Revision of Trogulidae Sundevall, 1833

(Arachnida: Opiliones)

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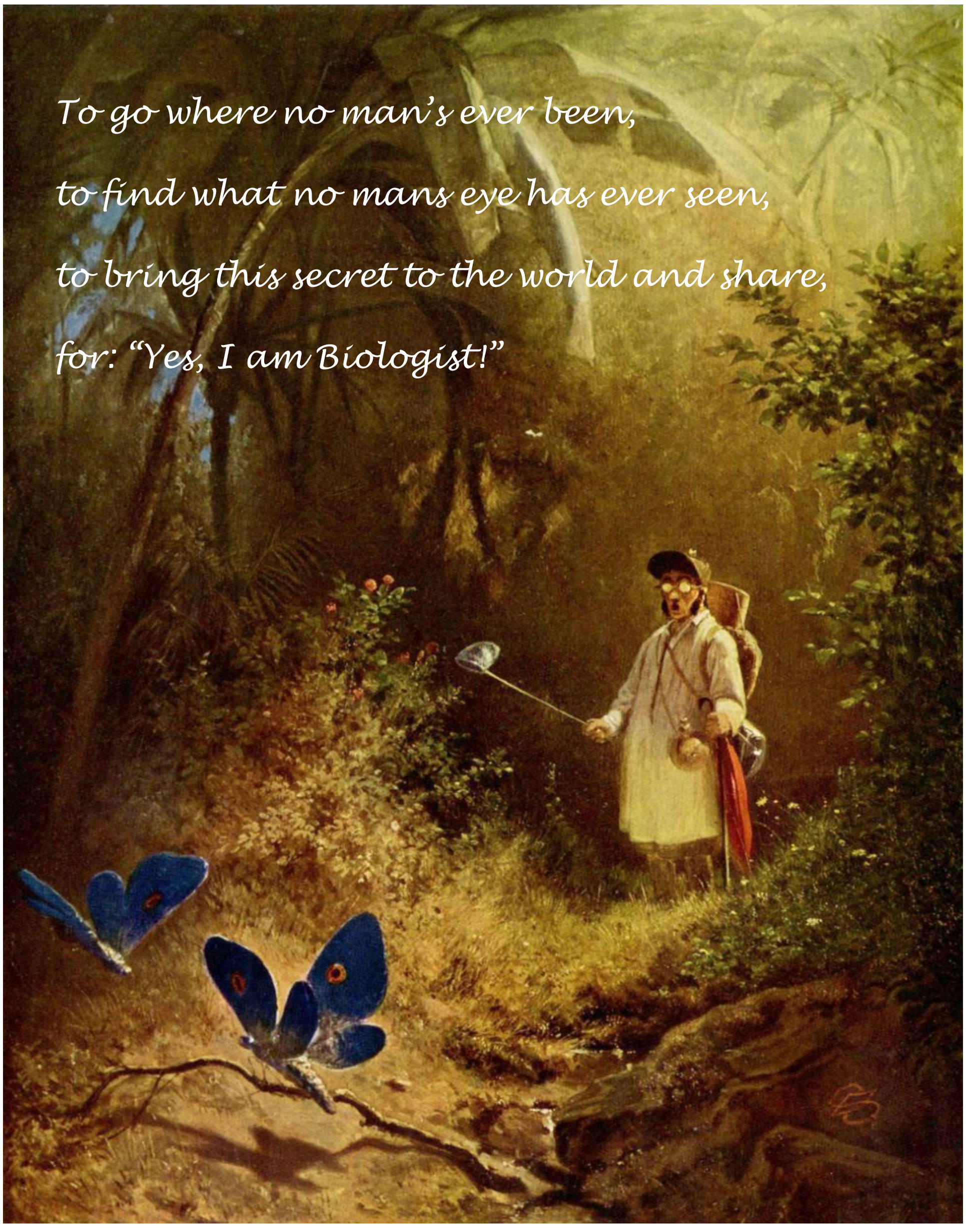


To go where no man's ever been,
to find what no mans eye has ever seen,
to bring this secret to the world and share,
for: "Yes, I am Biologist!"

"Der Schmetterlingsjäger" Carl Spitzweg (1840)

To my family and friends.

For you I am thoroughly thankful!

The chapter 4 has been accepted for publication and the chapter 5 has been published in a slightly modified version:

Chapter 4:

SCHÖNHOFER, A.L., MARTENS J. (in press): Revision of the genus *Trogulus* Latreille: the *Trogulus hirtus* species-group (Opiliones: Trogulidae). In Kropf, C. & Horak, P. (eds). Towards a natural history of arthropods and other organisms. In memoriam Konrad Thaler. Contributions to Natural History **12** (accepted 4.5.2007).

Species epithets to be used for the decription of new species in the published version of this chapter are here addressed as “manuscript name” [man.n.] prior to publication.

Chapter 5:

SCHÖNHOFER, A.L., MARTENS, J. (2008): Revision of the genus *Trogulus* Latreille: the *Trogulus coriziformis* species-group of the western Mediterranean (Opiliones: Trogulidae). Invertebrate Systematics **22** (5), 523-554.

Four species included in this chapter have been published in 2008. In this chapter I uphold “sp. nov.”. In the other chapters the authors are annotated.

Contents

1. Abstract

The relationship and phylogeny of the western Palearctic harvestmen family Trogulidae is investigated. The traditional system of seven genera and approximately 40 species appeared to be artificially composed but a phylogenetic approach and a comprehensive revision has long been sought after. Species are poorly characterised due to their uniform morphology and species evaluation is furthermore complicated by the variability of the few characters used for species delineation. To meet these demands a molecular genetic analysis is accomplished using the nuclear 28S rRNA gene and the mitochondrial cytochrome *b* gene. This analysis incorporates most genera and species of Trogulidae as well as a comprehensive set of Nemastomatidae and Dicranolasmatidae as outgroup taxa. Phylogenetic results of Bayesian analysis, Maximum Parsimony, Maximum Likelihood and Neighbor Joining are compared with distributional data, morphological characters and results of canonical discriminant analysis of morphometric characters and general congruence of these data sets is shown. To demonstrate the applicability of this method the revision of two species-groups within *Trogulus* is set out in detail. The *Trogulus hirtus* species-group and the *Trogulus coriziformis* species-group are revised. The former is in the central and north-western Balkan Peninsula. *T. tricarinatus* ssp. *hirtus* is raised to species level and four new species are described (*T. karamanorum* [man.n.], *T. melitensis* [man.n.], *T. pharensis* [man.n]; *T. thaleri* [man.n.]). The *Trogulus coriziformis* species-group is confined to the western Mediterranean area. *T. coriziformis*, *T. aquaticus* are re-described, *T. cristatus* and *T. lusitanicus* are re-established and four species are described as new (*T. balearicus*, *T. huberi*, *T. prietoi*, *T. pyrenaicus*). In both species-groups two further cryptic species probably exist but were not described. The species groups are shown to represent different phylogenetic levels and this information is used for the revisional work on the genus *Trogulus* as well as for the generic system of Trogulidae. Family status of Dicranolasmatidae is rejected and *Dicranolasma* is shown to be best incorporated within Trogulidae. *Calathocratus*, *Platybessobius* and *Trogulocratus* appear to be polyphyletic and are best to be united within *Calathocratus*, the oldest name of this set. The cryptic diversity within Trogulidae, especially in *Trogulus* and the composed genus *Calathocratus* rates to 150-235% and is thereby remarkably high for a group of the generally well researched European fauna. Genetic features of the group such as heteroplasmy, the possibility of major gene rearrangements and usability of the cytochrome *b* gene for phylogenetic studies in Opiliones are outlined.

2. General Introduction

The current discussions on biodiversity and its worldwide loss are mainly focused on centres of species richness in the tropics. However, it is important not to lose focus on the diversity of groups of organisms in those areas that have been well researched since the onset of systematic investigation. Cryptic species, a term which points to species not to be delimited by means of easy-to-recognise morphological characters, are still undiscovered and are often hidden among accepted taxa. Although difficult to recognise their uniqueness has to be outlined by taxonomists. As species they have important value for the understanding of evolution, biogeographical processes and may even turn out to exhibit still hidden potential as genetical, medical and chemical resources.

