RESEARCH ARTICLE



Trachymolgus purpureus sp. n., an armored snout mite (Acari, Bdellidae) from the Ozark highlands: morphology, development, and key to Trachymolgus Berlese

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Abstract

Trachymolgus purpureus Fisher & Dowling **sp. n.** is described from the Ozark highlands of North America. A diversity of imaging techniques are used to illustrate the species including low-temperature scanning electron microscopy (LT-SEM), stereomicrography, compound light micrography, and digitally created line drawings. Developmental stages (larva, nymphs, and adult) and morphology are illustrated and discussed, and terminological corrections are suggested. *Trachymolgus recki* Gomelauri, 1961 is regarded as being described from tritonymphs. A key to *Trachymolgus* is presented.

Keywords

LT-SEM, taxonomy, Prostigmata, new species, image diversity

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Introduction

Bdellidae Dugès, 1834 generally have a striated, unsclerotized integument. Exceptions occur in Cytinae Grandjean, 1938, which comprises three of the most distinctive bdelloid genera. *Cyta* Heyden, 1826 are common mites known for their stocky bodies, massive chelicerae, and unpaired fifth eye. *Rigibdella ignea* Tseng, 1978 from Taiwan have sclerotized, striated holodorsal shields (Tseng 1978; Lin and Zhang 2010). The only other bdellids with a sclerotized body are the subject of this study – *Trachymolgus* Berlese, 1923. *Trachymolgus* are infrequently collected mites with three described species. Instead of the typical fingerprint-like membranes of other Bdellidae, the integument of *Trachymolgus* is heavily sclerotized, divided into distinct sclerites, and dark (Fig. 1). The sclerites are foveolate, containing many indentions that create a characteristic reticulated patterning (Fig. 2a). These indentions have multiple small pits at the corners of the foveolae (Fig. 2b). This strange integument, combined with the rarity of collection, has rendered *Trachymolgus* the most enigmatic bdellid.

Berlese (1923) erected *Trachymolgus* to accommodate the distinctive snout mite Canestrini and Fanzago (1876) named *Bdella nigerrima. Trachymolgus niggerimus* (Canestrini & Fanzago, 1876) was originally collected in northern Italy (Padova) and subsequently reported from Sicily and Lugano, Switzerland (Thor 1931), Crimea, Ukraine (Vainshtein et al. 1978), Caucasus (Vainshtein et al. 1978), and from rodent nests in Bulgaria (Sosnina et al. 1965). Grandjean (1938) grouped *Cyta* and *Trachymolgus* into a new subfamily (Cytinae) based on the number of subcapitular setae and leg trichobothria, presence of pseudotracheae, and normal chelicerae (reduced in Spinibdellinae). Two other species were described later, both known only from their type localities: *T. recki* Gomelauri, 1961 in Georgia (former U.S.S.R.: Tbilisi and Kashtak) and *T. jesusi* Mejia-Recamier & Palacios-Vargas, 1999 in Mexico (Jalisco and Chamela). Undetermined species have been reported from a Buddhist temple on Shikoku Island, Japan (Nakamura et al. 2006), from the St. Lawrence Islands National Park, Canada (Smith et al. 1996), and we collected a third from Columbus, Ohio. Here, we describe and illustrate *Trachymolgus purpureus* sp. n. from the Ozark highlands of North America.

Material and methods

Specimens

Mites were collected primarily from leaf litter samples in the Ozark Mountains of Arkansas (U.S.A.), specifically Buffalo National River and Devil's Den State Park, and extracted using Berlese-Tullgren funnels. Approximately half of the specimens were slide-mounted with Hoyer's medium (see Krantz and Walter 2009 for preparation), and half are stored in 95% ethanol at -80°C. Slide-mounted specimens were dissected along the frontal plane. Five paratypes are deposited in the Ohio State University Acarology Collection, Columbus, Ohio. Four paratypes each are deposited in the Field Museum of Natural History, Chicago, Ill., and the National Mite Collection, National Museum of Natural History, Smithsonian Institution, located in Beltsville, Md. All other type specimens are deposited in the Acari Collection of the University of Arkansas, Fayetteville, Ark.

Terminology

An effort is made to implement terminology that is broadly applicable and well accepted across acariforms despite conventions used among bdelloid authors. Thus, two terms have been renamed herein. First, "hypostome" is used by many (Atyeo 1960; van der Schyff et al. 2004; Hernandes and Feres 2006; Krantz and Walter 2009) to refer to the entire subcapitulum, though it more accurately refers only to the portion anterior to the oral opening (Evans 1992; Krantz and Walter 2009). Thus, in addition to the subcapitulum itself, its setae have been renamed herein to ventral subcapitular setae (*vs*) and dorsal subcapitular setae (*ds*).

Second, the major idiosomal divisions of bdelloids are regularly referred to as the "propodosoma" and "hysterosoma" (Bdellidae: Atyeo 1960, Mejia-Recamier and Palacios-Vargas 1999, Hernandes et al. 2007; Cunaxidae: Meyer and Ryke 1959, Swift 1996, Den Heyer and Castro 2009). However, acariform segmentation is a debated topic with recent views favoring a radically reduced podosoma leaving the major idiosomal divisions (when viewed dorsally) the opisthosoma and aspidosoma (Grandjean 1969; Coineau 1974; Evans 1992; Krantz and Walter 2009). With regard to the posterior portion, hysterosoma is already widely used and accurately refers to the idiosoma posterior to the sejugal furrow (metapodosoma and opisthosoma). Moreover, it is independent of segmentation hypotheses. Therefore, we retain the use of hysterosoma. However, propodosoma is hypothesis dependent. The Grandjean (1969) hypothesis of body organization suggests the propodosoma is highly reduced dorsally, rendering propodosoma inaccurate when referring to the anteriodorsal portion of the idiosoma. Instead, aspidosoma accurately describes this region. Therefore, we abandon the use of propodosoma when referring to the dorsal morphology of acariforms. However, until more evidence exists for segmentation homologies, we also avoid the use of aspidosoma for Bdelloidea. Prodorsum is widely used by acarologists, but is usually poorly defined and represents the opposite extreme from aspidosoma--straying too far from morphological hypotheses. An exception to this is in Oribatida (e.g., Sanders and Norton 2004), where it is often used as synonymous with the aspidosomal shield (=aspis) and is therefore hypothesis dependent. Thus we recommend restricting prodorsum to casual use. Proterosoma refers to the body anterior to the sejugal furrow (propodosoma, aspidosoma, and gnathosoma of Grandjean [1969]), and is a segmentation independent term that is already widely used in acarology. Therefore, we adopt proterosoma here.

With regard to hysterosomal setal notation, we follow the chaetotaxic system of Grandjean (1939, 1947) that has been widely adopted (e.g., van der Hammen 1970; Lindquist 1976, 1977; Kethley 1990). Proterosomal setal notation in this system is

currently problematic. Generally, we do not recommend the use of mixed approaches in terminology, especially given our attempts to utilize broadly applicable notations. However, recent suggestions in the proterosomal setal notation of bdelloids have rendered this system unreliable. In the Grandjean system, proterosomal setae are termed internal/external verticals (vi and ve) and internal/external scapulars (sci and sce). In Bdelloidea, sci are always external to sce, leaving the internal/external designations unintuitive. Den Heyer and Castro (2008a) noted this and proposed simply switching the terms when referring to bdelloids so that sce and sci are descriptive, which they have published since (Den Heyer and Castro 2008b, c; Den Heyer 2011). As a result, the literature now has sce and sci referring to both inner and outer scapulars. The homology of these setae with respect to other mites is not known. Therefore, until more evidence is provided for homology, we resort to a modified version of Atyeo (1960) when referring to proterosomal setae, which unambiguously relies on position: anterior and posterior trichobothria (at and pt), and lateral and median proterosomal setae (lps and mps).

Leg chaetotaxy follows Grandjean's system as reviewed by Norton (1977). However, leg chaetotaxy is poorly studied among Eupodina, and only distal tarsal setae are denoted presently, which has been adopted by other eupodine authors (e.g., Jesionowska 2010). Nevertheless, we believe Grandjean's system can be employed with other leg setae, and will readdress this in a more detailed forthcoming study.

Images

Most species descriptions include only a few image types; line drawings are most common in acarology (e.g., Mejia-Recamier and Palacios-Vargas 1999; Den Heyer and Castro 2008a, b, c; Łochyńska 2008). We believe image diversity increases accuracy, accessibility, and attractiveness of taxonomic products, and have therefore included many images and a range of imaging types. Other acarologists have also begun including image diversity in taxonomic works (e.g. Mąkol 2010; Wohltmann 2010; Pešić et al. 2011).

Line drawings were created digitally with Adobe Illustrator CS5 and a Wacom Cintiq 21UX tablet using procedures outlined in Fisher and Dowling (2010). Compound light micrographs were taken with a Leica DFC300 FX camera and a Leica DM2500 DIC light microscope. Stereomicrographs were taken with a Leica MZ 16 stereoscope and a Leica DFC 290 camera. Photographs were enhanced using Adobe[®] Photoshop CS4.

Low-temperature scanning electron micrographs (LT-SEM) were made using an S-4700 field emission scanning electron microscope (Hitachi High Technologies America, Inc., Pleasanton, Calif.) equipped with a Quorum CryoPrep PP2000 (Energy Bean Sciences, East Grandby, Conn.) cryotransfer system. To prepare specimens, mites were placed on 12 mm diameter ultra smooth carbon double sided adhesive tabs (Electron Microscopy Sciences, Hatfield, PA) which were adhered to flat speci-

men holders consisting of 16x30mm copper plates that were tacked on the edges to the tabs with a small dot of Tissue Tek (OCT Compound, Ted Pella, Inc., Redding, Calif.), which acted as the cyro-adhesive upon freezing. The samples were frozen conductively, in a Styrofoam box, by placing the plates on the surface of a pre-cooled (-96°C) brass bar whose lower half was submerged in liquid nitrogen (LN2). After 20–30s, the holders containing the frozen samples were transferred to a LN2 Dewar for future use or cryotransferred under vacuum to the cold stage in the pre-chamber of the cryotransfer system. Removal of any surface contamination (condensed water vapor) took place in the cryotransfer system by etching the frozen specimens for 10-15 min by raising the temperature of the stage to -90°C. Following etching, the temperature was lowered below -130°C, and a magnetron sputter head equipped with a platinum target, was used to coat the specimens with a very fine layer of platinum. The specimens were transferred to a pre-cooled (-130°C) cryostage in the SEM for observation. An accelerating voltage of 5kV was used to view the specimens. Images were captured using a 4pi Analysis system (Durham, N.C.). Images were sized and placed together into figures using Adobe® Photoshop 7.0 and CS4.

Taxonomy

Trachymolgus purpureus Fisher & Dowling sp. n.

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Diagnosis. Trachymolgus purpureus sp. n. is heavily armored with distinctive integument characteristic of Trachymolgus (Figs 1-2). Like T. jesusi, the integument is dark purple, whereas *T. nigerrimus* was described as black. Like *T. jesusi* and *T. nigerrimus*, there are two teeth on the fixed cheliceral digit. Like T. nigerrimus, T. purpureus has one tooth on the movable digit (T. jesusi have three) and a serrated edge proximal to the tooth (undescribed in other species). All stages have two pairs of eyes, unlike the larva, proto- and deutonymphs of *T. jesusi*, which lack eyes (tritonymphs and adults have two pairs). Trachymolgus purpureus pedipalpal basi- and telofemora are only fused dorsally. Trachymolgus jesusi pedipalp femora are completely fused, whereas T. nigerrimus are completely divided. Trachymolgus purpureus, like other Trachymolgus, have undivided femora on legs I-II (femora III-IV are divided). All other Bdellidae have divided femora on all legs. T. jesusi is the only bdellid reported to have undivided femora on legs II and III. The ontogeny of *T. purpureus* differs markedly from that described for T. jesusi, the only other species where ontogeny was investigated. Finally, there are many chaetotaxic differences on the appendages and venter between T. purpureus and T. jesusi. Most chaetotaxy of T. nigerrimus remain to be investigated. See Remarks for discussion of T. recki.

Imago description. Females and males similar, except for genitalia, size, and chaetotaxic differences noted in Table 1. Color dark purple; occasionally immatures and

Table 1. Leg chaetotaxy. Female (\mathcal{G}), male (\mathcal{J}), tritonymph (3N), deutonymph (2N), protonymph (1N), larva (L), pedipalp (Pp), legs I-IV (I-IV). Numbers represent setal counts for barbulate setae (undesignated), solenidia (s), and trichobothria (tr). Male setal counts that are not different from the female are denoted with an asterisk (*). Absent characters are denoted with a dash (-). Fused segments are denoted by fused cells. Numbers in parentheses denote occurrences of two solenidia on tarsus II in some specimens.

Stage		Coxa	Trochanter	Basifemur	Telofemur	Genu	Tibia	Tarsus
Ŷ	Рр	-	0	8	8	4	4;	1s
	Ι	7	2	1	8	4; 2s	8; 2s; 1tr	28; 5s
	II	7	2	2	.0	4; 1s	9; 1s	26; 1(2)s
	III	9	2	10	10	5; 1s	9; 1s	24; 1tr
	IV	8	2	10	10	5; 1s	9; 1tr	21; 1s
3	Рр	-	*		*	*	*	
	Ι	6	*	د	*	*	*	*
	II	6	*		*	*	*	*
	III	6	*	*	*	*	*	*
	IV	10	*	*	*	*	*	*
3 N	Рр	-	0	(5	4	4;	1s
	Ι	4	2	1	8	4; 2s	8; 2s; 1tr	24; 5s
	II	4	2	18		4; 1s	8; 1s	22; 1s
	III	4	2	9	9	4; 1s	9; 1s	20; 1tr
	IV	3	1	6	7	4; 1s	8; 1tr	19; 1s
2 N	Рр	-	0	4	-5	4	4;	1s
	Ι	4	1	1	2	4; 2s	7; 2s; 1tr	20; 5s
	II	2	1	1	1	4; 1s	6; 1s	18; 1(2)s
	III	4	1	6	6	4; 1s	6; 1s	16; 1tr
	IV	2	1	2	4	4; 1s	6; 1tr	15; 1s
1 N	Рр	-	0	4	4	4	4;	1s
	Ι	2	1		7	4; 2s	5; 2s	18; 4s
	II	1	1		6	4; 1s	5; 1s	16; 1s
	III	1	1	1	4	4; 1s	5; 1s	12; 1tr
	IV	0	0	(0	0	1	7
L	Рр	-	0		2	4	4;	1s
	Ι	3	0		7	4; 2s	5; 2s	16; 3s
	II	1	0	(6	4; 1s	5; 1s	14; 1s
	III	2	0	(5	4; 1s	5; 1s	12; 1tr
	IV	-	-	.	-	-	-	-

adults were collected from the Buffalo National River (Arkansas) with an internally green coloration, which rendered the normally purple mite teal; teal specimens returned to purple after a few days in 95% ethanol, and were indistinguishable from normal specimens when slide-mounted (we also collected *Penthaleus*, a normally black to dark blue mite, from the same habitat exhibiting green internal coloration). Integument divided into heavily armored sclerites with foveolate sculpturing (Fig. 2a). The foveolate indentions (foveolae) are bordered with pits (Fig. 2b). Measurements in Tables 2–5.

Table 2. Body measurements. Stage (St), female (\mathcal{Q}), male (\mathcal{S}), tritonymph (3N), deutonymph (2N), protonymph (1N), and larva (L), mean (M), standard deviation (S), range (R), number examined (n), idiosomal length (Idi L) and width (Idi W), and lengths of proterosomal shield (Pro), hysterosomal shield (Hys), lateral shield (Lat), subcapitulum (Sub), chelicerae (Chel), pedipalps (Ped), anal shield (Ana), genital shield (Gen), and legs I-IV (L I-IV). Absent characters are denoted with a dash (-). All measurements in micrometers.

St		Idi L	Idi W	Pro	Hys	Lat	Sub	Chel	Ped	Ana	Gen	Ι	II	III	IV
Ŷ	M	791	505	279	512	485	307	283	344	113	171	470	457	526	600
	S	24	14	9	16	11	13	7	4	5	9	9	13	6	37
	R	768-	488-	273-	495-	475-	285-	273-	338-	108-	160-	458-	438-	515-	538-
		838	525	298	540	503	323	295	350	120	190	483	478	533	665
	n	7	7	7	7	7	8	8	6	7	8	7	7	7	8
3	M	753	483	270	483	448	294	277	345	105	165	468	445	518	594
	S	52	25	10	45	34	8	9	7	8	9	16	13	21	25
	R	693-	465-	260-	425-	390-	288-	268-	338-	95-	150-	443-	435-	488-	555-
		825	500	283	545	475	305	293	355	118	175	483	465	540	628
	n	6	2	6	6	6	5	6	5	6	6	6	6	6	6
3N	M	684	452	259	268	134	258	242	301	95	102	393	378	451	509
	S	99	70	38	52	10	10	10	12	6	4	23	27	17	43
	R	588-	350-	230-	220-	126-	250-	228-	288-	88-	98-	363-	353-	438-	453-
		808	500	314	324	145	273	255	315	100	105	410	405	475	553
	n	4	4	4	3	3	5	5	5	5	3	4	4	4	4
2N	M	549	375	213	227	88	225	204	249	77	61	331	318	373	391
	S	77	53	26	17	-	4	7	3	3	2	5	3	7	8
	R	500-	330-	191-	205-	-	220-	198-	225-	73-	60-	328-	315-	365-	380-
		665	450	250	241		230	213	260	80	63	338	323	383	398
	n	4	4	4	4	1	4	4	3	4	2	4	4	4	4
1N	M	508	375	168	325	-	171	162	210	65	30	265	n/a	305	288
	S	-	-	-	-	-	1	2	2	2	2	4	n/a	-	285-
															290
	R	-	-	-	-	-	170-	160-	206-	64-	25-	263-	n/a	-	4
							172	163	213	65	30	265			
	n	1	1	1	1	-	2	2	2	2	2	2	n/a	1	2
L	M	323	243	118	88	-	137	128	195	48	-	210	200	238	-

Dorsal idiosoma (Fig. 3). **Idiosoma** dorsally armored with two large tergites: proterosomal and hysterosomal shields (see Terminology). Dorsal membrane (between proterosomal and hysterosomal shields and between dorsal and lateral shields) striated and accompanied with raised bumps similar in size to the foveolate indentions (Figs 4, 5a-b). **Proterosoma** ending anteriorly in a crenulated, tri-lobed shelf (crown) covering the stigmata. Two pairs of eyes present. Two pairs of minutely barbulate trichobothria: anterior (*at*) and posterior trichobothria (*pt*). Barbules are difficult to discern with light microscopy (Fig. 5c). Two pairs of barbulate setae are present: lateral proterosomal (*lps*) and median proterosomal setae (*mps*). Setae *lps* are oriented dorsomedially and lay in a groove posterior to the first pair of eyes (Fig. 5d); *mps* are the longest barbulate setae.

Table 3. Dorsal setal measurements. Female (\mathcal{Q}), male (\mathcal{J}), tritonymph (3N), deutonymph (2N), protonymph (1N), and larva (L), mean (M), standard deviation (S), range (R), number examined (n), anterior and posterior trichobothria (*at* and *pt*), lateral and medial proterosomal setae (*lps* and *mps*). All measurements in micrometers.

Stage		at	lps	pt	mps	C ₁	<i>c</i> ₂	d_{I}	e,	f_{I}	f_2	h,	h,
Ŷ	Μ	182	56	214	103	74	90	81	75	70	82	67	69
	S	23	11	18	8	6	17	8	3	5	12	3	4
	R	163-	40-75	200-	93-	65-83	60-	70-90	73-78	65-75	75-	63-70	63-75
		208		238	113		115				105		
	n	3	7	4	7	5	7	4	4	3	6	5	7
8	M	186	64	214	98	76	83	77	76	66	69	65	68
	S	4	7	15	4	1	8	7	5	11	8	7	5
	R	180-	58-75	200-	93-	75-78	78-95	65-85	70-83	55-78	58-78	55-78	63-75
		190		230	100								
	n	4	6	3	5	3	4	5	4	3	6	6	6
3N	M	166	53	174	74	56	66	53	53	53	63	51	56
	S	18	4	2	3	6	6	1	2	4	3	1	7
	R	155-	48-58	173-	70-78	50-65	60-73	53-55	50-55	48-55 6	60-65	50-53	48-65
		188		175									
	n	3	5	2	4	5	4	4	4	4	4	4	4
2N	Μ	136	39	183	63	41	46	38	40	44	60	47	47
	S	2	1	-	3	4	4	0	2	4	2	2	3
	R	135-	38-40	175-	60-65	38-45	40-50	38	38-43	40-50	58-63	45-50	43-50
		138		190									
	n	2	4	1	3	3	4	4	4	4	4	4	4
1N	Μ	111	21	155	48	30	38	30	35	43	51	36	47
	S	34	8	49	-	-	4	-	-	3	1	1	1
	R	88-	15-26	120-	-	-	35-41	-	-	41-45	50-52	35-37	46-48
		135		190									
	n	2	2	2	1	1	2	1	1	2	2	2	2
L	M	105	20	118	43	30	33	33	40	40	43	40	40

Two pairs of heavily sclerotized, cylindrical, internally directed structures are apparent (Fig. 5e-f) that we interpret to be apodemes. **Hysterosoma** folding over posterior, shelf-like portion of proterosoma; with three lyrifissures (*ia*, *im*, and *ip*) and seven barbulate setae as follows: c_1 , c_2 , d_1 , e_1 , f_1 , f_2 , and h_1 . Posteriorly, the hysterosomal shield folds inward between the $f_{1,2}$ and h_1 forming a curved lateral furrow isolating h_1 on a raised area.

