard 1990), both *Kymachrysa* and *Ceraeochrysa* males are recovered at couplet 45. However, the two species can be differentiated with the following changes and additions to the couplet:

45 Fore wing narrow (length : breadth > 2.8 : 1); anal veins not crassate; radial crossveins (between R and Rs) usually straight; median plate [= gonarcal bridge] with dorsal horns [= gonocornua] (Brooks and Barnard 1990, fig. 268)......**45A**

– Fore wing broad (length : breadth ≤ 2.8 : 1); anal veins crassate; radial crossveins (between R and Rs) usually sinuate; median plate [= gonarcal bridge] without dorsal horns [= gonocornua] (Brooks and Barnard 1990, figs 335, 346) .... ***Chrysopodes* Navás**

45A Fore wing with veins between gradate veins straight; dorsum of T9+ect invaginated apically, but fused at least basally (male and female); male with ventral apodeme of S8+9 not elongated, extending anteriorly at most to margin of S8, not beyond; spermatheca cylindrical, with U-shaped or J-shaped bend opening to bursa copulatix.. ***Ceraeochrysa* Adams**

– Fore wing with veins between gradate veins sinuate (wavy); dorsum of T9+ect separate (unfused or divided) dorsally (male and female); male with ventral apodeme of S8+9 elongate, extending anteriorly beyond margin of S8; spermatheca pillbox-shaped, with velum opening to bursa copulatrix via small bursal duct.. ***Kymachrysa* gen. n.**

Catalog of *Kymachrysa* species

Kymachrysa placita (Banks, 1908), comb. n.

Chrysopa placita Banks, 1908: 259 [MCZ, Lectotype, designated by Tauber and Flint 2010: 61].

Ceraeochrysa placita (Banks). First combination in *Ceraeochrysa* by Adams (1982: 73). Removed from *Ceraeochrysa* by Tauber (2003: 484). Combination reinstated by Freitas et al. (2009: 568), but subsequently considered uncertain by Tauber and Flint (2010: 64).

Chrysopodes (*Neosuarius*) *placitus* [= *placita*] (Banks). First combination in *Chrysopodes* (*Neosuarius*) by Tauber (2003: 484). Removed from *Chrysopodes* by Freitas et al. (2009: 568). Generic and subgeneric association with *Chrysopodes* (*Neosuarius*) considered uncertain by Tauber (2010: 12).

Chrysopa forreri Navás, 1913-14 [1914]: 97 [Syntype, The Natural History Museum, London (BMNH)]. Junior subjective synonym of *Cer. placita* by Adams (1982: 73). Recognized as a junior subjective synonym of *Ceraeochrysa intacta* (Navás) by Tauber and Flint (2010: 62).

Chrysopa intacta Navás, 1912: 199 [Neotype, Canadian National Collection, Ottawa, (CNC), designated by Garland 1985: 138]. Junior subjective synonym of *Cer. placita* by Garland (1985: 137). Recognized as a valid species, with uncertain generic assignment by Tauber and Flint (2010: 62).

Species specific characters. The species was most recently re-described by Freitas et al. (2009: 568). Externally, it is recognized by its characteristic broad, dark brown facial markings (Fig. 4) and broadly cleft tarsal claws (Fig. 8C). The distinctive male features include: microtholi absent (Fig. 8A); ventral apodeme of S8+9 convex, with smooth curve; gonocornua broad, touching each other mesally (Fig. 6). Female character states include: spermathecal invagination small (< 1/4th the width of the spermatheca), shallow (< 1/2 the depth of the spermatheca); basal section of spermathecal duct smooth, without hairiness (Fig. 3). The larvae and biology are unknown.

Geographic distribution. We have seen specimens or reliable reports only from the USA (AZ: Chafee, Cochise Co.; CO: Clear Creek, Larimer, Jefferson Co.; NM: Cibola Co.; UT: Uintah Co.; WY: Albany Co.).

Kymachrysa intacta (Navás, 1912), comb. n.

Chrysopa intacta Navás, 1912: 199 [Original syntype reported to have been retained in Navás collection, probably destroyed; Neotype, CNC; designated by Garland (1985: 137)]. Junior subjective synonym of *Cer. placita* by Garland (1985: 137).

Ceraeochrysa intacta (Navás), genus *incertae sedis*. Recognized as a valid species, with uncertain generic assignment by Tauber and Flint (2010: 62).

Chrysopa forreri Navás, 1913-14 [1914]: 97 [Syntype, BMNH]. Junior subjective synonym of *Cer. intacta* by Tauber and Flint (2010: 61).

Ceraeochrysa chiricahuae Freitas & Penny, in Freitas et al. 2009: 594 [Holotype, CAS]. Junior subjective synonym of *Cer. intacta* by Tauber and Flint (2010: 61).

Remarks. In addition to the citations listed above that refer to synonymies and nomenclatural changes, Garland and Kevan (2007: 59) provide a list of references containing information on *K. intacta* under the name *placita*/*placitus* [as *Chrysopa*, *Ceraeochrysa*, *Chrysopodes* (*Neosuarius*), *Oviedus*]; other references include Tauber and de León (2001, as *Ceraeochrysa placita*); Tauber (2010: 12, as *Chrysopodes placitus*); Tauber et al. 2014: Suppl, Material, as *Ceraeochrysa placita*, *incertae sedis*).

Species specific characters. This species was re-described by Tauber et al. (1998, 2000, as *Ceraeochrysa placita*), Tauber (2003, as *Chrysopodes placita*), and Freitas et al. (2009: 594, as *Ceraeochrysa chiricahuae*). Adults are recognized by their slender, red markings on the head and thorax (Fig. 5) and narrowly cleft tarsal claws (Fig. 8D; also see Garland 1982, fig. 74k), as well as their distinctive male and female genitalia. The male features include: microtholi sometimes present (see below); ventral apodeme of S8+9 irregular, with several small curves and a mesal bend; gonocornua narrow, separated from each other basally (Fig. 7). In the female, the spermathecal invagination is large (~1/3rd the width of the spermatheca) and relatively deep (> ½ the depth of the spermatheca), and the basal section of the spermathecal duct is hairy (Fig. 3).

Specimens of *K. intacta* from eastern and western North America appear very similar to each other, but we found some geographic variation of note. First, the male abdominal sternites are densely covered with microtholi on our specimens from California (Alameda, Kern, and Sierra Counties) (Fig. 8B). In contrast, microtholi are very sparse or absent on specimens from Utah (Wasatch County) and Colorado (Larimer County), and absent from specimens from New Hampshire (Belknap County) and New York (Tompkins and Schuyler Counties) (as in Fig. 8 for *K. placita*; also see Garland 1982). Second, larvae (second and third instars) from the west were reported to have somewhat denser abdominal setation than those of the east (Tauber et al. 1998). And, finally, the length of the stalk that supports the egg is considerably longer in east-

