

Zeitschrift: Contributions to Natural History : Scientific Papers from the Natural History Museum Bern

Herausgeber: Naturhistorisches Museum Bern

Band: - (2009)

Heft: 12/3

Artikel: Revision of the genus Trogulus Latreille: the Trogulus hirtus species-group (Opiliones: Trogulidae)

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DOI: <https://doi.org/10.5169/seals-787023>

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Revision of the genus *Trogulus* LATREILLE: the *Trogulus hirtus* species-group (Opiliones: Trogulidae)

Axel L. Schönhofer & Jochen Martens

ABSTRACT

Contrib. Nat. Hist. 12: 1207–1251.

A molecular genetic analysis of the cytochrome *b* gene (*cyt b*) revealed a monophyletic group of six widely separated but closely related haplotype clusters (4.8–21.4% distance values) among minute representatives of *Trogulus* LATREILLE, 1802 from the Balkan Peninsula. All representatives have in common a large penial stylus that is sickle-like and strongly curved to the right side (in ventral view). All representatives of the individual clusters differ slightly but distinctly by external morphology (size, bristles on legs and body, pattern of body papillae) and most of them to a lesser degree by male genital morphology. The genetically defined clusters are allopatrically distributed and we assign them species rank. According to the oldest available name this *cyt b* clade is here named the *Trogulus hirtus* species-group; it includes six species: *T. hirtus* DAHL, 1903 (raised from subspecies to species level; central Croatian coast from the Gulf of Kotor to the mouth of the Neretva River), *T. falcipenis* KOMPOSCH, 2000 (NW Balkans from SE Carinthia to N Slovenia), *T. karamanorum* sp. nov. (central Balkans from SE Serbia and S Croatia to E Greece), *T. thaleri* sp. nov. (central Croatian coast, Makarska riviera), *T. pharensis* sp. nov. (central Croatian coast, Hvar Island) and *T. melitensis* sp. nov. (central Croatian coast, Mljet Island). They can be further separated into two distinct sub-clades, the *Trogulus hirtus* clade and the *Trogulus falcipenis* clade. The *Trogulus tricarinatus* species-group, which is also represented in the Balkans and which includes species of equally small size, is not closely related to the *Trogulus hirtus* species-group and not discussed here. To define species within the *Trogulus hirtus* species-group by external and genital morphology alone would lead to considerable underestimation of *Trogulus* diversity and species richness in the Balkans.

Introduction

Among European Opiliones, the genus *Trogulus* LATREILLE, 1802 is considered as one of the "exceedingly difficult animals to deal with" (Hansen & Sørensen 1904) as far as systematics, taxonomy and evolutionary biology are concerned. External morphology of *Trogulus* is extraordinarily homogeneous. Traditionally, species limits in *Trogulus* were drawn by few, only minor differences in body size, eye interdistance, relation of tarsus II segment length and genital morphology, but clear-cut characters to delimit species remained difficult to establish. Furthermore, the degree of geographical variation in external and internal characters is questionable, and, consequently, so are species limits. As a result, most species described during the last three decades did not shed new light on the situation but rather obscured it because previously described similar species were not re-characterised carefully enough. Consequently, *Trogulus* systematics simply represents a nightmare even within the fairly small central European species set. Considering the high degree of morphological homogeneity in *Trogulus*, cryptic species can be expected, further complicating the evaluation of species limits in the genus.

Here we present the second paper of a series in which we try to shed new light on *Trogulus* systematics and evolutionary biology. Our overall attempt is based on establishing a molecular phylogeny of specimens from as many different parts of the geographic range of the genus as possible, in order to recognize groups of closely related haplotype clusters. Not unexpectedly, we found many more clearly separated groups of populations than there are described species. This did not clear the situation at all and we decided to work through *Trogulus* by each clade of the molecular tree and to present our results step by step. This paper represents a combination of molecular, morphological and biological data that allow us to re-evaluate species limits. The logic applied here is that groups of similar haplotypes widely separated from each other on the molecular tree may, as a first approach, represent biological species. This is to be evaluated further by distributional and biological data, and, hopefully and finally, by morphological characters. We further speculate that *Trogulus* species may well be defined by external and genital morphology and that morphological characters have been so far overlooked due to the lack of molecular backing. This attempt has so far proven to be successful within the recently revised *Trogulus coriziformis* species-group (Schönhofer & Martens 2008), species of which were clearly assignable upon morphological characters, although a clear morphological characterisation of the species-group as a whole failed due to its high morphological diversification. Likewise, we will show that this approach turned out to be successful for the *T. hirtus*

species-group. Apart from two already named taxa, we recognized four additional species which are clearly distinguishable by cytochrome b gene (cyt b) characters. They are very similar in respect to external and genital morphology, but are nevertheless distinguishable by these characters. In contrast to the *T. coriziformis* species-group the phylogenetic distances of the *T. hirtus* species-group to other species-groups as well as between assigned species is lower. We will show that this does influence the significance of morphological characters for species-group and species recognition and subsequently give an idea of the usability of characters on different phylogenetic levels within *Trogulus*.

Material and Methods

Material: Essential for the molecular part of this study was fresh material, most of which we collected ourselves (Tab. 1). In addition to that we were able to study an extensive material from several private and public collections which are listed below. We are most grateful to all of the collection holders; without their help this study would not have been possible.

Abbreviations:

CCD	Collection of C. L. Deeleman-Reinhold, in the collection of Naturalis, National Museum of Natural History, Leiden, The Netherlands
CIK	Collection of Dr. Ivo Karaman, Department of Biology and Ecology, Novi Sad University, Serbia
CJM	Collection of Prof. Dr. Jochen Martens, Institute of Zoology, University of Mainz, Germany
CMK	Collection of Marjan Komnenov, Skopje, Republic of Macedonia
CNS	Collection of Tone Novak and Ljuba Slana, Slovenj Gradec, Slovenia
CRO	Collection of Roman Ozimec, in the collection of the Croatian Biospeleological Society (collection CBSC), hosted by the Croatian Natural History Museum (CNHM), Zagreb, Croatia
IZRK	Inštitut za raziskovanje krasa (Slovenian Karst Research Institute, Postojna, Slovenia)
MHNG	Muséum d'Histoire naturelle, Genève, Switzerland (Dr. Peter Schweninger)
MNHP	Muséum national d'Histoire naturelle, Paris, France (Dr. Arturo Muñoz-Cuevas)
NHMW	Naturhistorisches Museum, Wien, Austria (Dr. Jürgen Gruber)

SMF	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (Dr. Peter Jäger)
ZMB	Naturhistorisches Forschungsinstitut, Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin, Germany (Dr. Jason Dunlop)

Methods: Molecular genetics: We used 12 samples of the *Trogulus hirtus* species-group for our molecular analysis. Seven sequences of the main *Trogulus* species-groups (represented by *T. tricarinatus* LINNAEUS, 1758, *T. martensi* CHEMINI, 1983, *T. huberi* SCHÖNHOFER & MARTENS, 2008, *T. graecus* DAHL, 1903 and an undescribed species from Macedonia) were incorporated in the dataset for the phylogenetic reconstruction. For hierarchical outgroup rooting we used a sequence of other Trogulidae genera (*Anelasmacephalus cambridgei* (WESTWOOD, 1874), *Trogulocratus sinuosus* (SØRENSEN, 1873) and an unnamed *Platybessobius* species from Turkey (Tab. 1).

Tissue, mainly muscle, was removed from the opisthosoma and its DNA was extracted using the High Pure PCR Template Preparation Kit (Roche Diagnostics). About 630 bp of the mitochondrial cyt b were amplified using the primer combination Cytb-for: 5'-GAG-GAC-AAA-TAT-CTT-TTT-GAG-GAG-CTA-3' (position in *Limulus polyphemus* AF216203, bps 9189–9213) and Cytb-rev-deg: 5'-TCN-ACN-GGA-CRN-GMN-CCA-ATT-CAN-GTT-A-3' (position in *Limulus polyphemus* AF216203, bps 9789–9816). Primers were generated from an alignment of Chelicerata mitochondrial sequences available from GenBank (*Limulus polyphemus* AF216203 [Lavrov & al. 2000], *Mesobuthus gibbosus* AJ716204 [Gantenbein-Ritter & al. 2005], *Varroa destructor* AJ493124 [Navajas & al. 2002], *Ornithoctonus huwena* NC_005925 [Qiu & al. 2005]) and from our own *Trogulus* sequences. PCR was performed using pure Taq™ Ready-To-Go™ PCR Beads (GE Healthcare). The PCR protocol was 35 cycles of 94°C for 30 s, 40°C for 30 s and 72°C for 30 s with a final extension in 72°C for 8 min. Sequencing of the PCR products was performed with BigDye™ v. 3.0 and v. 3.1 Dye Terminator Cycle Sequencing Kits (Applied Biosystems) according to the manufacturer using primers as mentioned; reactions were electrophoresed with the ABI 377 automatic sequencer. Sequences were automatically edited using Genotyper (Version 2.0, Perkin Elmer) and further manually edited and aligned using Sequence-Navigator 1.0.1 (Perkin Elmer) and Quick Align 1.6.0b. The identity of each sequence was checked using NCBI-Blast.

An appropriate substitution model for the molecular dataset was estimated with Modeltest 3.6. (Posada & Crandall 1998). According to the Akaike information criterion (Posada & Buckley 2004) the best fit model for the cyt b dataset was the HKY+I+G model with the following likelihood settings: Empirical

Taxon	Voucher	Country	Locality	Acc. no cyt b
<i>Anelasmoecephalus cambridgei</i>	3846	Germany	Alzey, Nieder-Wiesen	FJ373241*
<i>Platybessobius</i> sp.	5118	Turkey	Izmir, Nif Dağı	FJ373212*
<i>Trogulocratus sinuosus</i>	5090	Italy	Abruzzo, Prov. Chieti, Bomba	FJ664886
<i>Trogulus falcipenis</i>	4952	Slovenia	Topla Valley near Črna	FJ664887
<i>T. graecus</i>	5083	Greece	Igoumenitsa	FJ373223*
<i>T. hirtus</i>	4969	Montenegro	Herceg-Novı, Monastir Savina	FJ664888
<i>T. huberi</i>	5344	Portugal	Algarve, ca. 50 km N Faro, Alte, near Hotel Alte	FJ373224*
<i>T. karamanorum</i> sp. nov.	3025	Greece	W Makedonia, Pindos Mts., Grevena Smixi	FJ373215*
<i>T. karamanorum</i> sp. nov.	4882	Montenegro	N Ulcinj, Camp Valdanos	FJ664889
<i>T. karamanorum</i> sp. nov.	4889	Macedonia	Gjonovitze Cave near Gostivar	FJ664890
<i>T. karamanorum</i> sp. nov.	4933	Macedonia	S Skopje, Skopska Crna Gora Mt., Monastir Sveti Ilija	FJ664891
<i>T. karamanorum</i> sp. nov.	4877	Montenegro	Rumija Mountain, Ostros	FJ664892
<i>T. martensi</i>	4068	Germany	Rheinland-Pfalz, Bad Kreuznach	FJ664893
<i>T. melitensis</i> sp. nov.	CRO4	Croatia	MIjet island, Soline, Bjeajka	FJ664894
<i>T. pharensis</i> sp. nov.	4881	Croatia	Hvar, banks of road 116, near Sinje špilje	FJ664895
<i>T. pharensis</i> sp. nov.	5155	Croatia	Hvar, entrance of tunnel from Plitve to Zavala	FJ664896
<i>T. sp. Macedonia</i>	4900	Macedonia	Sveti Jovan Bigorski near Rostuše	FJ373220*
<i>T. thaleri</i> sp. nov.	4938	Croatia	church Porat near Podaca	FJ664897
<i>T. thaleri</i> sp. nov.	4985	Croatia	Drvenik	FJ664898
<i>T. tricarinatus</i>	5312	Germany	Sachsen, Dresden, park near botanical garden	FJ373214*
<i>T. cf. tricarinatus</i>	4981	Macedonia	Belasica Mountain, above Bansko	FJ664899
<i>T. cf. tricarinatus</i>	5096	Greece	Corfu, Portes	FJ664900

Tab. 1. List of specimens included within the molecular genetic analysis of the cytochrome b gene. All numbers except CRO 4 refer to specimens of Collection J. Martens (CJM). Accession numbers with an asterisk correspond to Schönhofer & Martens (2008).

base frequencies: $\pi A=0.3515$, $\pi C=0.2898$, $\pi G=0.0473$, $\pi T=0.3114$; proportion of invariable sites $I=0.3733$; Ti/Tv ratio=4.2356; gamma shape parameter $\alpha=0.8245$. Phylogenetic analysis was performed using PAUP 4.06b (Swofford 2001). Phylogenetic trees were constructed under different approaches: Neighbor Joining and Maximum Parsimony (NJ, Saitou & Nei 1987; MP, Farris 1983), Maximum Likelihood (ML, Schmidt & al. 2002) and Bayesian inference of phylogeny (with MrBayes 3.1.2; Huelsenbeck & Ronquist 2003). If not specified default settings were used.

Robustness of clades was estimated by 2.000 bootstrap replicates (Felsenstein 1985), and via Bayesian posterior probabilities using Markov chain

Coxa II interdistance: distance between prolateral sides of left and right coxa II

Coxa IV interdistance: distance between **lateral** sides of left and right coxa IV

Eye interdistance: distance between outer borders of left and right lens

Length of hairs: from emergence out of papillae to tip (in lateral view)

Body length: total length from front cap to rear end of opisthosoma

Leg II: total length of stretched leg II, from tip to border of coxa II

Body width: maximum width of opisthosoma

DSII: distal segment of tarsus II

BSII: basal segment of tarsus II

MtII: metatarsus of leg II

MtIV: metatarsus of leg IV

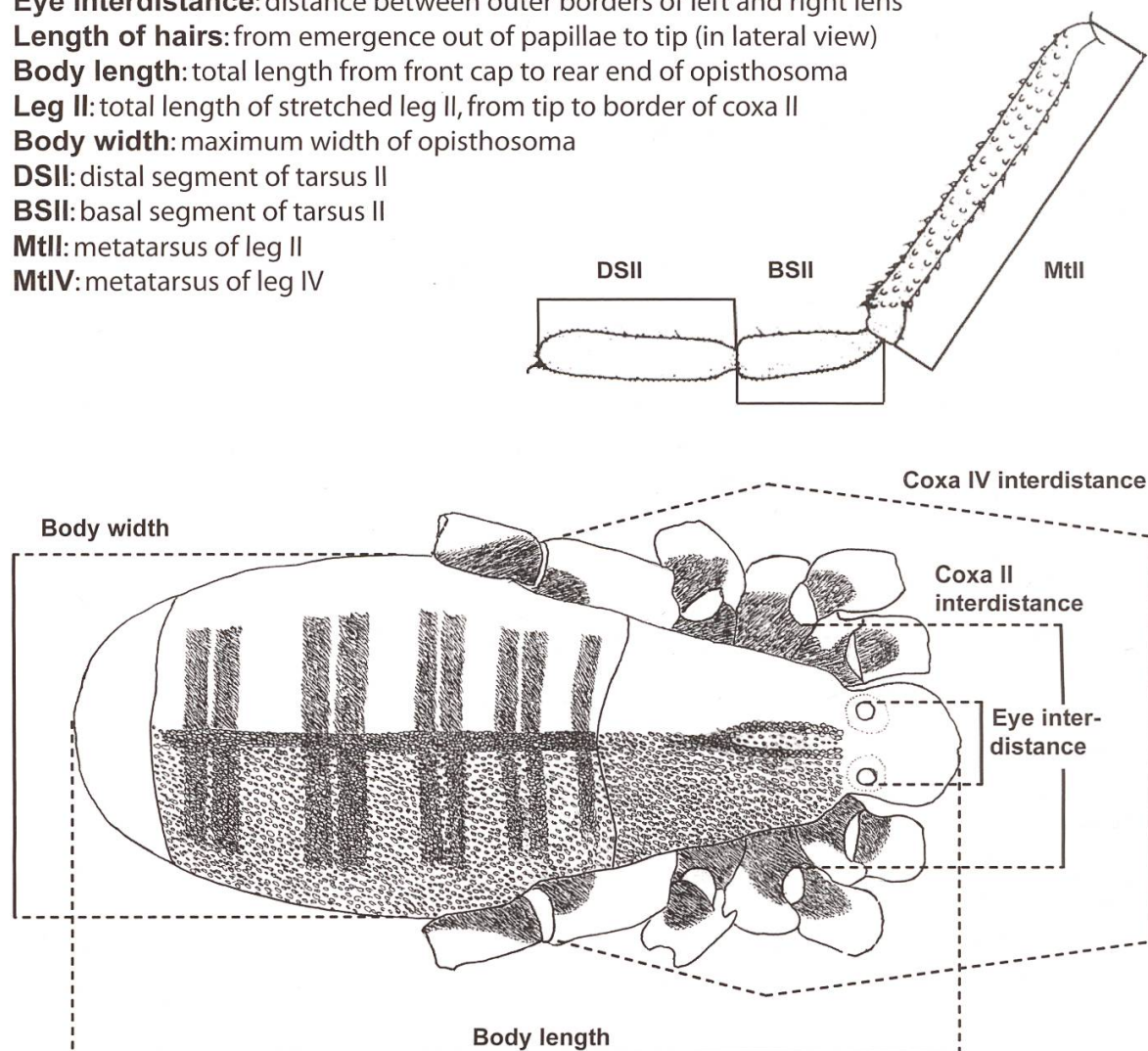


Fig. 1. Schematic drawing of *T. karamanorum* sp. nov., dorsal view with coxae, trochanters and tarsus and metatarsus II, lateral view (above), with indication of measurement distances. Also indicated are: Blackish parts of coxae and trochanters, densely papillated median and transversal ridges on opisthosoma and Y-shaped ridge on prosoma enclosing zone of weak papillation (see Fig. 13t–v, w–y).

Monte Carlo (lset: nst=2, rates=gamma, ngammacat=4, code=metmt, 4 replicates, 500.000 generations, samplefreq=100, burnin=1.000). Genetic distances were calculated in PAUP using uncorrected p-distances and excluding ambiguous data.

Morphology: Specimens were examined under a stereomicroscope and morphological features were drawn with a camera lucida or photographed with a Wild MPS52 Kodak. Morphometrical data were obtained using a microscope with an ocular micrometer disc. Abbreviations of morphological terms are explained in Fig. 1 (see also definitions in Schönhofer & Martens 2008).

Geographical information: UTM data were acquired from publications and provided by collectors. GPS data of accuracy to seconds were taken in the field with a Garmin Geko 201 or provided by collectors. Data of an accuracy to minutes were reconstructed using internet services (www.wikipedia.org, www.viamichelin.com, www.tageo.com), a variety of cartographic sources and the program Encarta Professional (version 2003).