Ventral idiosoma (Fig. 4). **Lateral shields** each posteriorly containing one lyrifissure (*ih*) and one barbulate seta (h_2). Podocephalic canals lead from the posteriolateral edges of the gnathosoma and curve around coxal field I, and are visible externally (Figs 1a, 4). Ventral membrane is striated but lacks bumps. **Genital region** covered with one pair of genital shields each containing more than 20 barbulate setae. There are six pairs of paragenital setae; one unpaired median seta between coxal field IV; three pairs of genital papillae; one pair of genital tracheae associated with the genital papillae that leads into the body anteriorly from the anterior-most genital papilla, and

Table 4. Gnathosomal measurements. Female (\mathcal{Q}), male (\mathcal{J}), tritonymph (3N), deutonymph (2N), protonymph (1N), and larva (L), mean (M), standard deviation (S), range (R), number examined (n), dorsal subcapitulars (*ds*), proximoventral subcapitulars (*pvs*), distoventral subcapitulars (*dvs*), adorals (*ad*), dorsal end setae (*des*), ventral end setae (*ves*), cheliceral distal seta (*cds*), and cheliceral proximal seta (*cps*). All measurements in micrometers.

Stage		ds	pvs	dvs	ad	des	ves	cds	cps
9	M	46	52	26	19	196	180	48	51
	S	4	6	2	2	10	22	5	5
	R	43-53	43-63	23-28	15-23	175-203	130-193	40-53	43-55
	n	5	7	7	8	7	7	8	7
3	Μ	41	44	25	15	199	182	44	46
	S	7	6	4	4	16	9	3	6
	R	33-48	38-50	18-28	10-20	185-225	173-193	40-48	40-55
	n	4	3	5	5	5	5	6	5
3N	Μ	37	41	27	16	168	158	38	36
	S	1	2	4	3	8	5	1	5
	R	35-38	38-43	20-30	13-20	160-180	153-165	38-40	30-40
	n	4	5	5	5	5	5	3	3
2N	Μ	31	36	21	14	143	133	37	31
	S	2	2	3	1	3	3	3	1
	R	28-33	33-38	20-25	13-15	140-145	130-135	33-40	30-33
	n	4	4	4	4	3	3	4	4
1N	Μ	20	30	20	13	121	115	29	32
	S	-	-	-	-	118-125	113-118	-	-
	R	-	-	-	-	5	4	-	-
	n	1	1	1	1	2	2	1	1
L	Μ	19	30	24	12	100	85	30	34

ending in spoon-shaped platytracheae near coxal field I (Fig. 6a). Female with long, telescoping ovipositor that approaches body length (Fig. 6b); with 16 setae. Male amphoid sclerites each with nine setae. Unpaired median cylindrical structure interpreted as an apodeme between coxal field III (Fig. 8). Anal region with two pairs of sclerites: anal shields and paranal shields, each usually containing three pairs of barbulate setae. Either side of both anal and paranal shields may have one to two extra setae (symmetrically or asymmetrically). Legs (Figs 4, 7): coxal fields I-III distinct, coxal field IV indistinguishably fused medially with venter; sclerotized, inwardly directed cylindrical structures (interpreted here as apodemes) are readily apparent on coxal field II and III (Fig. 8). Trochanters, femora, and genua sclerotized, with pitted, sculptured armor, especially II and III (Figs 4, 9a); other podomeres unsclerotized with papillated striations (Fig. 9b). Podomeres with eight possible setal rows positioned ventrally (unpaired), medioventrally (paired), lateroventrally (paired), laterally (paired), laterodorsally (paired), and dorsally (unpaired). Base of the ambulacrum surrounded with two pairs of setae: prorals (p) and unguinals (u). Proximally, the dorsal setae are as follows: iterals (it), tectals (tc), and fastigials (ft). The tectals are paired on all legs except IV;

Table 5. Ventral setal measurements. Female (\bigcirc) , male (\bigcirc) , tritonymph (3N), deutonymph (2N), proto-
nymph (1N), and larva (L), mean (M), range (R), number examined (n), anal setae (as), paranal setae (ps),
genital setae (gs), paragenital setae (ps), unpaired median seta (ums). Absent characters are denoted with a
dash (-). All measurements in micrometers.

Stage		as	as_2	as ₃	as ₄	as ₅	ps ₁	ps2	ps3	long	short	pgs	ums
										gs	gs		
Ŷ	M	43	43	44	40	-	43	52	54	34	17	41	30
	S	1	2	3	-	-	4	3	2	2	2	2	1
	R	42-45	41-46	41-49	-	-	39-48	47-55	52-56	31-37	14-20	38-46	29-32
	n	6	6	5	1	-	6	5	5	7	6	7	4
8	Μ	45	43	42	41	43	45	51	52	35	18	42	37
	S	4	7	2	3	-	3	1	6	5	4	6	3
	R	40-51	35-56	40-44	37-43	-	42-50	50-52	45-62	27-44	14-21	34-48	35-40
	n	6	6	5	4	1	6	5	6	6	3	6	3
3N	Μ	37	37	38	36	-	42	43	45	27	18	32	26
	S	2	3	3	-	-	2	4	4	2	2	2	1
	R	35-40	35-41	35-40	-	-	40-44	40-47	40-49	25-30	16-20	30-35	25-27
	n	4	4	3	1	-	4	4	4	4	3	4	3
2N	Μ	30	29	29	32	-	35	39	38	21	-	23	28
	S	5	1	2	1	-	2	3	2	2	-	3	3
	R	24-35	28-30	26-30	31-33	-	32-36	34-42	35-40	19-23	-	21-25	25-30
	n	4	4	4	2	-	4	4	4	2	-	2	3
1N	Μ	24	25	22	-	-	27	32	37	24	19	24	25
	S	0	1	2	-	-	4	3	4	-	-	-	-
	R	24	24-25	20-23	-	-	24-30	30-34	34-40	-	-	-	-
	n	2	2	2	-	-	2	2	2	1	1	1	1
L	Μ	20	21	23	-	-	-	-	-	-	-	-	-

fastidials are paired only on leg I, and are absent on leg IV. Other setal homologies remain to be investigated. Baculiform solenidia present on genua I-IV (σ), tibiae I and III (γ), and tarsi I, II, and IV (ω); short, ceratiform solenidia present on tibiae I and II (γ); and a short solenidion present on tarsi I that has the appearance of being raggedly broken, interpreted here as the famulus (ϵ). Trichobothria present on tibiae I and IV, and tarsus III. Apotele with barbulate ungues and pulvilli with tenant hairs (Fig. 9c-d). Leg arthrodial membrane is unsculptured.

Gnathosoma (Fig. 10). **Subcapitulum** (Fig. 10a) foveolate and armored posteriorly, longitudinally striated anteriorly (Fig. 11a); ventrally with two pairs of smooth adoral setae (*ad*), one pair of smooth anterior setae (*avs*), and one pair of barbulate posterior setae (*pvs*); dorsally with one pair of smooth, thin, straight setae (*ds*) that are hidden under the chelicerae in life; ending in three pairs of lateral lips (Figs 10a, 11d). Oral opening located midway between ventral setae (Fig. 11b). Gnathosomal membrane unsculptured. **Pedipalps** (Fig. 10b) entirely striated (Fig. 11e), becoming more papillated-striated distally (Fig. 11f); femora partially fused dorsally; terminal setae (*ves* and *des*) finely barbulate (Fig. 11f). **Chelicerae** (Fig. 10c) with foveolate armoring basally, and longitudinal striation distally (Fig. 11c); with two dorsal barbulate setae. Fixed digit ending in a hook, and with two teeth (one small and one large and triangular); movable digit with one small tooth and a serrated edge proximal to the tooth (Fig. 10d).

Immatures description. Measurements and chaetotaxy of immatures are given in Tables 1–6. Developmental stages are illustrated in Figures 13–16. Like other mites, developmental stages can be easily recognized by leg number (larvae have six legs) and genital development (Fig. 17). Chaetotaxic differences and femoral divisions are also helpful (Tables 1, 6). All immature stages appear soft bodied (despite dorsal sclerites) and vary in color from light green or purple to yellowish-white (Fig. 12).

Due to the unique armored morphology of *Trachymolgus*, other interesting developmental changes are present. These are discussed below.

Dorsal sclerites and setae. None of the immature stages of T. purpureus have complete dorsal shields as seen in the adult. This is unlike T. jesusi, which was described as having an armored tritonymph and unsclerotized proto- and deutonymphs. In T. purpureus, all stages have dorsal sclerites. Shield sculpturing is underdeveloped in the larva with foveolate indentions absent but pits present (Fig. 13); protonymphs also lack foveolate indentions, but the pits are more organized, reminiscent of the indentions (Fig. 14); deutonymphs begin to develop foveolate indentions (Fig. 15), which are nearly complete in the tritonymph (Fig. 16). The proterosomal shield of the larva does not encompass the posterior pair of eyes, and the anterior crown is not developed, leaving the gnathosomal membrane appearing as a collar. The protonymph has a welldeveloped proterosomal shield that encompasses all eyes and has a complete crown. Hysterosomal shield of the larva only encompasses c_i and d_j ; nymphal stages also encompass e_1 . Small sclerotized regions containing pits, but not foveolate indentions, are present around c_2 in the deuto- and tritonymphs. A posterior shield encompassing h_1 , contiguous with the hysterosomal shield in adults, is present in nymphal stages, but not larvae. Larvae completely lack f_{a} .

Lateral shields. Lateral shields are present in deuto- and tritonymphs (Figs 15, 16), but do not encompass h_2 or *ih*, as in adults (Fig. 3). Furthermore, in addition to lateral shields, larvae lack h_2 . Lyrifissure *ih* was not found in any immature stage.

Pseudotracheae. As described for *T. jesusi*, pseudotracheae are lacking in the larva and protonymph, but are well-developed in the deutonymph (Fig. 17).

Membranes. As discussed above, adult *T. purpureus* striations are accompanied with bumps (Fig. 5b), unlike other bdellid membranes that exhibit fingerprint-like striations. However, larvae and protonymphs lack bumps and have typical fingerprint-like striations (Figs 13, 14). Membrane bumps begin to develop on the deutonymphal dorsum (Fig. 15), and are well developed in the tritonymph (Fig. 16). All stages have normal, fingerprint-like striations on the venter.

Remarks. In the early 1980s, *Trachymolgus* was collected by Cal Welbourn on a rocky bluff in the Buffalo National River (Arkansas). John Kethley recollected three specimens from the same bluff a few years later. Another specimen (one female) was collected by Evert Lindquist in the St. Lawrence Islands National Park, Canada (Smith et al. 1996), but the specimen has since been lost. Since then, we have col-

Stage	Adoral Setae	Anal Setae	Paranal Setae	Genital Setae	Paragenital Setae	Femora III divided	Femora IV divided
Ŷ	2	3 (4)	3	>20	6	yes	yes
8	2	3 (5)	3 (4)	>20	6	yes	yes
3N	2	3 (4)	3	6	5	yes	yes
2N	2	3 (4)	3	1	5	yes	yes
1N	2	3	3	0	0	yes	no
L	1	3	1	-	-	no	no

Table 6. Recognizing life stages. Female (\mathcal{Q}), male (\mathcal{J}), tritonymph (3N), deutonymph (2N), protonymph (1N), and larva (L). Numbers represent setal counts; those in parentheses denote counts when extra setae are present. Absent characters are denoted with a dash (-).

lected this seemingly restricted, rare mite from a wide variety of microhabitats including litter, talus, rock outcrops and bluffs, moss, cedar stands, hardwood stands, and in both wet and dry conditions. Furthermore, the range is potentially not restricted to the Ozark highlands. Amusingly, we collected one tritonymph and one adult from leaf litter less than 200ft from where the Ohio State University Summer Acarology Course is taught (downtown Columbus, Ohio). Morphologically, these specimens cannot yet be distinguished from *T. purpureus*, potentially extending the range to eastern U.S. We were able to extract DNA from one of these specimens and will publish our findings later.

Biogeography. The known distribution of North American *Trachymolgus* is Mexico (*T. jesusi*), Ozark highlands (*T. purpureus*), central Ohio (undet. species), and the northern Appalachian mountains (undet. species). Other groups have a similar distribution, and the biogeographic affinity between the Ozark and Appalachian mountains, and between Mexico and the eastern U.S. has been well documented. Examples include mosses (Crum 1952; Redfearn 1986), higher plants (Braun 1955; Dressler 1954; Miranda and Sharp 1950; Watson 1891), fungi (Miranda and Sharp 1950; Sharp 1948), snakes, flying squirrels, and plethodontid salamanders (see Martin and Harrel 1957). Recently, a mite was implicated as sharing this affinity (Skvarla et al. 2011). It is tempting consider *T. purpureus* as representative of these biogeographic events, but much more sampling is necessary before this conclusion can be justified.

Temperature tolerance. *T. purpureus* seems to have extremely high temperature tolerances. They were found crawling on rock surfaces in direct sunlight during a drought in the hottest and driest time of year (August), and were collected near the surface during the winter. When preparing live specimens for LT-SEM, mites are set atop a metal bar that is subjected to liquid nitrogen fumes which freezes them midstride for imaging. When *T. purpureus* was subjected to liquid nitrogen temperatures however, they would simply run, curl their legs, and roll off the plate (see Fig. 18a). This made imaging live specimens very difficult.

Silk production. LT-SEM imaging illuminated another behavioral characteristic of *T. purpureus*. Though other bdellids have been known to orally produce silk to tether prey (Alberti 1973; Krantz and Walter 2009), silk production in *Trachy-molgus* was not previously known. When subjected to liquid nitrogen, *T. purpureus* would charge its gnathosoma with silk, making investigation of chelae impossible on living specimens (Fig. 11d). One specimen tethered itself to the plate before rolling off (Fig. 18), potentially using silk as a dragline as has been described in many spiders.

Feeding behavior. We observed a tritonymph of *T. purpureus* feeding on a small mite approximately 200–250m long. Unfortunately, the prey could not be retrieved for identification. The tritonymph fed with prey elevated from the ground. There seemed to be a droplet surrounding the bite site, interpreted here as silk seen in Figures 11d. We hypothesize that *T. purpureus* uses a drop of silk at the bite site to act as a gasket when sucking prey fluids.

Type material (27 individuals on slides). HOLOTYPE: female, collected from leaf litter, USA, Arkansas, Washington Co., Devil's Den State Park (35°46.817 N, 94°14.750 W), 23 Sep 2009, by JR Fisher & MJ Skvarla, APGD 09-0923-006.

PARATYPES: Female (n=7): 2 individuals collected from leaf litter on rocky slope, USA, Arkansas, Washington Co., Devil's Den State Park (35°46'50.1N, 94°14′45.9″W), 28 Aug 2008, by APG Dowling, APGD 08-0828-004 • 2 individuals collected from leaf litter on rocky slope, USA, Arkansas, Washington Co. Devil's Den State Park (35°46'50.1"N, 94°14'45.9"W), 30 Aug 2009 by JR Fisher, APGD 09-0830-001 • 1 individual collected from leaf litter, USA, Arkansas, Newton Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W), 7 Sep 2009 by JR Fisher, APGD 09-0907-005 • 1 individual collected from American beech leaf litter, USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf (35°52.062 N, 093°24.092 W), 14 Mar 2010 by JR Fisher, APGD 10-0314-019 • 1 individual collected from litter on rocky bluff, USA, Arkansas, Newton Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W), [date unknown] by Cal Welbourn, OSAL 0061853. Male (n=5): 1 individual collected from rocky overhang, USA, Arkansas, Washington Co., Devil's Den State Park (35°46'50.1N, 94°14'45.9"W) by APG Dowling, APGD 08-0822-001 • 1 individual collected from cedar litter, USA, Arkansas, Washington Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W) by JR Fisher, APGD 09-0802-006 • 1 individual collected from leaf litter on rocky slope, USA, Arkansas, Washington Co. Devil's Den State Park (35°46'50.1"N, 94°14'45.9"W), 30 Aug 2009 by JR Fisher, APGD 09-0830-001 • 1 individual collected from leaf litter on rocky slope, USA, Arkansas, Washington Co. Devil's Den State Park (35°46'50.1"N, 94°14'45.9"W), 30 Aug 2009 by JR Fisher, APGD 09-0830-003 • 1 individual collected from leaf litter, USA, Arkansas, Newton Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W), 7 Sep 2009 by JR Fisher, APGD 09-0907-005. 1 individual collected from leaf litter, USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf (35°52.062 N, 093°24.092 W), 10 Apr 2010 by APG Dowling. Tritonymph (n=6): 3 individuals collected from cedar litter, USA, Arkansas, Washington Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W) by JR Fisher, APGD 09-0802-006 • 1

individual collected from oak litter, USA, Arkansas, Washington Co., Buffalo National River, Steel Creek trail (36°01'56.2"N, 93°20'01.5"W) by JR Fisher, APGD 09-0802-001 • 1 individual collected from leaf litter, USA, Arkansas, Newton Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W), 7 Sep 2009 by JR Fisher, APGD 09-0907-005 ● 1 individual collected from litter on rocky bluff, USA, Arkansas, Newton Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W), [date unknown] by John Kethley, FMNH 2. Deutonymph (n=4): 3 individuals collected from cedar litter, USA, Arkansas, Washington Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W) by JR Fisher, APGD 09-0802-006. 1 individual collected from leaf litter on rocky slope, USA, Arkansas, Washington Co. Devil's Den State Park (35°46'50.1"N, 94°14'45.9"W), 30 Aug 2009 by JR Fisher, APGD 09-0830-002. Protonymph (n=2): 1 individuals collected from leaf litter on rocky slope, USA, Arkansas, Washington Co., Devil's Den State Park (35°46'50.1N, 94°14'45.9"W), 28 Aug 2008, by JR Fisher & MJ Skvarla, APGD 08-0828-004 • 1 individual collected from cedar litter, USA, Arkansas, Washington Co., Buffalo National River, Roark Bluff (36°01'56.2"N, 93°20'01.5"W) by IR Fisher, APGD 09-0802-006. Larva (n=1): 1 individual collected from oak litter, USA, Arkansas, Washington Co., Buffalo National River, Steel Creek trail (36°01'56.2"N, 93°20'01.5"W) by JR Fisher, APGD 09-0802-001.

Etymology. This species is named for the Latin "purpureus," meaning purple.

Notes on Trachymolgus recki, Gomelauri, 1961

T. recki was described from two specimens from Georgia (Gomelauri 1961). Unlike other *Trachymolgus*, the integument of *T. recki* was described as unarmored (despite having foveolate indentations and proterosomal crown) and yellowish. There was one tooth on the fixed digit, one pair of eyes, and the pedipalps were inconclusively described as "nearly fused" though they were completely fused in the illustration (Gomelauri 1961). There were 6–7 genital setae, and coxal field setae 3-4-4-5.

We have found that purple *T. purpureus* immatures lose color more readily than adults when slide-mounted, and some immatures are yellowish-white in life (Fig. 12b). Also, though deuto- and tritonymphal shields are foveolate, they are not as heavily sclerotized as in adults, which could give the appearance of being un-armored. Adults of *T. purpureus* and *T. jesusi* have higher setal counts with >20 and 10 genital setae, respectively, and coxal field setae 7-7-9-8 (female *T. purpureus*), 6-6-6-10 (male *T. purpureus*), and 8-5-11-10 (*T. jesusi*). Larvae, proto- and deutonymphs of *T. jesusi* were described as having highly reduced eyes. Gomelauri observed only one pair eyes in *T. recki*. This offers significant evidence to suggest the specimens used to describe *T. recki*

were immature. Since these specimens were said to have three pairs of genital papillae, we suggest the description of *T. recki* was based on tritonymphs. Therefore, *T. recki* is excluded from the key below.

Notes on Trachymolgus jesusi, Mejia-Recamier & Palacios-Vargas, 1999

Aspects of the morphology and development described for *T. jesusi* (Mejia-Recamier & Palacios-Vargas 1999), suggest major deviations from what is known from other Bdellidae. Unfortunately, we were unable to obtain type specimens of this species.