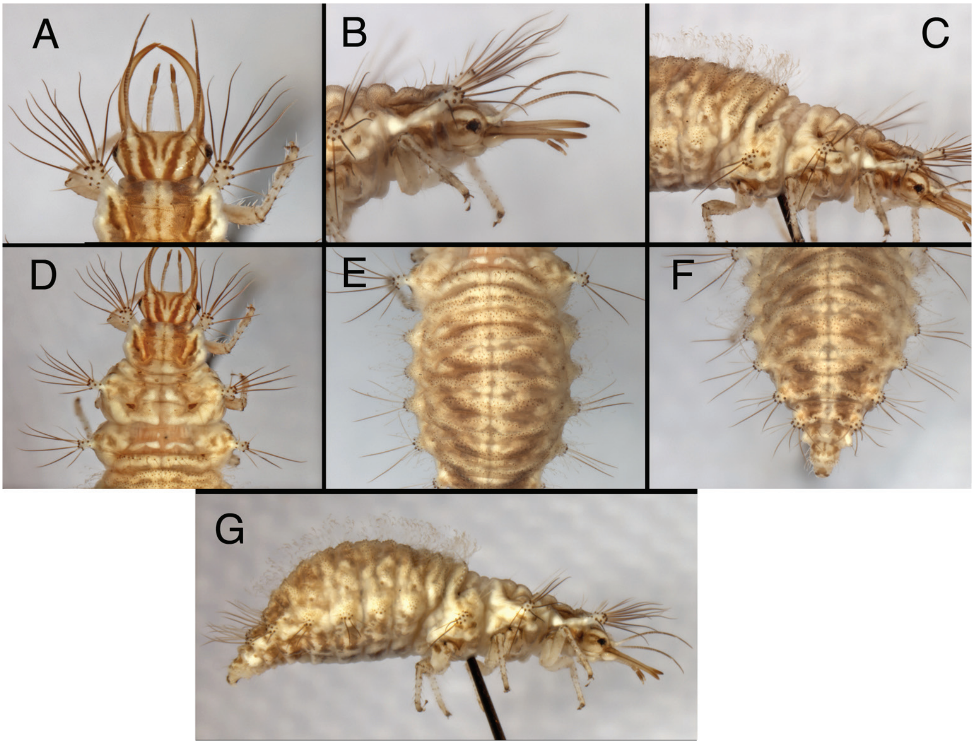

Figure 11. *Kymachrysa intacta* third instar. **A** Head (dorsal) **B** Head (lateral) **C** Thorax (lateral) **D** Thorax (dorsal) **E** Abdominal segments 1–4 (dorsal) **F** Abdominal segments 4–10 (dorsal) **G** Body (lateral). All New York, TRC.

ern than in western populations (eastern: 2.1–3.3 mm; western: 1.4–2.3 mm) (Tauber et al. 1998). Given the potential role of microtholi in courtship, we suspect that the above variation may indicate at least some reproductive isolation between eastern and western populations.

The larvae of *K. intacta* have been described (Tauber et al. 1998, 2000, Tauber 2003); for images, see Fig. 11 here. Below are some modifications and corrections to the earlier descriptions:

(a) Semaphorant A (L1): Thorax as figured by Tauber et al. (1998, Fig. 8), with following differences: Mesothorax with Sc1, Sc2 present anteriorly on folds as in *Chrysopodes* (see Tauber 2003, fig. 10); Sc3 present, posteromesal to lateral tubercles, with one medium-length and sometimes one small associated setae; S1 small or absent; S2 medium-length, mesal to Sc3, smooth to finely sabulose. Metathorax with Sc3 present, mesal to lateral tubercle, with one or two small associated setae (S1Sc3, S2Sc3); several very small setae anterior to Sc3, probably associated with a very pale Sc2.

(b) Semaphorant B (L3, L2): Prothorax with S1 and S1Sc1 smooth to very finely sabulose, not thorny. Mesothorax with Sc2 present mesal to lateral tubercles, with two small associated setae (S1Sc2, S2Sc2); S1 present, small; S2 small or absent; S3 of medium-length, slightly granular; S4 small, smooth; but S1Sc3 small, S2Sc3 slightly longer. Metathorax with posterior row of setae (R1) arising from large chalazae.

Geographic distribution. This species occurs broadly throughout North America. We have seen specimens or reliable records from: Canada (ON, QC; see Garland 1984); United States (AZ, CA, CO, MN, MO, NC, NH, NM, NV, NY, OR, TN, TX, UT, WS, WV, WY; see Penny et al. 1997); and Mexico (Dgo., D.F., Mich.; see Valencia Luna et al. 2006).

Kymachrysa placita and *K. intacta* were collected sympatrically in Rustler Park, Cochise Co., AZ, 6-Aug-1991, by R. & J. Robertson (CAS).

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Citation: Kerr PH (2014) The sequoia-loving sprite, a new genus and species of fungus gnat (Diptera, Mycetophilidae) from California. ZooKeys 437: 109–126. doi: 10.3897/zookeys.437.7932

Abstract

California is one of the most biologically diverse regions of the world, yet the diversity of fungus gnats (Mycetophilidae) remains largely undocumented within the state. A modest survey of these flies has led to the discovery of a new genus and species of gnat that lives alongside one of the most iconic trees in the world, the giant sequoia (*Sequoiadendron giganteum*). *Spritella sequoiaphila* **gen. et sp. n.** is described and illustrated and its status among other mycetophilid genera is analyzed and discussed.

Keywords

Systematics, fungus gnats, new genus, new species, California Floristic Province, *Spritella*, giant sequoia tree, *Sequoiadendron giganteum*

Introduction

California is home to one of the most biologically diverse regions of the world (Myers et al. 2000), although it is unknown exactly how many species of Mycetophilidae (Diptera) occupy the state. Recent monographs suggest that the family remains in need of rigorous taxonomic development. For example, the genera *Novakia* Strobl and *Azana* Walker were not known to occur in the state until 2007 and 2010, respectively (representing four new species; Kerr 2007, 2010); all three species of *Acomoptera* Vockeroth living in

California were undescribed until 2011 (Kerr 2011); both species of Californian *Phthinia* Winnertz were not described until 2014 (Fitzgerald and Kerr in press); and an additional seven new species (six of these California endemics) of *Megophthalmidia* Dziedzicki were only just recently discovered and described (Kerr 2014).

Our understanding of the diversity and distribution of Mycetophilidae and related flies in California will remain limited as long as material available for study is lacking in museums and other curated collections. In an effort to document latent diversity within the California Floristic Province, a modest collecting program has been conducted throughout the state over the last several years. Although woefully incomplete, this effort has generated over 5000 genus-level specimen identifications of fungus gnat specimens from over 170 different collecting events (nearly all Malaise traps) in 12 different California counties.

One of the most iconic symbols of the California Floristic Province is the giant sequoia groves of the Sierra Nevada Mountains. This habitat is special for its natural inhabitants as much as for the emotional reaction it inspires. The giant sequoia is the planet's largest living organism and found only in California, with some trees towering over 300 feet tall and having trunk diameters of over 55 feet. In 1853, when the 'Mother of the Forest' tree was cut down in Calaveras County for speculative commercial exploitation, it set off the first national awakening of environmentalist sentiments that called for the protections of public lands. This awareness, fostered by the popular publications of naturalist John Muir, led to the first protections of these trees in 1864 (Mariposa Grove in Yosemite Valley), and eventually led to the establishment of the United States National Park Service in 1872. Today, the magnificent 'Big Trees' bring over 5,000,000 people per year to visit parks that contain giant sequoia groves, generating tens of millions of dollars in tourist revenue for local economies every day (Thomas et al. 2014).

It was within giant sequoia forest habitat that an especially curious fungus gnat was recently discovered. Because of its unusual morphology – particularly, the unique wing venation of the male – the phylogenetic affiliation of this fly was not immediately clear. This paper describes this species, illustrates its morphology, and locates it within a systematic phylogenetic framework among currently known Mycetophilidae.