Results

The 22 trogulid sequences (*Anelasmocephalus*, *Platybessobius*, *Trogulus* and *Trogulocratus*) produced a 552-bp-long alignment. There were 175 variable sites (32.7%) in the alignment of which 134 (24.2%) were parsimony informative (only for ingroup sequences of the *T. hirtus* species-group). A NJ-tree is shown in Fig. 2 with support values indicated at the according nodes. Phylogenetic results were similar regarding topology of MP, ML and Bayesian inference. Support values at species-group level are generally low, indicating the saturation of cyt b due to repeated remutation of the 3rd codon position. This effect is most likely due to our limited sequence data. Unfortunately, we could not obtain an adequate number of sequences of other molecular markers for the *T. hirtus* species-group. Nevertheless, data sets of about 70 trogulid taxa combining 28S rRNA and cyt b data using Bayesian inference support monophyly of the few members available for the *T. hirtus* species-group (not shown, Schönhofer & Martens in press). Besides genetic data, genital morphology and geographical restriction strongly suggest treatment of the *T. hirtus* species-group as a monophyletic and independent evolutionary unit.

Phylogenetic reconstructions clearly reject a closer relationship between the *T. hirtus* species-group and the *T. tricarinatus* species-group (Fig. 2). *T. tricarinatus* represents a heterogeneous group of species summarised upon small body size and large ratio between the lengths of the tarsal segments II. Although traditionally assigned to *T. tricarinatus*, the *T. hirtus* species-group represents a discrete and convergent lineage. It originated from a diverse central Balkan group of *Trogulus*, today including as morphologically contrasting taxa as *T. torosus* SIMON, 1885 and *T. setosissimus* ROEWER, 1940 (Schönhofer & Martens in press). Within this group the closest relative to the *T. hirtus* species-group is represented by a minute *Trogulus* (here assigned to *T. tricarinatus* agg.) from Corfu (CJM 5096). It is clearly different in genital morphology and is to be considered as sister to the *T. hirtus* species-group (see Taxonomy, The *Trogulus hirtus* species-group). Changes in composition and number of ingroup taxa within the cyt b data set placed this taxon within the

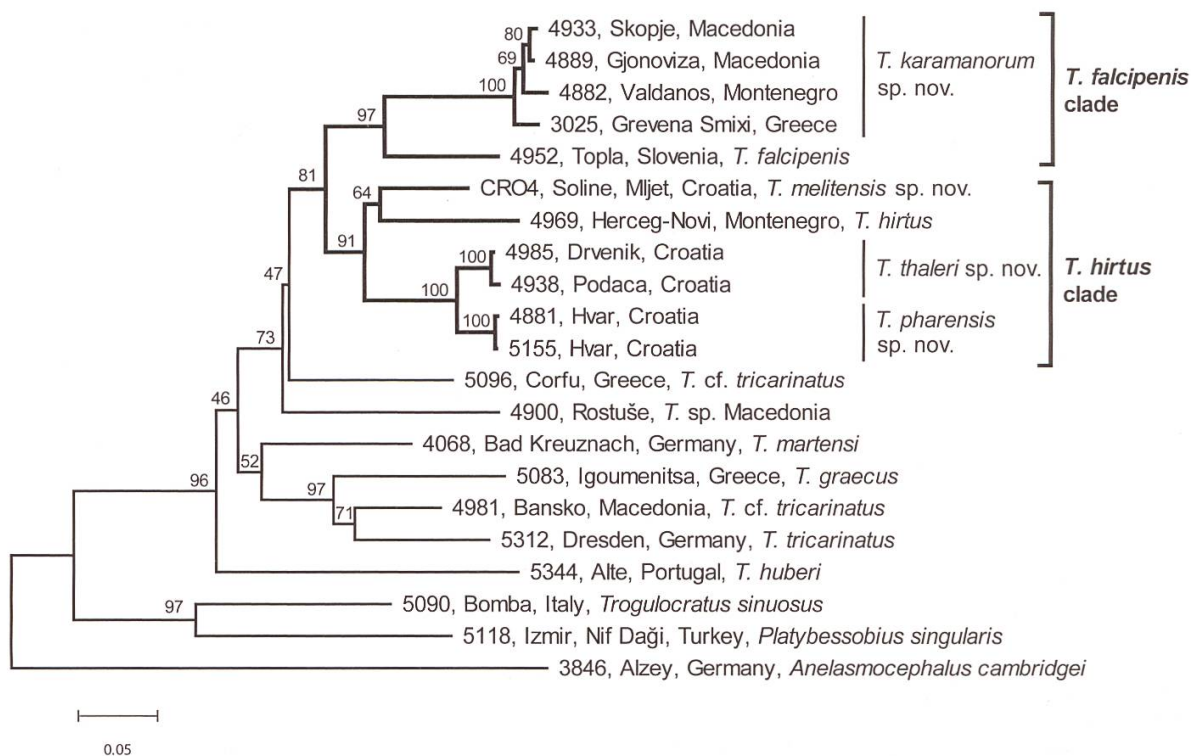


Fig. 2. Neighbor-Joining tree of the *Trogulus hirtus* species-group (552 bp, cytochrome b gene, bootstrap values after 2000 replications); *Trogulus hirtus* species-group is indicated by bold lines. All numbers except CRO4 refer to specimens of Collection J. Martens (CJM).

T. hirtus species-group but without support. This is due to the high mutational saturation of the cyt b which causes difficulties to resolve taxa on the species-group level. The same holds true for a morphologically clearly different *Trogulus* species from Macedonia (CJM 4900) sometimes affiliated with one of the clades within the *T. hirtus* species-group. Using a larger data set incorporating 28S rRNA, these taxa are not in conflict with the monophyly of the members of the *T. hirtus* species-group (not shown, Schönhofer & Martens in press).

The *T. hirtus* species-group is divided into two well-supported clades of four and two separate species, respectively (*hirtus* clade, *falcipenis* clade). The between-clade distance (16.8–21.7%) is similar to distances between other species-groups within *Trogulus* and indicates a long independent evolution. In comparison, the between-group distance of *T. martensi* (as representative of the *T. nepaeformis* species-group) to the *T. tricarinatus* species-group (from Germany and Macedonia, see Tab. 1) is 20.9–21.4%. Between-group distances of the above-mentioned *Trogulus* species-groups to the *T. coriziformis* species-group (20.8–26.8%) and the outgroup genera *Platybessobius* (27.8–30.2%), *Trogulocratus* (24.7–28.7) and *Anelasmaocephalus* (27.9–33.9) are noticeably larger.

Within-clade distances (Tab. 2) are nearly equal to each other (*T. hirtus* clade 13.6–16.9%; *T. falcipenis* clade 14.9–15.8%). The *hirtus* clade contains

four species, two of them closely related to each other (*T. pharensis* sp. nov. and *T. thaleri* sp. nov.), the two others are widely separated and of unresolved affinities (*T. hirtus*, *T. melitensis* sp. nov.). NJ and MP suggest a closer relationship between the latter two taxa but without bootstrap support. Probably, the *hirtus* clade split into a minimum of three lineages which diverged more or less simultaneously. A more recent split led to the sister species *T. pharensis* sp. nov. and *T. thaleri* sp. nov. (interspecific distances 4.8–5.9%). The *T. falcipenis* clade diverged into two clearly separated lineages: *T. falcipenis* and *T. karamanorum* sp. nov. The latter species evolved, probably as a consequence of its large mountainous distribution area, a set of quite different haplotypes (within-group distances 0.7–3.3%, neglecting a ambiguity-rich sequence from Rumija Mountain, CJM 4877).

Discussion

Species delineation within *Trogulus* has always been a challenge and there seemed no reliable way to recognize species by means of morphology alone, let alone relationships and phylogeny. Even in central Europe the discrimination of the well-researched *Trogulus* species *nepaeformis* (SCOPOLI, 1763), *closanicus* AVRAM, 1971 and *martensi*, seemed to be more or less arbitrary, at least not based on sound and easy-to-recognize characters. By means of molecular genetics, now introduced into *Trogulus* systematics and taxonomy, the situation becomes, beforehand, even worse. Well circumscribed genetic units ("clusters") emerge, the representatives of which, from the viewpoint of comparative morphology, seem to be (nearly) indistinguishable. Only at closer view, minute characters of external and genital morphology do help to separate these clusters. Characters have hitherto been overlooked, simply neglected or treated as variation.

Within the recently revised *T. coriziformis* species-group we showed species-worthy clusters to be defined by geographical restriction, as well as morphological characters (Schönhofer & Martens 2008). Its species exhibited high genetic distances, often exceeding the amount of other species-groups. This indicates long-lasting separation, in most cases connected with morphological diversification that today enables easier delineation of these species. On the other hand, the morphological boundaries of the *T. coriziformis* species-group became blurred and morphology can no longer be used to identify it unambiguously. In contrast, the *T. hirtus* species-group comprises a much younger evolutionary lineage comparable with one lineage within the *T. coriziformis* species-group. The *T. hirtus* species-group is outlined by its conserved

no.	Taxon	Voucher	1	2	3	4	5	6	7	8	9	10
1	<i>Anelasmacephalus cambridgei</i> , Germany	3846										
2	<i>Platybessobius</i> sp., Turkey	5118	30.4									
3	<i>Trogulocratus sinuosus</i> , Italy	5090	27.9	20.1								
4	<i>Trogulus falcipenis</i> , Slovenia	4952	32.1	28.2	27.7							
5	<i>T. graecus</i> , Greece	5083	29.8	29.1	27.4	21.6						
6	<i>T. hirtus</i> , Montenegro	4969	32.2	30.1	27.5	21.7	24.7					
7	<i>T. huberi</i> , Portugal	5344	33.9	28.1	27.7	25.2	24.2	26.1				
8	<i>T. karamanorum</i> sp. nov., Greece	3025	32.6	28.6	28.3	14.9	24.9	21.4	26.3			
9	<i>T. karamanorum</i> sp. nov., Montenegro, Valdanos	4882	32.6	28.9	28.6	15.1	26.0	20.2	25.7	2.9		
10	<i>T. karamanorum</i> sp. nov., Macedonia, Gostivar	4889	32.6	28.7	28.0	15.1	25.2	20.2	26.0	3.3	1.8	
11	<i>T. karamanorum</i> sp. nov., Macedonia, Skopje	4933	33.0	28.8	28.4	15.8	25.8	20.7	26.8	3.1	2.4	0.7
12	<i>T. karamanorum</i> sp. nov., Montenegro, Rumija	4877	29.9	24.8	24.7	12.0	20.5	16.9	23.0	4.3	3.0	3.6
13	<i>T. martensi</i> , Germany	4068	31.4	28.1	25.7	20.9	19.1	20.0	21.4	22.9	23.0	22.9
14	<i>T. melitensis</i> sp. nov., Croatia, Mljet	CRO4	31.0	29.0	26.1	17.8	22.8	13.8	23.2	19.4	18.4	17.9
15	<i>T. pharensis</i> sp. nov., Croatia, Hvar	4881	30.5	29.4	27.0	16.9	24.0	16.9	24.7	19.8	19.5	19.0
16	<i>T. pharensis</i> sp. nov., Croatia, Hvar	5155	29.8	29.3	26.3	16.8	23.5	15.9	24.2	19.2	19.0	18.4
17	<i>Trogulus</i> sp., Macedonia	4900	28.7	30.2	28.7	21.3	22.4	21.3	25.8	22.4	22.7	22.5
18	<i>T. thaleri</i> sp. nov., Croatia, Podaca	4938	31.6	29.2	26.7	17.4	22.4	13.9	24.5	20.7	20.4	19.9
19	<i>T. thaleri</i> sp. nov., Croatia, Drvenik	4985	31.5	29.4	26.2	17.4	22.6	13.6	24.0	20.5	20.2	19.7
20	<i>T. tricarlinatus</i> , Germany	5312	32.2	29.2	27.6	21.1	17.6	23.6	22.5	24.4	23.9	23.6
21	<i>T. cf. tricarlinatus</i> , Macedonia	4981	30.8	29.5	26.8	20.1	14.8	22.1	20.8	23.0	22.6	22.2
22	<i>T. cf. tricarlinatus</i> , Greece, Corfu	5096	29.8	27.8	27.8	17.4	22.1	19.0	23.1	18.7	19.3	18.4

no.	Taxon	Voucher	11	12	13	14	15	16	17	18	19	20	21
12	<i>T. karamanorum</i> sp. nov., Montenegro, Rumija	4877	4.3										
13	<i>T. martensi</i> , Germany	4068	23.1	18.9									
14	<i>T. melitensis</i> sp. nov., Croatia, Mljet	CRO4	18.3	14.6	18.0								
15	<i>T. pharensis</i> sp. nov., Croatia, Hvar	4881	19.6	16.8	19.4	14.7							
16	<i>T. pharensis</i> sp. nov., Croatia, Hvar	5155	19.0	16.1	18.7	13.6	0.2						
17	<i>Trogulus</i> sp., Macedonia	4900	22.7	19.8	18.7	21.3	19.5	18.6					
18	<i>T. thaleri</i> sp. nov., Croatia, Podaca	4938	20.5	16.9	18.2	13.0	5.9	4.8	19.1				
19	<i>T. thaleri</i> sp. nov., Croatia, Drvenik	4985	20.3	16.5	17.9	12.3	5.9	4.8	18.9	0.6			
20	<i>T. tricarlinatus</i> , Germany	5312	24.2	20.7	18.5	20.7	23.3	22.2	24.1	20.9	21.1		
21	<i>T. cf. tricarlinatus</i> , Macedonia	4981	23.2	19.6	14.7	19.0	22.7	22.1	22.0	21.4	21.4	13.5	
22	<i>T. cf. tricarlinatus</i> , Greece, Corfu	5096	18.9	16.9	18.8	18.7	20.0	19.6	19.4	19.7	20.0	20.2	18.5

Tab. 2. Uncorrected p-distances of 552 base pairs of cyt b within the *Trogulus hirtus* species-group and troglid outgroups. Distances are given in %, ambiguous positions are excluded; all numbers except CRO 4 refer to specimens of Collection J. Martens (CJM).

penial morphology but its species are difficult to distinguish upon morphological and morphometric characters. Species delineation is thereby supported by allopatry of closely related lineages and genetic characters. This conservation of male genital morphology beyond species boundaries seems to be a general trait within *Trogulus* and does conflict with the paradigmatic use of this character for species delineation within Opiliones (e. g. numerous examples in Martens 1978; Schönhofer & Martens in press). The lesson to be learned from the *T. hirtus* species-group is that in some groups of Opiliones genital morphological stasis may not facilitate the final decision to characterise species.

The question remains how to define genetically-based clusters in accordance with the Biological Species Concept as defined by Mayr (1942). In the case of allopatry of these clusters, so far recognized in the *T. hirtus* species-group, there is no reliable way to establish from field data and/or morphological characters alone, which taxonomic status is appropriate for these genetic units. Are these well-defined populations, subspecies of one or several widely distributed species, or do all these widely separated units represent species of their own? A look at genetic distances of our cyt b data set may help to facilitate the decision (Tab. 2). Within the *T. hirtus* species-group the lowest genetical distances are to be found in the closely related *T. thaleri* sp. nov. and *T. pharensis* sp. nov. (4.8–5.9%). We showed these taxa to be 'micro-allopatric' and apparently to be distinguished upon morphological characters. In Opiliones there is no consensus (like, e. g., in birds) above which level of cyt b differentiation biological species normally do exist.

Additionally, studies of the *Trogulus nepaeformis* radiation indicate that comparable genetic distances are coincident with morphospecies (Schönhofer & Martens in press). On the other hand, recent diversification processes obscure a clear cut-off value for a genetic determination of species, *T. karamanorum* sp. nov. being the best example. Presently, genetic distances higher than 5% cyt b represent useful guidance for species recognition within *Trogulus* but always need confirmation by other independent lines of evidence. For this instance, we characterised the subsequent species by genetic and in addition by morphological, biological and geographic characters of their own, to substantiate them as biological species, reproductively separated units in the sense of Ernst Mayr.

The *Trogulus hirtus* species-group

Molecular genetics: Almost all tree topologies support the species-group as a monophylum (Fig. 2) but with weak support in most analyses. Cyt b does only weakly support taxa at this phylogenetic level (see Results). A phylogeny including 28S rRNA data and about 70 representatives of *Trogulus* from the whole range of the genus revealed similar results (Schönhofer and Martens in press). This group of species is presently composed of six species which are distributed over the Balkan Peninsula from the southeastern Alps to northern Greece: *T. hirtus* DAHL, 1903, *T. falcipenis* KOMPOSCH, 2000, *T. karamanorum* sp. nov., *T. thaleri* sp. nov., *T. pharensis* sp. nov. and *T. melitensis* sp. nov. The *Trogulus hirtus* species-group can be divided into two genetically widely separated clades, the *T. hirtus* clade and the *T. falcipenis* clade (Fig. 2).

Morphology: The *T. hirtus* group species belong to the smallest in the genus *Trogulus* (♂ 3.8–5.05 mm, ♀ 3.85–5.5 mm). Geographically restricted species show little variation in body length (e. g., *T. thaleri* sp. nov.: ♂ 3.8–4.25 mm, ♀ 4.25–4.55 mm), whereas widespread and genetically diverse species like *T. karamanorum* sp. nov. exhibit considerably larger variation (♂ 3.85–4.7 mm, ♀ 4.05–5.5 mm). The eye mound is always flat, the eye interdistances relatively large. Papillae on dorsal side of body small, forming different patterns on the opisthosoma, caused by clearly defined regions of high and low papillae density (see *T. karamanorum* sp. nov., Figs. 1, 13w, y) or by very regularly spaced papillae (see *T. falcipenis*, Figs. 13g, i).

Penis morphology (Figs. 8–11, 13): Truncus rather stout, not dorsoventrally flattened as in most other *Trogulus* species, usually slightly broadened in its central third (in ventral/dorsal view), nearly parallel-sided in its lower third or tapering to basis (in lateral view), truncus dorsally and ventrally with a shallow furrow in most species. Glans similar to an asymmetrical (oblique) triangle (in ventral/dorsal view), in several species remarkably flattened dorsoventrally (seen in lateral view). Unique feature is a strong sickle-like stylus bent to the left side of the animal (dorsal view, in *T. tricarinatus* bent to the right), forming a more or less pronounced nearly half-circle. Glans sparsely set with medium-sized setae.