Key to adult *Trachymolgus* Berlese (excluding *T. recki*, likely a tritonymph – see above)

1	Movable digit with 3 teeth; pedipalp basi- and telofemur completely fused; leg
	basi- and telofemur III-IV completely fused; dark purple; Mexico T. jesusi
_	Movable digit with 1 tooth; pedipalp basi- and telofemur either divided or
	only partially fused dorsally; leg basi- and telofemur divided; dark purple to
	black
2	Pedipalp basi- and telofemur divided; black; Palaearctic
_	Pedipalp basi- and telofemur fused dorsally; dark purple; U.S.A

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Figures



Figure 1. *Trachymolgus purpureus* sp. n. **A** Lateral view of proterosoma, LT-SEM; **B–C** Stereomicrographs of live specimens.



Figure 2. Integument of *Trachymolgus purpureus* sp. n. LT-SEM. **A** Lateral view of eyes and *pt* showing foveolate indentions **B** Magnified view of foveolae and pits.



Figure 3. Dorsum of *Trachymolgus purpureus* sp. n. Lateral plates removed and displayed laterally. See text for abbreviations.



Figure 4. Venter of *Trachymolgus purpureus* sp. n. Podocephalic canal (*pc*), median seta (*ms*), paragenital setae (*pgs*), genital shield/setae (*gs*), paranal shield/setae (*ps*), anal shield/setae (*as*). Stippling denotes unstriated membrane.



Figure 5. Morphological aspects of *Trachymolgus purpureus* sp. n. **A** LT-SEM of lateral view **B** enlargement of lateral membrane showing striations accompanied with bumps **C** Base of pt showing minute barbules **D** Left lateral view of *lps* in a groove above anterior eye, pt removed **E** Compound light micrograph of proterosomal shield with apodemes in focus, appearing as four dark spots **F** Line drawing of proterosomal shield showing apodemes.



Figure 6. Ventral aspects of *Trachymolgus purpureus* sp. n. A Venter showing pseudotracheae, legs removed B Stereomicrograph showing extruded ovipositor.



Figure 7. Legs of *Trachymolgus purpureus* sp. n. Laterodorsal view of distal podomeres. Fastigials (*ft*), iterals (*it*), prorals (*p*), tectals (*tc*), unguinals (*u*), and famulus (ε). Stippling denotes unstriated membrane. Asterisk (*) denotes solenidion found in only a few specimens.



Figure 8. Coxal fields of *Trachymolgus purpureus* sp. n. **A** Compound light micrograph of venter showing apodemes on coxae II & III **B** Line drawing with emphasis on apodemes.



Figure 9. Legs of *Trachymolgus purpureus* sp. n. LT-SEM. **A** Leg II, showing sclerotized, pitted sculpturing on telofemur and genu **B** Tarsus I showing papillated striations **C** Apotele II showing barbulate ungues **D** Enlargement showing tenant hairs.



Figure 10. Gnathosoma of *Trachymolgus purpureus* sp. n. **A** Subcapitulum **B** Pedipalp **C** Chelicera **D** Chela enlarged. Ventral end seta (*ves*), dorsal end seta (*des*), lateral lips (*l*), adorals (*ad*), anterioventral subcapitular setae (*avs*), oral opening (*o*), posterioventral subcapitular setae (*pvs*), dorsal subcapitular setae (*ds*). Stippling denotes unstriated membrane.



Figure 11. Gnathosoma of *Trachymolgus purpureus* sp. n. LT-SEM. **A** Ventral view of gnathosoma showing subcapitular sculpturing **B** Dorsal view of subcapitulum showing position of oral opening (*o*) **C** Lateral view of gnathosoma showing cheliceral sculpturing **D** Magnified view of distal gnathosoma showing lateral lips and silk charge **E** Dorsolateral view of removed pedipalp showing striations **F** Ventrodistal view of right pedipalp showing papillated striations, finely barbulate *ves*, and solenidion.



Figure 12. Nymphs of *Trachymolgus purpureus* sp. n. **A** Stereomicrograph showing greenish nymph, deutonymph shown **B** Stereomicrograph showing yellowish-white nymph,



Figure 13. Larva of *Trachymolgus purpureus* sp. n. See dorsal illustration (Fig. 3) for labeling. Stippling denotes unstriated membrane. Note *f2* is lacking.



Figure 14. Protonymph of Trachymolgus purpureus sp. n. See Fig. 3 for labeling.



Figure 15. Deutonymph of *Trachymolgus purpureus* sp. n. Lateral plates removed and shown laterally. See Fig. 3 for labeling.



Figure 16. Tritonymph of *Trachymolgus purpureus* sp. n. Lateral plates removed and shown laterally. See Fig. 3 for labeling.



Figure 17. Genital development of immature *Trachymolgus purpureus*. **A** Protonymph (note weak sclerotization) **B** Deutonymph **C** Tritonymph.



Figure 18. LT-SEM of silk production in *Trachymolgus purpureus* sp. n. **A** Lateral habitus showing frozen mite with legs curled, attached to LT-SEM plate with silk tether **B** Enlargement of anterior gnathosoma and silk tether.

RESEARCH ARTICLE



Two new genera of Nanophyidae with six desmomeres (Coleoptera, Curculionoidea)

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Abstract

A new genus *Lyalia* is described in Nanophyidae and three species are included in it: *Lyalia curvata* **sp. n.** (Vietnam), *L. robusta* (Pic, 1921), **comb. n.** (from *Nanophyes*) (Java, Bali, Laos) and *L. albolineata* (Pajni & Bhateja, 1982), **comb. n.** (from *Ctenomerus*) (India: Assam). *Ctenomerus lagerstroemiae* G. A. K. Marshall, 1923 is a **syn. n.** of *L. robusta*. Thus, the genus *Ctenomerus* Schoenherr, 1843 is restricted to the Afrotropical Realm. *Kantohia* **gen. n.** is erected for *Kantohia taiwana* (Kantoh & Kojima, 2009) (from *Shiva*) (Taiwan). A key to the Nanophyinae genera with six desmomeres is presented.

Keywords

Nanophyidae, *Lyalia, Kantohia*, new genus, new species, Oriental Region, East Palaearctic, Afrotropical Region, systematics

Introduction

The family Nanophyidae Gistel, 1848 includes at present 29 genera and 309 species grouped in two subfamilies, Corimaliinae Alonso-Zarazaga, 1989 and Nanophyinae Gistel, 1848. They are small (0.75–5 mm) weevils but adults of most species do not

measure more than 2.5 mm. They are usually strictly monophagous or oligophagous on different plant families, where their larvae cause galls on aerial parts or develop in fruits.

Their systematics is extremely difficult and based mainly on structures of the male genitalia (Alonso-Zarazaga 1989; Lyal and Curran 2003) for a neat separation of the genera and the species. Thus female specimens not accompanied by males are in many cases of doubtful ascription.

A study of the type specimens of Oriental Nanophyidae in M. Pic's collection housed in the Muséum National d'Histoire Naturelle (Paris, France) (Alonso-Zarazaga and Perrin in preparation) led to the discovery that one of his species represented the same Asiatic genus that the first author had already considered different from the African *Ctenomerus* Schoenherr, 1843. The discovery of a second, new, species has led us to describe together the new genus and prepare a synopsis of the group. The recently described *Shiva taiwana* Kantoh & Kojima, 2009 shows considerable differences to any of the hitherto known genera and is placed in a new genus.

Materials and methods

Specimens of the new genus *Lyalia* were studied from the collections of the MNHN (Muséum National d'Histoire Naturelle, Paris, France) and of the NHM (The Natural History Museum, London, UK). Those dissected were soaked overnight in lukewarm soapy water and later rinsed with distilled water. The abdomen was separated and placed in lukewarm 10% potash solution overnight for digestion of soft tissues. Genitalia and terminalia were studied in temporary glycerine slides and later mounted in DMHF (5,5-dimethyl-hydantoin formaldehyde resin) in acetate cards pinned under each specimen.

Descriptions were made using a binocular LeicaWild MZ8, provided with a photographic tube. Photographs were taken with an Olympus C7070WZ. Extended focus images were generated with CombineZP 7.0 by Alan Hadley and edited with Adobe Photoshop CS 5.0 if required. Microscope slides were studied under a light microscope and drawings were made using a drawing tube.

Taxonomic treatment

Lyalia Alonso-Zarazaga & Perrin, gen. n. urn:lsid:zoobank.org:act:B89C6848-6BF3-466C-AC99-F53CFDF006C5 http://species-id.net/wiki/Lyalia

Type species. Lyalia curvata Alonso-Zarazaga & Perrin sp. n. Gender feminine.

Description. With the characters of the tribe Nanophyini as considered in Alonso-Zarazaga (1989). Size large: 3.1–4.1 mm
Integument polychrome, varying from black to testaceous or reddish, mostly on elytra, but these not fasciate.

Vestiture of whitish, yellowish or dark (black, piceous) piliform scales, on elytra banded rather than fasciate, scales directed obliquely towards outer margin in the interstriae 1–5 (except the line closest to the suture, being parallel mostly on basal half), parallel to the striae on interstria 6 and oblique towards sutural margin on interstriae exterior to 6. Tibial comb setae dark. Specialized setae on odd elytral interstriae, pronotum, head, and legs.

Rostrum more or less cylindrical, long: $1.35-1.47 \times as$ long as pronotum in male, $1.64-1.86 \times in$ female, weakly to moderately curved, in side view prorostrum visibly tapered in males, less so in females. Epistome with a median triangular tooth, flanked on each side by a small rounded notch; in the female of *L. curvata*, epistome convex and asymmetrical, tooth displaced to the right. Mandibles with one external seta. Mentum oblong-rhombic, with a small median seta on each side; postmentum with one pair of setae just behind prementum.

Antennae with 6 desmomeres; scape slightly claviform in the apical fourth, $1.30-1.45 \times as$ long as funicle, not reaching level of front margin of eye in resting position; funicle clearly longer than club, 3^{rd} desmomere oblong, at least $1.15 \times as$ long as 4^{th} , 3^{rd} club segment hardly longer than 1^{st} and 2^{nd} together, and a little asymmetrical in males.

Head. Frontal angle flat in side view. Eyes medium-sized, not touching on frons, frons as wide as $0.35-0.41 \times \text{rostral apex}$.

Elytra short, subcordate-triangular, maximum width across humeral calli, outer basal angles marked, separately rounded at apex, leaving an obtuse sutural angle; 8th elytral interstria crenulate-keeled along the basal 3rd-4th, continuous across humeral callus, reaching more or less level of half way along metasternum; 10th elytral stria complete, at apex joining 1+10, 2+9, 3+8, 4+5, 6+7 (usual arrangement in the family). Second and third striae more or less curved to the suture in the basal third, 2nd and 3rd interstriae accordingly reduced in width, 4th widened.

Ventral areas. Mesocoxae separated $0.65-0.78 \times$ width of a mesocoxa and 0.65-0.85 separation of metacoxae. Abdomen with suture I weak, limited to a short streak on each side, or absent, with suture IV present, but not functional, in males; 5th ventrite shorter than distance between hind metacoxal margin and suture II; suture IV absent in females in the median third. Male pygidium normal, moderately convex.

Legs. Femora incrassate, with 1+2–3 teeth; hind femora exceeding elytral apex by a short distance. All three pairs of tibiae mucronate in male, unarmed in female. Tarsi robust, first tarsomere apically concave and acutely angled.

Genitalia and terminalia. Male: Penis (¹) depressed, pedon with sides more or less parallel, apex more or less ogival to triangular, symmetrical. Temones shorter than pedon. Tectum thin, rather inconspicuous. Endophallus with denticles in the median part and a long basal flagellum exceeding a little the total length of penis (temones in-

¹ We have not taken into account the genitalia figured by Pajni and Bhateja (1982) for *L. albolineata*, because of its extreme simplicity, which could be due to the immaturity of the specimen.

cluded), basal part of flagellum inflated, remainder slightly undulate to apically curved, apex more or less widely funnel-shaped. Two *frena* visible in *L. curvata*. Tegmen with dorsal plate slightly notched medially at apex, bearing a high number of long apical setae (18–24) on each lobe; *fenestrae* and *linea arquata* marked, continuous at middle; *prostegium* projected cephalad in an angle, narrowly rounded at apex, with two paramedian careniform reinforcements, protruding on the ventral face and beyond apical margin of *prostegium* (*L. curvata*). Spiculum gastrale with manubrium longer than arms, these without wings (sclerotized pouches in Lyal and Curran 2003).

Female: Ovipositor slightly sclerotized; gonocoxites very obliquely ending cephalad, more strongly sclerotized at apex, baculi wide, styli elongate, apically setose; vagina with several weak, distant teeth; bursa copulatrix without sclerotizations; spermatheca of the usual kind in the family, with a long cornu.

Etymology. This genus is named in honour of our good colleague and friend Dr Christopher H.C. Lyal (Natural History Museum, London), one of the best world experts on weevils (Coleoptera Curculionoidea), having recently published a revision of two Oriental genera (Lyal and Curran 2003).

Included species. This genus includes for the moment three nominal species in the Oriental Realm, two of them having been wrongly placed in the Afrotropical genus *Ctenomerus* Schoenherr, 1843: *Ctenomerus lagerstroemiae* G.A.K. Marshall, 1923 (Java), a synonym, and *C. albolineatus* Pajni & Bhateja, 1982 (India: Assam). Two others have been found in the collections of the Muséum National d'Histoire Naturelle (Paris) by the senior author: *Nanophyes robustus* Pic, 1921 (described from Java) and one undescribed species in the Barbier collection, coming from Vietnam.

Lyalia curvata Alonso-Zarazaga & Perrin, sp. n.

urn:lsid:zoobank.org:act:90833E1A-D7B9-4A4C-A60F-E81060B5E3DE http://species-id.net/wiki/Lyalia_curvata Figs 1–2, 4–5, 8, 13–17

Description. (holotype). *Measurements* (in μ m): Body length (without rostrum): 3140; (standard): 2890. Rostrum: length: 1440; width (mesorostral and basal): 251, (apical): 272. Distance from antennal insertion to base: 880. Frons: width: 94. Eye: length: 356. Scape: length: 785; maximum width: 99. Desmomeres 1–6 (length × width): 157 × 79; 115 × 73; 94 × 73; 63 × 79; 63 × 84; 52 × 84. Club (length × width): 451 × 178; 3rd segment: length: 241. Pronotum: length: 980; width (basal): 1600, (apical): 620. Elytra: length: 2400; maximum width: 1920. Mesocoxal distance: 272. Mesocoxal diameter: 356. Metacoxal distance: 325.

Integument. General colour reddish brown, club and apices of onychia and rostrum piceous brown, remainder of antennae and legs lighter testaceous brown, apices of femoral teeth blackened.

Vestiture of yellowish piliform scales with golden reflections, in two dense parallel and separate rows on frons, on pronotum dense on sides and on a very narrow midline,



Figures 1–3. Types of *Lyalia* Alonso-Zarazaga & Perrin gen. n. l *L. curvata* Alonso-Zarazaga & Perrin sp. n., male holotype, dorsal view 2 Do., lateral view. 3 *L. robusta* (Pic), male lectotype. Scale: 1 mm.

separated from the lateral patches at base by dense brownish squamules and near apex by a region of dense mixed yellow and brown squamules, on elytra the yellow scales forming a band in the apical half of 1st interstria, with some mixed brownish scales, 2nd interstria with a basal patch and a band in the apical two thirds, 3rd as 2nd but with no basal patch, 4th completely covered of yellow scales, 5th as 4th but a brown basal patch and a line mixed with brown squamules on median third, 6th covered by yellow scales, except a short line of brown squamules on median third, 7th and 8th with brown scales on humeral calli, 7th also with brown scales on apical half, 9th and 11th also densely covered in yellow scales throughout. Ventral parts densely covered with yellow scales, legs sparsely so.

Rostrum in dorsal view 5.29 × as long as wide at apex, 1.47 × as long as pronotum, metarostrum parallel-sided, prorostrum widening towards apex, 5-carinate, median keel hardly surpassing middle of prorostrum, finer and more convex than paramedian keels, these wider and less convex, surpassing a little apex of median keel, all three widening before disappearing, lateral keels fine and acute up to apex, keels separated by densely punctate and pubescent sulci, weakly and confusedly so on prorostrum; in side view, rostrum moderately curved, sublateral keel acute up to apex, except where interrupted by scrobe, prorostrum weakly tapering towards apex.

Antennae inserted at basal 0.61 of rostrum, scape $7.93 \times as$ long as wide and $3.13 \times as$ long as mesorostral width, 1.44 as long as funicle, first 3 desmomeres clearly oblong, 4th subtransversal, 5th and 6th clearly transversal, club short, 0.83 × as long as funicle, shortly fusiform, 2.53 × as long as wide, last segment 1.15 × as long as the first two together, weakly asymmetrical.

Head subconical, eyes slightly oblong and convex, from $0.35 \times as$ wide as rostral apex, with two dense longitudinal rows of scales on each side.



Figures 4–7. Types of *Lyalia* Alonso-Zarazaga & Perrin, gen. n. 4 *L. curvata* Alonso-Zarazaga & Perrin sp. n., male holotype, rostrum, dorsal view 5 Do., lateral view 6 *L. robusta* (Pic), male lectotype, rostrum, dorsal view 7 Do., lateral view. Scale: 1 mm.

Pronotum transversally troncoconical, $1.63 \times as$ wide as long, sides almost straight, hardly constricted behind apex, base $2.58 \times as$ wide as apex, basal crenulated keel interrupted at middle, with very dense teeth (7 in 100 µm), punctures very fine (6–7 µm in diameter) and denser in basal half, separated 1–3 diameters in apical half.

Elytra very convex, very shortly oval, $1.25 \times as$ long as wide, widest at humeral calli, sides rather parallel behind these and then arched to apex, basal keel teeth similar to the pronotal keel ones, striae deep, interstriae $3-4 \times$ wider than striae, with 7–8 rows of scales, interstrial punctures as small as those on pronotum, but much denser, 2^{nd} and 3^{rd} striae strongly curved towards suture in basal third, 2^{nd} interstria usually less than $1.4 \times as$ wide as interstria 1 at same level.

Legs. Profemora 2.13 × as long as wide, with 1+2 teeth on each femur, largest tooth 0.30 × as long as width of femur, protibiae straight, robust, 5.61 × as long as wide, inner margin weakly bisinuate, punctures longitudinally undulate, other legs similar, mucros short and robust. First protarsomere 1 1.25 × as long as wide, 2^{nd} 1.1 ×, 3^{rd} 0.83 ×, onychium 4.5 ×, surpassing lobes of 3^{rd} by half its length.

Ventral areas. Third ventrite without visible lateral fovea, 5th ventrite weakly trisinuate at apex (Fig 8). Pygidium moderately convex.

Genitalia. Tegmen with dorsal plate oblong, tapering to apex, this widely rounded with a very small median notch, 18-19 very long macrochaetae on each side of it, some of these subapical, most apical, *fenestrae* medially continuous, well conspicuous, *linea arquata* marked, *prostegium* subtriangular, median projection with two shorter projections on each side ending paramedian longitudinal ventral keels. Penis in dorsal view with sides of pedon subparallel, a little wider near middle, $1.4 \times$ as long as temones, apical plate roundly triangular with sides slightly concave, tectum hardly visible. Endophallus with two ill-defined *frena* and several teeth, and a subrectilinear flagellum $1.06 \times$ as long as the whole penis.

Female. (paratype). *Measurements* (in μ m): Body length (without rostrum): 3370; (standard) = 3170. Rostrum: length: 1800; width (at apex): 304, (mesorostrum): 251, (at base): 272. Distance to antennal insertion from base: 920. Frons: width: 115. Eye:



Figures 8–9. Abdominal ventrites: 8 *Lyalia curvata* Alonso-Zarazaga & Perrin, sp. n., male holotype 9 *Lyalia robusta* (Pic), male lectotype. Scale: 1 mm.

length: 335. Scape: length: 817; maximum width: 84. Desmomeres 1–6 (length \times width): 147 \times 63; 115 \times 63; 73 \times 68; 63 \times 73; 68 \times 84; 53 \times 89. Club: 472 \times 159; 3rd segment: length: 262. Pronotum: length: 1100; width (at base): 1700, (at apex): 700. Elytra: length: 2520; maximum width: 2100. Mesocoxal distance: 283. Mesocoxal diameter: 366. Metacoxal distance: 356.

As male, but *rostrum* in dorsal view 5.92 × as long as wide at apex, 1.64 × as long as pronotum, metarostrum parallel-sided, prorostrum weakly widening to apex, 5-carinate, keels as in male, sulci in prorostrum as irregular lines with confuse punctures; in side view rostrum moderately curved, prorostrum with margins subparallel to apex.

Antennae inserted at basal 0.51 of rostrum, scape $9.73 \times as$ long as wide and $3.25 \times as$ long as mesorostral width, $1.56 \times as$ long as funicle, this as in male, but a little more robust; club narrower, $0.91 \times as$ long as funicle, fusiform, $3.00 \times as$ long as wide, last segment $1.25 \times as$ long as two first together, hardly asymmetrical.