Materials and methods

Terminology for thoracic, wing, and genitalic morphology is consistent with Kerr 2011, which follows Söli (1997), McAlpine (1981), Vockeroth (1981), and Matile (1990). The terms "genitalia" and "terminalia" are used interchangeably. Genitalia were macerated in 10% KOH at approx. 95 °C for 15–20 minutes to remove soft tissue, then rinsed in distilled water and dilute glacial acetic acid, and dissected in water. All genitalia preparations were placed in a small genitalia vial containing glycerol, and pinned beneath the specimen. Figures were made using Adobe Illustrator and Adobe Photoshop Creative

Suite software, with digital images taken using a Nikon DS-Fi1 scope-mounted digital camera. Habitus images were taken with the same digital camera (or the Nikon DS-Fi2), using an LED dome lighting system (Kerr et al. 2008). Material examined is deposited in the California State Collection of Arthropods, Sacramento, CA (CSCA), as indicated in square brackets after the transcribed specimen label data.

All measurements are made in millimeters. Ranges are given for body length, wing length, and the mean for each of these values is provided. Measurements of the holotype are given in square brackets. The number of individuals measured is noted in parentheses. All measurements are of critical-point dried specimens.

Key to the sciophiline genera lacking a posterior wing vein fork (Mycetophilidae: Sciophilinae: "*Azana* group" *sensu* Matile 1998) (Modified from Matile 1998)

1 Posterior vein forked, sometimes incomplete at the base; mediotergite setose or not .... **(Other Sciophilinae)**

– Only one posterior wing vein; mediotergite setose **2**

2 (1) M_2 absent or present in the form of a vein more or less obsolete at the base **8**

– Anterior fork complete **3**

3 (2) Wing macrotrichia oriented toward base of wing; sc-r and R_4 present (R_4 occasionally absent); metepisternum with fine setae .... ***Monoclona*** **Mik**

– Wing macrotrichia oriented toward wing apex; sc-r and R_4 present or absent; metepisternum bare **4**

4 (3) Sc-r present, R_4 present or absent; tibia II without sensory organ **6**

– Sc-r and R_4 absent; tibia II bearing sensory organ **5**

5 (4) Subcostal wing vein not exceeding (or just barely exceeding) the apex of the basal cell; second palpal segment strongly dilated; male tergite IX large, lacking modified setae .... ***Cluzobra*** **Edwards**

– Subcostal wing vein clearly exceeding the apex of the basal cell; second palpal segment weakly dilated; male tergite IX short, bearing a pair of modified paddle-shaped bristles .... ***Afrocnemia*** **Matile**

6 (4) R_4 present; anterior basalare setose; anepisternum bearing short setae; subcostal vein usually less than half length of wing membrane ...... ***Parvicellula*** **Marshall**

– R_4 absent; anterior basalare bare; anepisternum bare or bearing short setae; subcostal vein usually half length of wing membrane or longer **7**

7 (6) Anepisternum bare or with small setae; katepisternum bare; sc-r proximal of Rs .... ***Acnemia*** **Winnertz**

– Anepisternum with small setae near upper margin; katepisternum with setae; sc-r distad of Rs .... ***Spritella*** **gen. n.**

8 (2) Subcostal very short, free at apex; r-m longitudinal, the basal cell small and rectangular .... ***Azana*** **Walker**

– Subcostal ending in C or R, r-m longitudinal or not **9**

9 (8) Subcostal long, ending in R; r-m long and longitudinal; anepisternum setose .... ***Neotrizygia* Tonnoir & Edwards**

– Subcostal short, ending in C; r-m long or short; anepisternum setose or bare... **10**

10 (9) Sc-r present, anepisternum setose.. ***Trizygia* Skuse**

– Sc-r absent, anepisternum bare **11**

11 (10) Wing macrotrichia directed toward the wing apex; r-m oblique; M_1 entire; R_4 present (New Zealand) or absent (South America)..... ***Paratrizygia* Tonnoir**

– Wing macrotrichia directed toward the wing base; r-m longitudinal, the basal cell small rectangular; M_1 incomplete at the base; R_4 absent.......................... .... ***Neoaphelomera* Miller**

Taxonomy

Spritella gen. n.

http://zoobank.org/BAA00509-5AFE-42E3-9A05-B10FE54A83E3

Type species. *Spritella sequoiaphila* gen. et sp. n., by current designation.

Diagnosis. Three ocelli, antennae with 14 cylindrical flagellomeres, maxillary palpus 4-segmented, scutum raised above level of head, upper half of anepisternum with setae, ventro-posterior area of katepisternum with microsetae, tibial spurs 1:2:2. Wing membrane with macrotrichia; costa produced beyond tip of R_5; subcosta long, ending at C, approximately at midpoint of wing; sc-r present, arising beyond origin of Rs; r-m missing because Rs and M_1 touching or r-m present, short; M_2 arising from discal cell basad of origin of Rs or at base of M_1; cubital vein unforked, A_1 well developed, reaching beyond origin of Rs. Male gonostylus without basal appendages.

Spritella gen. n. resembles *Acnemia* Winnertz by its lack of a posterior fork and foreshortened medial stem. However, the new genus is readily separated from *Acnemia* by the presence of setae on the anepisternum and katepisternum; sc-r arising well beyond origin of Rs; and by having male gonostylus without a basal process. Other sciophiline genera that also lack the cubital fork include *Afrocnemia* Matile, *Cluzobra* Edwards, *Monoclona* Mik, and *Parvicellula* Marshall. In the new genus, crossvein sc-r is clearly present unlike in *Afrocnemia* and *Cluzobra*; R_4 is absent unlike in *Parvicellula*; and the macrotrichia of wing membrane are decumbent, directed toward wing apex unlike in *Monoclona*. The long subcostal vein of *Spritella* gen. n. (relative to wing length) and position of sc-r relative to Rs is also distinctively different from these genera.

Description. Head shape in anterior view subequal, approximately as long as wide; medial eye margins farther apart dorsally than ventrally; antennal eye notch present, at least two ommatidia deep; interommatidial setulae present between all ommatidia; ocelli three, nearly linear; lateral ocellus between 1× and 1.5× its own diameter from eye margin, between 2.5× and 3× its own distance from median ocellus; all ocelli dorsad of eye margin; occipital suture from median ocellus to occiput absent; frontal suture between median ocellus and ventral margin of frons complete, suture between lateral ocelli and eyes also present; frons with setae; face approximately 2× longer than wide, parallel-sided along most of length, bearing setulae throughout; face and clypeus separated by complete suture; clypeus ovate, approximately one-half length of face, covered with short setae. Antennal scape and pedicel subequal in size; scape with setae approximately 2× scape length; pedicel setae approximate length of pedicel; antennal flagellomeres 14, cylindrical, approximately 3× longer than wide, approximately the same length but thinner distally, densely covered with short setae. Palp with 4 visible segments, none with apparent sensory pit.