Distribution (Fig. 3): From the south-eastern border of the Alps (NE Italy, locally in southern Carinthia/Austria, western and central Slovenia) through Croatia southwards along the Dinaric Alps to Montenegro, Albania (few records so far), Republic of Macedonia and north-eastern Greece (Pindos Mts.). The large gaps in the distributional record are apparently due to low sampling

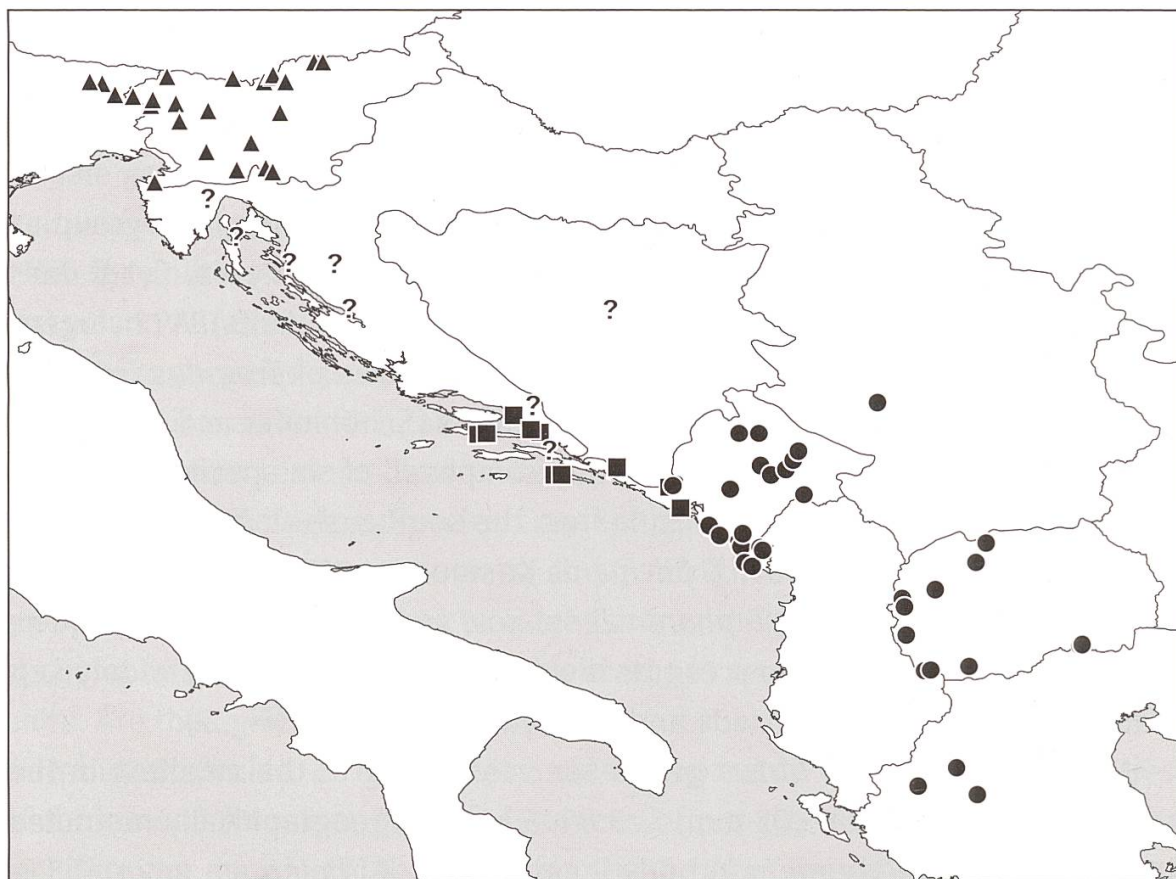


Fig. 3. Distribution of the *Trogulus hirtus* species-group: Triangles: *T. falcipenis*; squares: *T. hirtus* clade (including *T. hirtus*, *T. melitensis* sp. nov., *T. pharensis* sp. nov., *T. thaleri* sp. nov., see Fig. 5); circles: *T. karamanorum* sp. nov.; question marks: specimens of the *T. falcipenis* clade not treated here due to insufficient material (compare *Trogulus* sp. "Velebit", see Fig. 12).

activity in Herzegovina and Albania.

Similar species: The *Trogulus tricarinatus* species-group is characterised by equally small species and by a similar external morphology. In the Balkans several species of that group occur amidst the species of the *T. hirtus* species-group (pers. observation). However, the position of the *tricarinatus* group on the molecular tree is quite distant from that of the *T. hirtus* group (Fig. 2). Furthermore, the male genital morphology in the two species-groups is fundamentally different. Females of the *T. hirtus* group species and the *T. tricarinatus* group species are difficult to tell apart; determination should always be based on males.

Komposch (2000) mentioned one female from Corfu, Greece (Gasturi, M. Beier, leg. 2. IV. 1929, 4 ♀ 3 juv., NHMW) as possibly belonging to *T. falcipenis*. The series in question originally contained 4 females of three different species (pers. observation), one of which was never reported from Corfu or the nearby mainland and specimens have different colorations due to remarkably different soil incrustations. This appears to be a mixed sample and the geographical information is doubtful. On the other hand, we have at our disposal

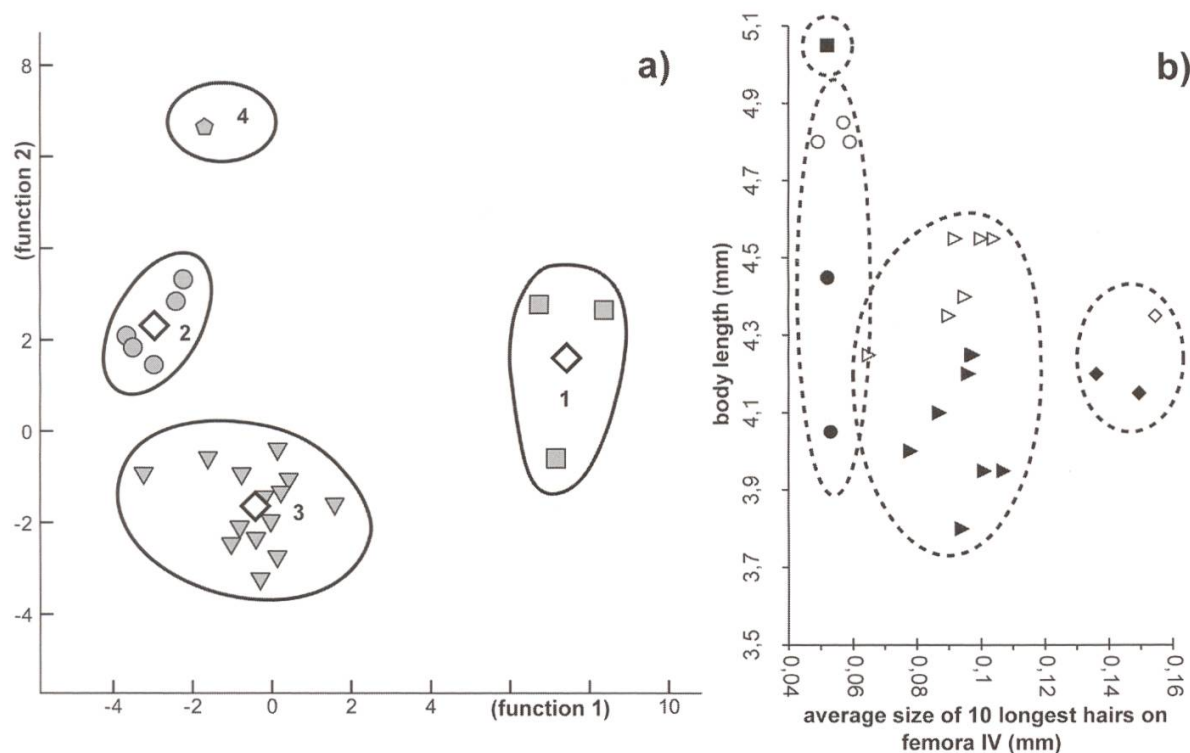


Fig. 4. – a: Results of the canonical discriminant analysis to separate four species within the *Trogulus hirtus* clade. The discriminant function incorporated average of 10 longest hairs of tibia IV, length of distal segment of tarsus IV and length of tibia II as the most significant characters to classify 100% of all included specimens correctly. *Trogulus hirtus* DAHL, *T. pharensis* sp. nov., *T. thaleri* sp. nov. and *T. melitensis* sp. nov. – 1/squares: *T. hirtus*; 2/circles: *T. pharensis* sp. nov.; 3/triangles: *T. thaleri* sp. nov.; 4/pentagon: *T. melitensis* sp. nov.; Rhombs: centroids.

– b: Scatterplot showing length of hairs on femur IV against body size of species of the *T. hirtus* clade. Rhombs: *T. hirtus*; triangles: *T. thaleri* sp. nov.; circles: *T. pharensis* sp. nov., squares: *T. melitensis* sp. nov.; black symbols: males, empty symbols: females.

several recently collected series of remarkably small specimens of *Trogulus* (here assigned to the *T. tricarinatus* species-group, CJM 5096) from Corfu, resembling one of these females. It clearly does not belong to the *T. hirtus* species-group due to the lack of a sickle shaped penial stylus. We consider it sister to this species-group without affinities to the *T. tricarinatus* species-group (see Results).

Key to the species of the *Trogulus hirtus* species-group

Affiliation of specimens to the *T. hirtus* species-group is possible by size (♂ 3.8–5.05 mm, ♀ 3.85–5.5 mm) in combination with male genital morphology: The massive stylus of the glans penis is strongly bent to the right side in the unremoved penis (in ventral view; genital operculum slightly to be slit laterally, then bent upwards). Females of similar body size may belong to other species-groups and are identifiable only together with males from the same

locality. Considering geographical restriction of the species, the key is valid for both sexes. Soil encrustations may be removed by dabbing (not brushing) with a stiff brush.

- 1 Occurring in a narrow belt along the Croatian coast from the mouth of the Cetina River to the Gulf of Kotor and on adjacent islands (Figs. 3, 5). Mainland taxa with conspicuously long and perpendicular bristles on all legs (Figs. 5b–c, 6e–h, i–m), island taxa (known from Mljet and Hvar) with shorter bristles (Figs. 5a, d, 6a–d, n–q). Papillae on femur II considerably longer than broad; if papillae are different in shape males are larger than 4.8 mm in body size **2**
- 1* Widely distributed from the south-eastern border of the Alps throughout the Dinaric Alps to Pindos Mts. in northern Greece, occurring north and south of the former group (Fig. 3). No long hairs on legs and body. Femur II with papillae as broad as long **5**
- 2 Length of hairs on legs at least half the leg diameter, often longer, perpendicular, well-developed on femur II, femur, patella and tibia IV (Figs. 5b–c, 6f–h, k–m), coat of hairs giving the legs a shiny appearance, long hairs on rear end of opisthosoma (Figs. 7a, d). Distributed in Croatian coastal areas and their hinterland **3**
- 2* Hairs on legs and body inconspicuous, only on femur II long hairs present (Figs. 6b, o), on femur IV short hairs bent sharply anteriorly (Figs. 5a, d, 6c, p); no long hairs on rear end of opisthosoma (Figs. 7g, k). Endemic to the islands of Hvar and Mljet **4**
- 3 Longest hairs on leg IV nearly as long as diameter of femur, perpendicular, hairs bent posteriorly in distal third (Figs. 5c, 6l). Body coated with long scattered bristles, also on rear end of opisthosoma (Figs. 7a, b). Occurrence from the Gulf of Kotor within a narrow coastal strip of 10–20 km width to the Neretva plain (Fig. 5) ***hirtus***
- 3* Longest hairs on leg IV distinctly shorter than diameter of femur, slightly bent anteriorly (Figs. 5b, 6g), body not coated with conspicuously scattered hairs. Rear end of opisthosoma only with short thickened hairs (Fig. 7d). Occurring in a small belt on the western flanks of the Biokovo Mt. from the mouth of the Cetina River to the Neretva plain (Fig. 5) ***thaleri* sp. nov.**
- 4 Endemic to Hvar Island; hair coat developed only on leg II as thin scattered hairs (Fig. 6b), hairs on femur IV short and sharply bent anteriorly (Figs. 5a, 6c); body size of males 4.0–4.5 mm, of females 4.8–4.9 mm
..... ***pharensis* sp. nov.**
- 4* Endemic to Mljet Island; hair coat on body and legs short and inconspicuous, body size of males about 5 mm (of females unknown), largest species of the species-group ***melitensis* sp. nov.**

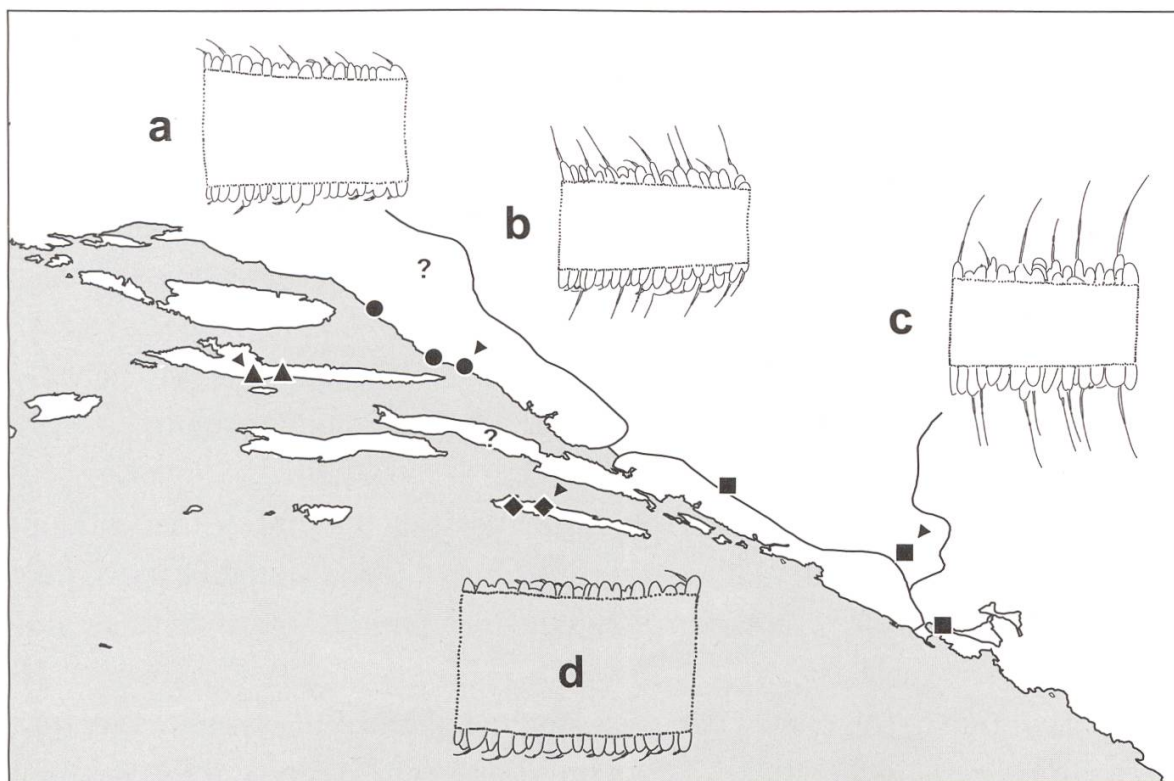


Fig. 5. Distribution of species of the *T. hirtus* clade and parts of femur II (dorsal and ventral papillae and hairs are indicated; left is anterior): a/triangles *T. pharensis* sp. nov. (Hvar Island), b/circles *T. thaleri* sp. nov. (Makarska Riviera), c/squares *T. hirtus* (south-eastern Croatian coast and hinterland), d/rhombs *T. melitensis* sp. nov. (Mljet Island), question marks: localities of members of the *T. hirtus* clade not assigned to species. Arrows point to type localities.

- 5 Endemic to the south-eastern Alps (NE Italy, Slovenia, SE Austria, Fig. 3); eyes about half their diameter from lateral border of front cap (Figs. 13h, l); dorsal papillation regular, without pattern (Figs. 13g, i, k, m); no Y-shaped ridge on dorsal prosoma, without a zone of widely spaced papillae, lacking soil encrustation (Figs. 13h, l); metatarsus III (when leg stretched backwards) surpasses rear end of opisthosoma; truncus penis parallel-sided in distal third (in ventral and lateral view; Figs. 14e–f) ***falcipenis***
- 5* Endemic to the southern Dinaric Alps (Montenegro, Republic of Macedonia, Greece, Fig. 3); eyes about their diameter from lateral border of front cap (Figs. 13u, x); dorsal papillation irregular, sometimes with pattern similar to Figs. 1, 13t, v–w, y; Y-shaped ridge on dorsal prosoma present, this part with widely spaced papillae and usually with soil encrustation (Figs. 13x–y, removed in 13u–v); metatarsus III (when leg stretched backwards) ends at rear end of opisthosoma. Truncus penis constricted in distal third (in ventral view, Fig. 14m) and broadened (in lateral view, Fig. 14l) ***karamanorum*** sp. nov.

The *Trogulus hirtus* clade

Molecular genetics (Fig. 2): The clade is supported by all phylogenetic reconstructions with high bootstrap support. It comprises the species *T. hirtus* DAHL, 1903, *T. thaleri* sp. nov., *T. pharensis* sp. nov. and *T. melitensis* sp. nov.

Morphology: Within the *hirtus* clade, the hair coat is the most useful character to distinguish species on a morphological basis. Although species differentiation within the clade is reliable upon a small set of morphometric characters (Fig. 4a), differences in length, angle and form of hairs on femur II and IV are most significant (Figs. 4b, 5–7).

Genital morphology (Figs. 8–11) is rather variable and not distinct enough for a reliable characterisation of the individual species. Compared to the *T. falcipenis* clade the glans in general is distinctly longer and larger, thus the stylus less long and massive.

Ecology: Due to their small body size, the members of the clade are restricted to permanently humid habitats. As the islands and parts of the Dalmatian coast are only little covered by forests nowadays, distributions are probably rather patchy and individual species rare.

Distribution (Figs. 3, 5): Restricted to a small belt of 20–30 km width along the Dalmatian coast and to the adjacent islands (Hvar, Mljet), from Montenegro, Gulf of Kotor to the mouth of the Cetina River in Croatia. The small distribution areas of the individual species are remarkable and in contrast to the much larger areas of the species of the *falcipenis* clade (see below). More island finds are to be expected.