Often cryptic diversity can be expected to be present in groups of organisms whose taxonomy is confused and where species delineation and descriptions are obscure. Within the European harvestmen the family Trogulidae is such a group, not only in respect to species taxonomy but also for its questionable generic concept and family relationships. Many new species have been described in recent times but closely related ones were rarely outlined and a general revision has long been overdue. Apparently this group of soil-dwelling Opiliones rejects a purely morphological approach to systematic understanding. They exhibit only few morphological characters useful for species recognition in combination with variation that is difficult to resolve.

Within the last two decades molecular genetics have shown to be extremely useful to delineate cryptic diversity in almost all groups of organisms. To obtain a molecular phylogeny of the group preliminary a molecular genetic approach of Trogulidae systematics was chosen using the mitochondrial cytochrome *b* gene (cyt*b*) and the nuclear 28S rRNA gene (28S). Results were corroborated with evidence from morphometrical and distributional data to finally evaluate morphological characters for use in species determination.

Sufficient material became available to revise two species-groups within the genus *Trogulus* (chapters 4, 5) and to outline the necessary taxonomic treatment of genera within Trogulidae (chapters 6.4.1, 6.4.2) making this molecular genetic approach successful. In addition a systematic concept based on distribution and genital morphology is proposed for *Trogulus* (chapter 6.4.3). The use of genital morphology in species systematics of *Trogulus* is discussed and a minimum distance value for the cyt*b* gene is proposed to be indicative for lineages worth to be investigated for the existence of possible cryptic species (chapter 6.4.4).

Subsequently the amount of cryptic diversity within Trogulidae could be estimated (chapter 6) and the family is shown to be useful for biogeographic investigations (chapter 5.4.3).

3. Material and Methods

This chapter summarises all applied methods of the chapters 4 to 7. Detailed data on material used for genetic analysis and morphological investigation is listed in the respective chapter.

3.1. Material

Essential for the molecular genetic part of this study was fresh and sufficiently preserved material. For morphology we could largely rely on our own material, as well as studying extensive material from several private and public collections listed below. Full accounts of the material examined are available in the respective chapters 4 (Table 4.1), chapter 5 (Table 5.1), chapter 6 (Table 6.1) and chapter 7 (Table 7.1).

BMNH	The Natural History Museum, London, UK (Janet Beccaloni)
BRINS	Belgian Royal Institute of Natural Sciences, Brussels, Belgium (Georges Wauthy)
CCD	Collection of C. L. Deeleman-Reinhold, in the collection of Naturalis, National Museum of Natural History, Leiden, The Netherlands
CCP	Collection Carlos Prieto, Universidad del País Vasco, Bilbao, Spain
CEI	Collection Étienne Iorio (Attaché au Muséum national d'Histoire naturelle (MNHN), Nice, France
CIK	Collection Ivo Karaman, Department of Biology and Ecology, University of Novi Sad, Serbia
CIS	Collection Institute Spéologie, material of Stefanie Avram hosted by the „Grigore Antipa" National Museum of Natural History, Bucharest (not accessed).
CJM	Collection Jochen Martens, Institut für Zoologie, Universität Mainz, Germany
CMK	Collection Marjan Komnenov, Skopje, Republic of Macedonia
CMR	Collection Maria Rambla, Universitat de Barcelona, Spain (Dr. Carles Ribera)
CNS	Collection of Tone Novak and Ljuba Slana, Slovenj Gradec, Slovenia
CRO	Collection Roman Ozimec (Croatian Biospeleological Society), hosted by the Croatian Natural History Museum (CNHM), Zagreb, Croatia

CVS	Collection of Vladimír Shilhavy, probably housed by the National Museum, Prague, Czech Republic (material not accessed).
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Dr. Jenö Kontschán)
IZRK	Inštitut za raziskovanje krasa Postojna (Slowenian Karst Research Institute)
MG	Museum Gothenburg, Sweden (material not accessed).
MHNG	Muséum d’Histoire Naturelle, Genève, Switzerland (Dr. Peter Schwendinger)
MNHP	Muséum national d’Histoire naturelle, Paris, France (Dr. Arturo Muñoz-Cuevas)
MSNB	Museo Civico di Scienze Naturali, Bergamo, Italy (Dr. Paolo Pantini)
MTSN	Museo Tridentino di Scienze Naturali, Trento, Italy (material not accessed).
MV	Museo Civico di Storia Naturale, Verona, Italy (Roberta Salmaso)
NHMB	Naturhistorisches Museum Basel, Switzerland (Dr. Ambros Hänggi)
NHMW	Naturhistorisches Museum, Vienna, Austria (Dr. Jürgen Gruber, Christoph Hörweg)
SMF	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (Dr. Peter Jäger)
ZIUV	Zoological Institute University of Istanbul, Turkey (material not accessed).
ZMB	Naturhistorisches Forschungsinstitut, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (Dr. Jason Dunlop)
ZMC	Zoological Museum, Copenhagen, Denmark (Dr. Nikolaj Scharff)

3.2. Molecular Genetic

3.2.1. Laboratory protocols

Tissue, mainly muscle, was removed from the opisthosoma. DNA was extracted using the High Pure PCR Template Preparation Kit (Roche Diagnostics, Mannheim, Germany). In total, 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, 9189–9213 bp) and Cytb-revdeg: 5'-TCN-ACN-GGA-CRN-GMN-CCA-ATT-CAN-GTT-A-3' (position in *Limulus polyphemus* AF216203, 9789–9816 bp). Primers were generated from an alignment of Chelicerata mitochondrial sequences available from GenBank (*Limulus polyphemus* AF216203 [LAVROV et al. 2000], *Mesobuthus gibbosus* AJ716204 [GANTENBEIN-RITTER et al. 2005], *Varroa destructor* AJ493124 [NAVAJAS et al. 2002], *Ornithoctonus huwena* NC_005925 [QIU et al. 2005]) and from our own *Trogulus* sequences.

Additionally cyt*b* was amplified in combination with the internal primers Cytb-for int: 5'-CAA-CCW-GAA-TGA-TAY-TTY-YTA-TTT-GC-3' (combined with Cytb-rev-deg, 185 bp) and Cytb-rev int: 5'-GCA-AAT-AR-AAR-TAT-CAT-TCW-GGT-TG-3' (combined with Cytb-for, 393 bp) designed upon an alignment of the previously sequenced Trogulidae fragments.

In total, 1240 bp of the nuclear 28S rRNA (28S) were amplified using the primer combination ZX1: 5'-ACC-CGC-TGA-ATT-TAA-GCA-TAT-3' and ZR2: 5'-GCT-ATC-CTG-AGG-GAA-ACT-TCG-G-3' (MALLATT & SULLIVAN 1998). To obtain additional sequences we designed internal primers: ZRint1: 5'-GAC-TCC-TTG-GTC-CGT-GTT-TCA-AGA-C-3', ZXint1: 5'-ACT-TTG-AAG-AGA-GAG-TTC-AAG-AG-3' and ZXint2: 5'-CCG-ACC-CGT-CTT-GAA-ACA-CGG-ACC-3'. We used an alignment of our own *Trogulus* sequences and Chelicerata mitochondrial sequences available from GenBank (*Pettalus thwaitesi* DQ518018 (SHARMA et al. 2009), *Limulus polyphemus* AF212167 (WINCHELL et al. 2002), *Pandinus imperator* AY210830, *Aphonopelma hentz*i AY210803 (MALLATT et al. 2004), *Paraphrynus* sp. AY859594, *Mastigoproctus giganteus* AY859587, *Siro rubens* AY859602, *Calocheiridius* cf. *termitophilus* AY859558, *Eremobates* sp. AY859572 (MALLATT & GIRIBET 2006), *Misumenops asperatus* AY210461 (PASSAMANECK & HALANYCH 2006)). Internal fragments were amplified using a combination of ZX1 and ZRint1 (890 bp) or ZR2 and ZXint1 (880 bp).