Thorax (Fig. 2) raised, scutum dorsad of head position; short setae distributed throughout scutum, acrostichal setae present, bristles present along lateral margins of scutum; postalar wall and callus separated by carina; scutellum clearly wider than long, narrower than scutum; antepronotum and proepisternum with bristles; anepisternum with setae dorsally; anterior basalare bare; anapleural suture incomplete; katepisternum with setae ventro-posteriorly; anepimeron bare; anepisternum with few inconspicuous setulae; laterotergite raised ventrally, with bristles and shorter setae; metepisternum bare; mediotergite with three bands of bristles ventrally and shorter setae that extend along dorsoventral length, medially. **Wing** membrane covered with microtrichia and macrotrichia that are arranged irregularly; C ending beyond R_5; dorsal surface of humeral vein without setae, ventral surface with setae; subcostal vein setose on both sides, ending in C, approximately at midpoint of wing; sc-r present, arising distad of origin of Rs; R_1 setose on dorsal and ventral surfaces, although bare basad of Rs vein ventrally; vestigial M vein within discal cell present or absent; R_4 not present, r-m present or absent (R_5 joining M_1 at junction with Rs); M_1 setose above, bare below; M_2 setose above, bare below, either arising from bM, from junction of M_1 and Rs, or from base of M_1; cubital vein unforked, setose above, bare below, ending at wing margin; CuP strong at base, extending apically as weak fold; anal vein strong, setose on both sides (less so ventrally), extending beyond origin of Rs. **Legs** elongate; coxae with dark, erect setae and lighter, shorter decumbent setae; femora with short, appressed setae and microtrichia; mid tibial organ absent; tibial spur formula 1:2:2; tibiae with short, appressed setulae and short, erect setae that are no longer than half widest width of tibia; tarsal claws small; empodium developed.

Abdomen with segments of subequal width; sternites with two longitudinal fold lines along length; in male, segments 8 modified so that genitalia orient upwards. **Male terminalia** with enlarged, hood-like epandrial sclerite (tergite IX); cerci and epiproct reduced; hypoproct with lightly sclerotized anterior apodemes; gonocoxites widely separated, joined by narrow medial bridge; gonostyli simple, without subtending appendages, inwardly-directed, and arising from middle area of gonocoxites. **Female terminalia** with first cerci elongate, second cerci ovoid, sternite 8 clearly larger than tergite 8.

Etymology. The genus name is feminine, derived from the English “sprite” and the Latin ending “-ella”, as a diminutive.

Spritella sequoiaphila sp. n.

http://zoobank.org/8135BBEC-1424-401B-9320-53205C3AD187
Figs 1–13

Type material. Holotype: ♂, "USA: CA: USA: CA: Tulare Co.: Whitaker Forest, EshomCrk.Drainage, nr. tree#142, 36.7062°N, -118.9319°W, 1650masl, YPT, 3.vi–16.vii.2010 P.H. Kerr" / "HOLOTYPE 10F761♂ *Spritella sequoiaphila* Kerr 2014" [red label]. Deposited in CSCA, dissected specimen mounted on gray point, terminalia in glass vial marked "10F761 HT" on pin below specimen. Type locality indicated in Fig. 14.

Paratypes: 1 ♂, USA: CA: Calaveras Co., Calaveras Big Trees SP, S. grove fire rd., nr. Beaver Creek, MT#1, 38°15.41'N ,120°15.25'W 1385masl, 22.v.–11.vi.2007 P.H. Kerr & A.R. Cline 07LOT086" [CSCA]; 7 ♂♂, 8 ♀, "USA: CA: Tulare Co.: Whitaker Forest, E.EshomCrk.Drainage, nr. tree#142, 36.7062°N, 118.9319°W, 1650masl, MT, 3.vi–16.vii.2010 P.H. Kerr CSCA10L174" [CSCA]; 8 ♂♂, 3 ♀, "USA: CA: Tulare Co: Whitaker's Forest, Ridge S. of Eshom Crk., 1620masl, 36.7011°N, 118.9363°W, MT, 3.vi–16.vii.2010 P.H. Kerr CSCA10L175" [CSCA]; 4 ♂♂, 2 ♀, "USA: CA: Tulare Co.: Whitaker Forest, E.EshomCrk.Drainage, nr. tree#142, 36.7062°N, -118.9319°W, 1650masl, YPT, 3.vi–16.vii.2010 P.H. Kerr CSCA10L258" [CSCA]; 1 ♂, "USA: CA: Glenn Co., Atchison Campsite pine forest, ex: Malaise, elev. 1310m, 20–24.v.2012, colls: K. Will, K. Yao, N. Grady-Grot, 39°45'00"N,122°55'33"W, CAL2012.v.23.5" [EMEC].

Diagnosis. This species may be distinguished by the characters of the genus and by the male genitalia; particularly the gonostylus which has two apical lobes, the ventral one being distinctly sclerotized and darkened.

Description. Male. Body length (n=4): 4.6–6.6, 5.7 [4.6] mm. Wing length: 5.3–5.9, 5.6 [5.9] mm (n=4).

Coloration (Figs 1, 2). Head brown; face and clypeus brown; palpomeres light brown to brown. Antennal scape and pedicel yellowish light brown, base of first flagellomere yellowish light brown, otherwise brown; all remaining flagellomeres brown. Thorax variously yellow, yellowish to orangish brown to brown; scutum yellowish light brown dorsally, with faint brown band postero-medially, orangish brown to brown laterally; scutellum light brown to brown; antepronotum, proepisternum, anepisternum, and katepisternum brown; anepimeron light brown; laterotergite and anepisternum brown; metepimeron and metakatepisternum brown to dark brown; halteres yellowish light brown; mediotergite yellowish light brown. Wing membrane lightly brown infuscated. Coxae dark brown; femora yellowish light brown; tibiae slightly darker yellowish light brown; tarsi brown. Abdominal segments light brown to brown, lighter in color near anterior margin on segments 1–6. Terminalia brown.

Head. Ocelli slightly raised; middle ocellus smaller than (approx. 0.5× size of) lateral ocelli. Face with golden brown setae laterally, mostly bare medially. Antenna length 2.7–3.0, 2.9 [2.7] mm (n=4); about 2× length of thorax, shorter than abdomen. Palpus with four visible palpomeres, slightly longer than width of head (anterior view); length of palpomeres 1 and 2 nearly subequal (palpomere 2 longer); palpomere 3 ap-

Figure 1. *Spritella sequoiaphila* sp. n., habitus [holotype male, # 10F761]. Scale bar = 1 mm.

prox. 5× longer than wide; palpomere 4 approx. 10× longer than wide, subequal to or shorter than combined length of palpomeres 1–3.

Thorax and Abdomen. Wing as Fig. 3; Rs distinctly elongate; vestigial M vein present within discal cell; M_1 arises from R_{4+5} at origin of Rs so that r-m not present; M_2 weak at base. Tergite 8 reduced (Fig. 4), with setae on posterolateral margin, and a