Frons $0.38 \times$ as wide as rostral apex.

Pronotum as in male, but $1.55 \times$ as wide as long, base $2.43 \times$ as wide as apex, basal crenulate keel with dense teeth, these larger (5 in 100 µm near middle).

Elytra a little wider than in male, $1.20 \times as$ long as wide, teeth in the basal crenulate keel larger than those of pronotum (4 in 100 µm on base of 1st stria).

Profemora with 1+3 teeth, largest tooth $0.33 \times as$ long as width of femur, others with 1+2, tibiae still more robust than in male, $4.85 \times as$ long as wide, mucros absent.

Ventral areas. 5th ventrite weakly convex, apex rounded-subtruncate.

Genitalia. Ovipositor weakly sclerotized, gonocoxites ending very obliquely cephalad, apex strongly sclerotized, styli elongate, ca. 2 × as long as wide, their apex shortly setulose, vagina with some distant weak teeth, *bursa copulatrix* without sclerotizations, spermatheca with long cornu.

Variability. The male paratype has a length (without rostrum) of 4030 μ m, a length (standard) of 3770 μ m and a ratio Lrostrum/Lpronotum of 1.44. Golden coloration of scales is a bit more extended than in the holotype, and all femora show 1+3 teeth. In



Figures 10–17. *Lyalia robusta* (Pic). 10 Penis, lateral view 11 Penis, dorsal view 12 Flagellum of endophallus. *Lyalia curvata* Alonso-Zarazaga & Perrin, sp. n. 13 Penis, lateral view 14 Tube of penis, dorsal view 15 Tegmen, dorsal view 16 Tegmen, lateral view 17 Female genitalia. Scale: 1 mm.

general in Nanophyidae, number of extra (small apical) teeth is related with femur size, the femora in females (which are usually larger than males) and larger males showing an increase in number; in a single specimen, it is usual to see an increase in the front and hind femora with respect to the mid femora, which are shorter than the others. Material examined. Holotype: 1 male, labelled as follows: yellowish: Jardin Botanique; yellowish: SAIGON / 17-VII-50 / J. BARBIER; yellowish: MUSEUM PARIS / Coll. / J. Barbier; white: AZ-0001; red: HOLOTYPE &/ LYALIA CURVATA / n. sp./ Alonso-Zarazaga / et Perrin 2011 (Perrin's handwriting). Specimen coming from Coll. Barbier, now included in the General Collection.

Paratypes: 1 female, labelled: yellowish: Jardin Botanique; yellowish: SAIGON / 15-VI-50 / J. BARBIER; white: COTYPE (in red); yellowish: MUSEUM PARIS / Coll. / J. Barbier; white: Nanophyes maximus nsp (Pic's handwriting); white: AZ-0002; red: PARATYPE Q/ LYALIA CURVATA / n. sp./ Alonso-Zarazaga / et Perrin 2011 (Perrin's handwriting). To our knowledge this nominal taxon by Pic has never been described. These two specimens are close to a bottom label stating: "Nanophyes major / maximus, barbieri / et testaceicollis in litt. / selon Zherikhin 1997". 1 male: Saigon; Nanophyes / maximus / Pic (locality and identification: Hoffmann's handwriting); MUSEUM PARIS / 1968 / Col. A. HOFFMANN; AZ-0313; red: PARATYPE &/ LYALIA CURVATA / n. sp./ Alonso-Zarazaga / et Perrin 2011 (Perrin's handwriting); white: Exchange /M.N.H.N. It lacks the left antenna beyond the scape, left midleg beyond base of tibia (broken), onychium of right midleg and tarsi of both hindlegs. This specimen was probably part of the Barbier's series and transferred to Hoffmann's collection "à la Hoffmann" (Perrin, 1998). It has been agreed that this specimen will be transferred to the Coll. Alonso-Zarazaga (MNCN, Madrid).

Etymology. This species is named *curvata* (curved) after the peculiar curved run of the 2nd and 3rd striae towards suture in their basal third. It is a Latin adjective.

Distribution. This species is known only from its type locality, Saigon (now Thành phố Hồ Chí Minh or Ho Chi Minh City) in Southern Vietnam. Nothing is known about its host plant, but it will probably be a species of *Lagerstroemia* (Lythraceae).

Lyalia robusta (Pic, 1921), comb. n.

http://species-id.net/wiki/Lyalia_robusta Figs 3, 6–7, 9–12

Nanophyes robustus Pic, 1921: 4. Ctenomerus lagerstroemiae G.A.K. Marshall, 1923: 268, syn. n.

Description. (lectotype of *L. robusta*). Measurements (in µm): Body length (without rostrum): 3610, (standard): 3510. Rostrum: length: 1780, width: 304. Distance of antennal insertion from eye: 1100. Frons: width: 126. Eye: length: 335. Scape: length: 963, maximum width: 94. Desmomeres 1–6 (length × width): 188 × 73; 157 × 73; 110 × 83; 94 × 83; 94 × 105; 94 × 94. Club: 544 × 136; 3rd segment: length: 293. Pronotum: length: 1230, width (at base): 1940, (at apex): 916. Elytra: length: 2830; maximum width: 2410. Mesocoxal distance: 314. Mesocoxal transverse diameter: 471. Metacoxal distance: 471.

Integument. Colour testaceous, rostrum, antennae, tarsi, base of head, sides of pronotum, two lines (one basal, one median) along 5th interstria and base of humeral calli brownish, two longitudinal paramedian spots on pronotum brownish, blackened at middle, a line on the first third of the 1st and 2nd interstriae (the very base excepted) and of the 3rd, and the 10th and 11th up to metacoxal level, the front 2/3 of the 9th, the median third of 7th and 8th and the tips of the femoral teeth blackish.

Vestiture of dense piliform scales, most of these yellow, blackish or piceous brown on the two pronotal spots and on the lines on interstriae 1, 3, and 5, directed cephalad on pronotum, on elytra caudad and parallel on sutural half of interstria 1 and on interstria 6, obliquely pointing to costal margin on outer half of interstria 1 and on interstriae 2–5, obliquely directed to sutural margin on interstriae 7–11.

Rostrum in dorsal view subcylindrical, $5.86 \times as$ long as wide at apex, $1.45 \times as$ long as pronotum, strongly 5-carinate, median keel reaching middle of prorostrum, paramedian keels approaching the lateral keels and reaching apex of rostrum, like the lateral ones; punctures very small, stronger and denser on prorostrum; in side view, rostrum slightly curved, prorostrum weakly tapering apicad.

Antennae inserted at basal 0.62 of rostrum, scape $10.2 \times as$ long as wide, $3.17 \times as$ long as mesorostral width, $1.31 \times as$ long as funicle, 3 first desmomeres clearly oblong, 5th slightly transverse and asymmetrical, club subfusiform, very short, $0.74 \times length$ of funicle, $4.0 \times as$ long as wide, its last segment $1.17 \times as$ long as other two together.

Head conical, eyes rounded, weakly convex, frons $0.41 \times as$ wide as rostral apex, with two longitudinal lines of pubescence on each side.

Pronotum strongly troncoconical, transverse, $1.58 \times as$ wide as long, base $2.11 \times as$ wide as apex, sides slightly convex in basal third and weakly constricted in apical third, basal crenulated keel densely toothed (4 teeth per 100 µm at middle), interrupted at middle, punctures very fine (10 µm in diameter) and dense at base, sparser in apical half.

Elytra very convex, shortly oval, $1.17 \times as$ long as wide, widest at humeri, evenly arched to posterior fourth, then quickly arched to apex; basal keel with teeth as large and dense as that of pronotum; striae deep, very fine, interstriae 7–10 × as wide as striae, with 7–8 rows of pubescence, punctures $0.5-1.0 \times as$ wide as those of pronotum, as dense as in basal half of pronotum.

Ventral areas. Third ventrite with a very small lateral fovea on each side, 5th ventrite moderately convex, apex medially notched, with a strong transverse pleat in the anterior margin of the notch (Fig 9). Pygidium moderately convex, without particular features.

Legs. Meso- and metafemora with 1+2 teeth.

Genitalia. Tube of penis in dorsal view with straight, parallel sides, apical plate ogival, median point slightly blunt, sides of apical plate convex, tectum rod-like, weak, temones shorter than half the tube; in side view, tube depressed, the apical plate inflexed, straight. Endophallus without visible sclerotizations, flagellum 1.15 × as long as penis, inflated in basal fifth, apex slightly funnel-shaped. Tegmen unknown.

Female. Lectotype of *C. lagerstroemiae.* Measurements (in μ m): Body length (without rostrum): 3850, (standard): 3770. Rostrum: length: 2230; width (at apex):

314, (mesorostrum): 262, (base): 283. Distance of antennal insertion from base: 1020. Frons: width: 115. Eye: length: 325. Scape: length: 932; maximum width: 84. Desmomeres 1–6 (length × width): 199 × 68; 147 × 63; 115 × 84; 84 × 84; 84 × 105; 73 × 94. Club: 482 × 168; 3^{rd} segment: length: 251. Pronotum: length: 1280; width (at base): 1960, (at apex): 916. Elytra: length: 3010; width: 2410. Mesocoxal distance: 314. Mesocoxal transverse diameter: 450. Metacoxal distance: 419.

As in male, but 1st elytral interstria immaculate. *Rostrum* in dorsal view subcylindrical, 7.09 × as long as wide at apex, metarostral sides a little convergent to mesorostrum, this weakly dilated, prorostral sides widening towards apex in curve, $1.73-1.86 \times as$ long as pronotum, weakly 5-carinate, median keel reaching almost to apex, low, almost flat, paramedians and laterals more convex, reaching apex, sulci between these moderately punctate, densely pubescent on metarostrum, sparsely and minutely pubescent on prorostrum ; in side view, moderately curved, prorostrum with margins parallel.

Antennae inserted at basal 0.44–0.46 of rostrum, scape 11.1 × as long as wide, $3.56 \times as$ long as mesorostral width, $1.33 \times as$ long as funicle, desmomeres as in male, antennal club 0.69 × as long as funicle, 2.87 × as long as wide, much more robust than in male, last segment 1.09 × as long as the other two together.

Frons $0.37 \times$ as wide as rostral apex, rest as in male.

Pronotum as in male, $1.53-1.60 \times$ as wide as long, very strongly troncoconical, base $2.14-2.21 \times$ as wide as apex. *Elytra* as in male, but a little more elongate, $1.24-1.28 \times$ as long as wide, teeth of basal keel less dense (3 in 100 µm at base of 1st stria). *Profemora* with 1+3 teeth, meso- and metafemora as in male.

Material examined. Lectotype of *Nanophyes robustus*: 1 male, found in the Pic collection, apparently dissected by V. Zherikhin. The specimen lacks both fore legs at the trochanter-femur level, the onychium of the right metatarsus, the abdominal tergites, the tegmen and a part of the manubrium of the spiculum gastrale. One wing was already separately prepared. It carries the following labels: Giava / Matte / 1909; printed: 134; Miarus gen? / sp? (Java); yellow: Pic's handwriting: type; red: TYPE; Pic's handwriting: Nanophyes / robustus / nsp; yellow, printed: Museum Paris / Coll. M. Pic; Shiva / robustus (Pic) / V. Zherikhin 95; red: LECTOTYPE & / LYALIA ROBUSTA / Pic /Alonso-Zarazaga / et Perrin des. 2011 (Perrin's handwriting). The specimen has been remounted by the first author and given the revision number AZ-0143.

Syntypes of *Ctenomerus lagerstroemiae*: species based on 6 females, housed in the NHM (Entomology), of which we have received two in study. One of them is here selected as lectotype. It carries the labels: round, circled blue: SYN- / TYPE; MID-JAVA. / 1919. / L. Kalshoven; Fruit borer; Ex / Lagerstroemia / speciosa; G.A.K. Marshall / Coll. / B. M. 1950–255; 3; 2; LYALIA / ROBUSTA / Pic / Alonso-Zarazaga det. 2010; red: LECTOTYPE 2 / CTENOMERUS / LAGERSTROEMIAE / Marshall /Alonso-Zarazaga / et Perrin des. 2011 (Perrin's handwriting). It has been added the revision database number AZ-0311. This specimen was incorrectly labelled as a male, and we have added a female label. The other specimen has been labelled with database number AZ-0312.

Distribution. This species is known from the island of Java (Indonesia), without any further detail. It has been recently recorded from the island of Bali (Pura Taman musi, Buleleng prov.) (Kantoh and Kojima 2009b) and from Laos (Ban Thad Son, Vientiane prov.) (Kantoh and Kojima 2009c).

Biology. This species seems to be trophically linked to *Lagerstroemia indica* L. (= *Lagerstroemia speciosa* (L.) Pers.) (Lythraceae), a widely distributed plant in SE Asia. The larvae bore in the fruits (Marshall 1923; Van Emden 1938).

Comment. It is curious that this synonymy was already known to Van Emden (1938: 27), who treated the Javan Kalshoven's specimens as *N. robustus* when describing their larval characters. He followed G.A.K. Marshall's identification, who also seems to have been aware of it at that time, but never published it.

Lyalia albolineata (Pajni & Bhateja, 1982), comb. n.

http://species-id.net/wiki/Lyalia_albolineata

Ctenomerus albolineatus Pajni & Bhateja, 1982: 464

Remarks. This species was incorrectly placed in the Afrotropical genus *Ctenomerus* based solely on the presence of 6 desmomeres and a crenulated keel on 8th interstria. The original description does not state the condition of the 10th stria, but the presence of the peculiar oblique elytral pubescence and the characters of the male genitalia are enough, in our opinion, to place it in this new genus.

This species is perhaps a synonym of *L. robusta*, since we have been unable to find robust characters to separate them. In particular the short temones of penis, the apparent lack of large structures in the endophallus and the shape and proportions of the antennal segments are very reminiscent of this species. The study of more material is desirable.

It is only known from the Indian state of Assam: Kaziranga and Tejpur, Chardaur, without any definite host plant ("ex a forest tree").

Kantohia Alonso-Zarazaga & Perrin, gen. n.

urn:lsid:zoobank.org:act:FCA32BC1-5CFE-4D01-9972-FDAF7FECC552 http://species-id.net/wiki/Kantohia

Type species. Shiva taiwanus Kantoh & Kojima, 2009. Gender feminine.

Description. The single originally included and type species was thoroughly described by Kantoh and Kojima (2009). Some important characters, however, were absent from this description and are added here, through Mr. Kantoh's courtesy. In their discussion of the placement of this species, the authors stated that they were defining *Shiva* as a genus having "8th elytral interval shortly crenulate distad of humeral callus", a character which is in contradiction with the original description of the genus, where Pajni and Bhateja (1982) state that the elytra show "interval 8 not granulate or carinate

on basal 0.33", and with the hundreds of specimens of this genus seen by the senior author. Consequently, this species cannot be placed in the genus *Shiva* nor in any other known presently to the authors.

The generic description, thus, coincides with the specific one given by Kantoh and Kojima (2009), adding: Size small: 2.0–2.5 mm. Rostrum short: ca. as long as pronotum in male, ca. $1.3 \times$ in female. Third desmomere subisodiametric, as long as 4^{th} . Club longer than funicle. Tenth stria erased or fused to 9^{th} between metacoxal and suture II level. Crenulate keel on 8^{th} elytral interstria complete on humeral callus, ending at mid-metasternal level. First tarsomere of all tarsi apically weakly and roundly notched. Apical plate of pedon asymmetrical. Temones as long as pedon. Flagellum slightly shorter (ca. 0.92 ×) than penis.

Etymology. It is a great pleasure to name this new genus after Mr. Junnosuke Kantoh, young Japanese entomologist, with our wish for a long and fruitful career.

Kantohia taiwana (Kantoh & Kojima, 2009), comb. n.

http://species-id.net/wiki/Kantohia_taiwana

Shiva taiwanus Kantoh & Kojima, 2009a: 165

Remarks. The penis and the spiculum gastrale of this species are distinctive. It is known only from Taiwan and was captured on flower buds of *Lagerstroemia subcostata* Koehne.

Discussion

The new genus *Lyalia* differs clearly from *Ctenomerus* by some important characters of the body structure. In *Ctenomerus*, the head and rostrum form an angle near 135°, mesocoxae are at least as widely separated as metacoxae, 10th stria is erased between the metacoxal and suture II levels, and the elytral vestiture is constantly ordered in parallel with the striae. In addition, the tegmen of the single species whose male genitalia is known to us (the type species, *C. serratorius* Gyllenhal, 1843) shows 2 long, deeply cleft and widely divergent parameroid lobes. *Lyalia* seems to be close to genera like *Meregallia* Alonso-Zarazaga, 1990 and *Damnux* Lyal, 2003, because of the peculiar oblique disposition of the elytral vestiture in some of the interstriae, and other features of the genitalia, but these have 5 desmomeres.

On the other hand, *Kantohia* was confused with *Shiva*, a genus with similar external appearance but with a complete 10th stria and no elytral crenulation on the 8th interstria. The evaluation of the phylogenetic relationships must wait until some other genera now being studied are described.

The genera of Nanophyidae with 6 desmomeres were keyed by Alonso-Zarazaga (1989). Since then, one more genus has been described, *Oxycorax* Alonso-Zarazaga,

1990. This was originally described as a subgenus of *Shiva* Pajni & Bhateja, 1982 (Alonso-Zarazaga, 1990) and later raised to genus (Alonso-Zarazaga and Lyal 1999). Moreover, *Temnalysis* Alonso-Zarazaga, 1989 was found to be a synonym of *Pseudorobitis* Redtenbacher, 1868, a genus misplaced in a different group (Curculionidae Orobitidinae) (Giusto 1993). That key has now become obsolete, and a new one is offered below:

1	Stria 10 complete
_	Stria 10 erased or fused to 9 between metacoxal and suture II level
2	Interstria 8 with a complete crenulate keel running up to the basal third of
	elytron. Flagellum of penis conspicuously longer than penis
_	Interestria 8 not visibly crenulate in basal third. Flagellum of penis conspicu-
	ously shorter than penis
3	Procoxae acutely projecting in both sexes, trochanters inserted laterally on pro-
	coxa. Rostrum almost straight. Eyes visibly separated on frons Oxycorax
_	Procoxae rounded at apex, trochanters apical or subapical. Rostrum conspic-
	uously curved. Eyes closely approximated on frons, leaving one row of hairs
	on midline
4	Interstria 8 not visibly crenulate in basal third. Humeral callus obsolete or ab-
	sent. Intermesocoxal distance $0.3-0.4 \times$ the intermetacoxal one <i>Hexatmetus</i>
_	Interstria 8 crenulate, at least partially. Humeral callus developed. Intermeso-
	coxal distance more than $0.75 \times$ the intermetacoxal one 5
5	Interstria 8 not crenulate on callus, keel reaching basal third. Arms of spicu-
	lum gastrale unwinged. Tegmen with parameroid lobes not or hardly devel-
	oped, at most separated by a small notch. Flagellum conspicuously shorter
	than penis. Body integument monochrome black Pseudorobitis
_	Interstria 8 crenulate on callus, keel reaching basal or apical third. Arms of
	spiculum gastrale winged. Tegmen with parameroid lobes deeply cleft. Flagel-
	lum at least as long as penis. Body integument maculate
6	Apex of tarsomere 1 deeply emarginate in V. Crenulate keel of interstria 8
	reaching apical third of elytron. Parameroid lobes very long, widely sepa-
	rated
_	Apex of tarsomere 1 subtruncate to roundly notched. Crenulate keel of in-
	terstria 8 reaching basal 3 rd of elytron (mid-metasternum level). Parameroid
	lobes short, narrowly separatedKantohia

This artificial key, however, does not show the real affinities of the genera. *Lyalia* seems to be related to *Shiva* (or at least some species groups of it), *Meregallia, Damnux* and *Kantohia*, while a relationship with the other close Oriental genus, *Pseudorobitis*, could be grounded on the short temones and the similar meso- and metacoxal distances.

Key to species

The known species of the genus *Lyalia* can be separated as follows. Size is given excluding rostrum.