Beside cyt*b* and 28S the mitochondrial fragments NADH dehydrogenase subunit I (ND1) and 16S rRNA (16S, HWANG & KIM 1999) were investigated for usability for phylogenetic analysis of taxa on species level. To obtain sequences of ND1 the primers ND1-N = LR-N 12945: 5'-CGA-CCT-CGA-TGT-TGA-ATT-AA-3' and ND1-J = LR-J 12261: 5'-TCG-TAA-GAA-ATT-ATT-TGA-GC-3' were used (HEDIN 1997, CROUCHER 1998, JOHANNESEN & VEITH 2001). 540 bp of 16S were amplified using the primer combination 16S A-L: 5'-CGC-CTG-TTT-ATC-AAA-AAC-AT-3' and 16SB-H: 5'-CCG-GTC-TGA-ACT-CAG-ATC-ACG-T-3' (PALUMBI et al. 1991). Additionally 374-397 bp long fragments of 16S were amplified by internal primers Trog ND1-J: 5'-ACA-CCG-GTC-TGA-ACT-CAA-ATC-A-3' and Trog 16S-Nd: 5'-GCT-GCG-GTA-TTT-T(G/A)A-CTG-TAC-3' designed upon an alignment of the previously sequenced 540 bp fragments.

The PCR was performed using pure *Taq* Ready-To-Go PCR Beads (GE Healthcare, Little Chalfont, UK). The PCR protocol for cyt*b* and fragments 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. For 28S (and fragments) 40 cycles of 94 °C for 45 s, 65 °C for 45 s. and 72 °C for 1 min, 45 s. with a final extension in 72 °C for 8 min were used (M. Hedin, pers. comm., modified from MALLATT & SULLIVAN 1998). The PCR protocol for ND1 was 30 cycles of 94 °C for 30 s, 47 °C for 30 s and 72 °C for 30 s with a final extension to 72 °C for 2 min (JOHANNESEN& VEITH 2001). For 16S (and internal fragments) 30 cycles of 94 °C for 30 s, 60 °C for 30 s and 72 °C for 30 s with a final extension to 72 °C for 2 min were used (further details in SCHÖNHOFER 2004).

Sequencing of the PCR products was performed with BigDye *v*. 3.0 and *v*. 3.1 Dye Terminator Cycle Sequencing Kits (Applied Biosystems, Darmstadt, Germany) using primers as mentioned; reactions were electrophoresed with ABI 377 and ABI 3130 automatic sequencer.

In few cases cloning of amplified fragments was accomplished using TOPO TA Cloning® Kit (Invitrogen, Karlsruhe, Germany) or pGEM®-T and pGEM®-T Easy Vector Systems (Promega, Mannheim, Germany) and transferring ligated vectors into chemically competent Echerichia coli cells (TOP10 One Shot™, Invitrogen, or JM109 High Efficiency Cells, Promega). Colonies were picked and checked for positive inserts by amplification using the promoter primers T7: 5'-TAA-TAC-GAC-TCA-CTA-TAG-GG-3' and SP6: 5'-ATT-TAG-GTG-ACA-CTA-TAG-AA-3'. Both primers were used for direct sequencing of positive clones. Vector regions were identified and exclude from sequences using NCBI VecScreen.

3.2.2. Phylogenetic analysis

Sequences were automatically edited using Genotyper (Version 2.0, Perkin Elmer) and Sequencing Analysis 5.2 (Applied Biosystems) 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 datasets was estimated with Modelltest 3.6. (POSADA & CRANDALL 1998) according to the Akaike information criterion (POSADA & BUCKLEY 2004). The 28S/cyt*b*-alignment was tested for heterogeneity using the partition homogeneity test (FARRIS et al. 1994), implemented in PAUP, to assess the appropriateness of combining the data partitions (results see chapters 4 to 6).

Phylogenetic analysis was performed under different approaches: Neighbor Joining (NJ, SAITOU & NEI 1987), and Maximum Parsimony (MP, FARRIS 1983), Maximum Likelihood (ML, SCHMIDT et al. 2002, both implemented in PAUP 4.06b, SWOFFORD 2001) and Bayesian inference of phylogeny (with MrBayes 3.1.2, HUELSENBECK & RONQUIST 2001). In PAUP we conducted heuristic searches with 100 random addition replicates and tree-bisection-reconnection (TBR) branch swapping.

Robustness of clades was estimated by 1.000 and 2.000 bootstrap replicates for NJ and MP (Felsenstein 1985) and via Bayesian posterior probabilities using Markov chain Monte Carlo (MCMC, 500.000 generations, samplefreq=100, burnin=1.000, 4 replicates) conducting four independent runs to avoid entrapment in local optima. Genetic distances were calculated in PAUP using uncorrected p distances and excluding ambiguous data setting "pairwise deletion". The preferred analyses in chapters 4 to 7 differ due to journal requirements.

3.3. Morphological examination and morphometry

Specimens were examined under a stereomicroscope and morphological features were drawn with a camera lucida or photographed with a Wild MPS52 Kodak or a Nikon D80. Measurements (in mm, otherwise indicated) were taken using a microscope with an ocular micrometer disc. A WACOM Tablett Digitizer 2 UD-1218-R (A3) and the program Adobe Photoshop CS2 were used to prepare drawings. For a few drawings, final inking was done using rotring Rapidograph 0.18, 0.25 and 0.35.

Morphometric distances to be included in the discriminant analysis and the species descriptions are listed below, are explained and abbreviated for Appendix 12.4 and illustrated in Fig. 3.1 and 3.2.

body length (BL): total length from front cap to rear end of opisthosoma
body width (BW): maximum width of opisthosoma
coxa II interdistance (CoxII): distance between prolateral sides of left and right coxa II
coxa IV interdistance (CoxIV): distance between lateral sides of left and right coxa IV
eye interdistance (Eyeout): distance between outer borders of left and right lens
interocular distance (Eyeout): distance between inner borders of left and right lens