Doubtful records: Croatia, Dalmatia, Mount Biokovo (field label: 2c+d), 1200–1300 m, from sieved litter, 1 unidentified ♂ (plus 2 ♂ of *T. thaleri* sp. nov.), C. Besuchet leg. 19. 5. 1984 (MHNG). This sample comprises two ♂ of *T. thaleri* sp. nov. and one additional ♂ of another species which probably also belongs to the *hirtus* clade (on grounds of genital morphology). There is no exact locality indication but obviously the specimens originate from two different localities. This single specimen indicates the presence of a yet undescribed taxon in the *T. hirtus* clade. We regard the following female as related to this male: Croatia, pass on road between Imotski and Zagvozd, ESE Split, *Pinus nigra*, N: 43° 26', E: 17° 08', 1 ♀, C. Deeleman leg. 22. 10. 1980 (CCD) [This specimen was declared paratype of *T. falcipenis* by Komposch 2000]. Specimens from Croatia (Oskorušno, east of Orebic, Pelješac (Poluotok) (N: 42° 58', E: 17° 20'), under *Pinus pinea*, 1 ♂ 1 ♀, C. Deeleman leg. 24. 10. 1980 (CCD)) were determined as *T. tricarinatus hirtus* by C. Komposch in 1999 but placed in *T. falcipenis* by Novak (2004a). They clearly belong to the *hirtus* clade but morphologically they are intermediate between *T. hirtus* and *T.*

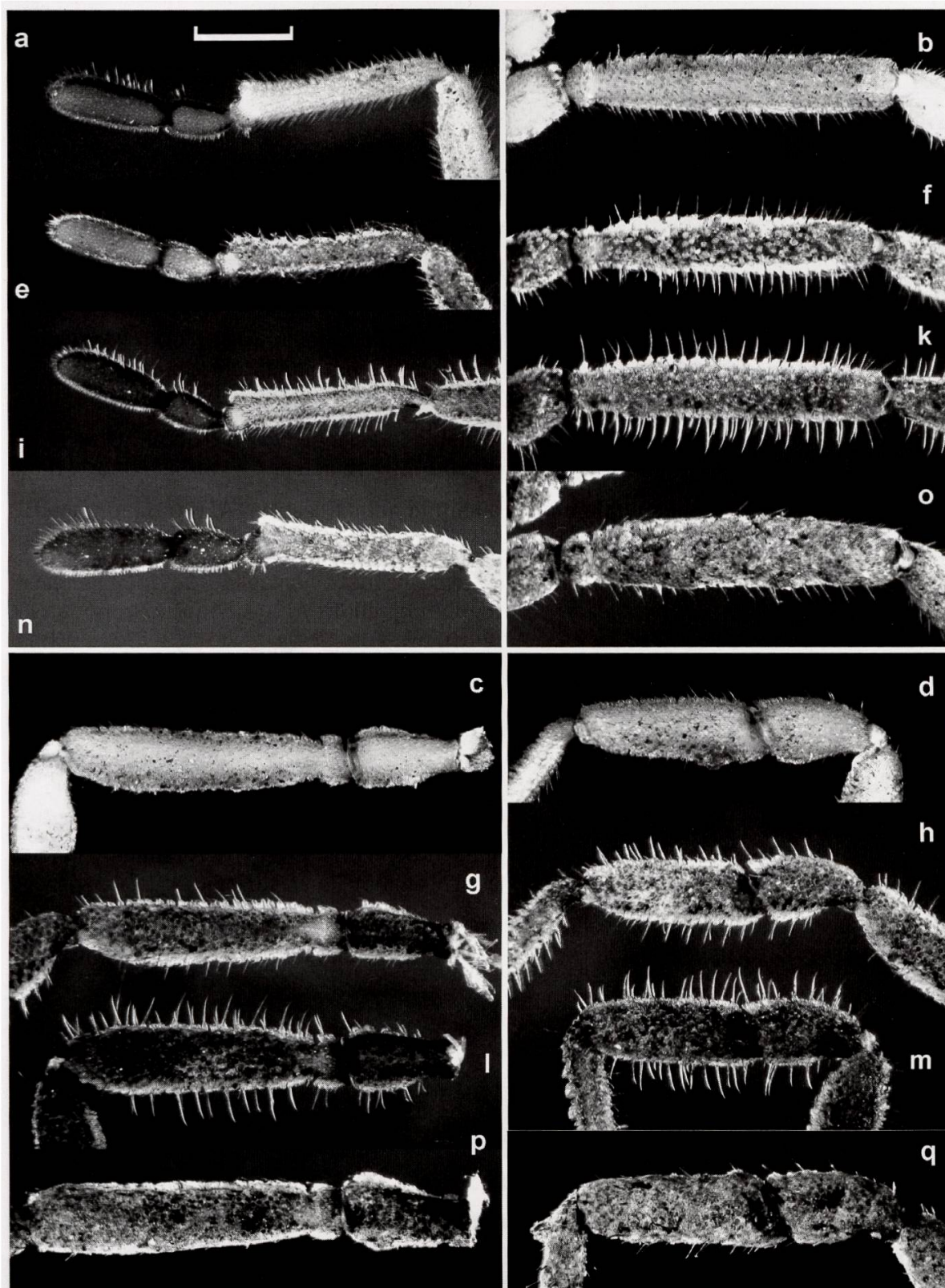


Fig. 6. Leg morphology of the species of the *Trogulus hirtus* clade, males (femur II dorso-lateral view, all other lateral view). – a–d: *T. pharensis* sp. nov. (Croatia, Hvar, near Sinje Spilje, CJM 4881); – e–h: *T. thaleri* sp. nov. (Croatia, Drvenik, CJM 4985); – i–m: *T. hirtus* (Montenegro, Herceg Novi, Monastir Savina, CJM 4969); – n–q: *T. melitensis* sp. nov. (Croatia, Mljet, Bjeajka, CRO 4). – Metatarsus and tarsus II (a, e, i, n); femur II (b, f, k, o); trochanter and femur IV (c, g, l, p); patella and tibia IV (d, h, m, q). Scale line 0.5 mm.

thaleri sp. nov. Further material and molecular genetic analysis may help to clarify the taxonomic status of these and related forms.

Species account

***Trogulus hirtus* DAHL, 1903, new rank** (Figs. 4, 5c, 6i–m, 7a–c, 8)

Trogulus tricarinatus hirta DAHL, 1903; Dahl (1903): Sitzber. Ges. naturforsch. Freunde Berlin: 289.

Trogulus tricarinatus hirtus – Roewer (1923): Weberknechte der Erde: 641 (diagnosis).

Trogulus tricarinatus hirta – Moritz (1971): Mitt. Zool. Mus. Berlin 47: 211 ("Kosusko" given as type locality).

Trogulus tricarinatus hirtus – Komposch (2000): Spixiana 23: 1–14 (discussion of taxonomic status).

Trogulus tricarinatus hirtus – Novak (2004a): Nat. Croat. 13: 235, 252 (localities).

Material examined: holotype: **Bosnia-Herzegovina**: southern Herzegovina, Konjsko (N: 42° 39', E: 18° 27'), 1000 m, oak forest, ♂, Verhoeff leg. (ZMB 11697 + microscopical slide 11697a). The type locality is given as "Kosusko" in Moritz (1971) and as "Kansko" in Komposch (2000). The original locality is given as "Konisko" but was (later?) changed to "Konsiusko". Accordingly I. Karaman confirmed that Kosusko is identical to the present Konjsko (pers. comm.; see Fig. 5).

Additional material examined: **Bosnia-Herzegovina**: Zavala, SE Vjetrenica cave, 350 m (N: 42° 50', E: 17° 58'), shrub forest, sieved, 2 ♂ 3 juv., J. Gruber leg. 6. 6. 1968, J. Gruber det. (NHMW 3154); Zavala, close to village, 300 m (N: 42° 50', E: 17° 58'), shrub forest, sieving, 3 juv., J. Gruber leg. 6. 6. 1968, J. Gruber det. (NHMW 3155). **Croatia**: southern Dalmatia, Castelnuovo (presently Kotor in Montenegro), Ragusa (presently Dubrovnik), Dricno (not located, probably region of Orjen), 1 ♀ 3 juv., Reitter leg. 1880, J. Gruber det. (NHMW 3273); **Montenegro**: Herceg Novi, Park of Monastir Savina, 50 m (N: 42° 27' 7.2", E: 18° 33' 12.5"), evergreen deciduous forest, very dense and dark, litter in stony debris, 1 ♂ 1 juv., I. Karaman leg. 1. 5. 1997 (CIK 1500); ibidem 1 ♂ 1 ♀ 1 juv., A. Schönhofer leg. 12. 5. 2006 (CJM 4969).

Molecular genetics (Fig. 2): The only sequenced specimen (CJM 4969) possesses many autapomorphies and cyt b distances of 13.8–16.9% to other

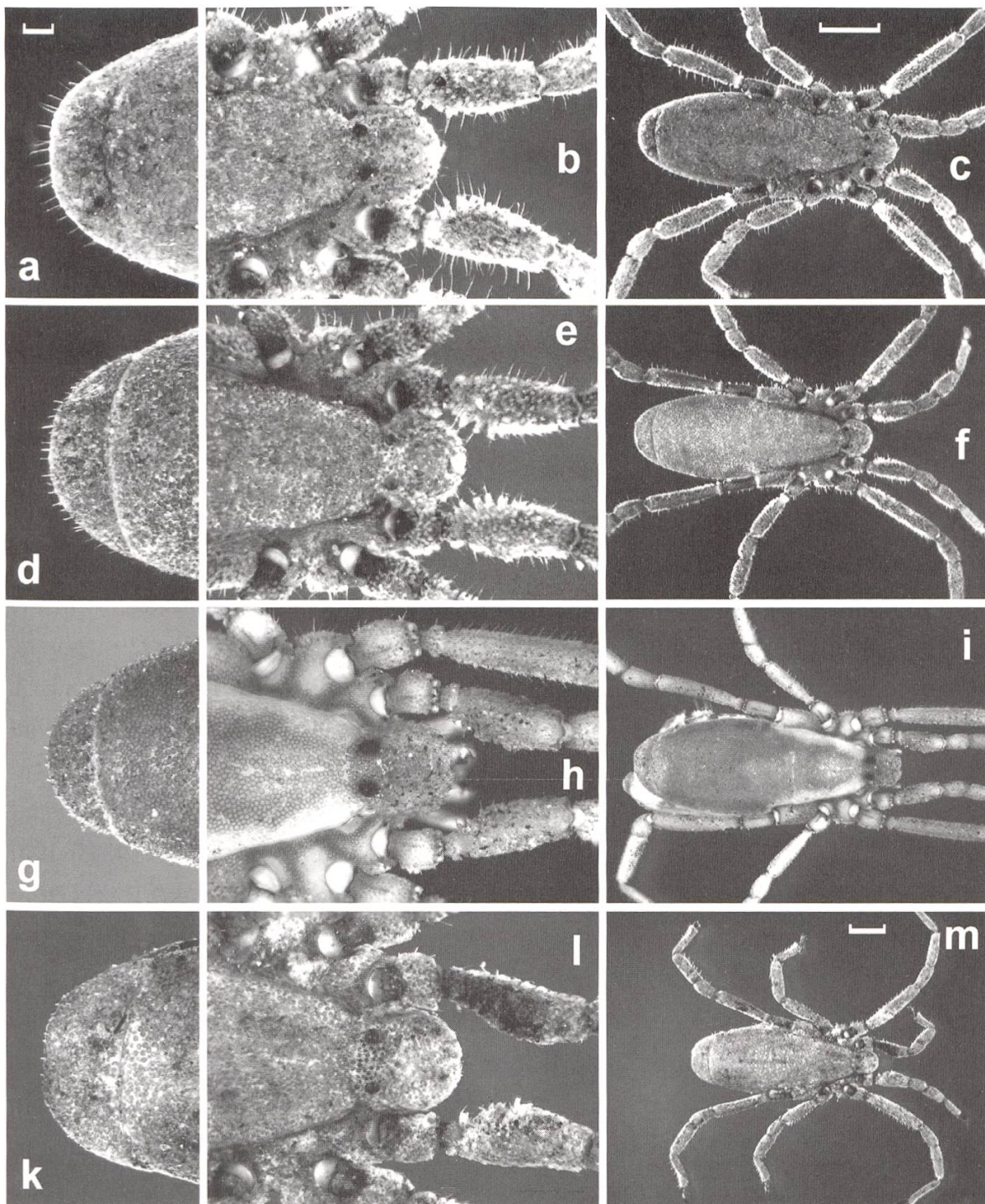


Fig. 7. Dorsal side of males of the *Trogulus hirtus* clade. – a–c: *T. hirtus* (Montenegro, Herceg Novi, Monastir Savina, CJM 4969); – d–f: *T. thaleri* sp. nov. (Croatia, Drvenik, CJM 4985); – g–i: *T. pharensis* sp. nov. (Croatia, Hvar, near tunnel to Zavala, CJM 4881); – k–m: *T. melitensis* sp. nov. (Croatia, Mljet, Bjeajka, CRO 4). – Caudal end of opisthosoma (a, d, g, k); prosoma with coxae I–IV and femur I (b, e, h, l); body with parts of legs I–IV (c, f, i, m). Scale lines 0.2 mm (a, b, d, e, g, h, k, l) and 0.1 mm (c, f, i, m).

taxa within the clade. A close relationship to *T. melitensis* sp. nov. is suggested by most topologies but with low support.

Diagnosis: Very small and robust *Trogulus*, conspicuously covered with long hairs perpendicular to the body surface, situated dorsally on the "shoul-

ders", along rear end of opisthosoma (Figs. 7a–c) and on all legs (there very distinct, Figs. 6i–m). Tips of hairs on legs bent anteriorly, well visible on femur IV (Figs. 5c, 6l). Body shape slightly more robust and broader than in *T. karamanorum* sp. nov. (Fig. 7c).

Similar species: Due to its hairy appearance *T. hirtus* can be easily told apart from *T. karamanorum* sp. nov., *T. melitensis* sp. nov. and *T. pharensis* sp. nov., which occur roughly in the same area but not in sympatry. In the northern part of its range *T. hirtus* may be confused with the somewhat less hairy *T. thaleri* sp. nov. but according to current knowledge both live in allopatry and differ in the shape of their hair coat on femur IV.

Description: Body (Figs. 7a–c): Area between branches of the Y-shaped ridge on dorsal prosoma deeply incised and partly void of papillae. Dorsal median ridge and transverse areas on opisthosoma pronounced, composed of densely packed upright papillae.

Eye mound and front cap (Fig. 7b): Front cap with long papillae, laterally without sharp contours and largely fused with the "shoulders". Eye mound very low, only slightly elevated; eyes separated by a shallow depression.

Hair coat (Figs. 5c, 6i–m, 7a–c): Hairs on femur II long, the longest in the *T. hirtus* species-group, more than half the diameter of the limb, hair tips bent posteriorly. Long hairs scattered all over the body, conspicuous at the shoulder, on the dorsal scutum and rear end of opisthosoma, mostly perpendicular to the surface. Hairs on femur IV shorter but otherwise as on femur II and bent posteriorly as well.

Measurements: **Body length:** ♂ 4.15–4.5 mm (n=5); ♀ 4.35–4.5 mm (n=2), length of 10 longest hairs on femur IV: 90–170 µm; average of 10 longest hairs per individual: 136–155 µm; – **DSII/BSII:** ♂ 1.59–1.88; ♀ 1.76–1.87; – **eye interdistance:** ♂ 0.33–0.36 mm; ♀ 0.36 mm; – **length of leg II:** ♂ 5.3–5.8 mm; ♀ 5.35–5.6 mm; – **length of tibia II:** ♂ 1.0–1.1 mm; ♀ 1.03–1.08 mm; – **length of tibia IV:** ♂ 0.94–1.04 mm; ♀ 0.97–1.02 mm; – **width of tibia IV:** ♂ 0.13–0.135 mm; ♀ 0.13–0.14 mm (difficult to measure); – **length of tibia IV/width of tibia IV:** ♂ 7.11–7.80; ♀ 7.07–7.85; – **body width:** ♂ 1.5–1.7 mm; ♀ 1.75–1.8 mm; – **length of distal segment of tarsus IV:** ♂ 0.15–0.16 mm; ♀ 0.14–0.16 mm (difficult to measure); – **length of median segment of tarsus IV:** ♂ 0.08–0.095 mm; ♀ 0.07–0.09 mm (difficult to measure); – **length of distal segment of tarsus IV/length of median segment of tarsus IV:** ♂ 1.7–2.0; ♀ 1.77–2.0; – **length of leg II/body length:** ♂ 1.28–1.33; ♀ 1.23–1.24.

Distal tarsal segment IV longer than in *T. thaleri* sp. nov., the central segment therefore quadrangular. Legs of *T. karamanorum* sp. nov. thicker and shorter than in *T. hirtus* and due to heavy incrustations difficult to measure.

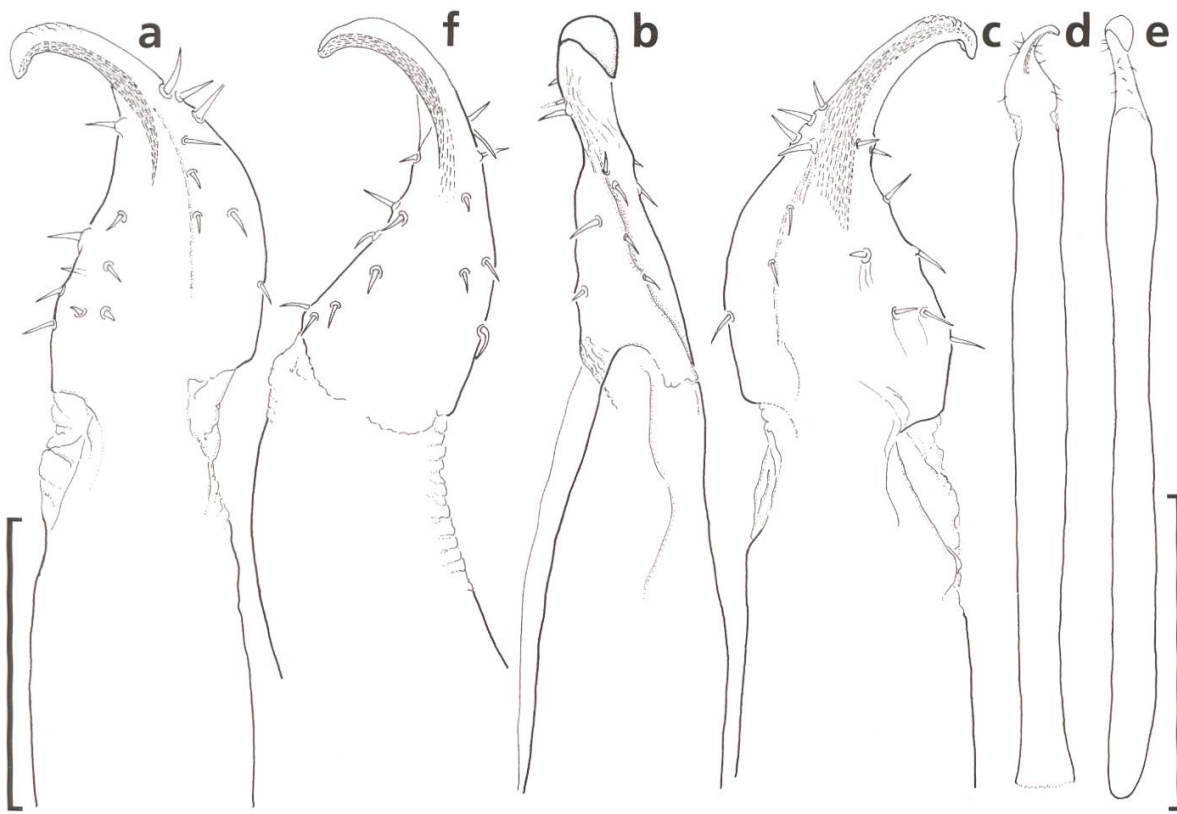


Fig. 8. *Trogulus hirtus*, penis morphology. Glans penis and distal part of truncus (a–c, f; a and f dorsal view; c ventral view; b lateral view); total penis (d–e; d ventral view, e lateral view). – a–e: Herceg-Novi (CJM 4969), – f: same locality (CIK 1500). Left scale line 0.1 mm (a–c, f), right scale line 0.5 mm (d–e).

Genital morphology (Fig. 8): Truncus most slender in central part (in lateral view) or in basal part (in ventral view); glans forming a sharp ridge on the right side (in lateral view, Fig. 8b), stylus relatively short and moderately bent. The male holotype was available to us only close to the publication of the present paper. Consequently we could not add additional drawings. Nevertheless, we can state that the penis of the holotype perfectly matches Figs. 8a–e.

Variability: Due to small material not yet fully established; the angle and conspicuous length of hairs on body and legs provide distinct and reliable characters; see Relationships.

Ecology: *T. hirtus* was recorded from evergreen Mediterranean hard-leaved forests at sea level and from shrub forest and oak forest at 200–1000 m. Permanently moist habitats with deep soil and leaf litter in sheltered valleys seem to be preferred; sieved from soil litter and collected under stones.

Distribution (Fig. 5): Along the Dalmatian coast in a small belt of 20–30 km width from Montenegro, the Gulf of Kotor to the mouth of the Neretva River in Croatia. Records range from sea level (Herceg-Novi) up to 1000 m (Konjsko).