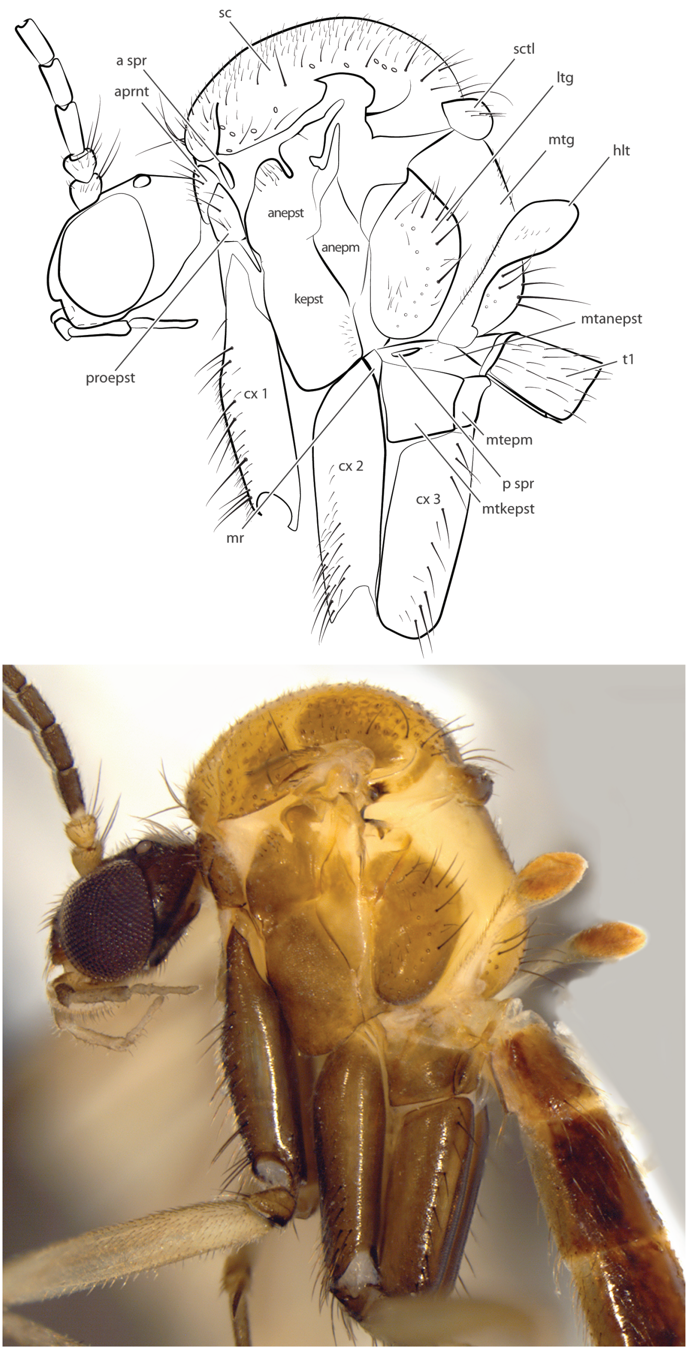

Figure 2. *S. sequoiaphila* sp. n., thorax, lateral view [paratype male, #11G040]. Abbreviations: **anepm** anepimeron **anepst** anepisternum **aprnt** antepronotum **a spr** anterior spiracle **cx** coxa **hlt** halter **kepst** katepisternum **ltg** laterotergite **mr** meron mtg mediotergite **mtanepst** anepisternum **mtepm** metepimeron **mtkepst** metakatepisternum **p spr** posterior spiracle **patg** paratergite **proepm** proepimeron **proepst** proepisternum **sc** scutum **sctl** scutellum.

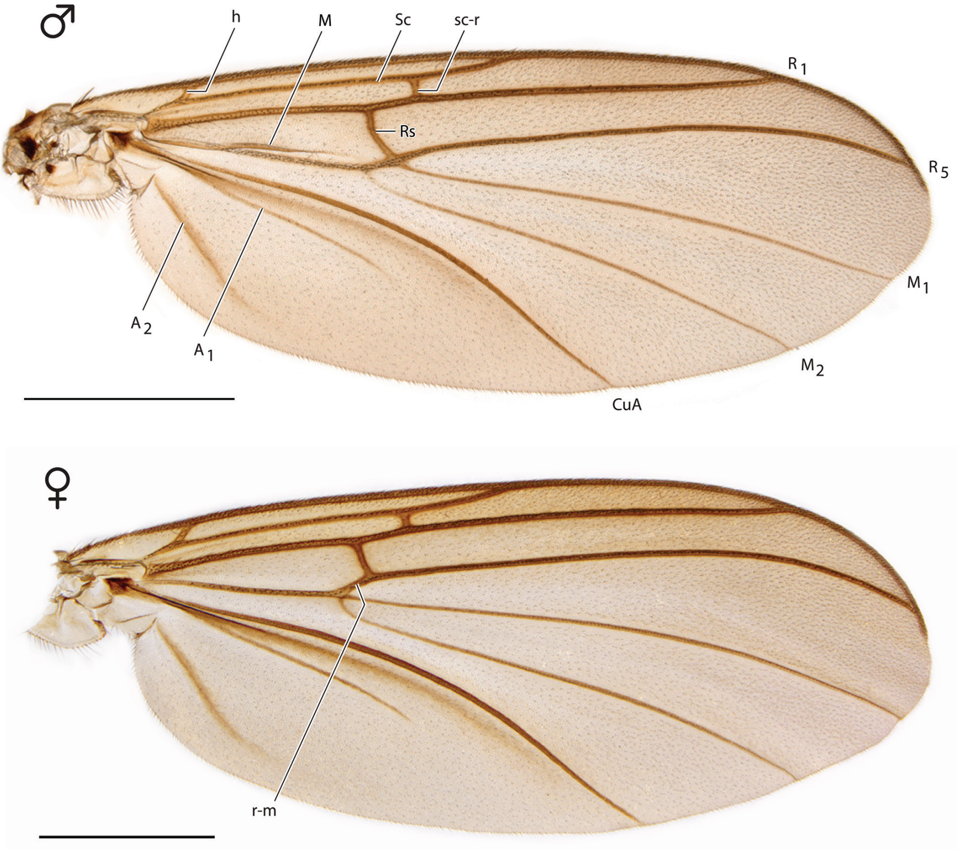

Figure 3. *S. sequoiaphila* sp. n., right wings [paratype male, #10F296; paratype female #14P342]. Scale bar = 1 mm.

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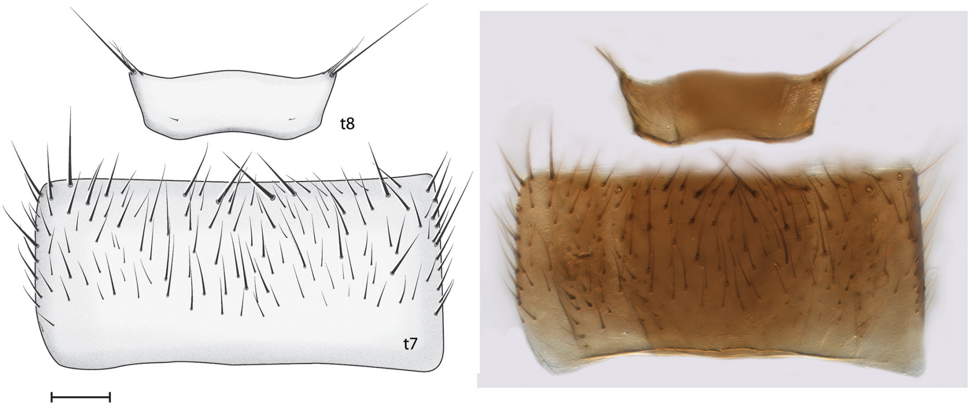

Figure 4. *S. sequoiaphila* sp. n., male abdominal tergites 7–8 [holotype, # 10F761]. Sternite 7 slightly visible below. **t** tergite. Scale bar = 0.1 mm.