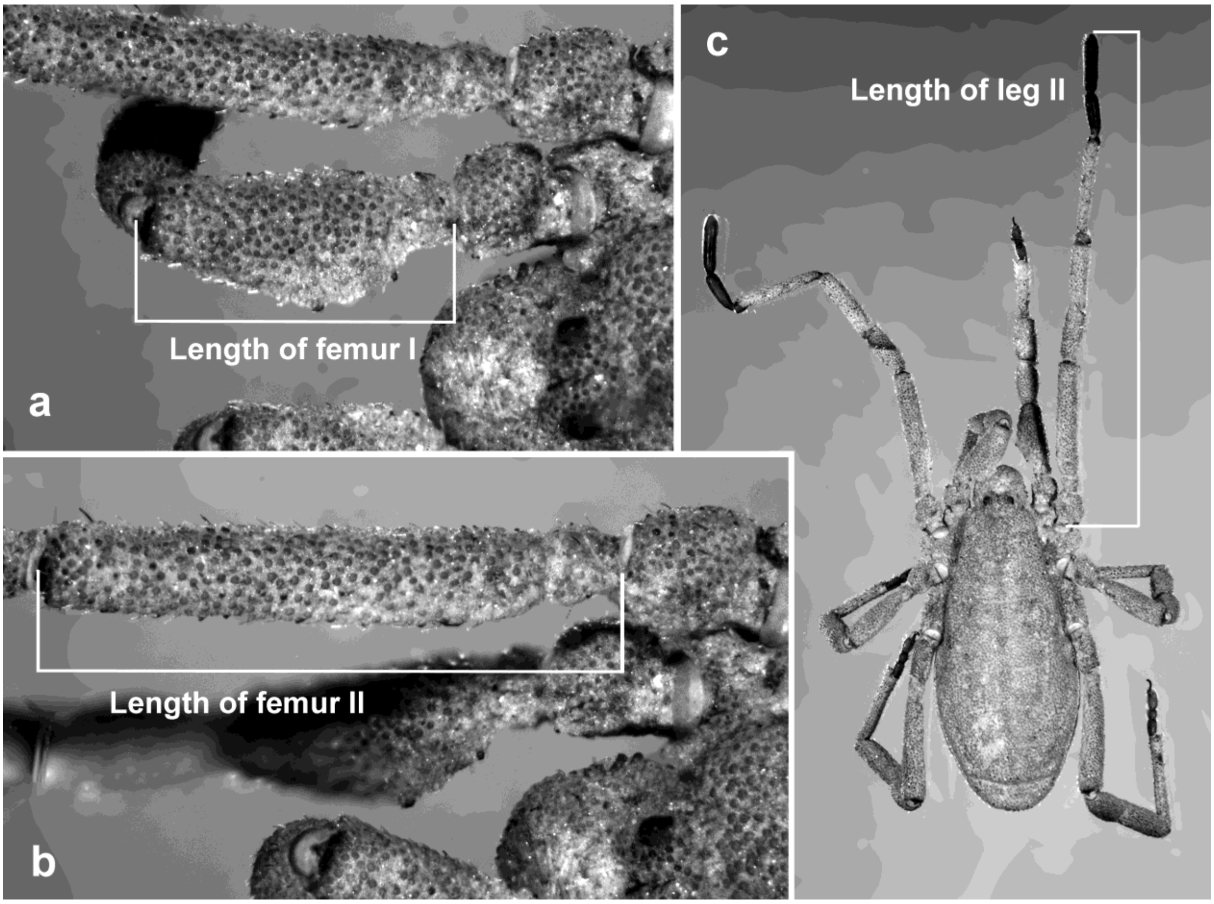


Fig. 3.1. (*a*–c): *Trogulus martensi* Chemini, dorsal view: Morphometric distances; (*a*): Length of femur I; (*b*): length of femur II; (*c*): length of leg II.

length of basal segment of tarsus II (BSII): measured from joint to joint

length of distal segment of tarsus II (DSII): measured from joint to end

length of distal segment of tarsus IV (DSIV): measured from joint to end

length of femur I (FemI): measured from joint to joint

length of femur II (FemII): measured from joint to joint

length of head cap (Lcap): taken from front of head cap to front margin of eye lens

length of leg II (LegII): total length of stretched leg II, from tip to border of coxa II

length of longest hairs on Femur IV: from tip to point of emergence

length of median segment of tarsus IV (MSIV): measured from joint to end

length of metatarsus II (MtII): measured from joint to joint

length of metatarsus IV (MtIV): measured from joint to joint

length of penis (Penis): taken from tip of stylus to base of truncus (not included in analysis)

length of tarsus IV (TaIV): all segments, measured from joint to end

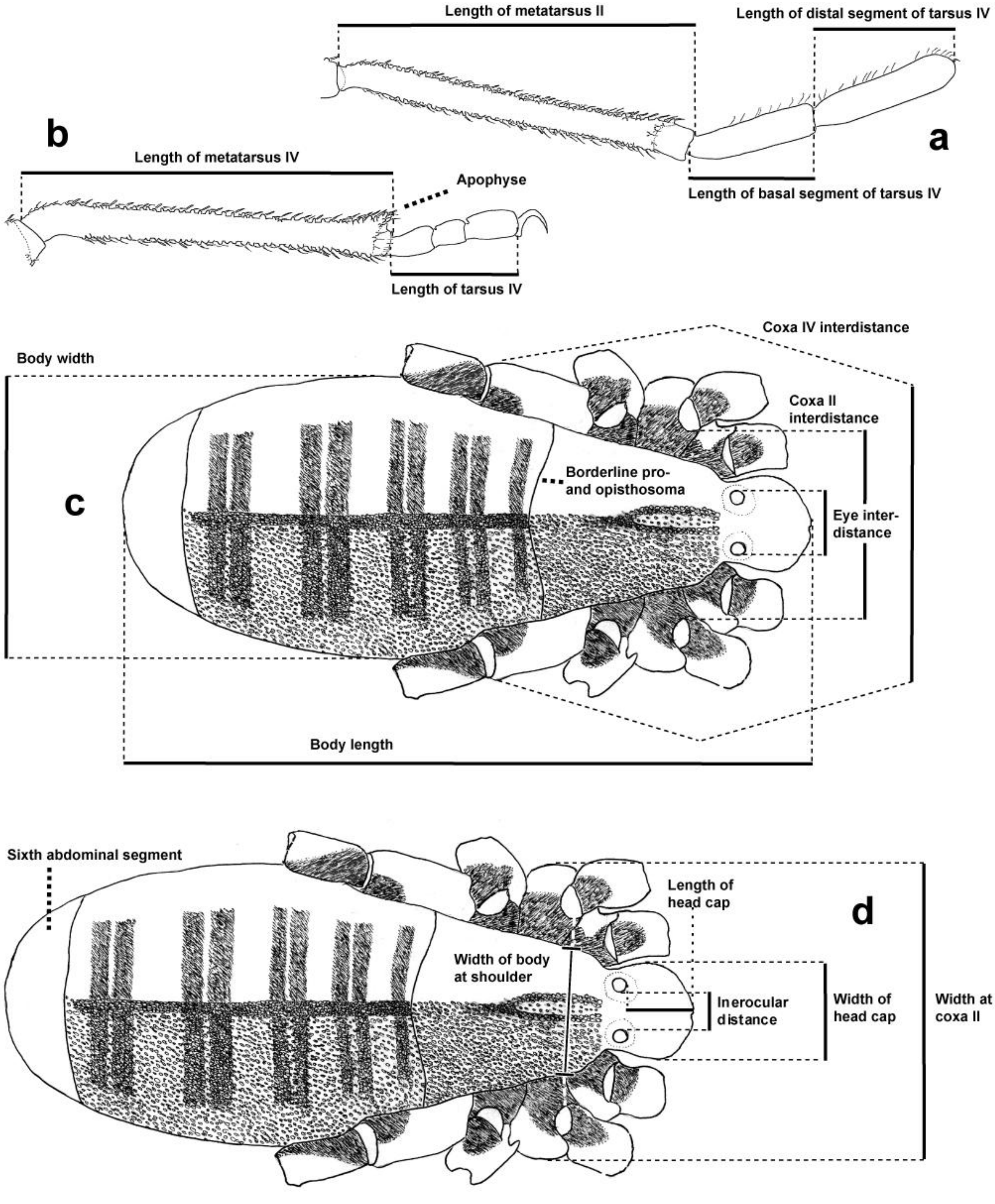


Fig. 3.2. Morphometric distances. (*a*–*b*): *Trogulus coriziformis* C. L. Koch, lateral view; (*a*): Tarsus and metatarsus of leg II; (*b*): Tarsus and metatarsus of leg IV; (c–d): Schematic drawings of *T. karamanorum* [man.n.], dorsal view with coxae, trochanters, with indication of measurement distances and further morphological features. 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.

width at coxa II (WcoxII): distance between lateral sides of left and right coxa II

width of body at shoulder (Should): width of prosoma between coxae II (shoulder)

width of head cap (Lcap): distance between lateral borders of head cap at the widest spot
width of metatarsus IV (MtIV): measured in midsection
length of hairs: from emergence out of papillae to tip (in lateral view)

Discriminant analysis was performed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). Data was processed corrected and uncorrected for body size, by including independent variables or using stepwise methods. Groups were defined as geographically isolated populations. The initial datasets included all considered groups but were recalculated after exclusion of groups assigned to 100%. Analysis of two groups-sets was performed to outline morphometric differences of similar groups. Results are given in Figs. 4.3, 4.11, 5.4 and 5.14 and are discussed in the "Measurements" section of the respective species (chapter 4.5.3 and 5.5.3). For the morphometric data matrices of chapter 4 and 5 refer to Appendix 12.4).