Discussion: The species was described by Dahl (1903) on the basis of its small size and the conspicuously long perpendicular bristles on all legs. It was originally regarded as a subspecies of the allegedly wide-spread *T. tricarina*.

tus. The available type material allowed correct identification of new material (CJM 4969; see above). Of the latter a cyt b sequence could be obtained. The type locality and the locality of specimen CJM 4969 are only about 20 km apart. Komposch (2000) discussed the relationship between *T. hirtus* (sub *T. tricarinatus hirtus*) and *T. falcipenis* on the basis of genital morphology and informally suggested to raise *T. hirtus* to species level. This evaluation is confirmed by our results based on morphology and molecular genetics. However, *T. falcipenis* and *T. hirtus* are not closest relatives, instead they belong to different clades within the *T. hirtus* species-group.

***Trogulus thaleri* sp. nov.** (Figs. 4, 5b, 6e–h, 7d–f, 9)

Holotype: Croatia: Drvenik, *Pinus* and dense *macchia*, sieved from wet needles between stones, 33 m (N: 43° 09' 31.0", E: 17° 14' 57.0"), ♂, A. Schönhofer leg. 12. 5. 2006 (CJM 4985).

Paratypes: **Croatia**: same data as for holotype, 3 ♂ 4 ♀; Sveti Makarska near Makarska, 90 m (N: 43° 18' 54.4", E: 17° 00' 15.7"), valley with *Pinus* forest, near rocks on small stream, 1 ♀, A. Schönhofer leg. 15. 5. 2006 (CJM 4867); Church Porat near Podaca, dense *Laurus* stand under *Pinus* near source, sieved from deep cracks in stonewalls, 29 m (N: 43° 11' 0.4", E: 17° 09' 52.4"), 2 ♂ 2 ♀ 1 juv., A. Schönhofer leg. 14. 5. 2006 (CJM 4938); Dalmatia, Biokovo Mt. (field label: 2c+d), 1200–1300 m, sieved from soil and leaf litter, 2 ♂ (of 3 ♂ in the whole series), C. Besuchet leg. 19. 5. 1984 (MHNG; 1 ♂ in Coll. P. Mitov) [determined as *T. falcipenis* by P. Mitov].

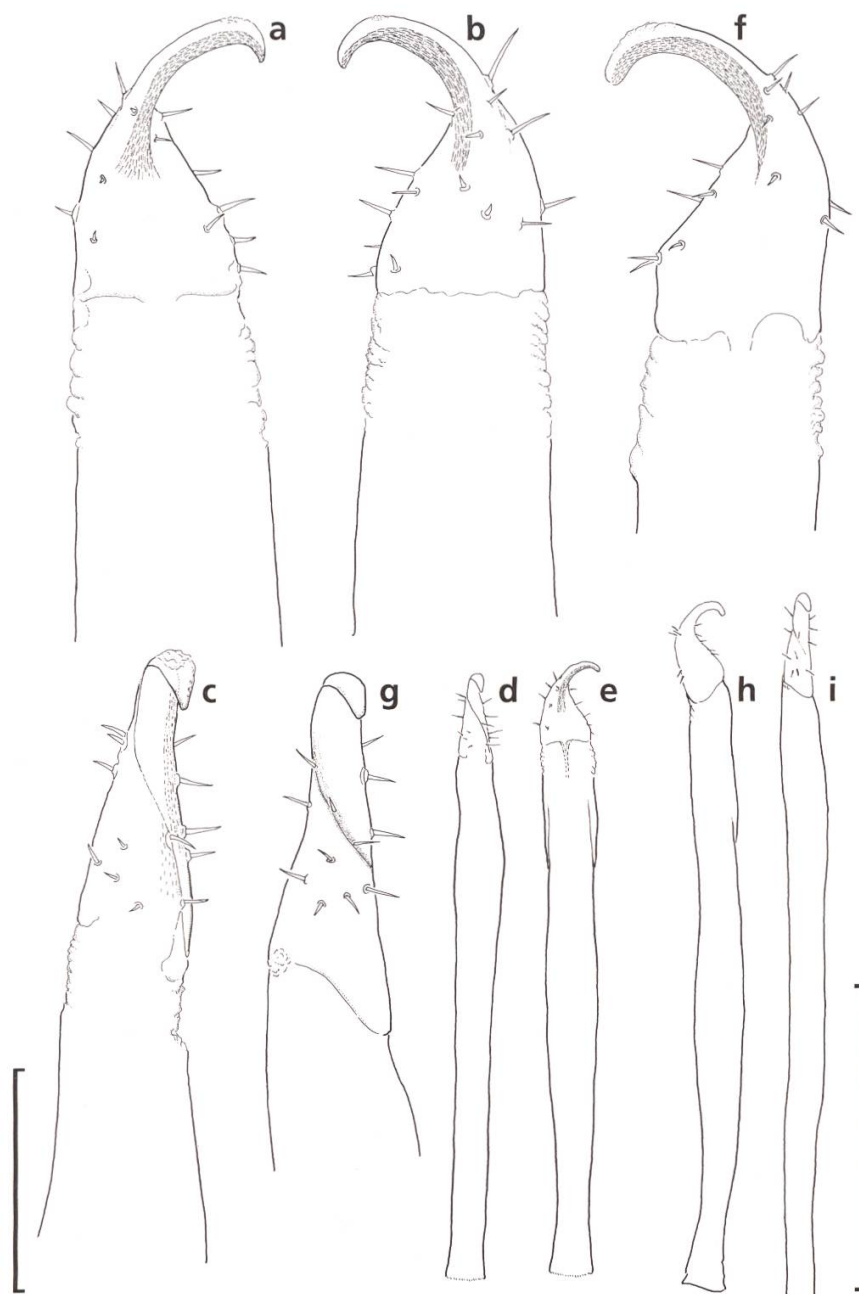
Molecular genetics (Fig. 2): The taxon is supported by all topologies and is close to *T. pharensis* sp. nov. Both species live in close geographic proximity (Fig. 5). The distance value between them amounts to only 4.8–5.9% and is relatively low (note the intraspecific distances of *T. karamanorum* sp. nov. populations which amount to 3.5%). However, morphological differences to *T. pharensis* sp. nov. are pronounced and point to species status.

Diagnosis: A very small and slender *Trogulus* conspicuously covered with long hairs (Figs. 6e–h, 7d–f), inserted nearly perpendicularly but slightly pointing anteriorly, bristles also on the "shoulders", on the rear end of opisthosoma (Fig. 7d) and on all legs (Figs. 6e–h). Conspicuous hairs on dorsum largely missing. Hairs on femur IV straight, tips not bent anteriorly and about one third shorter than in *T. hirtus* (Fig. 5b). Body shape more slender than in *T. hirtus* (Fig. 7f).

Similar species: *T. thaleri* sp. nov. (Croatian coast) is similar to *T. pharensis* sp. nov. but clearly allopatric. Both species can easily be told apart by com-

Fig. 9. *Trogulus thaleri* sp. nov., penis morphology.

Glans penis and distal part of truncus (a–c, f–g; a ventral view; b, f dorsal view; c, g lateral view); total penis (d–e, h–i; d, i lateral view; e, h ventral view). – a–e: Drvenik, type locality (CJM 4985), f–i: Podaca (CJM 4938). – Left scale 0.1 mm (a–c, f–g), right scale line 0.5 (d–e, h–i).



parison of the hair coat on femur IV. *T. pharensis* sp. nov. is on average larger than *T. thaleri* sp. nov.

Description: Body (Figs. 7d–f): Similar to *T. pharensis*; Y-shaped median ridge on dorsal prosoma indistinct; area between branches of the Y-shaped ridge narrow, partly void of papillae; papillae on opisthosoma irregularly spaced, leaving small bald spots; from a distance a few transverse rows of different density recognizable on opisthosoma, not visible when soil-encrusted; median ridge indistinctly developed in females (last two characters best seen at low magnification).

Eye mound and front cap (Fig. 7e): Cap with long lateral papillae, thus without sharp contours, longish to roundish; eye interdistance variable; "shoul-

ders" without long papillae and therefore clearly outlined; eye mound flat, only slightly elevated; eyes separated by a shallow to deeply incised depression.

Hair coat (Figs. 6e–h, 7d–e): Hairs on femur II long, about half the diameter of the limb including the papillae, straight, not bent at tip; long hairs scattered all over the body, inconspicuous on dorsum, conspicuous at the shoulder and rear end of opisthosoma, mostly perpendicular to surface; hairs on femur IV shorter than on femur II, pointing slightly anteriorly; hairs generally shorter than in *T. hirtus*.

Measurements: – **Body length**: ♂ (n=7) 3.8–4.25 mm; ♀ (n=7) 4.25–4.55 mm, on average smaller than *T. pharensis* sp. nov.; length of 10 longest hairs on femur IV: 50–130 µm; average of 10 longest hairs per individual: (65–) 78–107 µm; – **DSII/BSII**: ♂ 1.58–1.84; ♀ 1.55–1.74; – **eye interdistance**: ♂ 0.33–0.37 mm; ♀ 0.35–0.39 mm; – **length of leg II**: ♂ 5.05–5.7 mm; ♀ 5.2–5.7 mm; – **length of tibia II**: ♂ 1.01–1.13 mm; ♀ 1.05–1.15 mm; – **length of tibia IV**: ♂ 0.91–1.03 mm; ♀ 0.96–1.07 mm; – **width of tibia IV**: ♂ 0.10–0.125 mm; ♀ 0.11–0.125 mm (difficult to measure); – **length of tibia IV/width of tibia IV**: ♂ 7.4–10.3; ♀ 8.0–8.9; – **body width**: ♂ 1.4–1.5 mm; ♀ 1.6–1.7 mm; – **length of distal segment of tarsus IV**: ♂ 0.12–0.14 mm; ♀ 0.12–0.13 mm (difficult to measure); – **length of median segment of tarsus IV**: ♂ 0.06–0.075 mm; ♀ 0.06–0.075 mm (difficult to measure); – **length of distal segment of tarsus IV/length of median segment of tarsus IV**: ♂ 1.67–2.17; ♀ 1.67–2.0; – **length of leg II/body length**: ♂ 1.26–1.37; ♀ 1.21–1.25.

Distal tarsal segment IV shorter than in *T. hirtus*, the central segment being higher than long. Other characters show little difference to the closely related *T. melitensis* sp. nov. and *T. pharensis* sp. nov.

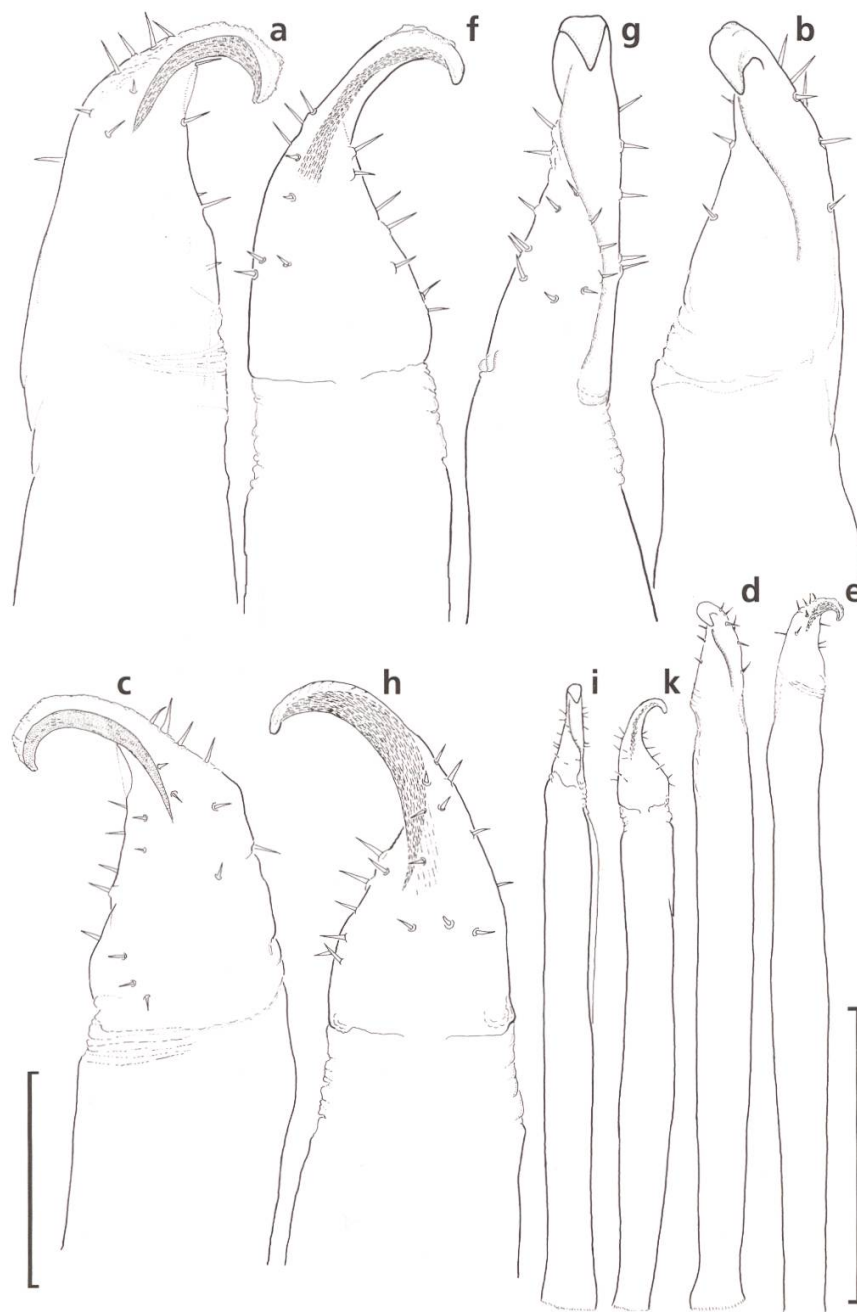
Genital morphology (Fig. 9): Truncus slightly enlarged in its distal part (in lateral and ventral views), slightly tapering to basis in lower half (in lateral and ventral views); glans relatively short, stylus long and distinctly curved, nearly forming a half-circle; short setae of glans longer than in other species of the *T. hirtus* group.

Variability: Low; form and position of the hairs are constant.

Distribution (Fig. 5): Croatia, Dalmatian coast from Makarska along the western foothills of Biokovo Mountain south to the mouth of the Neretva River, northwards probably up to the mouth of the Cetina River and restricted to the south-western part of Biokovo Mountain. One record from Biokovo between 1200–1300 m is doubtful; the data may correspond to different localities in that mountain massif (see *hirtus* clade, Discussion).

Ecology: Collected in association with *Pinus* as dominant tree, lower vegetation with *Laurus* in sheltered valleys. Sieved from deep cracks between rocks and stonewalls from deep humus deposits. Occurring locally in high

Fig. 10. *Trogulus pharensis* sp. nov., penis morphology. Glans penis and distal part of truncus (a–c, f–h; a, f ventral view; c, h dorsal view; g, b lateral view); total penis (d–e, i–k; i, d lateral view; k, e ventral view). – a–e: Hvar, near Sinje špilje (CJM 4881), – f–k: Hvar, tunnel from Pitve to Zavala (CJM 5155, holotype). Left scale line 0.1 mm (a–c, f–h), right scale line 0.5 mm (d–e, i–k).



population densities, mostly in association with *Cyphophthalmus* species.

Derivatio nominis: The species name honours Konrad Thaler (19. 12. 1940, Innsbruck – 11. 07. 2005, Stubai Alps), one of the most distinguished contemporary European arachnologists. His profound contributions to systematics, taxonomy, morphology and ecology of Alpine and Mediterranean arachnids are countless and will stand for long. He is greatly missed by the community of arachnologists worldwide.

Discussion: See *hirtus* clade.

***Trogulus pharensis* sp. nov.** (Figs. 4, 5a, 6a–d, 7g–i, 10)

Holotype: **Croatia**: Hvar Island, close to entrance of the road tunnel from Pitve to Zavala, 201 m (N: 43° 08' 25", E: 16° 40' 25"), sieved from needles and moss on stonewalls, *Pinus* forest, ♂, A. Schönhofer leg. 14. 5. 2006 (CJM 5155).

Paratypes: **Croatia**: Same data as for holotype, 1 juv.; Hvar Island, banks of road 116, stone cliff near Sinje špilje, 229 m (N: 43° 08' 41.3", E: 16° 45' 11.9"), under mossy stones shaded by forest, sieving of humus, 1 ♂ 3 ♀ 1 juv., A. Schönhofer leg. 14. 5. 2006 (CJM 4881).

Molecular genetics (Fig. 2): The cyt b distance between *T. pharensis* sp. nov. and the most closely related species, *T. thaleri* sp. nov., is only 4.8–5.9%. See details under *T. thaleri* sp. nov.

Diagnosis: A small and slender *Trogulus* endemic to Hvar Island. Bristles on body and legs short, inserted perpendicular to the body surface and slightly pointing anteriorly, long and conspicuous only on leg II (Fig. 6b), inconspicuous on the "shoulders" and along the rear end of the opisthosoma (Fig. 7g). Hairs on femur IV straight and about one third shorter than in *T. thaleri* sp. nov. (Figs. 5a, 6c), body size on average larger than in *T. thaleri* sp. nov. (Fig. 7i).

Similar species: See *T. thaleri* sp. nov.

Description: Body (Figs. 7g–i): Similar to *T. thaleri* sp. nov. in overall appearance.

Eye mound and front cap (Fig. 7h): Similar to *T. thaleri* sp. nov. No specific characters recognized.

Hair coat (Figs. 6a–d): Inconspicuous, long hairs especially on leg II (femur II), hairs on femur IV short, pointing anteriorly at an acute angle.

Measurements: ♂ (n=2); ♀ (n=3): – **Body length**: ♂: 4.05–4.45 mm; ♀: 4.8–4.85 mm, on average larger than *T. thaleri* sp. nov.; length of 10 longest hairs on femur IV: 30–70 µm; average of 10 longest hairs per individual: 49–59 µm; – **DSII/BSII**: ♂ 1.72–1.81; ♀ 1.63–1.83; – **eye interdistance**: ♂ 0.35–0.37 mm; ♀ 0.38–0.41 mm; – **length of leg II**: ♂ 5.1–5.6 mm; ♀ 5.4–5.6 mm; – **length of tibia II**: ♂ 1.0–1.11 mm; ♀ 1.07–1.14 mm; – **length of tibia IV**: ♂ 0.91–0.99 mm; ♀ 1.01–1.07 mm; – **width of tibia IV**: ♂ 0.12–0.13 mm; ♀ 0.125–0.14 mm (difficult to measure); – **length of tibia IV/width of tibia IV**: ♂ 7.59–7.8; ♀ 7.1–8.0; – **body width**: ♂ 1.5 mm; ♀ 1.7–1.8 mm; – **length of distal segment of tarsus IV**: ♂ 0.13–0.14 mm; ♀ 0.14–0.15 mm (difficult to measure); – **length of median segment of tarsus IV**: ♂: 0.07–0.085 mm; ♀ 0.07–0.09 mm (difficult to measure); – **length of distal segment of tarsus IV/length of inner segment of tarsus IV**: ♂ 1.34–1.43; ♀ 1.27–1.30; – **length of leg II/body length**: ♂ 1.26; ♀ 1.12–1.17.