Second and third elytral striae strongly shifted towards suture in basal third, 1 2^{nd} interstria usually less than $1.4 \times as$ wide as interstria 1 at same level (Fig 1). Club 0.83 \times as long as funicle. Male 5th ventrite weakly trisinuate at apex (Fig 8). Apical plate of pedon roundly triangular in dorsal view, sides slightly concave (Fig 14). Ventral margin of penis in side view straight for most of its length, prominent at base (Fig 13). Temones long, pedon $1.4 \times as$ long as temones (Fig 13). Endophallus with 2 frena and large teeth. Flagellum short, *ca*.1.06 × as long as penis (Fig 13).....*L. curvata* sp. n. Second and third elytral striae not or weakly shifted towards suture in basal third, 2^{nd} interstria at least $1.5 \times$ as wide as interstria 1 at same level (Fig 3). Club 0.69–0.74 × as long as funicle. Male 5th ventrite medially notched apically, with a strong transverse pleat in the anterior margin of the notch (Fig 9) (unknown in L. albolineata). Apical plate of pedon ogival in dorsal view, median point short and blunt (Fig 11). Ventral margin of penis in side view weakly bisinuate for most of its length, not prominent at base (Fig 10) (unknown in L. albolineata). Temones short, pedon 2.35-2.45 × as long as temones (Fig 10). Endophallus without visible frena, just with denticles. Flagellum longer, 1.15–1.20 × as long as penis......2 2 Male rostrum longer, $1.45-1.47 \times as$ long as pronotum. Scape ca. $1.3 \times as$ long as funicle in male. Male pronotum $1.58 \times$ as wide as long, base *ca.* $2.1 \times$ Male rostrum shorter, ca. $1.35 \times as$ long as pronotum. Scape $1.5 \times as$ long as funicle in male. Male pronotum 1.67 \times as wide as long, base *ca*. 2.5 \times as wide as apex L. albolineata

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RESEARCH ARTICLE



Apoxyria hirtuosa (Wiedemann, 1821) comb. n., lectotype designation, redescription and identification key to species of Apoxyria Schiner, 1866 (Asilidae, Laphriinae)

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Abstract

The type specimens of *Neodiogmites hirtuosus* (Wiedemann, 1821), two males and one female, deposited at the Museum für Naturkunde der Humboldt-Universität (ZMHB), Berlin were examined. The specimens show the diagnostic characters of *Apoxyria* Schiner, 1866: face strongly pronounced, swollen and curved hind tibia, and terminalia with epandrium large and hypandrium short and obtuse. A new combination is suggested, *Apoxyria hirtuosa* (Wiedemann, 1821), and lectotype and paralectotypes are designated. The species is redescribed, the male terminalia is described and illustrated for the first time, and an identification key to *Apoxyria* is presented.

Keywords

Neotropical, taxonomy, Laphystiini

Introduction

Dasypogon hirtuosus Wiedemann, 1821, a species classified in the subfamily Dasypogoninae (Papavero 2009), is known from Brazil, with no additional details of the collection locality, was described based on two males and one female without a holotype designation (i.e., syntypes) (Wiedemann 1821). Carrera (1949) transferred *D. hirtuosus* to *Laustauroides* Carrera, 1949 (Dasypogoninae) based on specimens collected in Brazil, however without examination of the type material. Subsequently, Artigas and Papavero (1988) synonymized *Laustauroides* with *Neodiogmites* Carrera, 1949, another genus of Dasypogoninae, and therefore the current name of the species is *Neodiogmites hirtuosus*.

During a revision of the genus *Neodigmites*, the three syntypes of *N. hirtuosus* were examined. It was apparent that this species is not a Dasypogoninae and consequently, is not a member of *Neodiogmites*. Here, we propose a new combination for this species, with a lectotype designation.

Material and methods

The specimens studied are deposited in the Museum für Naturkunde der Humboldt-Universität (ZMHB), Berlin, Germany. The material includes three syntypes, two males and one female; and their labels read only "Brazil". To observe the terminalia, it was detached from the abdomen and cleared in cold 10% KOH, followed by neutralization in acetic acid, dehydration in ethanol, and washing in distilled water. The dissected terminalia was placed in glycerin in a microvial pinned with the respective specimen. Morphological terms follow Cumming and Wood (2009).

Taxonomy

Apoxyria hirtuosa (Wiedemann, 1821) comb. n.

http://species-id.net/wiki/Apoxyria_hirtuosa Figs 1–7

- Dasypogon hirtuosus Wiedemann1821: 227; Wiedemann 1828: 402 (redescription); Walker 1854: 443 (check list); Schiner 1866: 679 (check list); Williston 1891: 67 (catalogue); Kertész 1909: 128 (catalogue);
- *Lastauroides hirtuosus*; Carrera 1949: 97, Fig. 27; 1958a: 146; Carrera and Vulcano 1961: 69 (prey); Carrera and Papavero 1962: 53 (check list); Hull 1962: 241, Figs 545, 1074, 1083 (check list); Martin and Papavero 1970: 29 (catalogue).
- *Neodiogmites hirtuosus*; Artigas and Papavero 1988: 213 (key), 151, Fig. 157; Papavero 2009:1 (catalogue); Geller-Grimm 2011 (online catalogue).

Type-material examined. Lectotype male (ZMHB), present designation, labeled: "Brazil\?, [without date] V. Olfers coll." A red label written "Lectotype" was added. Specimen in reasonable condition, head slightly dusty, flagellum and middle leg lost, right wing mounted on permanent slides, abdomen dissected and placed in a micro-vial with glycerin, pinned together with the specimen. Paralectotypes: 1 male and 1 female, same locality as lectotype. Paralectotype male (ZMHB) in reasonable condition, head with a



Figures 1–4. *Apoxyria hirtuosa* (Wiedemann, 1821) comb. n. **I** General lateral view of lectotype, male **2** General lateral view of paralectotype female **3** Frontal view of head of lectotype **4** Wing of lectotype. Scale = 1mm.

little dust, lacking flagellum, mesonotum broken posteriorly, abdomen cracked between the second and third segment. Paralectotype female (ZMHB) in good condition, but the mesonotum is perforated posteriorly and the left flagellum is lost.

Lectotype male: Measurements: 12.5 mm (body length excluding antennae); 9.0 mm (wings).

Diagnosis. Face pronounced, covered by yellow pruinescence; dorsocentral setae of the same length as the scutum setae, however black; scutellum covered by short yellow setae, with several yellow long and slender apical scutellar setae; wings with r₁ open.

Redescription: Lectotype male. Head (Fig. 3): face black, covered by yellow pruinescence that is denser on the sides, pronounced, not ending abruptly on upper part, occupying 2/3 of face; mystax black and yellow with some yellow setae between the antenna and facial swelling; frons black with sparse yellow pruinescence, yellow setae below and beside ocellar tubercle; vertex black; ocellar tubercle with several yellow setae; orbital setae yellow; postocular setae black with thin yellow setae between them; occiput black with yellow pruinescence, with black setae and yellow lower setae; proboscis black,



Figures 5–7. Terminalia of *Apoxyria hirtuosa* (Wiedemann, 1821) comb. n., lectotype male. **5** Dorsal **6** Ventral **7** Lateral. Scale = 1mm. Abbeviations: apc proc goncxl-apical process gonocoxal; cerc- cercus; epand- epandrium; epand arm- epandrial arm; 1° proc goncxl-first gonocoxal process; goncx-gonocoxito; gonst-gonostylus; hypd-hypandrium; proc cerc- process cercal; ph-phallus; 2° proc goncxl- second process gonocoxal.

apex obtuse, with short yellow setae ventrally; palpus black, longer than half length of proboscis, yellow setae basally and black on the remainder; antenna black, scape and pedicel almost the same length with black setae, scape with some basal yellow setae.

Thorax (Fig 1): black; second cervical sclerite black with sparse yellow pruinescence and black setae; antepronotum with black setae; postpronotum covered by yellow pruinescence and yellow setae laterally, some black setae mixed; postpronotal lobe with black setae anteriorly and yellow posteriorly; proepisternum and proepimeron with yellow pruinescence and yellow setae; scutum covered by short yellow setae; dorsocentral setae of the same length as the scutum setae, however black; two notopleural setae; three to four supra-alar setae and two postalar setae, all black; scutellum covered by short yellow setae, with several yellow long and slender apical scutellar setae; mesopleura covered by yellow pruinescence, except anteriorly on the anepisternum and katepisternum; anepisternum with yellow setae and some black setae posteriorly; katepisternum with yellow setae; katatergite with brownish setae.

Legs (Fig. 1): shiny black; coxae with yellowish pruinescence and yellow setae; femora covered by short yellow setae with some black setae on the dorsum; fore and hind tibiae covered by yellow setae, longer on ventral and posteroventral margin, and with dense short yellow setae on ventral margin which extend onto first tarsomere, these setae are also present on the hind tibiae, but are denser than on the other legs; fore tibia with anterodorsal, posterodorsal, and posteroventral rows of stout black setae; mid tibia covered by yellow and black setae of different lengths, with anterodorsal, posterodorsal, and posteroventral rows of stout black setae; tae; hind tibia covered by yellow and black setae of different lengths, with anterodorsal, posterodorsal, and posteroventral rows of stout black setae on ventral and posteroventral margins. Tarsi covered by short yellow setae and stout black setae; claws black; pulvilli yellowish.

Wing (Fig. 4): membrane slightly infuscate; veins brown; alula reduced, but a small lobe is still distinct; r_1 open, apex of R_{2+3} arching sharply anteriorly in 90° angle, R_4 strongly sinuate, R_4 and R_5 diverge from each other at the wing margin, r_5 open, m_3 closed and petiolate; cell cup closed; haltere yellow.

Abdomen (Fig 1): black, covered by short yellow setae, longer on the sides of anterior three tergites; posterior margin of tergites 6 and 7 reddish. Terminalia (Figs 5–7): terminalia reddish with black setae; epandrium long, with deep, rounded sulcus on apical fourth, forming long arms laterally; subepandrial sclerite with medial evagination forming laterally arms with rounded apex; cercus with two projections dorsally; gonocoxite with a claw-shaped projection on the apex and with two expansions, the second expansion with shell-shaped apex; gonostylus with rounded apex; hypandrium short and boomerang-shaped.

Female (Fig. 2): flagellum longer than scape and pedicel combined, with and a spine on the apex, black covered by brown pruinescence denser in the base; postpronotal lobe with black setae anteriorly; scutellum with some short black setae anteriorly; legs and abdomen with fewer setae than in male; terminalia pale brown.

Distribution: Brazil.

Discussion. After the original description of *Dasypogon hirtuosus* by Wiedemann (1821), the type specimens have not been examined until now. All the transfers to other genera were based on other specimens collected in Brazil (Carrera 1949; Artigas and Papavero 1988). The morphological study of the syntypes of this species revealed the lack of a spine on the prothoracic tibia, one of the most important characters to identify members of Dasypogoninae (Hull 1962; Papavero 1973; Dikow 2009). Moreover, the specimens studied have important characters that places them in the Laphriinae:

the male with only six abdominal tergites visible dorsally, as defined by Hull (1962), wings whit r_1 open, apex of R_{2+3} arching sharply anteriorly in 90° angle and R_4 strongly sinuate (Dikow 2009).

Among the genera of Laphriinae, the specimens show the diagnostic characters of *Apoxyria*: numerous long and slender apical scutellar setae, the face strongly pronounced, swollen hind femora, swollen and curved hind tibia, and terminalia with a large epandrium and short and obtuse hypandrium.

At the moment, the genus *Apoxyria* is known only from Brazil, now with three species: *Apoxyria apicata* Schiner, 1866, *Apoxyria americana* Carrera, 1955 and *Apoxyria hirtuosa*. There are insufficient data to determine their distributions in detail, because few specimens of this genus have been collected.

Key to species of Apoxyria Schiner, 1866.

1	R ₂₊₃ ends in R ₁ (not reaching C), cell r1close, petiolate; male with posterior
	margins of tergites 6-7 black (Brazil)A. apicata Schiner, 1866
_	$R_{2,3}$ ends in C, cell r1 open (Fig. 4); male with posterior margins of tergites
	6–7 either reddish or yellow
2	Mesonotum covered by short yellow setae (Fig 1); male with posterior margins
	of tergites 6-7 reddish; epandrial arms long and slender (Fig. 5) (Brazil)
_	Mesonotum covered by short black setae; male with posterior margins of
	tergites 6-7 yellow; epandrial arms short and thick (Fig. 66 from Artigas et
	al. 1997) (Brazil: Goiás and Santa Catarina)A. americana Carrera, 1955

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RESEARCH ARTICLE



Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species

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Abstract

The oviposition behaviour of four ant parasitoids was observed and filmed for the first time. The movies are available from YouTube (search for *Elasmosoma*, *Hybrizon*, *Kollasmosoma* and *Neoneurus*). Two of the observed species (*Neoneurus vesculus* **sp. n.** and *Kollasmosoma sentum* **sp. n.**) are new to science. A third species (*Neoneurus recticalcar* **sp. n.**) is described from Slovakia and Norway. Keys to the Palaearctic species of the genera *Neoneurus* and *Kollasmosoma* are added.

Keywords

Braconidae, Euphorinae, Neoneurini, *Neoneurus, Elasmosoma, Kollamosoma*, Ichneumonidae: Hybrizontinae, *Hybrizon*, biology, behaviour, Formicidae, *Formica, Cataglyphis, Lasius*, new species, key, Europe, Spain, Slovakia, Norway

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Introduction

In Europe the members of the small tribe Neoneurini Bengtsson, 1918 (Hymenoptera: Braconidae: Euphorinae) belong to three genera: *Elasmosoma* Ruthe, 1858, *Kollasmosoma* van Achterberg & Argaman, 1993, and *Neoneurus* Haliday, 1838 (van Achterberg and Argaman 1993). In the past Neoneurini were considered to form a separate subfamily, but recent DNA analyses indicate that it is part of Euphorinae Foerster, 1862 (Belshaw and Quicke 2000; Belshaw et al. 2001).

As far as the scanty biological information allows a conclusion, the Neoneurini are considered to be most likely koinobiont endoparasitoids of adult ants (Shaw and Huddleston 1991; Shaw 1992). According to Huddleston (1976) the strongly curved ovipositor, which is almost hook-shaped and forward-pointing when exserted (Figs 1, 23, 53), gives support to the supposition that the eggs are laid, possibly through the anus, into the metasoma of adult ant workers. With few exceptions Neoneurini have been found in association with formicine ants (Shenefelt 1969; Marsh 1979; Yu et al. 2007). These ants exude formic acid which is a powerful attractant for predatory ant species, and it seems likely that this exudate could serve also as a kairomonal stimulant to host-seeking hymenopterous parasitoids (Huddleston 1976; van Achterberg and Argaman 1993).

Elasmosoma species are predominantly associated with the genus *Formica* Linnaeus, 1758 (*Formica rufa* Linnaeus, 1758, *F. pratensis* (Retzius, 1783), *F. sanguinea* Latreille, 1798, *F. fusca* Linnaeus, 1758, and *F. rufibarbis* Fabricius, 1793), infrequently also with *Lasius niger* (Linnaeus, 1758), and species of *Camponotus* Mayr, 1861, and *Polyergus* Latreille, 1804, (Wasmann 1897; Schmiedeknecht 1914; Tobias 1971, 1986; Marsh 1979; Huddleston 1976). The observations by Panis (2007) on *E. berolinense* in southern France conflict with our observations; he reported oviposition through the intersegmental membrane at the base of the metasoma. Either this is an adaptation to parasitize workers of *Camponotus vagus* (Scopoli, 1763) or the identification of the parasitoid is perhaps incorrect.

The scanty biological information indicates that *Kollasmosoma* species are associated with species of the genus *Cataglyphis* Foerster, 1850. One *Kollasmosoma* species (*K. platamonense* (Huddleston, 1976)) was observed to approach the formicine desert ant *Cataglyphis bicolor* (Fabricius, 1793) from behind and remained in contact with the tip of the metasoma of the ant for less than one second (R.D. Harkness in Huddleston 1976). Similar oviposition behaviour is reported in this paper for another *Kollasmosoma* species (*K. sentum* sp. n.) with *Cataglyphis ibericus* (Emery, 1906) in Spain.

Neoneurus species are only associated with members of the genus *Formica* Linnaeus, 1758: *F. rufa* Linnaeus, *F. pratensis* (Retzius) and *F. subsericea* Say, 1836 (reported as *F. podzolica* Francoeur, 1973; Yu et al. 2007). Tobias (1971) found *Neoneurus auctus* (Thomson, 1895) in bark-beetle galleries (Scolytidae), but this may concern hibernating specimens.

For the identification of the tribe Neoneurini of the subfamily Euphorinae see van Achterberg (1990, 1993, 1997), for the identification of the Palaearctic genera see van Achterberg and Argaman (1993); for a key to the European *Elasmosoma* species see van Achterberg and Koponen (2003); for references to the genera and species, see Yu et al. (2007) and updates, and for morphological terminology see van Achterberg (1988).

The small subfamily Hybrizontinae Blanchard, 1845 (= Paxylommatinae Foerster, 1862; Wharton and van Achterberg 2000) is considered to belong to the family Ichneumonidae, but was often associated with Braconidae (van Achterberg 1976) or considered to be a separate family (Tobias 1988). The group is treated as a subfamily of the family Ichneumonidae Latreille, 1802, by Rasnitsyn (1980) and Yu and Horstmann (1997), and indeed the structure of the connection of the second and third metasomal tergites and the venation of the hind wing seem to indicate a closer relationship with the family Ichneumonidae (Sharkey and Wahl 1987; Wahl and Sharkey 1988). From analysis of the 28S ribosomal RNA from *Hybrizon* it may be concluded that the Hybrizontinae are at a basal position of the Ichneumonidae-lineage (Belshaw et al. 1998; Quicke et al. 2000; Belshaw and Quicke 2002).

Until now the biology of Hybrizontinae was poorly known and based on circumstantial evidence (van Achterberg 1999). Development was known to take place in ant-nests, from which they have been reared several times and where the naked pupae have been found among ant cocoons (Donisthorpe and Wilkinson 1930). Hybrizontinae are associated with ants of the genera Formica Linnaeus, Lasius Fabricius, 1804, Myrmica Latreille, 1804, and Tapinoma Foerster, 1850 (Yu et al. 2007). Donisthorpe (1915) and Donisthorpe and Wilkinson (1930) gave a detailed list of several species of probable hosts based on their own data and that of others (Arnold 1881; Ratzeburg 1848; Giraud 1857; Rudow 1883; Marshall 1891; Wasmann 1894, 1899; Cobelli 1906; de Gaulle 1908; Haupt 1913). According to that list Hybrizon buccatus (de Brébisson, 1825) was seen hovering over the nest entrance or over workers of *Formica* rufa, F. rufibarbis, F. sanguinea, Lasius alienus (Foerster, 1850), L. brunneus (Latreille, 1798), L. citrinus Emery, 1922, L. flavus (Fabricius, 1782), L. niger, Myrmica lobicornis Nylander, 1846, M. ruginodis Nylander, 1846, M. scabrinodis Nylander, 1846, and Tapinoma erraticum (Latreille, 1798). Ghilaromma fuliginosi was seen hovering over L. fuliginosus (Latreille, 1798). Eurypterna cremieri (Romand, 1838) was seen hovering over F. rufa, L. brunneus, L. fuliginosus and Camponotus herculeanus. More recently, Watanabe (1984) saw Ghilaromma fuliginosi (Wilkinson, 1930) hovering over L. fuliginosus, and Marsh (1989) refers to three specimens of H. rileyi (Ashmead, 1899) which were attracted to a disturbed nest of Lasius alienus. In The Netherlands females of Hybrizon buccatus were observed diving at Formica rufa worker ants during spring ant wars in the dunes near The Hague (van Achterberg 1999). In total, four genera of ants (Formica, Lasius, Myrmica and Tapinoma) belonging to three subfamilies (Formicinae, Myrmicinae and Dolichoderinae) have been considered as probable hosts of *H. buccatus*. This large range of host-parasitoid relationships needs, beyond the mere existence of hovering behaviour, direct confirmation of ovipositions. In the case of E. cremieri, Cobelli (1906) observed 20 ovipositions on the larvae transported by workers of L. fuliginosus, and Komatsu and Konishi (2010) photographed oviposition into larvae of *L. nipponensis* Forel, 1912. From the circumstantial evidence it was concluded that they probably are endoparasitoids of ants (Čapek 1970; van Achterberg 1976). Here we report that the egg of *Hybrizon buccatus* is laid in ant larva when they are transported outside of their nests. Komatsu and Konishi (2010) report oviposition by *E. cremieri* into the somatic cavity of the larva in less than a second. Konishi (2010) stated that the larvae are parasitized during their transport from the summer nest in a tree trunk to the winter ground nest in October; the adults of *E. cremieri* emerge from the summer nest in the tree trunk from late September to end of October. It remains a mystery how this large parasitoid. In addition, Komatsu and Konishi (2010) described and illustrated oviposition by a new Japanese genus and species into larvae of *Myrmica kotokui* Forel, 1911. For the recognition of the subfamily Hybrizontinae and for the identification of European genera and species, see Tobias (1988) and van Achterberg (1999).