3.4. Processing of distributional data

GEOGRAPHICAL INFORMATION: GPS data of accuracy to seconds were taken in the field with a Garmin Geko 201 or provided by collectors. Data of accuracy to minutes were reconstructed using internet services (www.geonames.org, www.maps.google.de, www.wikipedia.org, www.viamichelin. com, www.tageo.com), a variety of cartographic sources and the program Encarta Professional (version 2003). UTM data were acquired from publications and provided by collectors. UTM was converted to decimal degrees using Geographic Translator (GEOTRANS 2.4.1., National Geospatial-Intelligence Agency, United States, based on the World Geodetic System 1984 (WGS84)). In few cases geographic information could not be specified to minutes. If this information was included the imprecision is indicated (GPS not accurate).

DISTRIBUTION MAPS: For drawings of distribution maps the software DIVA-GIS 5.2.0.2 was used to map distribution points in decimal degrees on the respective areas. Final distribution maps and distribution areas were drawn using Adobe Illustrator CS3 13.0.2.

4. Revision of the genus *Trogulus* Latreille: the *Trogulus hirtus* species-group (Opiliones: Trogulidae)

4.1. 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.

This is the second paper of a series which tries to shed new light on *Trogulus* systematics and evolutionary biology. This 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 many more clearly separated groups of populations were found than there are described species. This did not clear the situation at all and it was decided to work through *Trogulus* by each clade of the molecular tree and to present the results step by step. This paper represents a combination of molecular, morphological and biological data that does allow 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. It is further speculateed 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 (chapter 5), 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, it will be shown that this approach turned out to be successful for the *T. hirtus* species-group. Apart from two already named taxa, four additional species are recognized 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. This study 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.

4.2. Material

Twelve samples of the *Trogulus hirtus* species-group were used for 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 sequences of other Trogulidae genera (*Anelasmocephalus cambridgei* (Westwood, 1874), *Trogulocratus sinuosus* (Sørensen, 1873) and a *Platybessobius* sp. from Turkey were used (Tab. 4.1).

In addition to that I was able to study an extensive material from several private and public collections (see chapter 3.1). According data is listed with the respective species in chapter 4.5.

Tab. 4.1. 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 chapter 5.

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

4.3. Results

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 base frequencies: πA=0.3515, πC=0.2898, πG=0.0473, πT=0.3114; proportion of invariable sites I=0.3733; Ti/Tv ratio=4.2356; gamma shape parameter α=0.8245.

The 22 trogulid sequences (*Anelasmocephalus, Platybessobius, Trogulus* and *Trogulocratus*) produced a 552-bp-long alignment. There were 175 variable sites (32.7%) in thealignment 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. 4.1 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 the limited sequence data. Unfortunately, an adequate number of sequences of other molecular markers for the *T. hirtus* species-group could not be obtained. 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 (Fig. 6.2). 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. 4.1). *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 (chapter 6.4.3). 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 chapter 4.5.1). Changes in composition and number of ingroup taxa within the cyt*b* data set placed this taxon within the *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 speciesgroup 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

Tab. 4.2. Uncorrected p-distances of 552 base pairs of cyt*b* within the *Trogulus hirtus* species-group and trogulid outgroups. Distances are given in %, ambiguous positions are excluded; all numbers except CRO 4 refer to specimens of Collection J. Martens (CJM).

no.	Taxon	Voucher	1	2	3	4	5	6	7	8	9	10
1	*Anelasmocephalus cambridgei*, Germany	3846										
2	*Platybessobius* sp., Turkey	5118	30.4									
3	*Trogulocratus sinuosus*, Italy	5090	27.9	20.1								
4	*Trogulus falcipenis*, Slovenia	4952	32.1	28.2	27.7							
5	*T. graecus*, Greece	5083	29.8	29.1	27.4	21.6						
6	*T. hirtus*, Montenegro	4969	32.2	30.1	27.5	21.7	24.7					
7	*T. huberi*, Portugal	5344	33.9	28.1	27.7	25.2	24.2	26.1				
8	*T. karamanorum* [man.n.], Greece	3025	32.6	28.6	28.3	14.9	24.9	21.4	26.3			
9	*T. karamanorum* [man.n.], Montenegro, Valdanos	4882	32.6	28.9	28.6	15.1	26.0	20.2	25.7	2.9		
10	*T. karamanorum* [man.n.], Macedonia, Gostivar	4889	32.6	28.7	28.0	15.1	25.2	20.2	26.0	3.3	1.8	
11	*T. karamanorum* [man.n.], Macedonia, Skopje	4933	33.0	28.8	28.4	15.8	25.8	20.7	26.8	3.1	2.4	0.7
12	*T. karamanorum* [man.n.], Montenegro, Rumija	4877	29.9	24.8	24.7	12.0	20.5	16.9	23.0	4.3	3.0	3.6
13	*T. martensi*, Germany	4068	31.4	28.1	25.7	20.9	19.1	20.0	21.4	22.9	23.0	22.9
14	*T. melitensis* [man.n.], Croatia, Mljet	CRO4	31.0	29.0	26.1	17.8	22.8	13.8	23.2	19.4	18.4	17.9
15	*T. pharensis* [man.n.], Croatia, Hvar	4881	30.5	29.4	27.0	16.9	24.0	16.9	24.7	19.8	19.5	19.0
16	*T. pharensis* [man.n.], Croatia, Hvar	5155	29.8	29.3	26.3	16.8	23.5	15.9	24.2	19.2	19.,0	18.4
17	*Trogulus* sp., Macedonia	4900	28.7	30.2	28.7	21.3	22.4	21.3	25.8	22.4	22.7	22.5
18	*T. thaleri* [man.n.], Croatia, Podaca	4938	31.6	29.2	26.7	17.4	22.4	13.9	24.5	20.7	20.4	19.9
19	*T. thaleri* [man.n.], Croatia, Drvenik	4985	31.5	29.4	26.2	17.4	22.6	13.6	24.0	20.5	20.2	19.7
20	*T. tricarinatus*, Germany	5312	32.2	29.2	27.6	21.1	17.6	23.6	22.5	24.4	23.9	23.6
21	*T.* cf. *tricarinatus*, Macedonia	4981	30.8	29.5	26.8	20.1	14.8	22.1	20.8	23.0	22.6	22.2
22	*T.* cf. *tricarinatus*, 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	*T. karamanorum* [man.n.], Montenegro, Rumija	4877	4.3										
13	*T. martensi*, Germany	4068	23.1	18.9									
14	*T. melitensis* [man.n.], Croatia, Mljet	CRO4	18.3	14.6	18.0								
15	*T. pharensis* [man.n.], Croatia, Hvar	4881	19.6	16.8	19.4	14.7							
16	*T. pharensis* [man.n.], Croatia, Hvar	5155	19.0	16.1	18.7	13.6	0.2						
17	*Trogulus* sp., Macedonia	4900	22.7	19.8	18.7	21.3	19.5	18.6					
18	*T. thaleri* [man.n.], Croatia, Podaca	4938	20.5	16.9	18.2	13.0	5.9	4.8	19.1				
19	*T. thaleri* [man.n.], Croatia, Drvenik	4985	20.3	16.5	17.9	12.3	5.9	4.8	18.9	0.6			
20	*T. tricarinatus*, Germany	5312	24.2	20.7	18.5	20.7	23.3	22.2	24.1	20.9	21.1		
21	*T.* cf. *tricarinatus*, Macedonia	4981	23.2	19.6	14.7	19.0	22.7	22.1	22.0	21.4	21.4	13.5	
22	*T.* cf. *tricarinatus*, 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

these taxa are not in conflict with the monophyly of the members of the *T. hirtus* species-group (Fig. 6.2).

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. 4.2) 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 *Anelasmocephalus* (27.9–33.9) are noticeably larger.