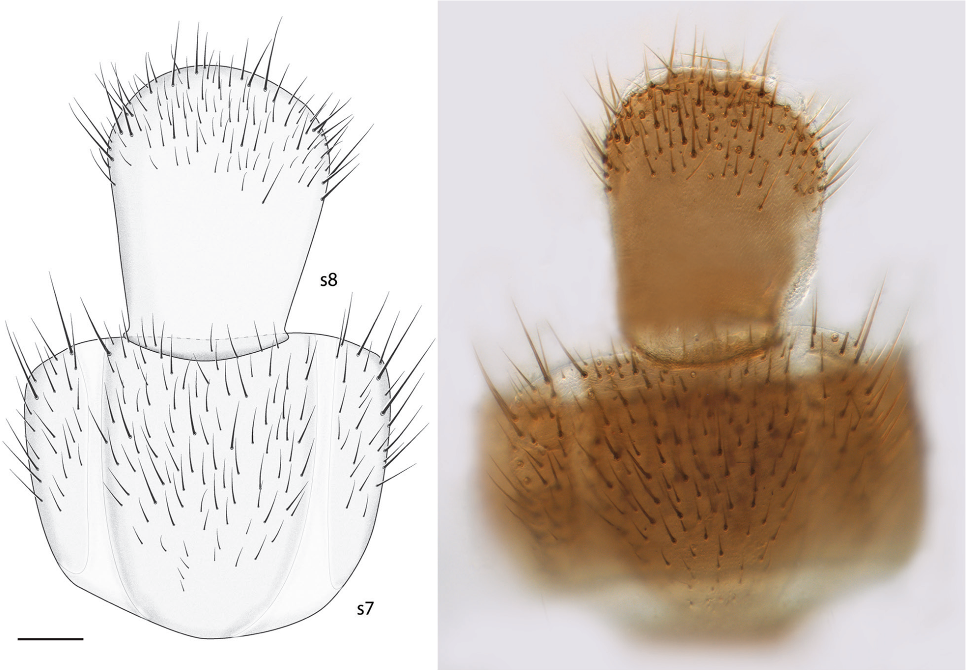

Figure 5. *S. sequoiaphila* sp. n., abdominal sternites 7–8 [holotype male, # 10F761] (looking through t7). **s** sternite. Scale bar = 0.1 mm.

pair of setulae sub dorsally; sternite 8 (Fig. 5) elongate, setose on posterior half, approximately half width of sternite 7.

Male Genitalia (Figs 6–9). Epandrium deeply emarginate both anteriorly and posteriorly, with pair of submedial apical fins (Fig. 6) and pair of short lateral processes (Fig. 8). Gonostyli with pair of setose apical lobes, the ventral one with dark sclerotization.

Female. Body length: 4.4–5.5, 5.1 mm (n=4). Wing length: 4.8–5.3, 5.1 mm (n=4). Antenna length 1.9–2.2, 2.1 mm (n=4).

Coloration. Similar to male.

Thorax. Wing as Fig. 3; Rs not as long as in male; vestigial M vein within discal cell absent; r-m present; M_2 arises at or near base of M_1.

Female Genitalia (Fig. 10). Tergite 8 narrow, expanded laterally; first cerci fused, approx. 2× longer than wide; second cerci ovoid; hypoproct elongate, subtending most of cercus 1; sternite 8 with deep medial cleft reaching anterior margin.

Etymology. The species epithet is an adjective, referring to its affiliation with giant sequoia groves ("sequoia-loving").

Phylogenetic analysis

The phylogenetic analysis was carried out by adding *Spritella seqoiaphila* gen. et sp. n. to the scored character matrix created by Borkent and Wheeler (2013), with minor

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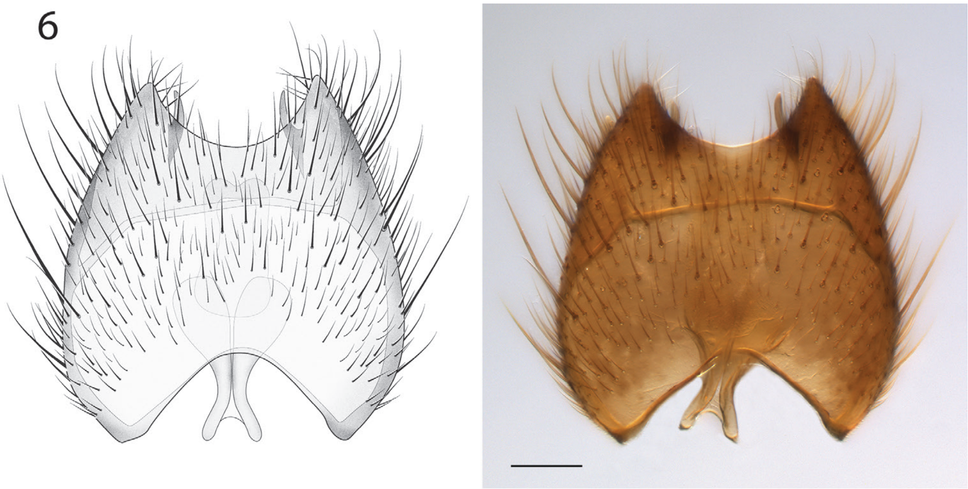

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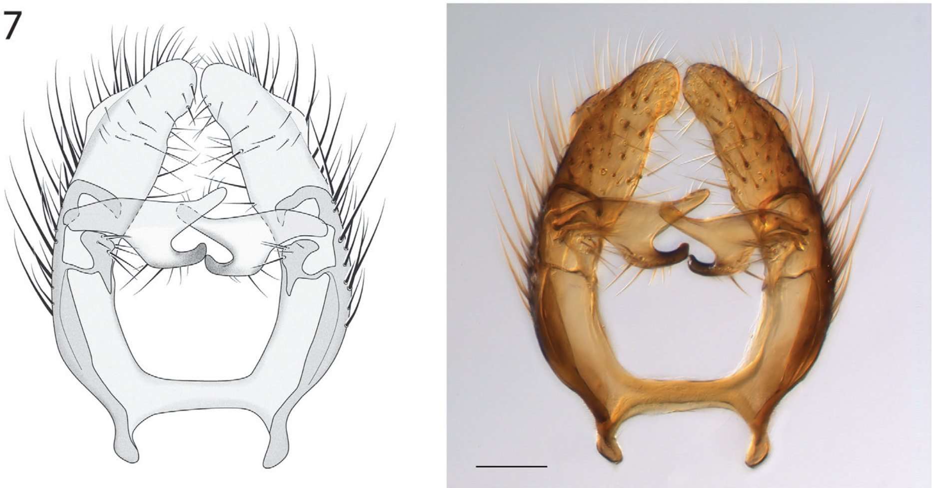

Figures 6–7. *S. sequoiaphila* sp. n., illustrations and photomicrographs of structures of the male genitalia, dorsal view [holotype male, # 10F761]. **6** epandrium **7** gonocoxites. Images same scale, scale bar = 0.1 mm.

modifications (Suppl. material 1). The following changes were made to avoid problems of non-independence: Character # 43, wing macrotrichia orientation (decumbent or reflexed), was changed to "?" for taxa whose wing macrotrichia was scored as absent (41: 1). For taxa whose ventral surface of subcostal vein was scored as bare (54: 0), character # 55 was not applicable and changed to "?" since the presence or absence of setae on the ventral base of subcostal vein was not free to vary (it was already scored as bare). The same type of non-independence was found in character # 57 which treats the dorsal side; the subcostal vein (bare or setose), was changed to "?" for taxa that had already been scored as bare in the previous character (56: 0). Character # 68, position of anterior fork origin, was changed to "?" for taxa whose anterior fork (M1 + M2) was scored as absent (67: 1). For taxa whose posterior fork was scored as absent (73:

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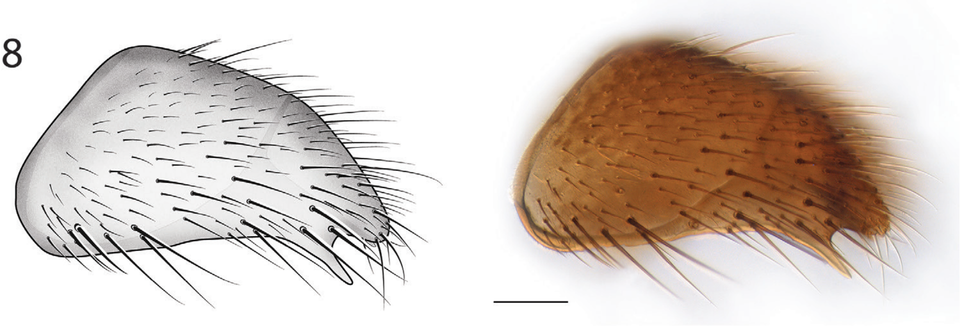

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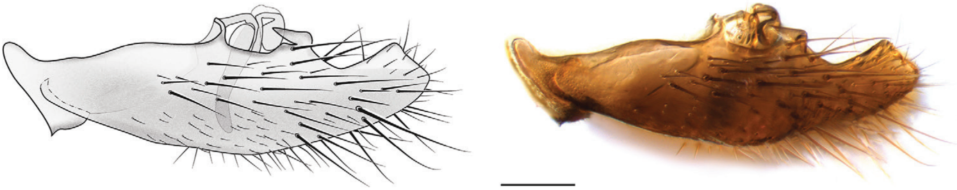

Figures 8–9. *S. sequoiaphila* sp. n., structures of the male genitalia, lateral view [holotype male, # 10F761]. **8** epandrium **9** gonocoxites. Scale bar = 0.1 mm.

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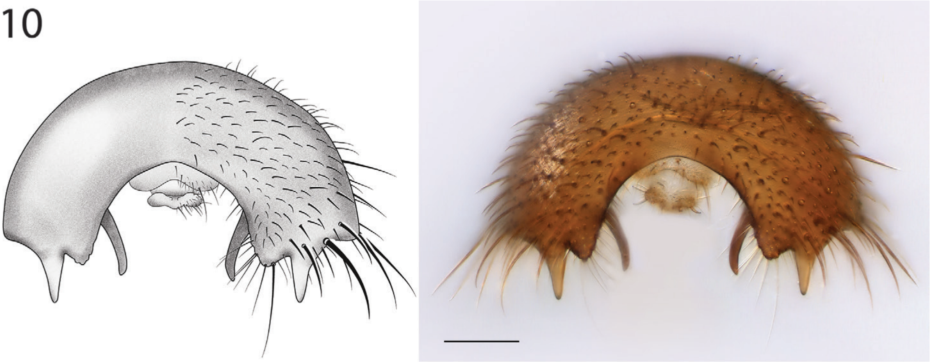

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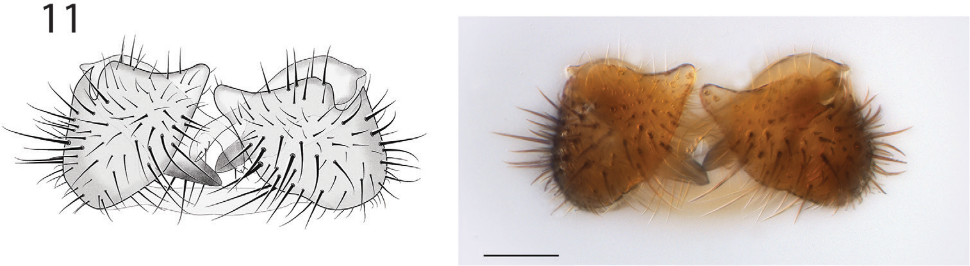

Figures 10–11. *S. sequoiaphila* sp. n., structures of the male genitalia, posterior view [holotype male, #10F761]. **10** epandrium **11** gonocoxites. Scale bar = 0.1 mm.

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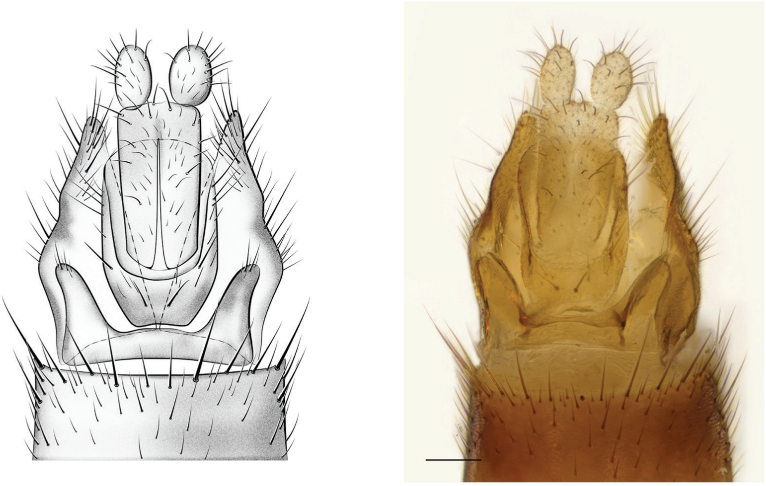

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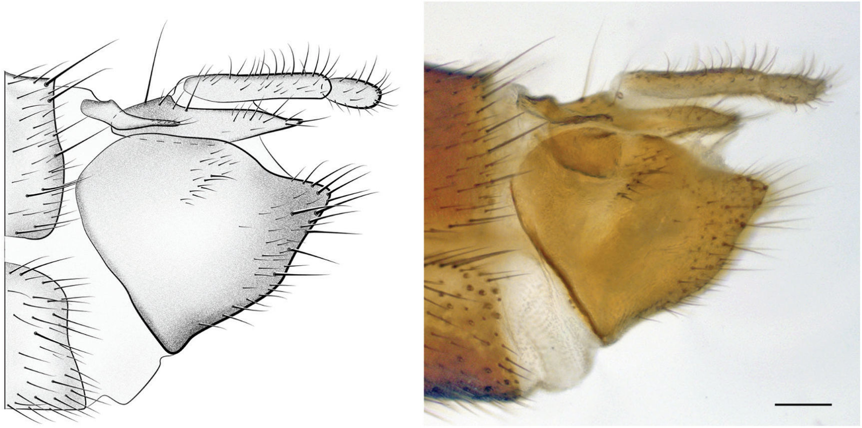

Figure 12–13. 12 *S. sequoiaphila* sp. n., structures of the female genitalia, dorsal view [# 14P342]. Scale bar = 0.1 mm **13** *S. sequoiaphila* sp. n., structures of the female genitalia, lateral view [# 14P342]. Scale bar = 0.1 mm

1), characters involving aspects of the posterior fork (74–76, 79) were changed to "?". Character #30, anapleural suture (single, double, or absent), was re-scored as "single" (30: 0) for *Acomoptera plexipus* (Garrett) and *A. vockerothi* Kerr since this character state could be verified with specimens in the CSCA collection.

All characters were scored for *S. sequoiaphila* except the following: 47, humeral vein (oblique or curved); 84, arrangement of vestiture of tibia (irregular, apical portion with parallel lines, or all in parallel lines); and 87, vestiture arrangement on tarsomeres (irregular or in parallel lines). Due to problems of interpretation and reproducibility, these characters were scored as "?" in the final matrix; I could not score these characters confidently for any taxa, including those used in the original Borkent and Wheeler (2013) matrix. For wing characters, the female (Fig. 3) was used to facilitate homology recognition.