Material and methods

Females of *Hybrizon buccatus* (de Brébisson) and *Elasmosoma luxemburgense* Wasmann were observed in Almazán (Soria, Spain) in July and August, 2010. *Kollasmosoma sentum* sp. n. and *Neoneurus vesculus* sp. n. were observed in Madrid (at the enclosed area of the Institute for Agriculture and Food Research and Technology (INIA), Carretera de La Coruña Km 7.5, Spain) in August and September, 2010. The oviposition behaviour for each species (comprising the grasping of the ant by the wasp and the insertion of the ovipositor, until departure by flight) was recorded in slow motion video, at a rate of 300 frames per second, with a Casio Exilim Pro EX-F1 digital camera and a Raynox DCR-250 Super Macro lens. The four short movies showing the oviposition behaviour of the four observed species are downloadable from YouTube (Appendices I–IV). RMNH stands for Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands; RMS for National Museums of Scotland, Edinburgh, RMSEL for Rocky Mountain Systematic Entomology Laboratory, Laramie, Wyoming, USA, and ZMUO for Zoological Museum, University of Oslo, Blindern, Oslo, Norway.

Braconidae Nees, 1811

Elasmosoma Ruthe, 1858

Elasmosoma Ruthe, 1858: 7. Type species by monotypy: *Elasmosoma berolinense* Ruthe, 1858 (examined).

Elasmosoma luxemburgense Wasmann, 1909

http://species-id.net/wiki/Elasmosoma_luxemburgense Figs 1–7

Oviposition behaviour. Oviposition of *Elasmosoma* spp. into the ants' metasoma has long been observed (Forel 1874; Olivier 1893; Pierre 1893; Wasmann 1897; Donisthorpe 1927; Kariya 1932), and adults of *Elasmosoma* have been reared from *Formica* nests on various occasions (Wasmann 1897; Watanabe 1935; Poinar 2004). Due to the very quick act of oviposition, few details are known about the accompanying behav-



Figure I. Elasmosoma luxemburgense Wasmann, female, Spain, Almazán. Habitus lateral.

iour of grasping the ant or about the location of ovipositor insertion. Wasmann (1897) supposed that *Elasmosoma* females lay the eggs between the abdominal segments; other authors, considering the strongly curved morphology of the ovipositor, have suggested that the eggs are probably laid through the anus (Huddleston 1976; van Achterberg and Argaman 1993). Here we report new observations on the oviposition behaviour of *Elasmosoma luxemburgense* on *Formica rufibarbis* Fabricius, 1793, comprising alighting and grasping the worker ant and ovipositor insertion.

The observations were made in Almazán (Soria, Spain) in August, 2010 on a warm and calm day between 12.26 PM and 13.38 PM. A group of 30 to 40 of *Formica rufibarbis* workers were present surrounding a nest entrance on the ground. They were excited and aggressive, carrying materials, entering and leaving the nest. Some cadavers of another species of ant and isolated fights indicated that a more extensive battle recently occurred. Forel (1874) noted that these struggle situations attract *Elasmosoma berolinense*, and possibly the formic acid exuded in the course of these fights serve as a kairomon to the parasitoid wasps (Huddleston, 1976). During the 72 minutes of observation, groups of 2–3 females of *E. luxemburgense* could be seen hovering over and attacking the ants at a height of 1–3 cm from the ground. A total of 50 attempts at oviposition was recorded (Movie *Elasmosoma*, Appendix I). The ants were aware of these attacks, turning around and chasing the wasps with open mandibles. On one occasion, a worker caught a wasp while flying (Movie *Elasmosoma*, last sequence).

The wasp attacks always come from behind, paralleling their longitudinal axis to those of the ants. When they are less than 1 cm from an ant they dart forward and the fore legs contact the dorsal surface of the metasoma first. Meanwhile the hind legs, arranged in curved shape, are situated to brace the apex of the metasoma (Fig. 2).

Contact with the fore legs is usually followed by hitting of the parasitoid's head on the host's metasoma. At this moment the middle and hind legs grasp the metasoma and the wasp folds its wings. The site chosen by the wasp for the initial hit of the fore legs, or the head, is usually the posterior margin of the first gastral segment (T1; Fig. 3), i.e., of a total of 48 hits observed, 44 were on the posterior margin of the first gastral segment (91.7%), three on the posterior margin of the second (6.3%), and one on the posterior margin of the third (2%).



Figure 2. I female of *Elasmosoma luxemburgense* approaches the ant's metasoma with the hind legs extended in curved shape (arrow) **2** the fore legs are darted forward (arrow) **3** when alighting the hind legs brace the apex of the ant's metasoma (arrow).



Figure 3. Two sequences of a female of *Elasmosoma luxemburgense* (red arrow) hitting on the posterior margin of the first gastral segment (yellow arrow) of *Formica rufibarbis*. After hitting, the wasp begins to fold its wings.

When the hit occurs at the posterior margin of the second or third gastral segments, the wasp climbs onto the metasoma, changing its position to reach the posterior margin of the first gastral segment (Fig. 4).

This locational preference for alighting may be visually stimulated by the differentiated border of the posterior margin of the first gastral segment, enhanced by the characteristic dark stripe behind it. The frame analysis in the film clip suggests that the wasp's head hits the posterior margin of T1 with the mandibles opened, and that a slight deformation of the suture between T1 and T2 is produced. Presumably, the modified structure of the T1-T2 suture is used by the wasp to secure its grasp. The tarsal modifications of *Elasmosoma* (vestigial tarsal claws and enlarged pulvillus; Shaw 1985, 2007) may be adaptations to effect this grasping behaviour. In the final arrangement, prior to oviposition, the fore tarsi usually grasp the posterior margin of the first gastral segment, and the hind tibiae and tarsi brace the apex of the metasoma on the fourth gastral segment, with the middle legs positioned near or somewhat posterior to the hind margin of the second gastral segment (Fig. 5).



Figure 4. I female of *Elasmosoma luxemburgense* approaches the ant metasoma **2** hits on the posterior margin of the third gastral segment **3** begins to climb **4** arrives at the posterior margin of the second gastral segment **5** reaches the posterior margin of the first gastral segment.



Figure 5. Arrangement of the legs of *Elasmosoma luxemburgense* grasping the ant's metasoma for oviposition.

This arrangement of the legs facilitates the appropriate position of the wasp's metasoma in order to insert the ovipositor into the posterior area of the last metasomal segment, between the pygidium and the hypopygium, probably through the anus. Poinar (2004) dissected the metasoma of the ant *Formica obscuriventris clivia* Creighton, 1940, a host of *Elasmosoma michaeli* Shaw, 2007, and found for the first time the wasp egg "just under the body wall of the ant's metasoma."

The precise moment of ovipositor insertion could be detected by the conspicuous downward-movement of the apex of the wasp's metasoma (Fig. 6 and first sequence of Movie *Elasmosoma*). Although one single movement of the apex of the metasoma normally occurred during oviposition, in some cases 2 or 3 consecutive movements



Figure 6. Insertion of the ovipositor by *Elasmosoma luxemburgense*. I the red arrow shows the wasp's metasoma separated from the ant's metasoma **2** the yellow arrow shows the metasoma of the parasitoid and of the ant joined during insertion of the wasp's ovipositor. The fore legs have now advanced their position towards the posterior margin of the first gastral segment.



Figure 7. Two sequences of failed attacks by *Elasmosoma luxemburgense*. I the wasp (red arrow) approaches the ant **2** the wasp hits the metasoma **3** the right hind leg of the ant (yellow arrow) strikes the wasp and **4** throws it off **5** the wasp approaches the ant **6** when alighting, the right hind leg of the wasp (yellow arrow) remains over the hind leg of the ant, impeding the grasp of the ant's metasoma **7** and **8** the wasp flies away.

were observed. On one occasion the same wasp alighted and oviposited two consecutive times in the same ant.

Oviposition attempts sometimes failed due to strong movements of the ant's metasoma, to strikes by the ant's legs, or because of defective alighting by the wasp (Fig. 7). Of a total of 50 oviposition attempts, 40 were successful (80%) and 10 failed (20%). The whole oviposition behaviour of *E. luxemburgense* (comprising grasping of the ant by the wasp and the insertion of the ovipositor, until taking off) lasted a mean of 0.727 seconds (95% confidence interval: 0.578–0.877; N = 38; SE = 0.074), with a median of 0.602 seconds (interquartile range: 0.480–0.900) (Fig. 79).

Kollasmosoma van Achterberg & Argaman, 1993

http://species-id.net/wiki/Kollasmosoma Fig. 8

Kollasmosoma van Achterberg & Argaman, 1993: 66. Type species by original designation: *Elasmosoma platamonense* Huddleston, 1976 (examined).

Key to species of the genus Kollasmosoma van Achterberg & Argaman

1 Scapus longer than pedicellus, somewhat longer than wide (Fig. 29); third antennal segment somewhat longer than fourth segment (Fig. 29); fore tarsus shorter than middle tarsus; face, frons and vertex transversely striate; hy-



Figure 8. Kollasmosoma sentum sp. n., female, holotype. Habitus lateral.

Dorsal face of propodeum about as long as metanotum or shorter (Figs 10, 37); inner spur of hind tibia of female normal and apically acute (Figs 13, 33); basitarsus of middle leg 2–3 times as long as second tarsal segment (Fig. 28); 3 Outer spur of hind tibia of female enlarged and apically obtuse (Fig. 33); fifth metasomal sternite of female without apical spine (Fig. 37); face moderately convex (Fig. 37); height of eye of female about 4.8 times width of temple in lateral view (Fig. 37); dorsal face of propodeum about as long as metanotum (Fig. 37); pedicellus of female less protruding and scapus much wider than long (Fig. 34); fore tarsus of female about 1.3 times as long as middle tarsus; Outer spur of hind tibia of female normal and apically acute (Fig. 13); fifth metasomal sternite of female with an apical spine (Fig. 14); face strongly convex (Fig. 9); height of eye of female about 3.6 times width of temple in lateral view (Fig. 9), of male about 2.8 times; dorsal face of propodeum shorter than metanotum (Fig. 10); pedicellus (= second antennal segment) of female more protruding and scapus slightly wider than long (Fig. 11), but much shorter in male; fore tarsus of female about 1.9 times as long as middle tarsus (of male about 1.2 times); West Mediterranean (Iberian Peninsula)



Figures 9–14. *Kollasmosoma sentum* sp. n., female, holotype. **9** head lateral **10** profile of posterior half of mesosoma **11** base of antenna lateral **12** fore leg lateral inner side **13** hind tarsus and tibial spurs lateral **14** apex of metasoma lateral. Scale-line = 1.0×, but of 11 1.5×.

Kollasmosoma sentum van Achterberg & Gómez, sp. n.

urn:lsid:zoobank.org:act:F4B69A39-303E-40D3-BE04-C2A076307DCD http://species-id.net/wiki/Kollasmosoma_sentum Figs 8–23

Type material. Holotype, \bigcirc (RMNH), "Spain, Madrid, Carretera de La Coruña km 7.5, 20.viii.2010, following adult workers of *Cataglyphis ibericus*, J.M. Gómez Durán, RMNH". Paratypes: 7 \bigcirc (RMNH (5), RMSEL (1)), topotypic, collected 3.ix. and 13.ix.2010; 1 \bigcirc (RMS), "(Spain), Granada, Orgiva, 3OS VF68, 500 m, 11241", "Leg. Jose Luis Ruiz de la Cuesta, 6.v.2009, 11241". The only known male paratype of *K. platamonense* from Spain probably also belongs here.

Oviposition behaviour. Few observations have been made on the biology of the small Palaeartic parasitoid genus *Kollasmosoma* van Achterberg & Argaman, 1993. *Kollasmosoma platamonense* is known to approach the ant *Cataglyphis bicolor* from behind, briefly contacting its metasoma (R.D. Harkness in Huddleston 1976); van Achterberg and Argaman (1993) reported this species hovering over the nest of *Messor semirufus*, but no oviposition was observed. *K. marikovskii* has been reared from *Formica pratensis* (van Achterberg and Argaman, 1993) and, finally, no information is available on the biology of *K. cubiceps* (Huddleston). Here we report some observations on oviposition by *Kollasmosoma sentum* sp. n. in the ant *Cataglyphis ibericus* (Emery, 1906). The observations were made in Madrid (at the enclosed area of the Institute for Agriculture and Food Research and Technology (INIA), Carretera de La Coruña Km 7.5, Spain) during August and September, 2010. The parasitized colony of *C. ibericus* had a polycalic nest with three entrances on the ground, forming a triangle of about 60 cm on



Figure 15. Baits were used to keep the ants quiet **I** *Messor barbarus* cadavers (red arrow) tied with a thread and fixed to the ground **2** honey (red arrow). Females of *Kollasmosoma sentum* sp. n. are indicated with a yellow arrow.

each side. This area was visited daily by females of *Kollasmosoma sentum* during the three weeks of observation. The wasps appeared in groups of 1-3 individuals at any time between 12 PM and 15.30 PM, in the hours of highest temperature (around 35° Celsius). The visits lasted between 30 and 90 minutes. The wasps hovered over the nest entrances or looked for worker ants in the surrounding area when going out to forage or when returning to the nest carrying prey (thus, walking slowly). The wasps' attacks usually occurred during the brief and characteristic stops of *Cataglyphis* ants when marching. The wasp was extremely fast, flying at a height of about 1 cm over the ground. In order to observe and record the wasp's oviposition behaviour, the very speedy workers of *C. ibericus* were kept quiet by means of baits such as *Messor barbarus* cadavers -a usual prey of this species- and honey (Fig. 15).

When the wasp approaches, the ant is often aware of its presence, aggressively turning around with opened mandibles, or extending the hind or middle legs to hit the wasp even if it comes from behind (Fig. 16). This defensive behaviour is very common and sometimes prevents the wasp from alighting and ovipositing.



Figure 16. Workers of *Cataglyphis ibericus* hitting females of *Kollasmosoma sentum* sp. n. (red arrow) with its legs (yellow arrow). I at the nest entrance **2** and **3** at the baits.

Kollasmosoma sentum attacks the ant from behind, and oviposition takes place into both the dorsal and ventral surface of the ant's metasoma, more rarely into its apex (Movie *Kollasmosoma*, Appendix II). (On one exceptional occasion, a wasp was observed attacking the ant's head). In all the cases observed (n= 22) the movements of the wasp's metasoma during oviposition, and hence the insertion of the ovipositor, followed the direction of the postero-anterior axis of the ant's metasoma, which suggests that the ovipositor may be inserted through an intersegmental membrane. Basically, two alighting strategies have been observed for achieving the postero-anterior insertion of the ovipositor; strategies that depend on the flight direction of the wasp's attack and on the inclination of the ant's metasoma, this last varying from an horizontal position to a vertical one, perpendicular to the ground surface and distinctive for the genus *Cataglyphis*.

1) Horizontal alighting: the wasp follows an ant with its metasoma in, or near, a horizontal position, approaches it from behind, in the direction of the longitudinal axis of the ant, and extends the fore legs until grasping the dorsal metasomal surface with its tarsi. With this grasp the wasp jumps over the ant's metasoma, lays down the middle and hind legs, and folds its wings before starting to oviposit (Fig. 17).

2) Vertical alighting: the wasp follows an ant having its metasoma arranged in vertical position, or forming an angle bigger than 45 degrees with the ground surface. It approaches the ant from behind, sometimes following a direction deviating from the longitudinal axis of the ant, and extends its fore legs until grasping the ventral metasomal surface with the tarsi. Now, with this grasp, the wasp accomplishes two kinds of rotational movements, which vary according to both the flight direction of the wasp and the inclination of the ant's metasoma. An example of this surprising pirouette, that fully involves the two rotations, occurs when the wasp, in horizontal flight, approaches an ant's metasoma placed in a vertical position (Fig. 18 and the first two sequences of Movie *Kollasmosoma*). After grasping the ant's metasoma with the tarsi, and being perpendicularly aligned with respect to it, the wasp starts a 180° rotation around its longitudinal axis. At the same time, the wasp rotates vertically, approaching the metasoma. As a result of both rotational movements, the wasp alights downwards, allowing it to insert the ovipositor following the direction of the postero-anterior axis of the ant's metasoma.

It is interesting that during the rotation movements of the wasp, its fore tarsi (Fig. 19) keep permanent contact with the ant's metasoma. To achieve rotation around



Figure 17. Horizontal alighting. I female of *Kollasmosoma sentum* sp. n. approaches an ant with the metasoma in horizontal position **2** extends the fore legs (yellow arrow) and grasps the metasoma with the tarsi **3** jumps over the metasoma placing the rest of its legs on it, and folds its wings.


Figure 18. Vertical alighting. I female of *Kollasmosoma sentum* sp. n. (blue arrow) grasps the ant's metasoma with its fore tarsi **2** starts a 180° rotation around its longitudinal axis **3** at the same time initiates a second rotation, moving vertically towards the ant's metasoma **4** alights downwards on the ant's metasoma.



Figure 19. Stereomicroscopic image showing the fore legs of a female of Kollasmosoma sentum sp. n.

its longitudinal axis (without lifting the legs off), the tarsi are placed slightly separated, one over the other, on the ventral surface of the ant's metasoma (Figs 20 and 21). If the right tarsus is placed over the left one, the wasp rotates counter clockwise; if the left



Figure 20. Arrangement of the fore legs a female *Kollasmosoma sentum* sp. n. for the rotation movement. I The wasp (the red arrow points the apex of its metasoma) approaches the ant's metasoma (blue arrow) and extends its fore legs (yellow arrow) 2 the right tarsus is placed over the left one 3 the wasp starts its counter clockwise rotation (yellow arrow points to separation between the fore legs) 4 the wasp alights downwards; at that moment the hind and middle legs (yellow arrow) grasp the ant's metasoma, and the fore legs move forwards.



Figure 21. Arrangement of the fore legs of the female of *Kollasmosoma sentum* sp. n. for the rotation movement. I the wasp (the red arrow points the apex of the metasoma) approaches the ant's metasoma and extends its fore legs 2 the right tarsus (yellow arrow) is placed over the left one 3 and 4 the wasp starts its counter clockwise rotation around its longitudinal axis 5 the wasp is in profile and the right fore leg hides the left one 6 the wasp alights downwards on the ant's metasoma.

tarsus is placed over the right one, the rotation is clockwise. This longitudinal disposition of the wasp's tarsi on the ant's metasoma is, therefore, a behavioural adaptation to enable the necessary rotation of the body before oviposition.

The rapid insertion of the ovipositor follows a uniform behavioural pattern. When alighting, the wasp grasps the ant's metasoma with its three pairs of legs and folds its wings. Immediately, the wasp moves gradually backwards toward a perpendicular position with respect to the metasoma surface, the apex of its metasoma remaining over the ant's metasoma. A good example is offered during horizontal alighting (Fig. 22): the body of the wasp goes back tending to the vertical position. Before reaching the vertical, the apex of the wasp's metasoma moves down, presumably inserting the ovipositor into the ant's metasoma. At the vertical position, the apex of the wasp's metasoma presses down on the ant's metasoma, completely attaching to it. The wasp continues leaning backwards some way beyond the vertical and, finally, takes flight backwards.

Regarding the oviposition behaviour of *Kollasmosoma sentum* sp. n., the probable function of the ventral spine, peculiar to this species, located on the fifth sternite (anterior to the hypopygium; Fig. 23) needs mention. Since the rapid insertion of the ovipositor occurs when the wasp is in or near a perpendicular position with respect to the surface of the ant's metasoma (most likely with the fore legs detached from it), the ventral spine could serve to fix the wasp's position and act as a supporting point for the oviposition movements of the wasp's metasoma.



Figure 22. Oviposition of *Kollasmosoma sentum* sp. n. I After alighting and folding its wings, the wasp begins to lean backwards (the red arrow points to the space between the apex of the wasp's metasoma and the ant's metasoma) 2 before reaching the vertical, the apex of the wasp metasoma moves down, presumably inserting the ovipositor 3 at the vertical position, the apex of the wasp's metasoma is completely attached to the ant's metasoma 4 and 5 the wasp continues leaning backwards 6 the wasp flies off backwards.

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Figure 23. I Detail of the moment of oviposition of *Kollasmosoma sentum* sp. n. showing the location of the ventral spine (red arrow) **2** stereomicroscopic image showing the ventral spine (red arrow) and the exserted ovipositor (yellow arrow).

The whole oviposition behaviour of *Kollasmosoma sentum* sp. n. (comprising the grasping of the ant by the wasp and the insertion of the ovipositor, until flight; Fig. 79) lasted a mean of 0.052 seconds (95% confidence interval: 0.047-0.057; N = 19; SE = 0.002), with a median of 0.050 seconds (interquartile range: 0.047-0.057).

Diagnosis. Outer spur of hind tibia of female normal and apically acute (Fig. 13); fifth metasomal sternite of female with an apical spine (Figs 14, 23); face strongly convex (Fig. 9); height of eye about 3.6 times width of temple in lateral view (Fig. 9); dorsal face of propodeum shorter than metanotum (Fig. 10); pedicellus of female distinctly protruding (Fig. 11); fore tarsus of female about 1.9 times as long as middle tarsus.

Description. Holotype, \mathcal{Q} , length of body 2.0 mm, of fore wing 1.4 mm.