Within-clade distances (Tab. 4.2) 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* [man.n.] and *T. thaleri* [man.n.]), the two others are widely separated and of unresolved affinities (*T. hirtus*, *T. melitensis* [man.n.]). NJ and MP suggest a closer relationship between the latter two taxa but without bootstrap support. Probably the

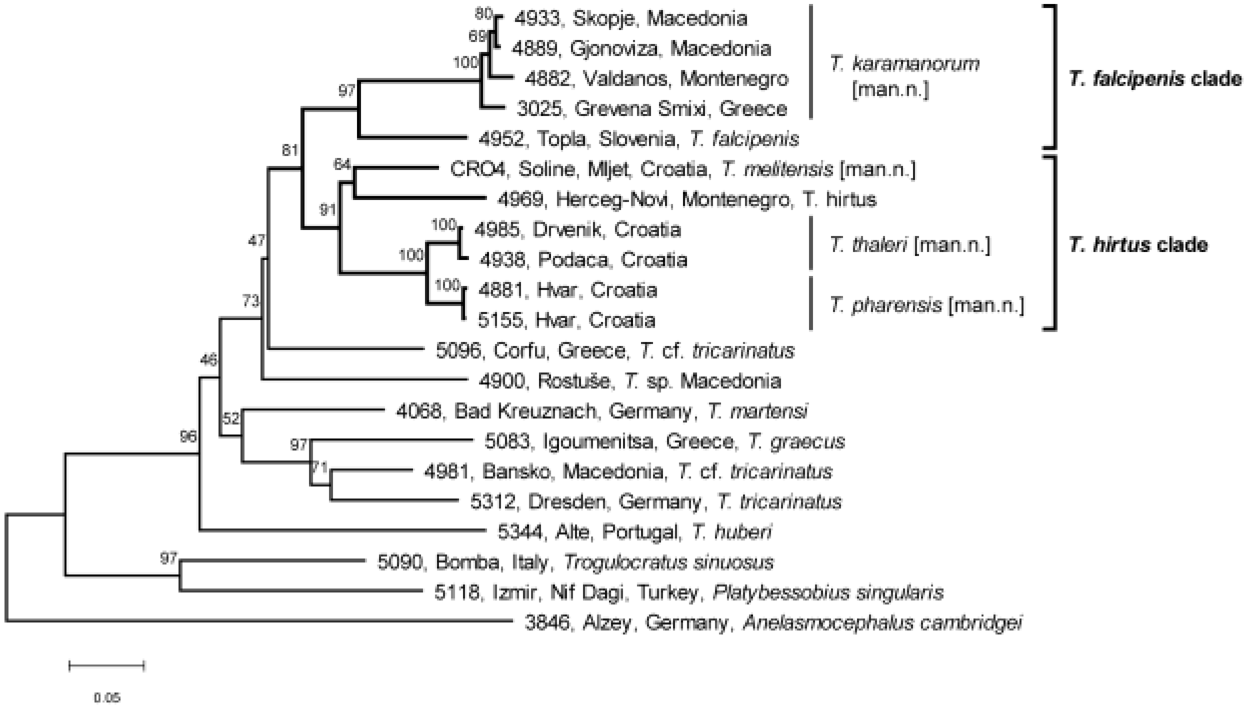


Fig. 4.1. Neighbor-Joining tree of the *Trogulus hirtus* species-group (552 bp, cytochrome *b* gene, bootstrap values after 2000 replications); *Trogulus hirtus* species-group is indicated by bold lines. All numbers except CRO 4 refer to specimens of Collection J. Martens (CJM).

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* [man.n.] and *T. thaleri* [man.n.] (interspecific distances 4.8–5.9%). The *T. falcipenis* clade diverged into two clearly separated lineages: *T. falcipenis* and *T. karamanorum* [man.n.] 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).

4.4. 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 species-worthy clusters were shown to be defined by geographical restriction, as well as morphological characters (chapter 5). 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 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, see chapter 6.4.4). 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 the cyt*b* data set may help to facilitate the decision (Tab. 4.2). Within the *T. hirtus* species-group the lowest genetical distances are to be found in the closely related *T. thaleri* [man.n.] and *T. pharensis* [man.n.] (4.8–5.9%). These taxa are shown to be 'microallopatric' 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 (chapter 6.4.4). On the other hand, recent diversification processes obscure a clear cut-off value for a genetic determination of species, *T. karamanorum* [man.n.] 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 the subsequent species are characterised by genetic and in addition by morphological, biological and geographical characters of their own, to substantiate them as biological species, reproductively separated units in the sense of Ernst Mayr.

4.5. Taxonomy

4.5.1. The *Trogulus hirtus* species-group

MOLECULAR GENETICS: Almost all tree topologies support the species-group as a monophylum (Fig. 4.1) but with weak support in most analyses. Cyt*b* does only weakly support taxa at this phylogenetic level (see chapter 7.4.4). A phylogeny including 28S rRNA data and about 70 representatives of *Trogulus* from the whole range of the genus revealed similar results (chapter 6, Fig. 6.2). 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* [man.n.], *T. thaleri* [man.n.], *T. pharensis* [man.n.] and *T. melitensis* [man.n.] The *Trogulus hirtus* species-group can be divided into two genetically widely separated clades, the *T. hirtus* clade and the *T. falcipenis* clade (Fig. 4.1).

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* [man.n.]: ♂ 3.8–4.25 mm, ♀ 4.25–4.55 mm), whereas widespread and genetically diverse species like *T. karamanorum* [man.n.] exhibit considerably larger variation (♂ 3.85–4.7 mm, ♀ 4.05–5.5 mm). The eye mound is always flat, the eye interdistance 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 chapter 4.5.3.2, *T. karamanorum* [man.n.], Figs. 3.2, 4.12*w*, *y*) or by very regularly spaced papillae (see chapter 4.5.3.2, *T. falcipenis,* Figs. 4.12*g*, *i*).

PENIS MORPHOLOGY (Figs. 4.7–4.10, 4.12): 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