Genital morphology (Fig. 10): Truncus quite stout and nearly parallel-sided,

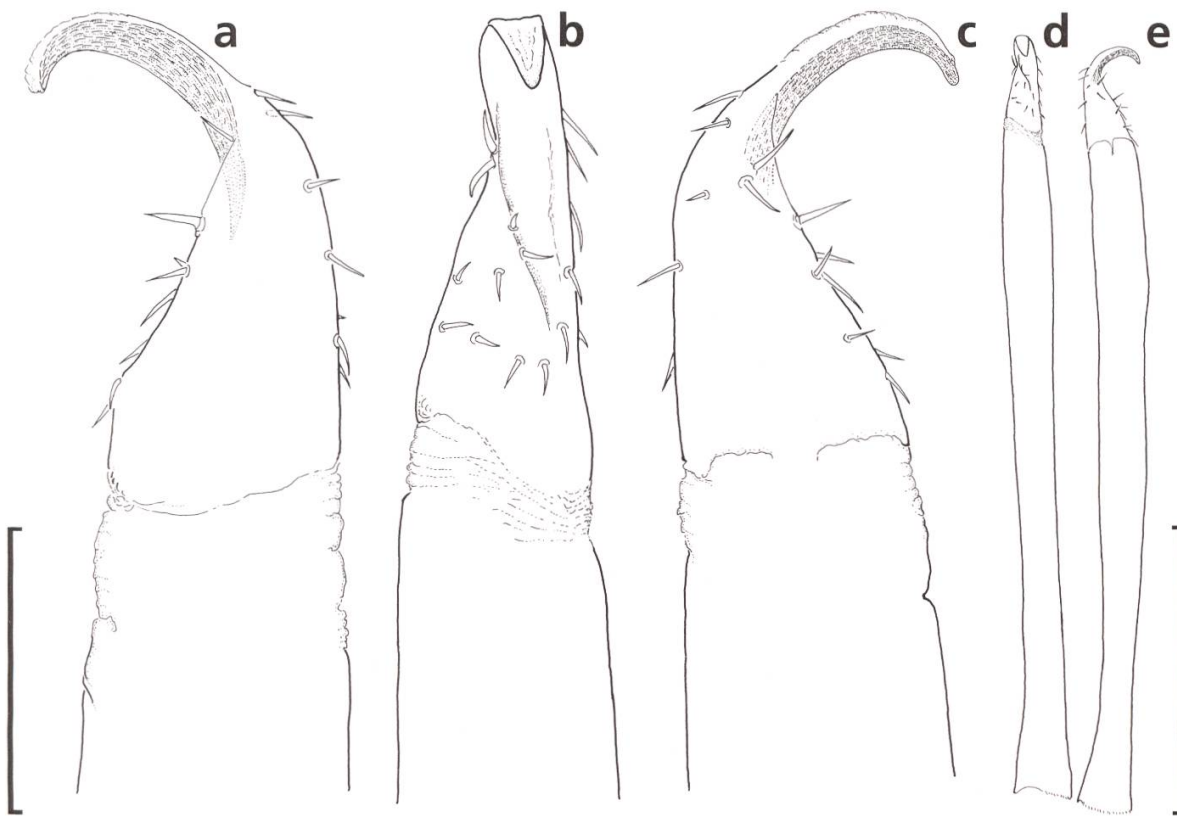


Fig. 11. *Trogulus melitensis* sp. nov., penis morphology. Glans penis and distal part of truncus (a–c; a dorsal view; b lateral view; c ventral view); total penis (d–e; d lateral view, e ventral view). – a–e: Mljet Island (CRO 4). Left scale line 0.1 mm (a–c), right scale line 0.5 mm (d–e).

only lower third to lower half slightly tapering to basis (in ventral and lateral views); glans relatively large, longish, not extremely flattened (in lateral view); stylus quite massive, strongly bent only in distal third to distal half.

Variability: Due to small material unresolved. Penis morphology quite variable. There is some variation in the angle at which the hairs are inserted on femur II; they always point anteriorly. Varying position of hairs on femur II from perpendicular to slightly bent anteriorly, but invariable on the same specimen. No distinction of different "bristle type" populations possible by means of cyt b sequences.

Ecology: Found in sheltered mossy microhabitats and in humus between stony debris in Mediterranean hard-leaved forests and in *Pinus* forest.

Distribution (Fig. 5): Croatia, endemic to Hvar Island.

Derivatio nominis: Name derived from Pharos, the ancient Greek name of the present island of Hvar.

Discussion: Although the cyt b distance between *T. thaleri* sp. nov. and *T. pharensis* sp. nov. is quite low, distinct morphological characters suggest species status of both genetic clusters. The average body size is considerably larger in *T. pharensis* sp. nov. and length and position of hairs on femur IV clearly separate the two species (see Fig. 5).

***Trogulus melitensis* sp. nov.** (Figs. 4, 5d, 6n–q, 7k–m, 11)

Trogulus tricarinatus hirtus – Novak (2004a): Nat. Croat. 13: 235, 253 (records).

Holotype: **Croatia**: Southern Dalmatia, Mljet Island, Soline, Bjeajka, in pit Jama u uvali šume Bjeajka (N: 42° 46', E: 17° 23'), ♂, J. Bedek, I. Boršić, T. Dražina leg. 18. 6. 2001 (CRO OP30101, here referred as to CRO 4).

Paratype: **Croatia**: Mljet Island, Blato, Kozarica, (N: 42° 46', E: 17° 23'), 1 ♀, Travnik leg. 30. 4. 1987 (TN 1112/1998); not examined.

Molecular genetics (Fig. 2): The species possesses many autapomorphies; its cyt b distance to the other taxa within the *hirtus* clade amounts to 13.8–16.9% (see *T. hirtus*).

Diagnosis: A small and slender *Trogulus* endemic to Mljet Island. Hair coat inconspicuous, no long bristles present on femur IV. By far the largest species in the *T. hirtus* species-group (male body size > 5 mm).

Similar species: Probably none. So far no other small *Trogulus* is known from Mljet. However, it is unknown if *T. melitensis* sp. nov. is actually restricted to Mljet.

Description: Body (Figs. 7k–m): Short Y-shaped median ridge on anterior dorsal prosoma; area between branches of the Y-shaped ridge narrow, only partly with widely spaced papillae; on opisthosoma papillae irregularly spaced, leaving small bare spots without papillae; dorsal ridge pronounced by closely packed papillae, well visible in low magnification.

Eye mound and front cap (Fig. 7l): Front cap oval, eyes about their interdistance away from lateral border of front cap; front cap laterally not obscured by long papillae; eye mound flat, only slightly elevated; eyes separated by a shallow depression.

Hair coat (Figs. 5d, 6n–q): Inconspicuous, much less developed than in other species of the *T. hirtus* species-group, thus similar to hair coat of the two species of the *T. falcipenis* clade; long hairs only on femur II, especially on dorsal ridge, femur IV with short hairs closely adpressed to surface of femur, hardly visible among papillae.

Measurements: ♂ (n=1): – **Body length**: ♂ 5.05 mm, largest species within *hirtus* species-group; – **length of 10 longest hairs on femur IV**: 40–70 µm; – **average of 10 longest hairs per individual**: 52 µm; – **DSII/BSII**: ♂ 1.71–1.74; – **eye interdistance**: ♂ 0.4–0.42 mm; – **length of leg II**: ♂ 6.1–6.25 mm; – **length of tibia II**: ♂ 1.14–1.18 mm; – **length of tibia IV**: ♂ 1.1–1.13 mm; – **width of tibia IV**: ♂ 0.15–0.16 mm (difficult to measure); – **length of tibia IV/width of tibia IV**: ♂ 6.9–7.5; – **body width**: ♂ 1.8 mm; – **length of distal seg-**

canonical discriminant analysis

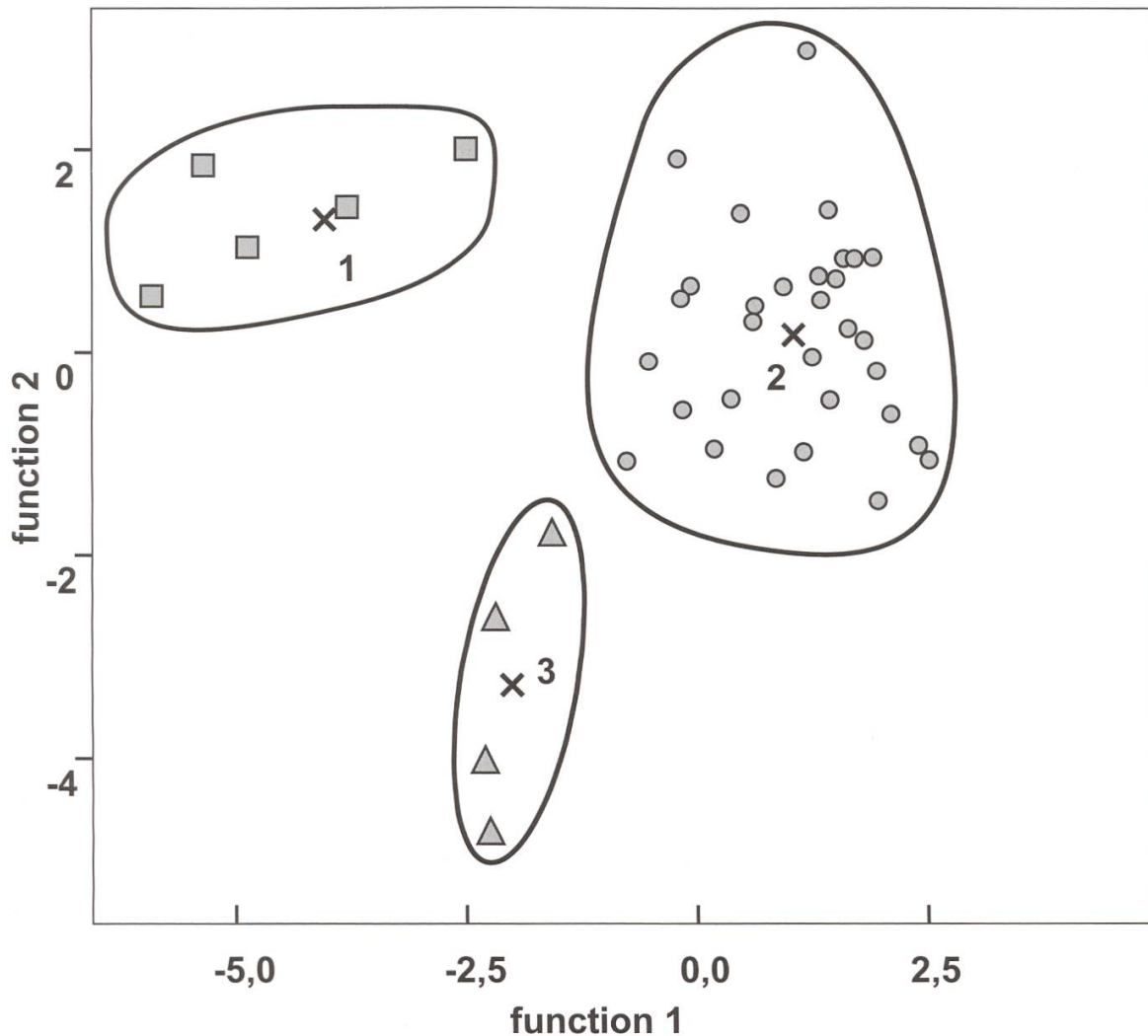


Fig. 12. Canonical discriminant analysis to distinguish *Trogulus falcipenis*, *T. karamanorum* sp. nov. and an unknown *Trogulus* species from Velebit Mts. – 1/squares: *T. falcipenis*; 2/circles: *T. karamanorum* sp. nov. 3/triangles: *Trogulus* sp. from Velebit. Crosses: centroids.

ment of tarsus IV: ♂ 0.175 mm (difficult to measure); – **length of median segment of tarsus IV:** ♂ 0.1 mm (difficult to measure); – **length of distal segment tarsus IV/length of inner segment of tarsus IV:** ♂ 1.75; – **length of leg II/body length:** ♂ 1.22.

Tarsus of leg III just reaches (when stretched backwards) rear end of opisthosoma.

Genital morphology (Fig. 11): Truncus conspicuously slender, most slender in lower two thirds, slightly enlarged distally and basally (in lateral view), tapering from below glans to basis and there slightly enlarged (in ventral view), glans slender (in dorsal/ventral view), moderately flattened (in lateral view), stylus strong, distinctly bent at tip; scattered setae medium-sized.

Variability: Due to small material no data available.

Ecology: No data available.

Distribution (Fig. 5): Croatia, according to present knowledge endemic to Mljet Island.

Derivatio nominis: Derived from Melita, the ancient Latin name for Mljet Island.

Discussion: As we assume *T. melitensis* sp. nov. to be restricted to Mljet Island, we assign a former record of *T. tricarinatus hirtus* from Mljet to the paratype series (see above).

The *Trogulus falcipenis* clade

Molecular genetics (Fig. 2): The clade possesses many autapomorphies and is supported in all calculated phylogenies by high bootstrap values. Between-group distance of cyt b of the *T. hirtus* and *T. falcipenis* clades amounts to 21.7%. Within the clade we distinguish two species, *T. falcipenis* KOMPOSCH, 2000 and *T. karamanorum* sp. nov., separated by distance values of 14.9–15.8%. Species differentiation within the clade is further supported by genital morphology and morphometric characters (Fig. 12).

Morphological characters: We could not identify morphological characters shared by both species of the clade except for the smaller glans penis in comparison to the species of the *T. hirtus* clade (see species accounts).

Distribution (Fig. 3): From the south-eastern Alps (NE Italy to W and C Slovenia and Austria in S Carinthia) to the south along the Dinaric Alps to the Pindos Mountains in Greece. Large distributional gaps are likely due to little sampling in Croatia, Herzegovina and Albania.

Doubtful records: The specimens listed below from Croatia (Velebit Mt. and Cres Island) and Herzegovina (Nemila) are very small (♂ 3.8–3.9 mm, ♀ 3.85 mm) and differ in penis morphology and morphometric distances (Fig. 12) from *T. falcipenis* and *T. karamanorum* sp. nov. As the limited and heterogeneous material is not likely to be used as a basis for describing a further species within this difficult group, new collections are needed to verify the relationship of these specimens. Croatia: Dalmatia, Cres Island, north, 200–300 m (N: 44° 58', E: 14° 24'), litter under oak trees, 1 ♂, C. Deeleman leg. 29. 10. 1980 (CCD) [paratype of *T. falcipenis*]; Velebit Mt., 400 m (N: 44° 43', E: 14° 54'), Boven Jablanac, splete i kamen, SE Rab, S Starigrad, Naquin, 1 ♂, C. Deeleman leg. 18. 10. 1980 (CCD), penis lost [paratype of *T. falcipenis*]; Velebit Mt., Velika Paklenica Gorge (UTM: WK 30), 300 m (N: 44° 18', E: 15° 28'), litter, sieving, 1 ♀, L. Slana, M. Stangelj, M. Slana-Novak & T. Novak leg. 5. 4. 1986 (CNS 41/1986); Studenci (UTM: WK 35), 580 m (N: 44° 43', E: 15° 20'), litter, sieving, 1 ♀, L. Slana, M. Stangelj, M. Slana-Novak, T. Novak leg. 4.

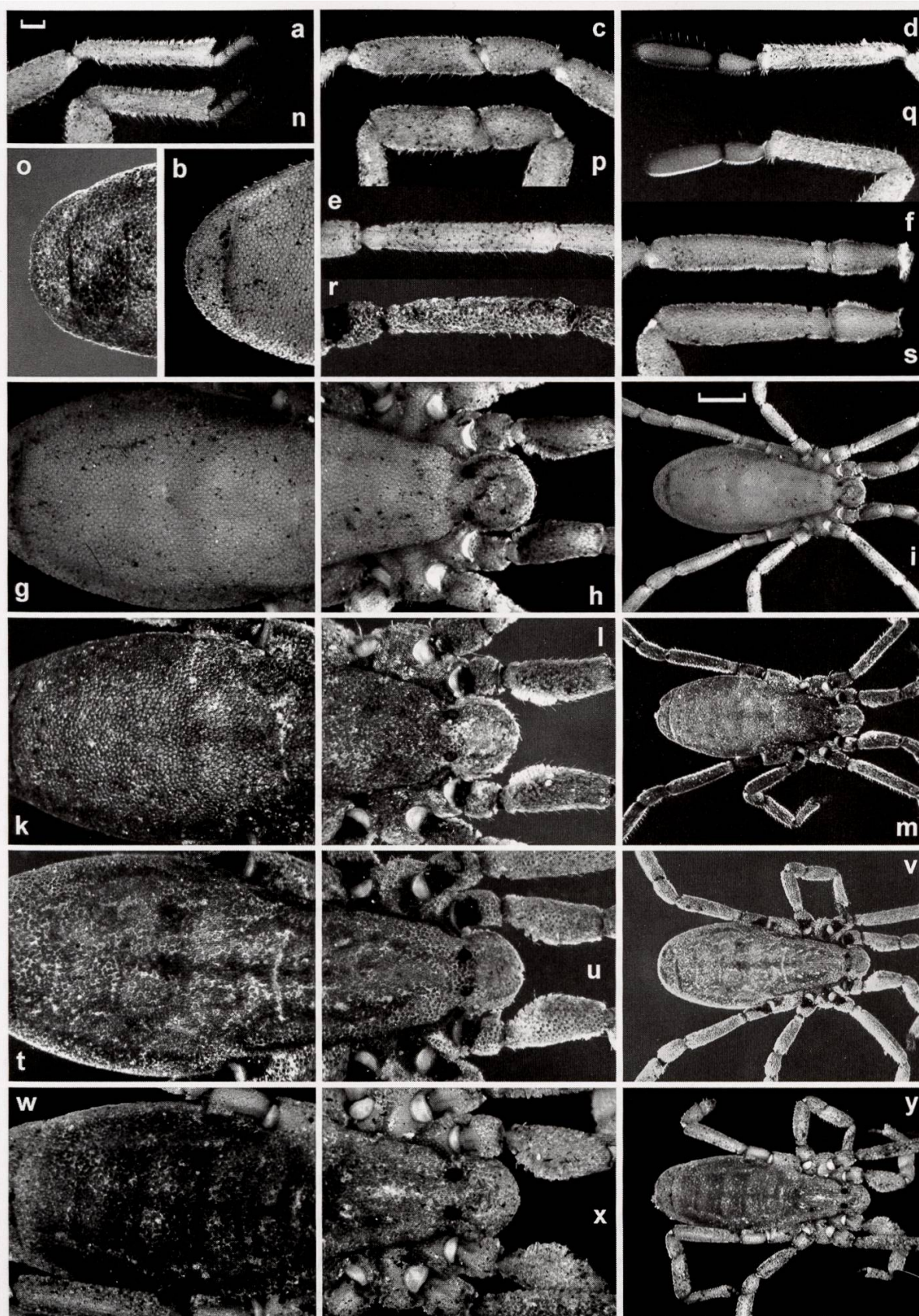


Fig. 13. Dorsal side and legs of males of the *Troglus falcipenis* clade. – a–m: *T. falcipenis* (a–i: Korschuta, paratype, CJM 3241; – k–m: Topla valley, CJM 4952); – n–y: *T. karamanorum* sp. nov. (n–v: Gjonovitze cave near Gostivar CJM 4889; – w–y: Camp Valdanos, N Ulcinj, CJM 4882). – Metatarsus and tarsus IV (a, n); patella and tibia IV (c, p); metatarsus and tarsus II (d, q); femur and trochanter IV (f, s); femur II (dorso-lateral view; e, r); scutum of opithosoma (g, k, t, w); prosoma, coxae I–IV and femora I (h, l, u, x); dorsal side of body with parts of legs (i, m, v, y). Scale line is 1.0 mm (i, m, v, y), for all others 0.2 mm.