Head. Length of third segment of antenna 0.5 times fourth segment, length of third, fourth and penultimate segments 0.5, 0.8 and 1.0 times their width, respectively, and basal segments with distinct setae; pedicellus distinctly protruding and larger than scapus; face strongly convex and densely setose (Fig. 9), without facial tubercles and bristles; length of eye 2.4 times temple in dorsal view; height of eye about 3.6 times width of temple in lateral view (Fig. 9); vertex superficially granulate and having a satin sheen; temples roundly narrowed behind eyes; OOL:diameter of ocellus:POL = 5:4:20; length of malar space 0.05 times height of eye, eye nearly touching base of mandible.

Mesosoma. Length of mesosoma 1.1 times its height; mesoscutum evenly granulate; scutellum granulate and distinctly convex; precoxal sulcus absent; mesopleuron superficially granulate, but speculum shiny and largely smooth; mesosternal sulcus narrow and micro-crenulate; metanotum without a median carina and longer than dorsal face of propodeum; propodeum finely rugulose, dorsal face much shorter than posterior face, with satin sheen, without a median carina and no medial areola and its spiracle small and far in front of middle of propodeum.

Wings. Fore wing: parastigma comparatively large (Fig. 8); vein SR distinctly pigmented; basal half of wing much less densely setose than its distal half. Hind wing: wing membrane sparsely setose basally. *Legs.* Hind coxa partly superficially micro-granulate, nearly smooth and with satin sheen; fore coxa nearly flat ventrally; all tarsal claws slender and simple; length of femur, tibia and basitarsus of hind leg 2.9, 4.5 and 4.0 times their width, respectively; fore femur moderately curved in dorsal view, compressed and apically without tooth; fore tibia without protuberances and evenly densely setose, its length 6.3 times its maximum width in lateral view; fore tarsus 1.9 times as long as middle tarsus and 1.6 times as long as fore tibia; fore tibia spur slightly curved and 0.7 times as long as fore basitarsus and 0.4 times fore tibia (Fig. 12); spurs of hind tibia acute apically, their length 1.1 and 1.0 times hind basitarsus.

Metasoma. Length of first tergite 0.6 times its apical width, its surface with satin sheen, granulate, basally and medially flat, and its spiracles not protruding and near apex of tergite; second and third tergites superficially granulate; second metasomal suture obsolescent; remainder of metasoma largely smooth and depressed; fifth sternite with a large and acute apical spine (Fig. 14); setae of metasoma spread and short; second tergite with sharp lateral crease; length of ovipositor sheath 0.05 times fore wing.

Colour. Black; face, clypeus, labrum, malar space, frons antero-laterally and medially, palpi, propleuron, tegula, wings basally, fore and middle legs white; scapus and pedicellus, and hind leg ivory, but hind tarsus dorsally infuscate; pronotal side with brown patch; veins brown; remainder of antenna, humeral plate largely, metasoma laterally, parastigma and pterostigma largely dark brown; wing membrane subhyaline.



Figures 24–27. *Kollasmosoma cubiceps* (Huddleston), female, paratype. **28**. *K. platamonense* (Huddleston), female, holotype. **29–30**. *K. marikovskii* (Tobias), female, holotype. **24** head lateral **25** hind tibial spurs lateral **26** profile of posterior half of mesosoma **27 28** middle tarsus and tibial spurs lateral **29** antenna lateral **30** head anterior. 24 scale-line = 1.0×, 25–28 1.4×, 29 30 after Tobias (1986).



Figures 31–43. *Kollasmosoma platamonense* (Huddleston), female, Israel, Eilot. **31** wings **32** palpi **33** hind tibial spurs **34** base of antenna **35** apex of antenna **36** mesosoma dorsal **37** habitus lateral **38** head anterior **39** fore leg **40** hind leg **41** fore tarsal spur **42** first-third metasomal tergites dorsal **43** head dorsal. 31 36–40 42 43: scale-line = 1.0×, 32–35 41: 2.2×.

Variation. Length of body 1.8–2.1 mm, of fore wing 1.1–1.4 mm, all females have 12 antennal segments; pronotal side may be largely brown.

Etymology. From "sentus" (Latin for "thorny, spiny"), because of the unique thorn-like spine of the fifth sternite of the female.

Neoneurus Haliday, 1838 http://species-id.net/wiki/Neoneurus Fig. 44

Neoneurus Haliday, 1838: 213 (no species). Type species (= first species included by Marshall (1897): Neoneurus halidaii Marshall, 1897 (examined; = N. auctus (Thomson, 1895); examined).

Key to Palaearctic species of the genus Neoneurus Haliday

1	Females: third and following antennal segments with short and adpressed setae; fore tibia widened subbasally (Figs 46, 49); metasoma apically with a strongly downcurved ovipositor and a short and elliptical ovipositor sheath (Fig. 53)
_	Males: third and following antennal segments with medium-sized and erect setae; fore tibia narrow subbasally (Figs 47, 50); ovipositor and ovipositor sheath absent
	Note. Males are unknown of the C. Asian <i>Neoneurus curvicalcar</i> Belokobyl- skij, 1986, and the European <i>N. vesculus</i> sp. n. and <i>N. recticalcar</i> sp. n.
2	Fore femur straight in dorsal view (Fig. 45) and comparatively narrow in lat- eral view (Fig. 46); face without facial tubercles and bristles (Fig. 48); fore tibia without protuberances (Fig. 46); fore basitarsus 0.7–0.9 times as long as fore tibia (Fig. 46); [fore tibial spur 0.3–0.5 times hind basitarsus and its apical
	half narrow (Fig. 46); vertex finely transversely striate or rugulose; tegulae pale yellowish; anterior subalar prominence pale dark brown; pedicellus brown, darker than yellowish scapus; only European species with entirely black or dark brown metasoma]; W & E Palaearctic <i>N. auctus</i> (Thomson, 1895)
_	Fore femur curved in dorsal view (Figs 51, 56, 59, 69) and comparatively wide in lateral view (Figs 50, 58, 70); face with pair of facial tubercles and a central bristle (Figs 52, 57, 60, 67); fore tibia with protuberances (Figs 49, 55, 58, 68); fore basitarsus about 0.5 times as long as fore tibia and apical half gradually narrowed (Figs 49, 55, 58)
3	Anterior subbasal tooth of fore tibia minute (Figs 49, 55); posterior longitu- dinal carina of fore tibia short (Figs 49, 55)
_	Anterior subbasal tooth of fore tibia wide triangular (Figs 58, 68); posterior longitudinal carina of fore tibia long, surpassing middle of tibia (Fig. 58)5
4	Fore tibial spur nearly straight and 0.7–0.8 times as long as fore basitarsus (Fig. 55); facial tubercles minute, with slender bristle and distance between



Figure 44. Neoneurus auctus (Thomson), female, Netherlands, Oostkapelle. Habitus lateral.

bristles 1.2-1.3 times width of scapus (Fig. 57); apical tooth of fore femur medium-sized (Fig. 56); fore tibia 4.5-5.0 times as long as wide (Fig. 57); mesopleuron sometimes partly pale yellowish medially; W Palaearctic Fore tibial spur strongly curved and 0.8–0.9 times as long as fore basitarsus (Fig. 49); facial tubercles medium-sized, with robust bristle and distance between bristles about equal to width of scapus (Fig. 52); apical tooth of fore femur minute (Fig. 51); fore tibia about 6 times as long as wide (Fig. 49); mesopleuron dark brown medially; W & E Palaearctic 5 Posterior longitudinal carina of fore tibia with a submedial thorn-like protuberance; facial tubercles thick and nearly as long as pedicellus; [fore tibial spur distinctly curved in both sexes]; E Palaearctic (Mongolia) Posterior longitudinal carina of fore tibia without a submedial thorn-like protuberance (Figs 58, 68); facial tubercles shorter than pedicellus (Figs 60, 67)..... 6 6 Pair of facial bristles minute, 0.2 times as long as pedicellus and distance between bristles about 1.2 times width of scapus (Fig. 60); posterior subbasal tooth of fore tibia small, narrow (Fig. 58); SW PalaearcticN. vesculus van Achterberg & Gómez, sp. n.

Pair of facial bristles medium-sized, about as long as pedicellus and distance between bristles about equal to width of scapus (Fig. 67); posterior subbasal tooth of fore tibia medium-sized, wide triangular or falcate (Fig. 68); E Palaearctic (Kazakhstan) N. curvicalcar Belokobylskij, 1986 7 Hind femur partly dark brown or black; fore tibial spur strongly curved; [vertex finely granulate; clypeus black]; Mongolia.......N. armatus Tobias, 1977 Hind femur yellowish-brown or brown, sometimes infuscate basally; fore 8 Length of fore tarsus 1.8-2.0 times fore tibia and tibia widened apically (Fig. 47); fore tibial spur straight or nearly so and with medium-sized setae (Fig. 47); clypeus with satin sheen and transversely striate; epistomal suture obsolescent laterally; vertex dorsally transversely striate or rugulose; W & E Length of fore tarsus 1.2–1.5 times fore tibia and tibia slender apically (Fig. 50); fore tibial spur moderately curved and with short setae (Fig. 50); clypeus shiny and smooth or nearly so; epistomal suture distinct laterally; vertex dorsally finely granulate or coriaceous; W & E Palaearctic.....

Neoneurus auctus (Thomson, 1895)

http://species-id.net/wiki/Neoneurus_auctus Figs 44–48

Synonyms. Neoneurus halidaii Marshall, 1897 (examined); Euphorus bistigmaticus Morley, 1909 (synonymised by Shaw (1992)).

Material. (all RMNH unless otherwise indicated) Austria (Aschbach, 1400 m; Bach, Lechtal, 1200 m), Bulgaria (Rogen; h. Teneran; Batak; Smoljanski esera; h. Erqupria; Jemkovo; m. Nektenica; Gababovo (all Rhodopi)), England (RMS: Midhurst Common, W. Sussex, hovering above and swooping down on *Formica rufa* L., with short abdominal contact observed; Ascot, Berkshire), Finland (Enontekiö, Lappland; Kangaslampi (RMS); Sb, Savonranta, Muhamäki, in window trap on dead aspen (Museum Helsinki), France (Pèzénar), Germany (Ottmaring, Bayern), Netherlands (Otterlo, with *Formica nigricans* Emery, 1909 (= *F. pratensis* Retzius, 1783); 't Harde; Naarden; Oostkapelle, Oranjezon), Norway (Bvardalen, flying over *Formica aquilonia* Yarrow; Sandfjellet, Bergen, id.; Lom, Lia, Oppland), Scotland (RMS: Morrone Birkwood, Aberdeenshire), Sweden (Romelson, Västerbotten (RMS)), Ukraine (Kanev). Mainly collected in May to early August, one specimen from Bulgaria was collected at the end of August. France and Netherlands are new records.

Notes. One male from Bulgaria (RMNH: H. Ruen, Rhodopi Mts, 29.vii.1969, A. Germanov) belongs to a related species; it has the fore tarsus 1.5 times as long as fore tibia, the fore tibial spur with rather long setae and straight and the vertex granulate.



Figures 45–48. *Neoneurus auctus* (Thomson), female, Netherlands, Oostkapelle, but 47 male, Norway, Lom. 49–52. *N. clypeatus* (Foerster), female, Netherlands, Meijendel, but 50 male of same locality. 45, 51 fore femur dorsal 46, 47, 49, 50 fore leg inner side lateral 48, 52 face dorsal. ast anterior subbasal tooth at apical tooth plc posterior longitudinal carina.

Neoneurus clypeatus (Foerster, 1862)

http://species-id.net/wiki/Neoneurus_clypeatus Figs 49–53

Material. Netherlands (Meijendel, dunes near The Hague; Rockanje, wet *Salix repens* dunes; Oostkapelle, Oranjezon; 't Harde). Mostly collected in August and September, but a few specimens were collected in May and June.



Figure 53. Neoneurus clypeatus (Foerster), female, Netherlands, 't Harde. Habitus lateral.

Synonyms. Elasmosoma viennense Giraud, 1871, syn. n. (examined). According to Shaw (1992) the holotype of *N. clypeatus* is a male and has the third and fourth antennal segments shorter and less densely setose and the hind tibial spurs and hind tarsal segments shorter than in the male holotype of *E. viennense*; the body, hind coxa and the antenna of the holotype of *N. clypeatus* are much paler than those of *E. viennense*. *E. viennense* has the tegulae pale yellowish; dark brown or brown, the clypeus yellowish-white, yellowish-brown or brown and dorsally darkened, the hind coxa yellowish; largely black or dark brown. However, the holotype of *N. clypeatus* is coloured as a typical female and it may be either just an anomaly or a female. In general, Foerster types are paler by ageing than types from other collections of similar age, including Giraud types and limited weight should be given to colour differences in general.

Notes. If the scapus and tegulae of a male are pale yellowish or whitish, the hind coxa largely yellowish-brown and the vertex finely granulate, the specimen may represent the unknown male of *N. vesculus* or *N. recticalcar*, the latter probably has a slenderer fore femur and tibia than the former.

Neoneurus recticalcar van Achterberg, sp. n.

urn:lsid:zoobank.org:act:FCFCE816-B847-4552-AAAF-5842B22A0138 http://species-id.net/wiki/Neoneurus_recticalcar Figs 54–57

Type material. Holotype, \bigcirc (RMNH), "Slovakia, Predna Hora, n[ea]r Murán, 25.vii-1.viii.2009, 850 m, 48°46'N, 20°06'E, Mal. traps, Schacht tr. [trap on southern face of sandy hill], C. v. Achterberg, RMNH'09". Paratypes: 2 \bigcirc (RMNH), same label data and EMT; 1 \bigcirc (ZMUO), "Norway, EIS 46, HES, Elverum, Starmoen NR [N], 11.vi.-29.vii.2004, UTM 32V WGS84, PN 4624 4907, L.O. Hansen/ E. Rindal, Malaise trap N: sandy pine forest".

Oviposition behaviour. Unknown.

Diagnosis. Fore tibia of female about 4.8 times as long as wide, slightly narrowed basally, with short carina and below it bristly setose and with a small anterior subbasal tooth (Fig. 55); mesosoma extensively marked with pale yellowish patches (Fig. 54); metasoma brownish-yellow, with first tergite entirely blackish and most tergites basally and apically dark brown, fore femur curved in dorsal view; fore spur straight and



Figure 54. Neoneurus recticalcar sp. n., female, holotype. Habitus lateral.

moderately wide. It does not run in the key by Shaw (1992) to any species because of having the long spur of the fore tibia combined with short facial spines. As indicated in our key it is similar to *N. clypeatus*, but easily to separate by the nearly straight fore tibial spur and minute facial tubercles.

Description. Holotype, \mathcal{Q} , length of body 3.3 mm, of fore wing 2.2 mm.

Head. Length of third segment of antenna 1.1 times fourth segment, length of third, fourth and penultimate segments 5.0,

4.7 and 7.0 times their width, respectively and basal segments without distinct setae; facial tubercles small and facial bristles 0.4 times as long as pedicellus, distance between bristles about 1.3 times width of scapus (Fig. 57); length of eye 3.2 times temple in dorsal view; vertex superficially granulate, with few superficial punctures and a satin sheen; temples directly narrowed behind eyes; OOL:diameter of ocellus:POL = 11:5:12; length of malar space 0.10 times height of eye.

Mesosoma. Length of mesosoma 1.4 times its height; mesoscutum superficially punctulate-granulate, but medio-posteriorly densely granulate; precoxal sulcus medially slightly impressed and with a few rugae; mesopleuron superficially granulate, but postero-dorsally shiny and largely smooth; mesosternal sulcus finely crenulate, rather narrow and moderately impressed; metanotum with a median carina, moderately protruding dorsally; propodeum finely granulate and with some rugulae, dorsal face about as long as posterior face, with satin sheen, with complete median carina and no medial areola, flat antero-medially and its spiracle small and far in front of middle of propodeum.

Wings. Fore wing: parastigma medium-sized (Fig. 54); basal half of wing nearly as densely setose as its distal half. Hind wing: wing membrane moderately setose basally.

Legs. Hind coxa largely superficially micro-granulate; fore coxa flat ventrally; all tarsal claws slender and simple; length of femur, tibia and basitarsus of hind leg 3.7, 7.6 and 7.0 times their width, respectively; fore femur curved in dorsal view, compressed and apically with medium-sized tooth; anterior subbasal tubercle of fore tibia small (Fig. 55) and longitudinal carina of tibia at basal 0.3, bearing a small posterior subbasal tooth, followed by bristly setae, area of tibia in between subbasal teeth concave (Fig. 56); fore tibia 4.7 times longer than its maximum width in lateral view; fore tibia spur straight, comparatively slender and about as long as fore basitarsus and 0.5 times fore tibia (Fig. 55); spurs of hind tibia acute apically, their length 0.8 and 0.7 times hind basitarsus.

Metasoma. Length of first tergite 1.6 times its apical width, its surface with satin sheen, granulate with some rugulae posteriorly, basally flat, medially convex and its spiracles slightly protruding and near middle of tergite; second tergite superficially granulate and anteriorly with some rugulae; second metasomal suture distinct but shallow; remainder of metasoma largely smooth and compressed; setae of metasoma spread, short, but second tergite and anterior half of third tergite glabrous; second tergite with sharp lateral crease; length of ovipositor sheath 0.06 times fore wing.

Colour. Dark brown or blackish; face (except narrow triangular patch mediodorsally), clypeus, labrum, malar space, palpi, temple ventrally, frons anteriorly (except in front of anterior ocellus), tegulae (but humeral plate brown medially), propleuron, fore and middle coxae, trochanters and trochantelli white or ivory; four basal segments of antenna, pronotal side postero-dorsally and ventrally, remainder of legs (but hind tibia and tarsus pale brown and fore telotarsus dark brown), mesoscutum antero-laterally, mesopleuron antero-dorsally, mesosternum posteriorly, third-sixth metasomal tergites (but anteriorly and posteriorly dark brown) and seventh tergite (except a pair of oblique dark brown stripes) and eighth tergite pale yellowish; posteriorly mesoscutum with narrow W-shaped patch brown; second tergite blackish anteriorly and its posterior half brown; veins pale brown; parastigma posteriorly, pterostigma and 1-R1 largely dark brown; wing membrane slightly infuscate.



Figures 55–57. *Neoneurus recticalcar* sp. n., female, holotype. **58–60.** *N. vesculus* sp. n., female, holotype. **55, 58** fore leg inner side lateral **56, 59** fore femur dorsal **57, 60** face dorsal. 55–57 scale-line = 1.0× 58–60 1.2×. ast = anterior subbasal tooth **at** apical tooth **plc** posterior longitudinal carina **pst** posterior subbasal tooth.

Variation. Length of body 3.3–3.4 mm, of fore wing 2.1–2.2 mm, all females have 16 antennal segments; distance between bristles 1.2–1.3 times width of scapus; mesoscutum sometimes with W-shaped patch medio-posteriorly and mesopleuron medially yellowish, and third (except base) and fourth antennal segments may be light brown.

Etymology. From "rectus" (Latin for "straight") and "calcar" (Latin for "spur"), because of the straight spur of the fore tibia.

Neoneurus vesculus van Achterberg & Gómez, sp. n.

urn:lsid:zoobank.org:act:E163C037-3738-4DA9-AC35-96C884DCBF5F http://species-id.net/wiki/Neoneurus_vesculus Figs 58–61

Type material. Holotype, ♀ (RMNH), "Spain, Madrid, Carretera de La Coruña km 7.5, 20.viii.2010, following adult workers of *Formica cunicularia*, J.M. Gómez Durán, RMNH". Paratypes: 11 ♀ (RMNH (8), RMSEL (2), RMS (1)), topotypic, collected 3.ix. 2010, 13.ix.2010, 24.vi.2011 and 27.vi.2011.



Figure 61. Neoneurus vesculus sp. n., female, holotype. Habitus lateral.

Oviposition behaviour. In recent years the oviposition behaviour of the genus *Neoneurus* was studied for the first time (Shaw 1992, 1993) with *Neoneurus mantis* Shaw, 1992. Shaw proposed a "raptorial hypothesis" to explain the greatly modified morphology of *Neoneurus* fore legs (compression of the fore femur, robustness and shortening of the fore tibia, enlargement of the tibial spur, development of a tibial carina often associated with sharp tubercles and spines, shortening of the tarsus and enlargement of the fore pulvillus). These features, together with the two peculiar spinules situated in the frontal area of the head, could serve to grasp the ant before oviposition. Here we confirm for *Neoneurus vesculus* sp. n. Shaw's raptorial hypothesis. While this author mentions the metasoma of *Formica pozdzolica* as the location for alighting and oviposition for *N. mantis*, our observations show that *Neoneurus vesculus* sp. n. alights and probably oviposits in the mesosoma of *Formica cunicularia* Latreille, 1789.