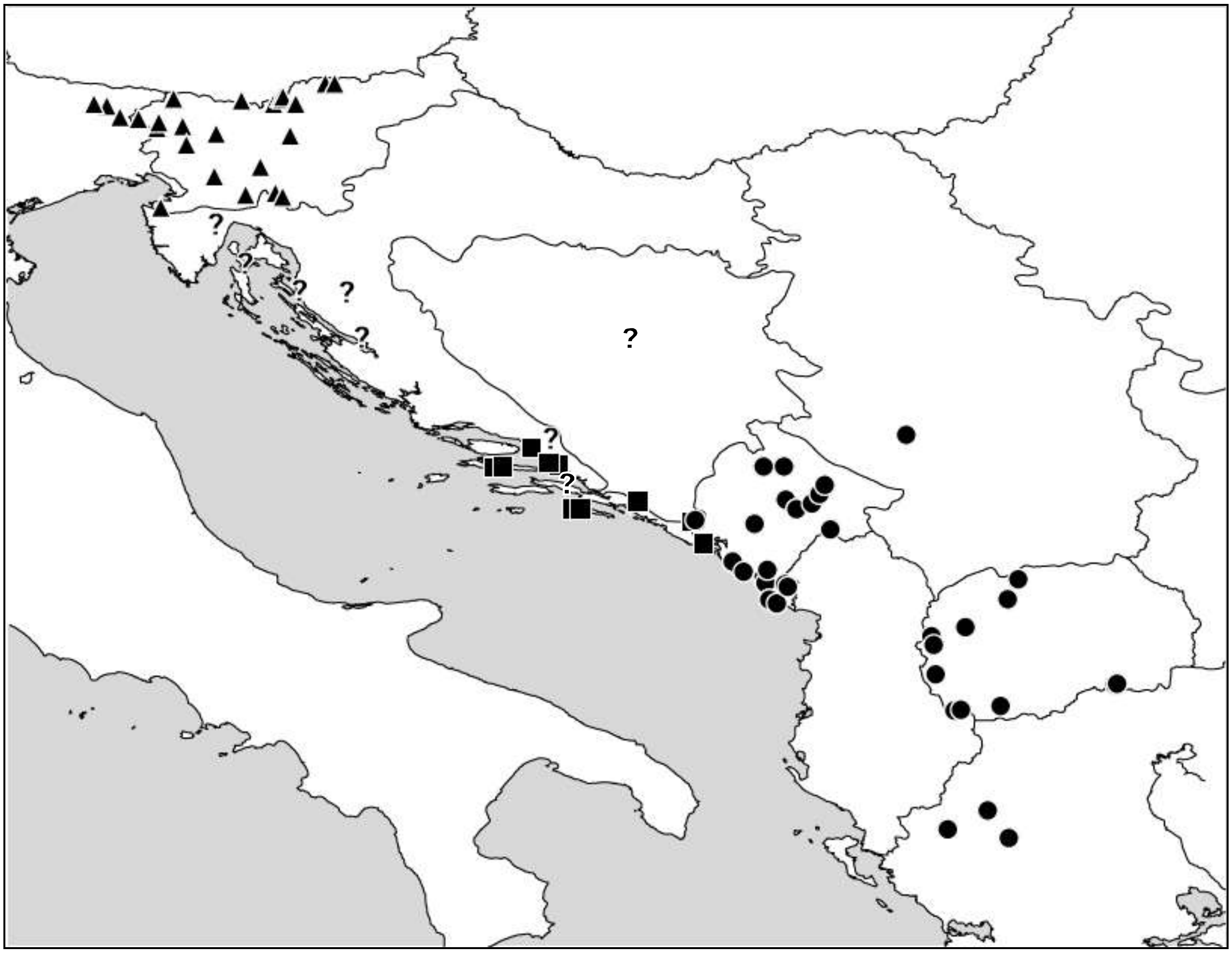


Fig. 4.2. Distribution of the *Trogulus hirtus* species-group: Triangles: *T. falcipenis*; squares: *T. hirtus* clade (including *T. hirtus* Dahl, *T. melitensis* [man.n.], *T. pharensis* [man.n.], *T. thaleri* [man.n.], see Fig. 4.4); circles: *T. karamanorum* [man.n.]; question marks: specimens of the *T. falcipenis* clade not treated here due to insufficient material (compare *Trogulus* sp. "Velebit", see Fig. 4.11).

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. 4.2): 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 activity in Herzegovina and Albania.

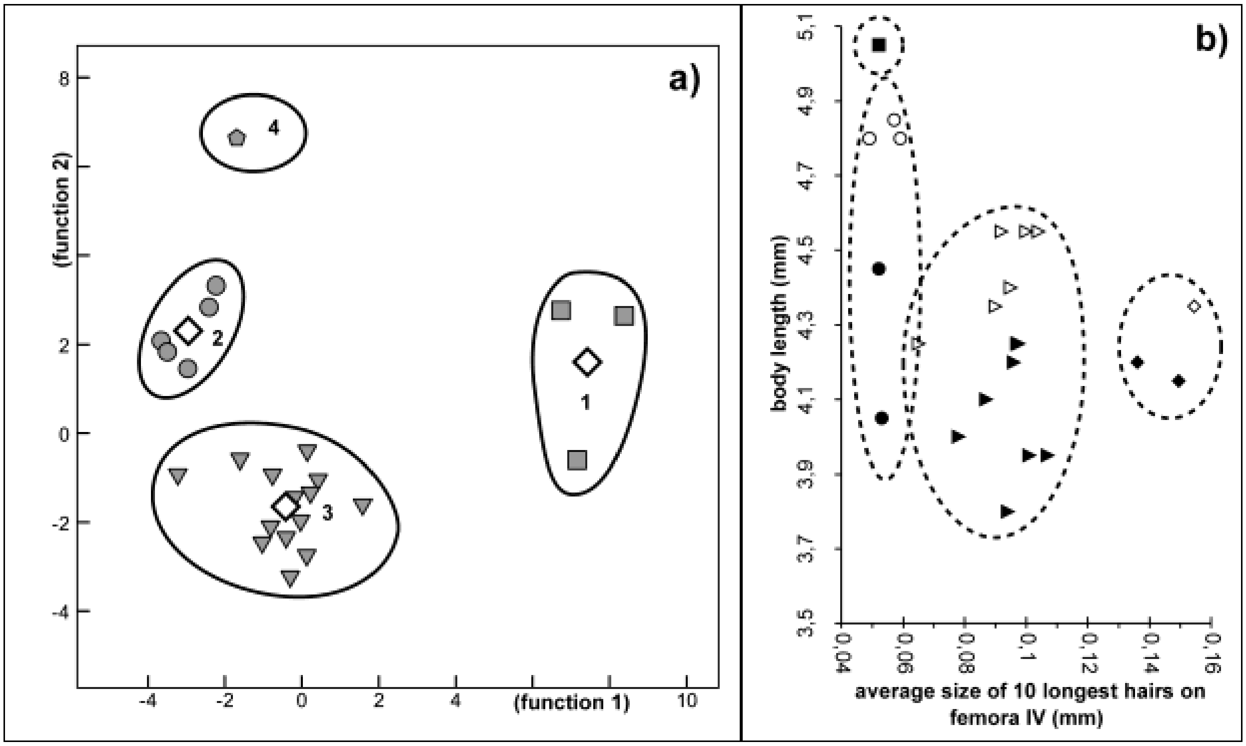


Fig. 4.3. (*a*) Results of the canonical discriminant analysis to separate four species within the *Trogulus hirtus* clade. The discriminant function incorporated average of 10 longest hairs of tibia IV, length of distal segment of tarsus IV and length of tibia II as the most significant characters to classify 100% of all included specimens correctly. *Trogulus hirtus*, *T. pharensis* [man.n.], *T. thaleri* [man.n.] and *T. melitensis* [man.n.] – 1/squares: *T. hirtus* Dahl; 2/circles: *T. pharensis* [man.n.]; 3/triangles: *T. thaleri* [man.n.]; 4/pentagon: *T.melitensis* [man.n.]. Rhombs: centroids. – (*b*) Scatterplot showing length of hairs on femur IV against body size of species of the *T. hirtus* clade. Rhombs: *T. hirtus* Dahl; triangles: *T. thaleri* [man.n.]; circles: *T. pharensis* [man.n.], squares: *T. melitensis* [man.n.]; black symbols: males, empty symbols: females.

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. 4.1). 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♀, 3juv., 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, several recently collected specimen of remarkably small specimens of *Trogulus* (here assigned to the *T. tricarinatus* species-group, CJM 5096) from Corfu resemble the female referred to by Komposch. It clearly does not belong to the *T. hirtus* species-group due to the lack of a sickle shaped penial stylus. It is considered sister to this species-group without affinities to the *T. tricarinatus* species-group (Figs. 4.1, 6.2-6.4).

4.5.2. 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. 4.2, 4.4). Mainland taxa with conspicuously long and perpendicular bristles on all legs (Figs. 4.4*b*–*c*, 4.5*e*–*h*, *i*–*m*), island taxa (known from Mljet and Hvar) with shorter bristles (Figs. 4.4*a*, *d*, 4.5*a*–*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. 4.2). 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. 4.4*b–c*, 4.5*f–h*, *k–m*), coat of hairs giving the legs a shiny appearance, long hairs on rear end of opisthosoma (Figs. 4.6*a*, *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. 4.5*b*, *o*), on femur IV short hairs bent sharply anteriorly (Figs. 4.4*a*, *d*, 4.5*c*, *p*); no long hairs on rear end of opisthosoma (Figs. 4.6*g*, *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. 4.4*c*, 4.5*l*). Body coated with long scattered bristles, also on rear end of opisthosoma (Figs. 4.6*a*, *b*). Occurrence from the Gulf of Kotor within a narrow coastal strip of 10–20 km width to the Neretva plain (Fig. 4.4) .... ***hirtus***

3* Longest hairs on leg IV distinctly shorter than diameter of femur, slightly bent anteriorly (Figs. 4.4*b*, 4.5*g*), body not coated with conspicuously scattered hairs. Rear end of opisthosoma only with short thickened hairs (Fig. 4.6*d*). 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. 4.4) .... ***thaleri* [man.n.]**