4. 1986 (CNS 42/1986); Mt. Zecjate (we consider this to be Mt. Zecjak, Dalmatia, Velebit Mt.) (N: 44° 42', E: 14° 59'), 1 ♀ (SMF 1355); Bosnien-Herzegovina: Nemila (N: 44° 19', E: 17° 54'), 1 ♀, Reitter leg. (NHMW) [paratype of *T. falcipenis*].

***Trogulus falcipenis* KOMPOSCH, 2000** (Figs. 3, 12, 13a–m, 14a–g)

Trogulus falcipenis; Komposch (2000): Spixiana 23 (1): 1–14 (partim: series from Austria and Slovenia).

Trogulus falcipenis – Novak (2004b): Gortania, 26: 22 (records).

Trogulus falcipenis – Novak, Delakorda & Novak (2006): Zootaxa, 1325: 270 (records).

Material examined: Holotype: **Austria**: Kärnten, Koschuta, Karawanken, S Zell-Pfarre, NW Koschutnik, between Koschutahaus and Grosalm, 1370–1410 m (N: 46° 27' 0", E: 14° 23' 04"), sieving of deep leaf litter in *Fagus sylvatica* forest on slope near tree line, dwarf *Fagus* bushes, ♂, C. Komposch leg. 4. 7. 1995 (NHMW 19105).

Paratypes (examined material only, for further records see Komposch 2000): **Austria**: Kärnten, Koschuta, Karawanken, S Zell-Pfarre, NW Koschutnik, between Koschutahaus and Grosalm, 1370–1410 m (N: 46° 27' 0", E: 14° 23' 04"), deep leaf litter in *Fagus sylvatica* forest on slope near tree line, W exposed, sieved, 1 ♂ (out of 1 ♂ 1 ♀), B. & C. Komposch leg. 6. 9. 1999 (CJM 3241); 1 ♀ (out of 4 ♀), from the same locality, B. & C. Komposch leg. 30. 7. 1999 (CJM 3242); **Slovenia**: Nanos, W Postojna, Rebrnica, E Lozice, (N: 45° 46', E: 14° 09'), 1 ♂, Ganglbauer leg. 25. 6. – 4. 7. 1894 (NHMW 19711).

New material examined: **Slovenia**: Topla valley near Črna, 931 m (N: 46° 28' 51", E: 14° 46' 07.4"), coniferous forest near stream, depressions with moss, very damp, sieving, 1 ♂ 1 juv., A. Schönhofer, T. Novak & N. Maicen leg. 18. 5. 2006 (CJM 4952); Snežnik Mt., 1450 m (N: 45° 36', E: 14° 26'), 1 ♀, J. Martens leg. 10. 7. 1974 (CJM 4796).

New material not investigated (data kindly provided by T. Novak, all det. by T. Novak): **Kroatia**: Istria, Učka Mt. (UTM: VL 31), 950 m (N: 45° 19', E: 14° 08'), pitfall traps, 1 ♂, 1 juv., F. Gasparo leg. 10. 9. – 6. 10. 1990 (CNS 100/2000); **Slovenia**: Village Kandrše, 13 km W Zagorje ob Savi, Jama v Lipovici (formerly Lovrinova jama), UTM: VM 91, 510 m (N: 46° 08', E: 14° 50'), 1 ♂, Kuštor & Novak leg. 16. 05. 1979, (IZRK 7025); N Goteniški Snežnik (UTM: VL 74), 1180 m (N: 45° 35', E: 14° 46'), leaf litter, *Fagus*, *Picea*, 1 ♀ 1 juv., L. Slana & T. Novak leg. 28. 5. 2000 (CNS 246/2000); Peca Mt., below

the monument, 700 m (N: 46° 29', E: 14° 45'), 1 ♂, F. Janžekovic leg. 10. 08. 1999 (CNS 66/2002); Peca Mountain, below the monument (UTM: VM 85), 1400 m (N: 46° 29', E: 14° 45'), 4 ♂ 1 ♀ 2 juv., F. Janžekovic leg. 10. 08. 1999 (CNS 75/2002); Peca Mountain, near cattle pen, (N: 46° 29', E: 14° 45'), 2 ♂, F. Janžekovic leg. 10. 08. 1999 (CNS 86/2002); Vršic Mt., Mihov dom, alpine hut shelter (UTM: VM 04), 1100 m (N: 46° 28', E: 13° 47'), 1 ♀, Vršic leg. 07. 1980 (CNS 641/2002); Oblakov vrh (UTM: VM 10), 700 m (N: 46° 03', E: 13° 54'), gravel with decomposing plant material, 1 ♂, T. Novak leg. 1. 8. 2000 (CNS 376/2000); Javorje, Peca Mountain, 9 km NW Topolšica, road 425 between Sleme and Crna na Koroškem (UTM: VM 95), 1340 m (N: 46° 09', E: 14° 10'), 1 ♀, M. Tajzel leg. 11. 10. 2000 (CNS 1219/2002); S of Ludranski Vrh, N Ljubno, Smrekovec Mt., near Podrta bajta (UTM: VM 84), 1300 m (N: 46° 25', E: 14° 52'), 1 ♀, M. Potocnik leg. 16. 09. 2000 (CNS 1374/2002); Bela pec Mt., northern slope (UTM: VM 84), 1370 m (N: 46° 25', E: 14° 53'), 1 ♂, M. Tajzel leg. 07. 08. 2000 (CNS 115/2003); Topla valley (UTM: VM 85), 1260 m (N: 46° 28', E: 14° 46'), 1 ♂, L. Slana & T. Novak leg. 12. 07. 2003 (CNS 182/2003); Olševa, Zadnji kraj (UTM: VM 74), 1380 m (N: 46° 25', E: 14° 41'), *Alnetum viridis*, leaf litter sieving, 1 ♀, L. Slana & T. Novak leg. 28. 06. 2003 (CNS 708/2003); Planinsko polje, northern margin, Vranja jama cave, (UTM: VL 48), 500 m (N: 45° 51', E: 14° 34'), 1 ♂, biology student leg. 23. 06. 1983 (CNS 82/2004); 250 m SE Sveti trije kralji (UTM: WM 16), 720 m, N: 46° 36', E: 15° 09', sieving of mixed forest leaf litter, 1 ♂, L. Slana & T. Novak leg. 20. 08. 2005 (CNS 89/2005); Kapunar Mt. (UTM: WM 16), 960 m (N: 46° 36', E: 15° 14'), *Fageto-Piceetum* leaf litter sieving, 1 ♂ 1 ♀ 1 juv., T. Novak leg. 19. 08. 2005 (CNS 98/2005).

Molecular genetics (Fig. 2): The only sequenced specimen (CJM 4952) shows many autapomorphies and distance values of 14.9–15.8% to the related *T. karamanorum* sp. nov. from the southern and central Balkans. This close relationship is strongly supported by all topologies.

Diagnosis (Figs. 13a–m): A very small *Trogulus*, the smallest within its geographical range; more slender and with longer legs than *T. karamanorum* sp. nov., eye interdistance larger, colouration with reddish tinge. Glans penis with a deep lateral trough (in ventral view). Metatarsus III (when leg stretched backwards) surpasses rear end of opisthosoma.

Similar species: Body clearly smaller than in species of the *Trogulus tricarinatus* species-group which are present in the *T. falcipenis* distributional range. In northern to southern inland Croatia there probably exists another very small species of the *T. hirtus* species-group (see doubtful records *falcipenis* clade). Due to the restriction of *T. falcipenis* to subalpine altitudes (roughly above 1000 m) a syntopic occurrence of both species is not likely.

Description: Body (Figs. 13g–m): No Y-shaped median ridge on dorsal prosoma; area irregularly elevated and only partly void of papillae, therefore no clear median stripe visible if soil-encrusted; papillation of opisthosoma regular, without changes of density, therefore no median and transversal ridges on opisthosoma present; suture between prosoma and opisthosoma clearly visible; body colouration partly reddish, blackish at joints between coxae and trochanters.

Eye mound and front cap (Figs. 13h, l): Eyes less than their diameter from lateral border of front cap, exposed to side of cap, giving the species a "wide-eyed" appearance; eye mound low, only slightly elevated, eyes separated by a shallow depression.

Measurements: ♂ (n=4), ♀ (n=2): – **Body length**: ♂ 4.35–4.6 mm, ♀ 4.5–4.7 mm; – **DSII/BSII**: ♂ 1.74–2.19; ♀ 1.61–1.97; – **eye interdistance**: ♂ 0.4–0.42 mm; ♀ 0.42–0.46 mm; – **length of leg II**: ♂ 5.85–6.6 mm; ♀ 5.7–6.1 mm; – **length of tibia II**: ♂ 1.16–1.35 mm; ♀ 1.18–1.24 mm; – **length of tibia IV**: ♂ 1.12–1.29 mm; ♀ 1.08–1.21 mm; – **body width**: ♂ 1.6–1.75 mm; ♀ 1.8 mm; – **coxa II interdistance**: ♂ 1.1–1.2 mm; ♀ 1.18 mm; – **coxa IV interdistance**: ♂ 1.92–2.0 mm; ♀ 2.04–2.05 mm; – **length of leg II/body length**: ♂ 1.34–1.43; ♀ 1.27–1.30. Metatarsus III (when leg stretched backwards) surpassing rear end of opisthosoma.

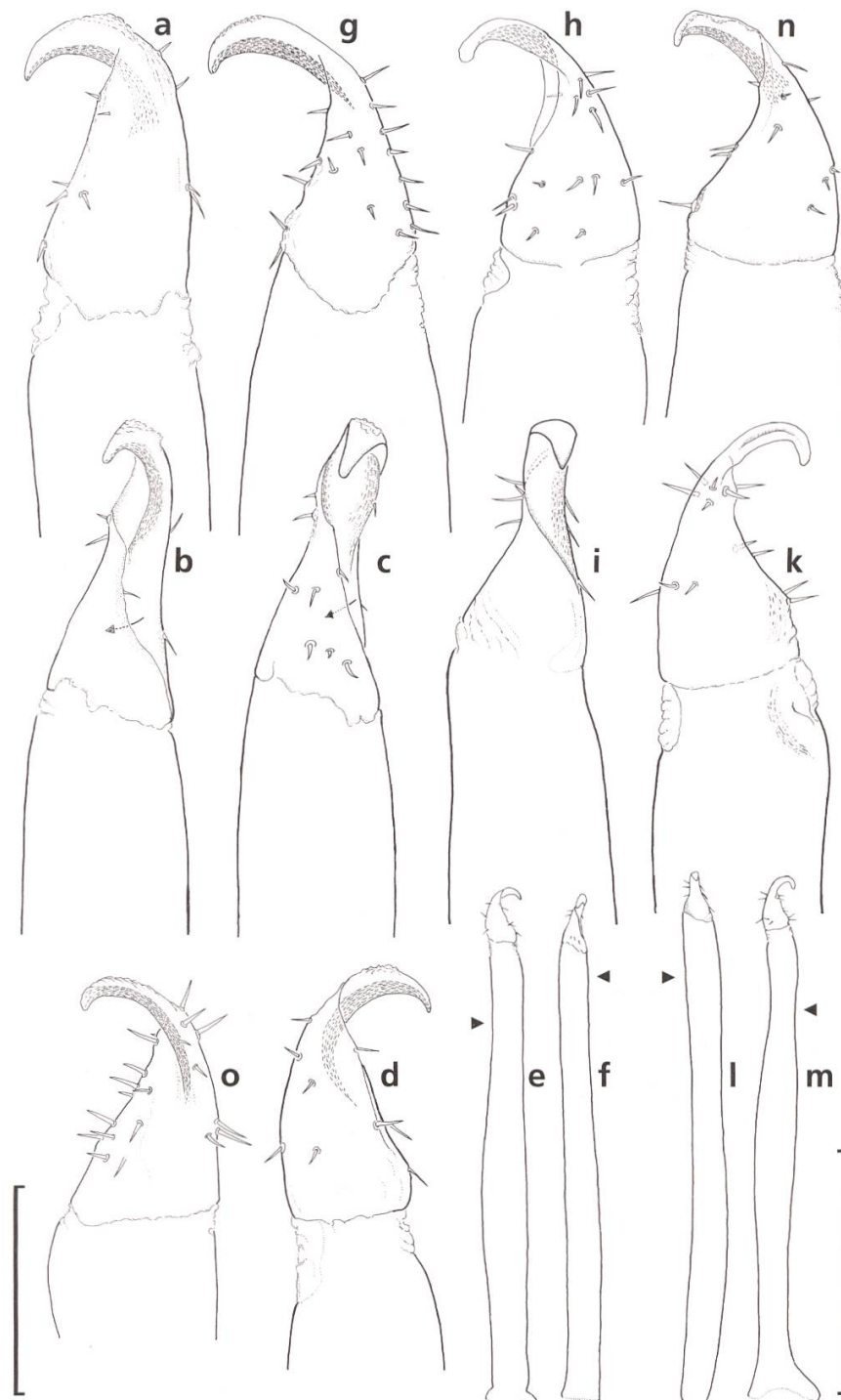
Genital morphology (Figs. 14a–g): Truncus slightly inflated in lower half, narrowing towards basis and glans (in ventral view), parallel-sided, with conspicuous cuticular borders (not indicated in Figs. 14e–f); glans slender, distinctly higher than broad (in dorsal/ventral view), a lateral deeply incised trough running all over length of glans below stylus (see arrows in Figs. 14b–c).

Variability: Due to the small material at our disposal not yet worked out. One male from Slovenia (Nanos) differs by its ratio of the tarsus II segments.

Ecology: According to Komposch (2000) confined to the subalpine belt of the south-eastern Alps; our own observations support this view. *T. falcipenis* lives in syntopy with other typical subalpine species like *Holoscotolemon unicolor* ROEWER, 1915, *Trogulus tingiformis* C. L. KOCH, 1848, *Paranemastoma bicuspidatum* C. L. KOCH, 1835 and *Nemastoma triste* C. L. KOCH, 1835 (syntopic with CJM 4952). Habitats range from humus cover of subalpine meadows and different forest types to wet moss-covered banks along streams in coniferous forest (see Komposch 2000).

Distribution (Fig. 3): Endemic to the south-eastern border of the Alps, ranging from north-eastern Italy (Prov. Udine) to western and central Slovenia, slightly crossing into SE Austria (Carinthia). The southern border is not yet identified but *T. falcipenis* is probably restricted to higher altitudes, thus

Fig. 14. Penis morphology of the species of the *T. falcipenis* clade. Glans penis and distal part of truncus (a–d, g–k, n–o; a, g, h, n, o dorsal view; b, c, i lateral view; d, k ventral view); total penis (e–f, l–m; f, l lateral view, e, m ventral view). – a–g: *T. falcipenis*. a–f: Topla-Tal, (CJM 4952), g: Koschuta, paratype (CJM 3241). – h–o: *T. karamanorum* sp. nov. h–m: Gjonovice (CJM 4889), n: Vermoša (NHMW 19713), o: Rumija Mt. (CJM 4877). – Left scale line 0.1 mm (a–d, g–k, n–o), right scale line 0.5 mm (e–f, l–m). Arrows in b and c indicate lateral trough of glans, in e–f, l–m they indicate differences in truncus symmetry.



confined to the southern Alps proper. Records from northern Croatia (Fig. 3, questionmarks) at lower altitude likely belong to a similar, yet undescribed taxon (treated here as *Trogulus* sp. "Velebit", see *T. falcipenis* clade). 54% of all records range from 1000–1800 m, only 15% are situated between 200 m and 700 m.

Discussion: While Komposch (2000) had no access to molecular genetic markers he regarded the *falcipenis* clade of the cyt b topology (Fig. 2) as a single species distributed from the south-eastern Alps to Montenegro and Albania (no records from Greece and the Republic of Macedonia were available

to him). The present results indicate genetic and morphological differences between the southern and northern populations, and they obviously belong to two distinct species. The type locality of *T. falcipenis* lies in south-eastern Austria and therefore the taxon name *T. falcipenis* applies to the northern populations; presently no records are known south of Slovenia. The paratype series of *T. falcipenis* are composed of more than one species.

***Trogulus karamanorum* sp. nov.** (Figs. 3, 13n–y, 14h–o, 15)

Trogulus falcipenis KOMPOSCH, 2000; Komposch (2000): Spixiana 23 (1): 1–14 (partim; records from Albania, Montenegro and Serbia).

Holotype: **Serbia**: Gostivar, 415 m (N: 41° 42' 04", E: 20° 55' 01.6"), near Gjonovica cave in dry *Carpinus* forest, sieving, ♂, A. Schönhofer, I. Karaman, M. Komnenov & S. Hristovski leg. 18. 4. 2006 (CJM 4889).