The modified matrix was analyzed using parsimony; 1000 heuristic search replicates and 500 bootstrap replicates were performed using *PAUP* 4.0b10* (Swofford 2001), with random-taxon-addition, tree bisection reconnection (TBR) branch swapping, steepest decent and 'MulTrees' options in effect. All characters were treated unordered and assigned equal weights. Mesquite (Maddison and Maddison 2011) was used to analyze character change and support in the phylogenetic tree.

Phylogenetic results and discussion

Parsimony heuristic searches found 61 most parsimonious trees (Fig. 14). The strict consensus of these trees differs from the results provided by Borkent and Wheeler (2013), although the underlying data matrix is largely the same. Bootstrap values above 50% support the monophyly of most genera while support for intergeneric relationships is largely lacking. A monophyletic Sciophilinae includes *Syntemna hungarica* Lundström and its sister lineage, although excludes species of *Aneura* Marshall, a genus normally thought to be included in the subfamily. Inside this group are two major lineages that contain the remaining taxa, sister to *Taxicnemis marshalli* Matile. Using implied weighting, Borkent and Wheeler (2013) may have found a similar tree, with *Syntemna* Winnertz as the sister to the rest of the Sciophilinae and *Phthinia* Winnertz and *Polylepta* Winnertz united as sister taxa.

Figure 14. Locality of *Spritella sequoiaphila* sp. n., showing 6-meter Malaise trap; Whitaker Forest (UC Berkeley Center for Forestry), Tulare Co. [CSCA10L258].

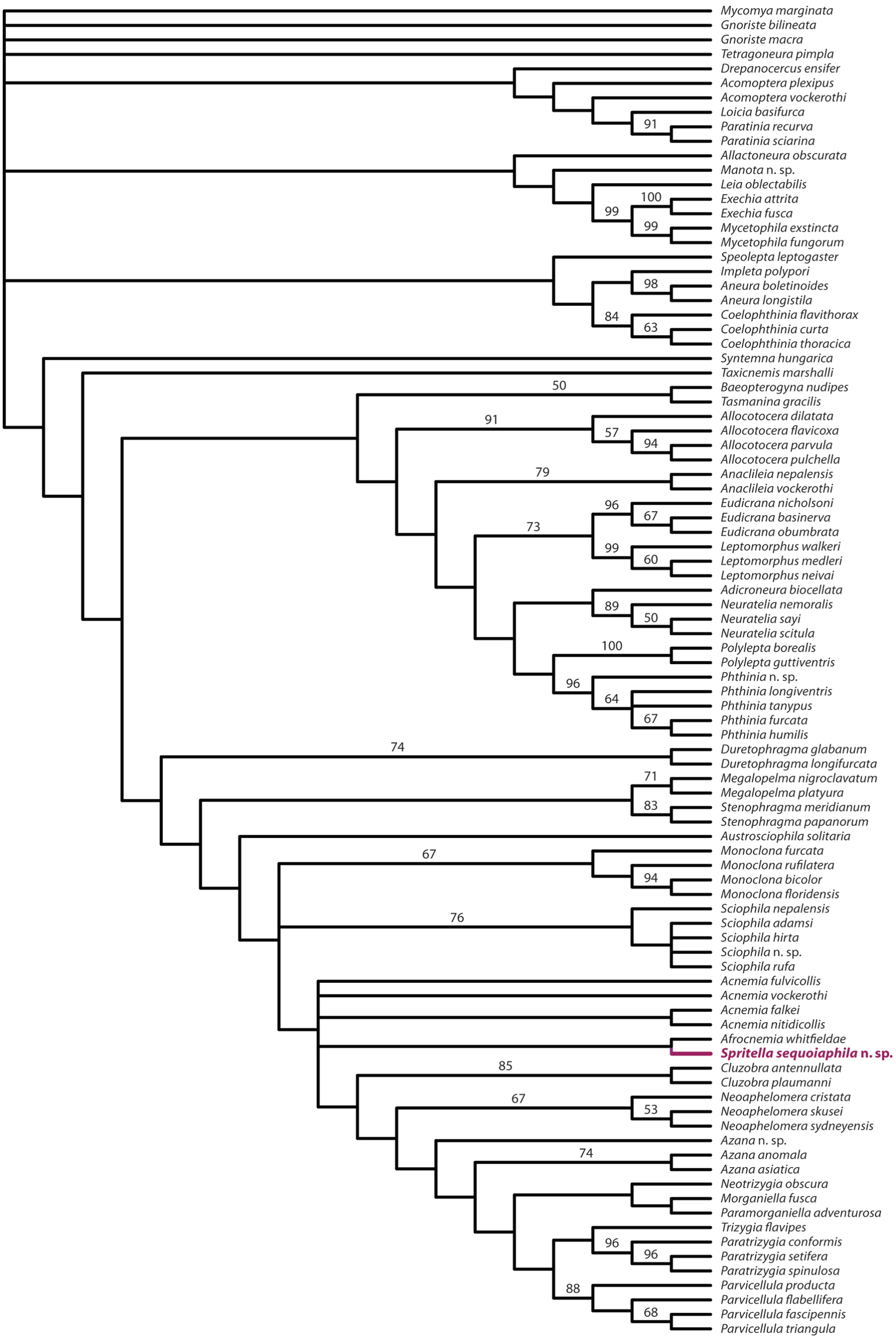

Figure 15. Strict consensus tree of 61 equally parsimonious trees from re-analysis of Borkent and Wheeler (2013), with the addition of *Spritella sequoiaphila* sp. n. Bootstrap values provided above branches where support ≥ 50% (500 reps).

The concept of the "*Azana* group" (Matile 1998) is recovered with the inclusion of *Morganiella fusca* Tonnoir and *Paramorganiella adventurosa* Tonnoir. This result is consistent with the composition of this group as suggested by Amorim and Oliveira (2008), although both *Morganiella* Tonnoir & Edwards and *Paramorganiella* Tonnoir have a complete posterior fork (character 73:0) unlike the other members of this group. *Sciophila* Meigen, which forms a trichotomy and may or may not be included in this group, also has a posterior fork that is complete (or interrupted basally; as in *S. interrupta*, *S. cincticornis*, and *S. fractinervis*). Within this clade, the new genus is included.

Spritella sequoiaphila is recovered sister to *Afrocnemia whitfieldae* Matile. The two genera are united by the ocellar arrangement being linear (6: 2) and the first flagellomere being slightly offset (20: 1). Along with most species of *Acnemia*, *Afrocnemia whitfieldae* and *Spritella sequoiaphila* have a distinctively short anterior wing vein fork. This character is difficult to score discretely for phylogenetic analysis (e.g., at what point is it "short" or "long"?) and was not scored by Borkent and Wheeler (2013) but appears to have phylogenetic signal that should be considered for future analyses.

Acnemia is recovered as a paraphyletic group, which is not especially surprising, since members of this genus can vary widely and in a way that suggests that this group is in need of systematic revision. Borkent and Wheeler (2013) did find that *Acnemia* are united by a unique synapomorphy, however, in that the gonostylar lobe bears one to three thin processes. These processes are lacking in *Spritella sequoiaphila*.

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Supplementary material 1

Data matrix in nexus format (modified from Borkent and Wheeler 2013)

Authors: Peter Kerr

Data type: NEXUS file with DNA data

Explanation note: Data matrix in nexus format (modified from Borkent and Wheeler 2013).

Link: doi: 10.3897/zookeys.437.7932.app