The observations were made in Madrid (at the enclosed area of the Institute for Agriculture and Food Research and Technology (INIA), Carretera de La Coruña Km 7.5, Spain) during August and September, 2010, in three colonies of *F. cunicularia* situated in the base of Atlas cedar trees (*Cedrus atlantica*). *Neoneurus vesculus* sp. n. could be seen around the nest entrances in the morning and in the afternoon, with a peak activity of oviposition attacks between 4–7 PM. Two strategies were observed (Fig. 62): a) the perching behaviour as described by Shaw (1993), the wasp standing on a grass stem, on a tree trunk (in both cases at a height less than 5 cm), or on the ground, until an ant approaches; a moment later the wasp takes flight and begins its attack (Movie *Neoneurus*, first sequence, Appendix III); b) the hovering behaviour -at a distance of about 1 cm- over ants leaving the nest entrance and going up the tree trunk at a height of 3 or 4 cm from the ground. Oviposition attacks following hovering behaviour (Movie *Neoneurus*, second sequence) increased in the afternoon, being then predominant over the perching behaviour.

When the ant moves up, the wasp approaches it from behind and waits until the ant's body is in a vertical position. Then, the wasp head hits the ant's mesonotum while the fore legs dart forward and brace the mesopleuron. The frame analysis reveals that the tibia are the part of the legs that firmly hold the mesopleuron (Figs 63–65).

After contact, the wasp's head is separated from the ant's body, the wasp's metasoma is placed vertically and its wings are folded. Then ovipositor insertion begins, during which time the middle legs can be seen to be sometimes holding the posterior part of the ant's mesosoma (Fig. 64). The wasp's metasoma is bent towards the posterior lower part of the ant's mesosoma, going between the metasoma and the hind leg of the ant. This occurred in a surprisingly asymmetric fashion: of 29 ovipositions observed, the wasp always bent its metasoma between the left hind leg of the ant and the left side of its metasoma. This suggests some asymmetrical morphology of the ovipositor system. According to the frame analysis, the ovipositor was inserted near the posterior coxal cavities, perhaps into the coxal cavities of the middle or hind legs or in the area between them (Fig. 66).

Oviposition was not always fully successful. Of a total of 25 attempts observed, 17 were completed, 4 were initiated but ended with the wasp and the ant -still joined-



Figure 62. Female of *Neoneurus vesculus* sp. n. I standing on the ground 2 on a grass stem and 3 hovering over the nest entrance.

falling to the ground, and in the other 4 cases the wasp failed to grasp the ant and flew away immediately. Hence, the grasping of the ant appears to be a critical moment of the oviposition process. Sometimes the wasp's head hit on the ant's pronotum instead of its mesonotum, or the wasp attacked an ant that was not in a vertical position. In these circumstances it had more difficulty holding the ant, whose vigorous movements usually resulted in oviposition failure. Other times the first hit of the wasp's head, together with the strong grasping of its fore legs, caused the ant to detach from the surface and fall down with the wasp.

The whole oviposition behaviour of *Neoneurus vesculus* sp. n. (comprising the grasping of the ant by the wasp and the insertion of the ovipositor, until taking flight) lasted a mean of 2.023 seconds (95% confidence interval: 1.352-2.694; N = 17; SE = 0.317), with a median of 1.507 seconds (interquartile range: 1.377-1.927; Fig. 79). Three outlier observations corresponded to ovipositions lasting more than 3 seconds due to the ant's vigorous movements which made it difficult for the wasps to bend their metasomata towards the postero-lower part of the ants' mesosomata.



Figure 63. 1 female of *Neoneurus vesculus* sp. n. hovering over the nest entrance **2** worker of *Formica cunicularia* showing the mesonotum (yellow arrow) where the wasp's head will hit, and the mesopleuron (red arrow) that will be braced by the wasp's legs **3** after the first hit, the wasp's metasoma is positioned vertically and its wings are folded.

On one occasion a strange behaviour was observed. One *Neoneurus* hovering over the nest entrance alighted on the tree trunk, turning and resting, 2 cm away from a worker. The ant approached and touched the apex of the wasp's metasoma with its antenna. Then the wasp curved its metasoma inward extruding the ovipositor. Finally, the ant attacked the wasp, held it by the wings, and transported it into the nest.

Discussion. The described oviposition behaviour of *Neoneurus vesculus* sp. n. fits well with the raptorial function predicted by Shaw for the modified morphology of the genus *Neoneurus*. The head spinules may fix the position of the wasp when its head hits the ant's mesonotum and the robust tibia are suitable for grasping the ant's mesosoma by the mesopleura. The location of the wasp when alighting on the ant, and the final arrangement of its body, allow the insertion of the ovipositor into the postero-lower part of the ant's mesosoma. These facts call for a re-examination, with high speed photography or video, of the oviposition behaviour of *Neoneurus mantis* in order to confirm the alighting and oviposition of this species in the ant metasoma, as mentioned by Shaw (1993). It may be remarked that this author several times dissected the ant's metasoma following the wasp's oviposition, and could not find the wasp's eggs. The possibility is open that *N. mantis*, and other species of the genus, have a similar oviposition behaviour to that of *Neoneurus vesculus* sp. n., and hence that the eggs are laid in the ant's mesosoma.



Figure 64. Position of wasp's tibiae (yellow arrow) of three *Neoneurus vesculus* sp. n. while bracing the ant's mesopleuron. In frame **3** the middle legs can be appreciated (red arrow) grasping the posterior part of the mesosoma just before the insertion of the ovipositor.



Figure 65. Two attack sequences of *Neoneurus vesculus* sp. n. **I** approaching a worker of *Formica cunicularia* and fixing its attention on the ant's mesonotum (yellow arrow) **2** hitting its head on the ant's mesonotum and extending the fore legs **3** bracing the ant's mesopleuron with its fore tibia (red arrow), then placing the metasoma vertically, parallel to the ant's body, and folding the wings prior to oviposition.

Diagnosis. Fore tibia of female about 4.0 times as long as wide, distinctly narrowed basally, with long carina and below it a double row of small pegs and with a wide triangular anterior subbasal tooth; mesosoma extensively marked with pale yellowish patches; metasoma brownish-yellow, with first tergite entirely blackish and most tergites basally and apically dark brown, fore femur curved in dorsal view; fore spur nearly straight and robust; facial tubercles small and facial bristles 0.2 times as long as pedicellus, distance between bristles about 1.2 times width of scapus. Runs in the key by Shaw (1992) to N. pallidus Shaw, 1992, from Canada (Ontario) and USA (Maryland, Michigan, North Carolina, Virginia and Colorado), but the new species has the third and fourth antennal segments pale yellowish (dark brown (except base of third segment) in N. pallidus); first metasomal tergite entirely blackish (dark yellowish-brown and medially irregularly black), apex and base of second-sixth tergites dark brown (entirely pale yellowish-brown except dark yellowish-brown base of second tergite), fore tibia with row of small pegs below carina (below carina largely smooth, but a few small pegs near apex), fore tibia of female 4.0 times longer than its maximum width in lateral view (4.5 times) and fore tibia of female distinctly narrowed basally (slightly narrowed; Fig. 4 in Shaw 1992).

Description. Holotype, \mathcal{Q} , length of body 2.8 mm, of fore wing 1.8 mm.

Head. Length of third segment of antenna 1.1 times fourth segment, length of third, fourth and penultimate segments 5.3, 4.8 and 2.5 times their width, respectively and basal segments without distinct setae; facial tubercles small and facial bristles 0.2 times as long as pedicellus, distance between bristles about 1.2 times width of scapus (Fig. 60); length of eye 1.5 times temple in dorsal view; vertex superficially granulate, with few superficial punctures and a satin sheen; temples directly narrowed behind eyes; OOL:diameter of ocellus:POL = 6:3:7; length of malar space 0.13 times height of eye.

Mesosoma. Length of mesosoma 1.4 times its height; mesoscutum superficially punctulate-granulate, but medio-posteriorly densely granulate; precoxal sulcus only medially impressed and with a few rugae; mesopleuron superficially granulate, but postero-dorsally shiny and largely smooth; mesosternal sulcus finely crenulate, narrow and rather shallow; metanotum with a median carina, not protruding dorsally; propodeum finely granulate and with some rugulae, dorsal face longer than posterior face, with satin sheen, only dorsally with a median carina and no medial areola, flat anteromedially and its spiracle small and far in front of middle of propodeum.

Wings. Fore wing: parastigma medium-sized (Fig. 61); basal half of wing nearly as densely setose as its distal half. Hind wing: wing membrane moderately setose basally.

Legs. Hind coxa nearly smooth, dorsally partly superficially micro-granulate; fore coxa flat ventrally; all tarsal claws slender and simple; length of femur, tibia and basitarsus of hind leg 3.9, 9.2 and 5.3 times their width, respectively; fore femur curved in dorsal view, compressed and apically with small tooth; anterior subbasal tubercle of fore tibia wide triangular (Fig. 58) and longitudinal carina of tibia at basal 0.6, bearing a small posterior subbasal tooth and apical half curved, followed by a row of small slender pegs, area of tibia in between subbasal teeth concave (Fig. 59); fore tibia 4.0 times longer than its maximum width in lateral view; fore tibial spur nearly straight



Figure 66. Insertion of the ovipositor by *Neoneurus vesculus* sp. n. **a** wasp metasoma **b** ant metasoma **c** wasp head; **d** ant head.



Figures 67–71. *Neoneurus curvicalcar* Belokobylskij, female, holotype. 67 head dorsal 68 fore tibia inner side lateral 69 fore femur dorsal 70 fore femur lateral 71 fore tibial spur. After Belokobylskij (1986).

and 0.9 times as long as fore basitarsus and 0.5 times fore tibia (Fig. 58); spurs of hind tibia acute apically, their length 0.7 and 0.6 times hind basitarsus.

Metasoma. Length of first tergite 1.4 times its apical width, its surface with satin sheen, granulate with some rugulae posteriorly, basally flat, medially convex and its spiracles slightly protruding and near middle of tergite; second tergite superficially granulate and anteriorly with some oblique rugulae; second metasomal suture obsolescent; remainder of metasoma largely smooth and compressed; setae of metasoma spread, short, but tergites glabrous anteriorly; second tergite with sharp lateral crease; length of ovipositor sheath 0.05 times fore wing.

Colour. Dark brown or blackish; face, clypeus, labrum, malar space, temple ventrally, pronotal side postero-dorsally and ventrally, frons antero-laterally, propleuron, palpi, coxae, trochanters and trochantelli white or ivory; four basal segments of antenna, remainder of legs (but hind tibia and tarsus brown and telotarsi dark brown), tegulae, mesoscutum antero-laterally and a W-shaped patch posteriorly, scutellum (except dark medial patch), mesopleuron antero-dorsally and medially, mesosternum posteriorly, second-fifth metasomal tergites (but anteriorly and posteriorly dark brown) and sixth-eighth tergites pale yellowish; veins pale brown; parastigma, pterostigma and 1-R1 largely dark brown; wing membrane slightly infuscate.

Variation. Length of body 2.6–3.0 mm, of fore wing 1.8–1.9 mm, all females have 16 antennal segments; mesoscutum medially, mesopleuron antero-medially and scutellum may be dark brown; third and fourth antennal segments pale yellow or brownish.

Etymology. From "vesculus" (Latin for "weak, little, poor") because this new species has poorly developed facial bristles.

Ichneumonidae Latreille, 1802

Hybrizon Fallén, 1813

http://species-id.net/wiki/Hybrizon

Hybrizon Fallén, 1813: 19 (no species). Type species (by subsequent monotypy, first included species): *Hybrizon latebricola* Nees, 1834 (= *H. buccatus* (de Brébisson, 1825)).

Notes. For a key to the European species, see van Achterberg (1999).

Hybrizon buccatus (de Brébisson, 1825)

http://species-id.net/wiki/Hybrizon_buccatus Figs 72–78

Paxylomma buccata de Brébisson, 1825: 23 (type lost).

Oviposition behaviour. Donisthorpe and Wilkinson (1930) found naked pupae of *H. buccatus* among the cocoons of the ant *Lasius alienus*, and concluded that *H. buccatus* is likely to be parasitoid of adult ants, as are the wasps of the genus *Elasmosoma*. Although authors such as Watanabe (1984) and Marsh (1989) suggested that *Hybrizon* species may be endoparasitoids of ant larvae, the adult-parasitism hypothesis has remained, being included in general revisions dealing with ants (Hölldobler and Wilson 1990; Schmid-Hempel 1998). Here we report larval-parasitism of *Hybrizon buccatus* of the ant *Lasius grandis* Forel, 1909.

The observations were made in Almazán (Soria, Spain) during July and August, 2010, on a permanent vertical trail of *L. grandis*, situated on a wall 60 cm high. The ants walked up and down, day and night, between two nest entrances of the same colony, one placed in the base and the other at the top of the wall (Fig. 73).

During the 3 weeks of observations, especially between 5–8 PM, one or two females of *H. buccatus* could be seen hovering over the trail, at 1 cm or less from the ants,



Figure 72. Hybrizon buccatus (de Brébisson), female, Spain, Madrid. Habitus lateral.

usually in the lower part of the trail (less than 15 cm from the base). They could remain almost stationary in the air for more than 5 minutes. Even in the absence of ants on the trail for a period of time, specimens of *H. buccatus* found the precise location of the trail and stayed hovering over it. Location of the trail may involve olfactory or visual clues or both. After a long set of video recording, and hundreds of workers passing through the trail, no oviposition of the wasp could be observed on adult ants. Sometimes the wasp followed and approached an ant with a very quick movement, even touching the ant metasoma with its fore legs, but without oviposition (Fig. 74). This rapid approaching behaviour must be the one referred to Giraud (1857) and Donisthorpe (1910), respectively, as "pounces" and "striking" at the ants, behaviour that led Donisthorpe and Wilkinson 1930) to conclude adult-parasitism for *H. buccatus*.

The analyse of video frames revealed oviposition of *H. buccatus* into the final instar larvae of *L. grandis* while being transported by worker ants. Two cases were recorded, one with the worker going upward, and the other with the worker going downward (Movie *Hybrizon*, Appendix IV). In the first case (Fig. 75) the wasp grasped the larva



Figure 73. Female of *Hybrizon buccatus* (left) hovering over a permanent vertical trail established between two nest entrances of a colony of *Lasius grandis* (right).



Figure 74. Female of *Hybrizon buccatus* approaches an ant and touches the metasoma with its fore leg (yellow arrow). Immediately, the wasp retreats the leg. No oviposition takes place.



Figure 75. Oviposition sequence of *Hybrizon buccatus*. **a** fore legs **b** hind legs **c** middle legs **d** apex of the metasoma. In frame **4** the wasp begins to bend the metasoma and folds the wings. In frame **5** the apex of the metasoma reaches the ant larva and oviposition takes place.

with its fore legs and placed its body in a vertical position over the adult ant. When the metasoma began to bend toward the larva, the middle legs seized the adult ant's head, and the wings were folded until oviposition finished. Throughout the process the hind legs remained in the air. The whole behaviour, comprising the grasping of the larva and the insertion of the ovipositor, until flying off, lasted 0.40 seconds.

In the second case (Fig. 76), contact of the fore legs with the larva can be seen, while the ovipositor is exserted. The middle legs are probably used to grasp the larva during the bending of the metasoma and oviposition. Again, the hind legs hang in the air. The whole behaviour lasted 0.58 seconds.

Specimens of *H. buccatus* twice ignored smaller larvae transported by workers of *L. grandis* (Fig. 77), which may indicate that only final instar larvae are selected for oviposition.

An unexplained aberrant behaviour was observed in Madrid (at the enclosed area of the Institute for Agriculture and Food Research and Technology (INIA), Carretera de La Coruña Km 7.5, Spain) in September, 2010, when a female of *H. buccatus* was hovering near a nest of *L. grandis* located at the base of an Atlas cedar tree (*Cedrus*)



Figure 76. The arrow points the exserted ovipositor of the female of *Hybrizon buccatus* while the fore legs grasp the ant larva.



Figure 77. Female of *H. buccatus* ignores a smaller ant larva transported by a worker.



Figure 78. Aberrant behaviour of a female of *Hybrizon buccatus*. **a** legs **b** apex of the metasoma touching the grass stem **c** wings.

atlantica). First, the wasp held the apex of a grass stem with its fore legs, and then grabbed it with all legs, bending the metasoma and folding the wings (last sequence of Movie *Hybrizon* and Fig. 78). The frame analysis revealed the movement of the apex of the wasp metasoma touching the stem. The whole behaviour lasted 0.30 seconds.

General conclusions

From the observations here recorded on the oviposition behaviour of four European ant parasitoid wasps, some general conclusions are offered. The grasping of the ant (or the larva, in the case of *Hybrizon buccatus*) appears to be a critical phase of the wasps' oviposition. In all four species the wings are folded after alighting on the ant and during the insertion of the ovipositor. The legs are used to grasp the ant's body, following different strategies according to the species. *H. buccatus* uses the fore and middle legs to hold the ant larva; *Neoneurus vesculus* sp. n. has especially adapted fore legs to grasp the ant mesosoma firmly, making secondary use of the middle and, probably, hind legs. *Elasmosoma luxemburgense* and *Kollasmosoma sentum* sp. n. use all three pairs of legs.

In all four species the fore legs are the first to grasp the ant (or the larva, in the case of *H. buccatus*). *Neoneurus vesculus* sp. n., and usually *E. luxemburgense*, hit the ant's body with their heads when alighting.

In order to grasp the host, the visual perception of these ant parasitoids seems highly developed, especially considering the extremely short time elapsing during the oviposition sequence (Fig. 79). *Hybrizon buccatus* detects the ant larvae transported by workers along the trails, most probably selecting the mature instars. *Neoneurus vesculus* sp. n. directly hits with its head on the ant's mesonotum. *Elasmosoma luxemburgense* tends to alight by fixing attention on the posterior margin of the first gastral segment of the ant. *Kollasmosoma sentum* sp. n. has different alighting strategies corresponding to the inclination of the host's (*Cataglyphis*) metasoma, always aligning itself with the longitudinal axis of the ant's metasoma.

The location of the oviposition insertion varies in the four species, each presenting particular situations. *H. buccatus* lays the egg into an ant larva, apparently without any locational preference, but with the difficulty of dealing with the moving transporter worker. *Neoneurus vesculus* lays the egg in the postero-ventral part of the ant's mesosoma, bending its metasoma between the hind leg of the ant and the metasoma, certainly the longer and most complex of the ovipositions observed. *Elasmosoma luxemburgense* lays an egg into the posterior area of the last metasomal segment, probably through the anus. *Kollasmosoma sentum* lays the egg in any location of the ant's metasomal surface, probably through an intersegmental membrane; its extremely fast oviposition seems well adapted to the very speedy workers of *Cataglyphis ibericus*, which usually march with the metasoma held in a vertical position.



Figure 79. Duration of the oviposition behaviour (comprising the grasping of the ant by the wasp and the insertion of the ovipositor, until taking off) of three neoneurine Euphorinae: *Neoneurus vesculus* sp. n. (N = 17), *Elasmosoma luxemburgense* (N = 38) and *Kollasmosoma sentum* sp. n. (N = 19). Interquartile ranges and outlier data are given.

Regarding the oviposition behaviour of the three neoneurines, the persistent defensive behaviour displayed by the ants is also significant. The ants are usually aware of the presence of the wasps, to which they turn towards with opened mandibles and sometimes catch them. Oviposition is also frequently impeded by the hits and movements of the ant's legs.

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Appendix I

Movie Elasmosoma. (doi: 10.3897/zookeys.125.1754.app1) File format: MOV

Explanation note: Females of the parasitoid wasp *Elasmosoma luxemburgense* ovipositing in workers of the ant *Formica rufibarbis*. In the last sequence a worker ant catches a wasp while flying. Recorded in slow motion video, at a rate of 300 frames per second. Almazán (Soria, Spain), August, 2010.

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Citation: Gómez Durán JM, van Achterberg C (2011) Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species. ZooKeys 125: 59–106. doi: 10.3897/zookeys.125.1754.app1

Appendix II

Movie Kollasmosoma. (doi: 10.3897/zookeys.125.1754.app2) File format: MOV

Explanation note: Females of the parasitoid wasp *Kollasmosoma sentum* ovipositing in workers of the ant *Cataglyphis ibericus*. Recorded in slow motion video, at a rate of 300 frames per second. Madrid, August and September, 2010.

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Appendix III

Movie Neoneurus. (doi: 10.3897/zookeys.125.1754.app3) File format: MOV

Explanation note: Females of the parasitoid wasp *Neoneurus vesculus* ovipositing in workers of the ant *Formica cunicularia*. Recorded in slow motion video, at a rate of 300 frames per second. Madrid, August and September, 2010.

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Appendix IV

Movie Hybrizon. (doi: 10.3897/zookeys.125.1754.app4) File format: MOV

Explanation note: Females of the parasitoid wasp *Hybrizon buccatus* ovipositing in the ant larvae transported by workers of *Lasius grandis*. In the last sequence a female of *H. buccatus* holds the tip of a grass stem with its legs, then bends the metasoma and touches the grass stem with its metasomal apex. Recorded in slow motion video, at a rate of 300 frames per second. Almazán (Soria, Spain), July and August, 2010.

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