Paratypes: **Albania**: N Albania, Vermoša, NNE Shkoder (N: 42° 35', E: 19° 42'), 2 ♂ 1 ♀, A. Penther leg. 17. 6. 1914 (NHMW 19713) [paratype of *T. falcipenis*]; **Herzegovina**: Orjen Mt., Bijela gora, Dubovac (region at Orovac), (N: 42° 40', E: 18° 29'), 2 ♂ 3 juv., I. Karaman leg. 11. 6. 2005 (CIK 1436); **Greece**: W Macedonia, Pindos Mts., Grevena, Smixi, 1150 m (N: 40° 03', E: 21° 07'), 2 ♂, A. Riedel leg. 2001 (CJM 3025); Epirus, Vikos Gorge near Monodendri, 1002 m (N: 39° 52' 53", E: 20° 45' 19"), oak forest, trunks covered by lichens and moss, sieved from leaf litter, 1 ♂, A. Schönhofer leg. 4. 4. 2006 (CJM 5350); road E92a between Penagia und Metsovo, 1084 m (N: 39° 48' 12", E: 21° 18' 25"), pine forest and subalpine meadows, sieved from wet moss and between stones near stream, 1 ♂ 1 ♀, A. Schönhofer leg. 2. 4. 2006 (CJM 5034); **Republic of Macedonia**: Same locality and data as for holotype, 1 ♂ 7 ♀ 10 juv.; Karaorman Mt., N Struga, Tašmaruništa, Mlečnik, 1007 m (N: 41° 16' 35.7", E: 20° 38' 50.2"), dry beech and oak forest, sieving litter, 2 ♂ 2 ♀ 4 juv., A. Schönhofer, I. Karaman leg. 21. 4. 2006 (CJM 5032); bridge Elenskok crossing river Mala reka on the road to Lazaropole, 665 m (N: 41° 32' 31.6", E: 20° 37' 47.9"), dry deciduous oak forest, sieving litter, 1 ♂ 3 ♀ 2 juv., A. Schönhofer & I. Karaman leg. 20. 4. 2006 (CJM 5022); Galičica Mt., road between Trpejca and Oteševo, 1500 m (N: 40° 57', E: 20° 49'), oak and beech forest, sieving litter, 2 ♂, A. Schönhofer & I. Karaman leg. 22. 4. 2006 (CJM 4994); S Skopje, Skopska Crna Gora Mt., Monastir Sveti Ilija (St. Ilija), 618 m (N: 42° 08' 0", E: 21° 23' 27.2"), valley with stream and deciduous forest, in stony debris and sieving near stream, 2 ♂, A. Schönhofer, I. Karaman & M. Komnenov leg. 16. 4. 2006 (CJM 4933); Galičica Mt., Leskoec, 1033 m (N: 40°

57' 27.3", E: 20° 52' 35.3"), oak forest with *Clematis*, sieving litter and under stones, 1 ♀, A. Schönhofer leg. 22. 4. 2006 (CJM 5349); Pelister Mt., Debel Rid S of Niže Pole, 1313 m (N: 40° 59' 25.2", E: 21° 14' 0.0"), river Ezerska Reka, open meadows with streams, *Caltha palustris* and other floral elements characteristic for C European highlands, birch and beech forest, sieving leaf litter and under stones, 1 ♀, A. Schönhofer & I. Karaman leg. 25. 4. 2006 (CJM 5352); Matka valley, 350 m (N: 41° 57' 13.5", E: 21° 17' 43.5"), W Skopje, small valley near dam, beech forest, sieving leaf litter under *Buxus* and digging in stony debris, 1 ♀, A. Schönhofer & M. Komnenov leg. 17. 4. 2006 (CJM 5353); Kožuf Mt., Smrdлива voda, 736 m (N: 41° 11' 31.7", E: 22° 16' 53.6"), beech forest near stream, sieving leaf litter, 4 ♂ 3 ♀ 1 juv., A. Schönhofer & I. Karaman leg. 26. 4. 2006 (CJM 5152); same locality, 1 ♀, S. Stanković leg. 21. 7. 2000 (CIK 1360); Bistra Mt., Monastir St. Jovan Bigorski, Radika-Tal bei Rostuše, 728 m (N: 41° 37' 7.6", E: 20° 36' 34.8"), beech forest on chalk debris, below stones and sieving chalk gravel, 1 ♂ 1 juv., I. Karaman leg. 5. 8. 1999 (CIK 1489); Šar planina Mt, Mountain house Jelak, under stone, 840 m (N: 42° 01' 39" E: 20° 51' 54"), 1 ♂, M. Komnenov leg. 1. 6. 2003 (CMK); Bistra Mt., Mavrovo, traps, 1 ♂, M. Komnenov leg. 18. 9. 1999 (CMK); **Montenegro:** Monastery Morača, Morača valley, 298 m (N: 42° 45' 52.8", E: 19° 23' 35.0"), dense forest on slope above rocks, heavy cover of moss and lichens, under stones and sieved, 2 ♂ 2 ♀ 1 juv., A. Schönhofer leg. 8. 5. 2006 (CJM 5136); same locality, 1 ♂, I. Karaman leg. 16. 8. 1985 (CIK 403c); same locality, 1 ♀ 1 juv., I. Karaman leg. 6. 5. 1997 (CIK 1522); Budva, 187 m (N: 42° 17' 36.1", E: 18° 49' 7.5"), forest of evergreen hard-leaved shrubs and *Erica arborea* with few large cherry trees, sieved and under stones, 1 ♀, A. Schönhofer leg. 10. 5. 2006 (CJM 5348); Durmitor Mts., Crno Jezero, 1450 m (N: 43° 09', E: 19° 05'), W Žabljak, on the lake shore, 1 ♂ 1 ♀, A. Ausobsky leg. 16. 9. 1974 (CJM 2817); Rumija Mt., 202 m (N: 42° 05' 20.9", E: 19° 17' 25.4"), near Ostros, *Castanea sativa* forest, sieving in moss covered clearings, 2 ♂ 3 ♀, A. Schönhofer leg. 9. 5. 2006 (CJM 4877); around Camp Valdanos, 0–100 m (N: 41° 57', E: 19° 09'), N Ulcinj, evergreen hard-leaved trees and olive plantation at small stream, sieved and under stones, 2 ♂ 3 ♀ 1 juv., A. Schönhofer leg. 10. and 11. 5. 2006 (CJM 4882); same locality, 1 ♂ 2 ♀ 1 juv., I. Karaman leg. 11. 5. 2000 (CIK 1494); same locality, 1 ♀, I. Karaman leg. 10. 5. 2005 (CIK 1466); Ostros, Šasko jezero (N: 42° 04', E: 19° 19'), 1 ♂, I. Karaman leg. 22. 10. 2004 (CJM 5355); southern Dalmatia, Petrovac na moru (formerly Castellastua) (N: 42° 12', E: 18° 55'), 3 ♂ 2 ♀, Stussiner leg. (MNHP 5168); Sustak boven Bar, 300 m (N: 42° 06', E: 19° 07'), *Quercus*, *Carpinus*, 1 ♂ 1 ♀, C. Deeleman leg. 14. 4. 1981 (CCD) [paratype of *T. falcipenis*]; Ulcinj (N: 41° 55', E: 19° 13'), 1 ♂ 2 juv., H. Schweiger leg. 2. 9. 1957 (NHMW 19712) [paratype of *T. falcipenis*]; Virpa-

zar, D. Seoca (N: 42° 13', E: 19° 08'), 1 ♂, I. Karaman leg. 1. 5. 2001 (CIK 1419); Bjelasica, NP Biogradska gora (N: 42° 54', E: 19° 36'), 1 ♀ 1 juv., S. Pešić leg. 28. 5. 2003 (CIK 1420); Gornja, river Morača, Dragovića polje (N: 42° 51', E: 19° 18'), 1 ♂, I. Karaman leg. 8. 6. 2000 (CIK 1425); Durmitor NP, Žabljak, Crno jezero (Black Lake) (N: 43° 09', E: 19° 06'), 1 ♀, S. Pešić leg. 30. 5. 1997 (CIK 1438); Bar, Rumija Mt., Sutorman pass (N: 42° 09', E: 19° 06'), 1 ♀ 1 juv., I. Karaman leg. 4. 5. 1997 (CIK 1451); Danilovgrad, S Tunjevo, Milovička vrela (N: 42° 38', E: 19° 01'), 1 ♀ 1 juv., I. Karaman leg. 26. 4. 1997 (CIK 1467); Bijelo Polje, at the main road, Ravna Rijeka, oak forest (N: 42° 59', E: 19° 39'), 1 ♂, B. Blesic leg. 10. 8. 1988 (CIK 983); Danilovgrad, S Tunjevo, Milovička vrela (N: 42° 38', E: 19° 01'), 1 ♂, I. Karaman leg. 6. 5. 2003 (CIK 1507); same data, 1 ♀ 1 juv., I. Karaman leg. 11. 4. 1997 (CIK 1495); Budva, Prijedor (N: 42° 17', E: 18° 49'), 1 ♀, I. Karaman leg. 16. 6. 2005 (CIK 1508b); Bjelasica, NP Biogradska gora, (N: 42° 49', E: 19° 32'), 1 ♀ 1 juv., S. Pešić leg. 25. 5. 1997 (CIK 1472); **Serbia**: 30 km SE Ivanjica, Deviči (N: 43° 26', E: 20° 23'), 1 ♀ 2 juv., I. Karaman leg. Aug. 1999 (CIK 1391); Tara Mt., Mitrovac, 1000 m (N: 43° 09', E: 19° 17'), 1 ♀, I. Karaman leg. 25. 8. 1982 (CIK 255) [paratype of *T. falcipenis*].

Molecular genetics (Fig. 2): Many autapomorphies and cyt b distance values of 14.9–15.8% separate *T. karamanorum* sp. nov. from the closely related *T. falcipenis*. The intraspecific variation ranges from 0.7–3.3%, indicating considerable local differentiation. The specimen from Rumija Mountain (CJM 4877) is clearly assigned to *T. karamanorum* but exhibits many ambiguous nucleotide positions. We consequently neglect genetic distances in this case.

Diagnosis (Fig. 13n–y): A small and compact *Trogulus* of the *T. hirtus* species-group, more robust than *T. falcipenis*. Eye interdistance smaller than in *T. falcipenis* and colouration without reddish tinge. Truncus penis inflated below glans (in lateral view, Fig. 14l). Legs shorter and more robust than in *T. falcipenis*. Metatarsus III (when leg stretched backwards) not surpassing rear end of opisthosoma.

Similar species: Within the distributional range of *T. karamanorum* sp. nov. minute representatives of the *T. tricarinatus* species-group occur. The presence of a sickle-like stylus is always distinctive for *T. karamanorum* sp. nov. (and other possibly still unknown species of the *T. hirtus* species-group). Note that the north-western distributional limit of *T. karamanorum* sp. nov. is not yet determined, especially in Croatia and Herzegovina co-occurrence with other species of the *T. hirtus* species-group seems to be possible. These might have a hairy appearance as far as they belong to the *T. hirtus* clade and should be easily distinguishable.

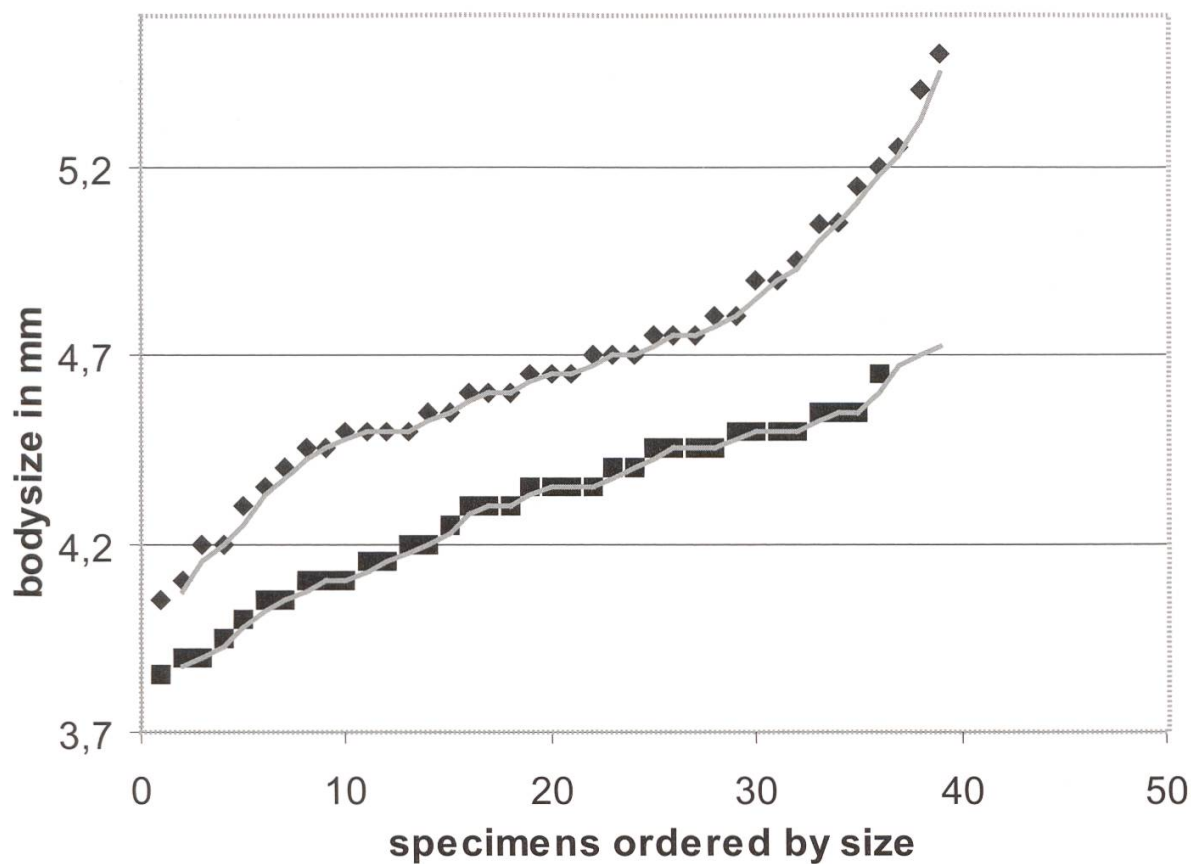


Fig. 15. Range of body size within the available sample of *Trogulus karamanorum* sp. nov. specimens. Increase in males (lower curve) is continuous, in females it is so only in the central part (upper curve). Each square refers to one individual.

Description: Body (Figs. 1, 13t–y): Y-shaped ridge on anterior part of prosoma; area between branches of the Y-shaped ridge with small and widely spaced papillae, and therefore with a clear median soil-encrusted stripe; on dorsal opisthosoma median and transversal ridges present, often arranged in complex patterns of papillae of different density (Figs. 1, 13t, v, w, y); irregular papillation often obscuring the suture between prosoma and opisthosoma; body colouration without reddish tinge, blackish at joints of legs.

Eye mound and front cap (Figs. 13u, x): Eyes about their diameter from lateral border of front cap, directed more dorsally than in *T. falcipenis*, giving a "normal-eyed" appearance; eye mound elevated, eyes separated by a depression.

Measurements: The data derived from specimens considered here as belonging to *T. karamanorum* sp. nov. is very heterogenous, probably reflecting the genetic and ecologic diversity within the species. Females are difficult to separate from other small representatives of *Trogulus* on the Balkans. Measurements given in parentheses indicate data taken from a single very large female from Sutorman Mt. which cannot be assigned to *T. karamanorum* sp. nov. with certainty.

Body length: 43 ♂ 3.85–4.7 mm, 44 ♀ 4.05–5.5 (5.6) mm; all other data referring to 16 ♂ 15 ♀: – **DSII/BSII:** ♂ 1.55–1.94; ♀ 1.53–1.83; – **eye inter-distance:** ♂ 0.36–0.42 mm, rarely up to 0.44 mm; ♀ 0.37–0.46 (–0.47) mm; – **length of leg II:** ♂ 5.1–6.0 mm; ♀ 5.15–6.0 (–6.2) mm; – **length of tibia II:** ♂ 1.03–1.24 mm; ♀ 0.99–1.21 mm; – **length of tibia IV:** ♂ 0.96–1.07 mm; ♀ 0.98–1.16 (–1.22) mm; – **body width:** ♂ 1.5–1.78 mm; ♀ 1.7–2.0 (–2.15) mm; – **coxa II interdistance:** ♂ 1.05–1.23 mm; ♀ 1.1–1.3 (–1.35) mm; – **coxa IV interdistance:** ♂ 1.71–2.08 mm; ♀ 1.93–2.25 (–2.5) mm; – **length of leg II/body length:** ♂ 1.21–1.31; ♀ 1.11–1.21.

Metatarsus III (when leg stretched backwards) reaching rear end of opisthosoma.

Genital morphology (Figs. 14h–m): Truncus more or less parallel-sided (in lateral view), distinctly inflated below glans, then constricted and enlarged for about the central half of truncus, then again distinctly constricted to the small but slightly enlarged basis (in ventral view); cross section of truncus square; glans stout, not elongated (see *T. falcipenis*), stylus distinctly more slender than in *T. falcipenis*, no trough present in glans below stylus (see *T. falcipenis*).

Variability: Quite large. Most variable are body size (Fig. 15), dorsal papillation and shape of truncus penis. The largest males and females come from the Rumija Mts. in Montenegro (CJM 4877). Morphological variability and ecological plasticity is paralleled by a large variety of cyt b haplotypes.

Ecology: This species occurs in a wide range of habitats, from evergreen Mediterranean shrub forest at low altitudes to shallow soils in dry *Quercus* and *Carpinus* forest from 600 to 1000 m, as well as in wet moss-covered banks in high-altitude *Pinus* forest. In contrast to other species of *Trogulus* in the region under consideration, it seems to prefer open woodland habitats where it was more commonly found than in valleys with stony debris. Our data hint at a continuous distribution from sea level to 1500 m without preference of a distinct range, except for Greece where *T. karamanorum* sp. nov. seems to be restricted to altitudes around 1000 m.

Distribution (Fig. 3): Large area in Montenegro, western Republic of Macedonia to Kozuf Mt. and Skopje, southern Serbia (Tara River Canyon, Ivanjica), southern Hercegovina (Orjen area) and probably in large parts of Albania and in north-western Greece. The northern border is still undetermined due to low sampling in Hercegovina. At present a border line can be drawn along Ivanjica, Tara River Canyon to Orjen Mt. The southern border is in the Pindos Mts. in north-western Greece; no records are available from Bulgaria.

Derivatio nominis: The name honours the Karaman family from Serbia who during the lifetime of three generations carried out important zoological

research in the Balkan Peninsula. Stanko L. Karaman (8. 12. 1889, Sarajevo – 17. 05. 1959, Skopje) is famous for his hydrobiology work with pioneering papers on stygobiotic crustaceans (Amphipoda, Isopoda, Thermosbenacea, Bathynellacea), taxonomy and faunistics on Balkan freshwater fishes and important contributions to Balkan Amphibia and Reptilia. Mladen S. Karaman (15. 01. 1937, Skopje – 18. 09. 1991, Kragujevac) contributed to taxonomy and zoogeography of freshwater fishes and on Orthoptera, on taxonomy and faunistics of Isopoda terrestria, various Decapoda and Branchiobdellidae leeches. Ivo Karaman (7. 4. 1963, Skopje) is a dedicated specialist on Balkan Opiliones, Isopoda and Orthoptera.

Discussion: Within the species of the *T. hirtus* species-group *T. karamanorum* sp. nov. covers the largest area and shows the highest amount of genetic differentiation and variation of external characters so far known. However, for the time being it seems not advisable to further split this complex. *T. falcipenis* and *T. karamanorum* sp. nov., the closest relatives, differ in shape of truncus penis, shape of glans and stylus. The deeply incised trough in the glans is present only in *T. falcipenis*.

Acknowledgements

We gratefully acknowledge loans and donations from the following colleagues: Ivo Karaman (University of Novi Sad), Tone Novak and Ljuba Slana (University of Maribor), Peter Schwendinger (Muséum d'Histoire naturelle, Genève), Arturo Muñoz-Cuevas (Muséum National d'Histoire Naturelle, Paris), Jürgen Gruber (Naturhistorisches Museum, Wien), Christa Deeleman-Reinhold (Ossendrecht), Roman Ozimec (Zagreb), Peter Jäger (Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main). I. Karaman accompanied A. S. on a successful collection trip to Serbia and Montenegro and gave access to his rich trogulid collection. T. Novak provided data and helped to collect *Trogulus falcipenis* in Slovenia. J. Gruber and P. Schwendinger provided helpful information on collections under their care and kindly revised an earlier version of the manuscript. The German Academic Exchange Service (Deutscher Akademischer Austauschdienst, Bonn) supported A. S. with a 2.5-months travel grant. The "Landesgraduiertenförderung Rheinland-Pfalz" provided a two-years grant to work on his PhD dissertation. "Wagner-Stiftung" and "Feldbausch-Stiftung", both at Fachbereich Biologie, Mainz University, provided annual travel grants for field work to J. M.

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