4 Endemic to Hvar Island; hair coat developed only on leg II as thin scattered hairs (Fig. 4.5*b*), hairs on femur IV short and sharply bent anteriorly (Figs. 4.4*a*, 4.5*c*); body size of males 4.0–4.5 mm, of females 4.8–4.9 mm .... ***pharensis* [man.n.]**

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* [man.n.]**

5 Endemic to the south-eastern Alps (NE Italy, Slovenia, SE Austria, Fig. 4.2); eyes about half their diameter from lateral border of front cap (Figs. 4.12*h*, *l*); dorsal papillation regular, without pattern (Figs. 4.12*g*, *i*, *k*, *m*); no Y-shaped ridge on dorsal prosoma, without a zone of widely spaced papillae, lacking soil encrustation (Figs. 4.12*h*, *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. 4.13*e–f*) .... ***falcipenis***

5* Endemic to the southern Dinaric Alps (Montenegro, Republic of Macedonia, Greece, Fig. 4.2); eyes about their diameter from lateral border of front cap (Figs. 4.12*u*, *x*); dorsal papillation irregular, sometimes with pattern similar to Figs. 3.2, 4.12*t*, *v–w*, *y*; Y-shaped ridge on dorsal prosoma present, this part with widely spaced papillae and usually with soil encrustation (Figs. 4.12*x–y*, removed in 4.12*u–v*); metatarsus III (when leg stretched backwards) ends at rear end of opisthosoma. Truncus penis constricted in distal third (in ventral view, Fig. 4.13*m*) and broadened (in lateral view, Fig. 4.13*l*) . ***karamanorum* [man.n.]**

4.5.3. Species accounts

4.5.3.1. THE *TROGULUS HIRTUS* CLADE

MOLECULAR GENETICS (Fig. 4.1): The clade is supported by all phylogenetic reconstructions with high bootstrap support. It comprises the species *T. hirtus* Dahl, 1903, *T. thaleri* [man.n.], *T. pharensis* [man.n.] and *T. melitensis* [man.n.]

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. 4.3*a*), differences in length, angle and form of hairs on femur II and IV are most significant (Figs. 4.3*b*, 4.4–4.6). Genital morphology (Figs. 4.7–4.10) 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.

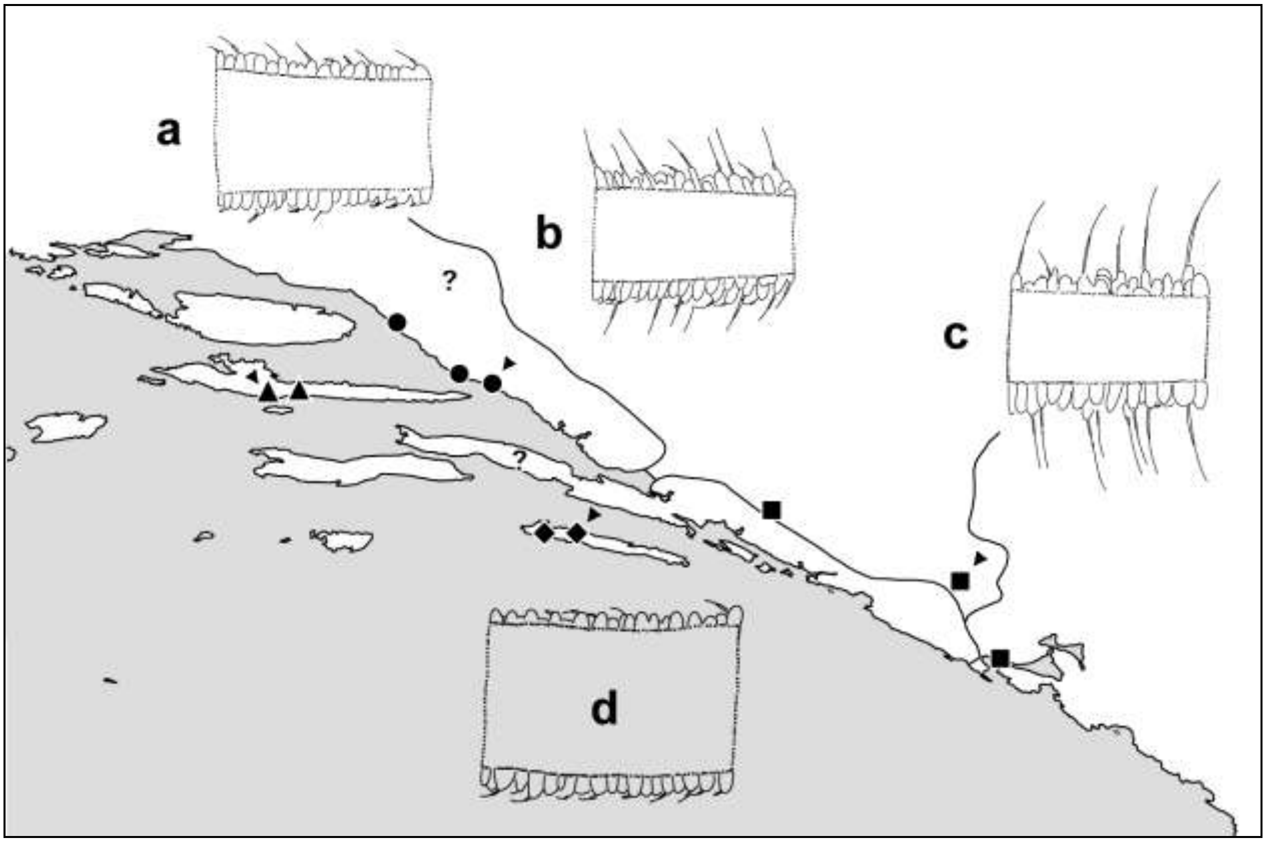


Fig. 4.4. Distribution of species of the *T. hirtus* clade and parts of femur II (dorsal and ventral papillae and hairs are indicated; left is anterior): *a*/triangles *T. pharensis* [man.n.] (Hvar Island), *b*/circles *T. thaleri* [man.n.] (Makarska Riviera), *c*/squares *T. hirtus* Dahl (south-eastern Croatian coast and hinterland), *d*/rhombs *T. melitensis* [man.n.] (Mljet Island), question marks: localities of members of the *T. hirtus* clade not assigned to species. Arrows point to type localities.

DISTRIBUTION (Figs. 4.2, 4.4): 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 (Figs. 4.2, 4.4). More island finds are to be expected.

DOUBTFUL RECORDS: Croatia, Dalmatia, Mount Biokovo (field lable: 2c+d), 1200–1300 m, from sieved litter, 1 unidentified ♂ (plus 2 ♂ of *T. thaleri* [man.n.]), C. Besuchet leg. 19. 5. 1984 (MHNG). This sample comprises two ♂ of *T. thaleri* [man.n.] 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. The following female is regarded 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. thaleri* [man.n.] Further material and molecular genetic analysis may help to clarify the taxonomic status of these and related forms.

Trogulus hirtus Dahl, 1903, new rank

(Figs. 4.3, 4.4*c*, 4.5*i–m*, 4.6*a–c*, 4.7)

Trogulus tricarinatus hirta DAHL 1903, Sitzber. Ges. naturforsch. Freunde Berlin: 289. – MORITZ 1971, Mitt. Zool. Mus. Berlin 47: 211 ("Kosusko" given as type locality).

Trogulus tricarinatus hirtus ROEWER 1923, Weberknechte der Erde: 641 (diagnosis). – KOMPOSCH 2000, Spixiana 23: 1–14 (discussion of taxonomic status). – 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. 4.4).

ADDITIONAL MATERIAL EXAMINED: **Bosnia-Herzegovina**: Zavala, SE Vjetrenica cave, 350 m (N: 42° 50', E: 17° 58'), shrub forest, sieved, 2♂, 3juv., 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, 3juv., 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♀, 3juv., 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"),

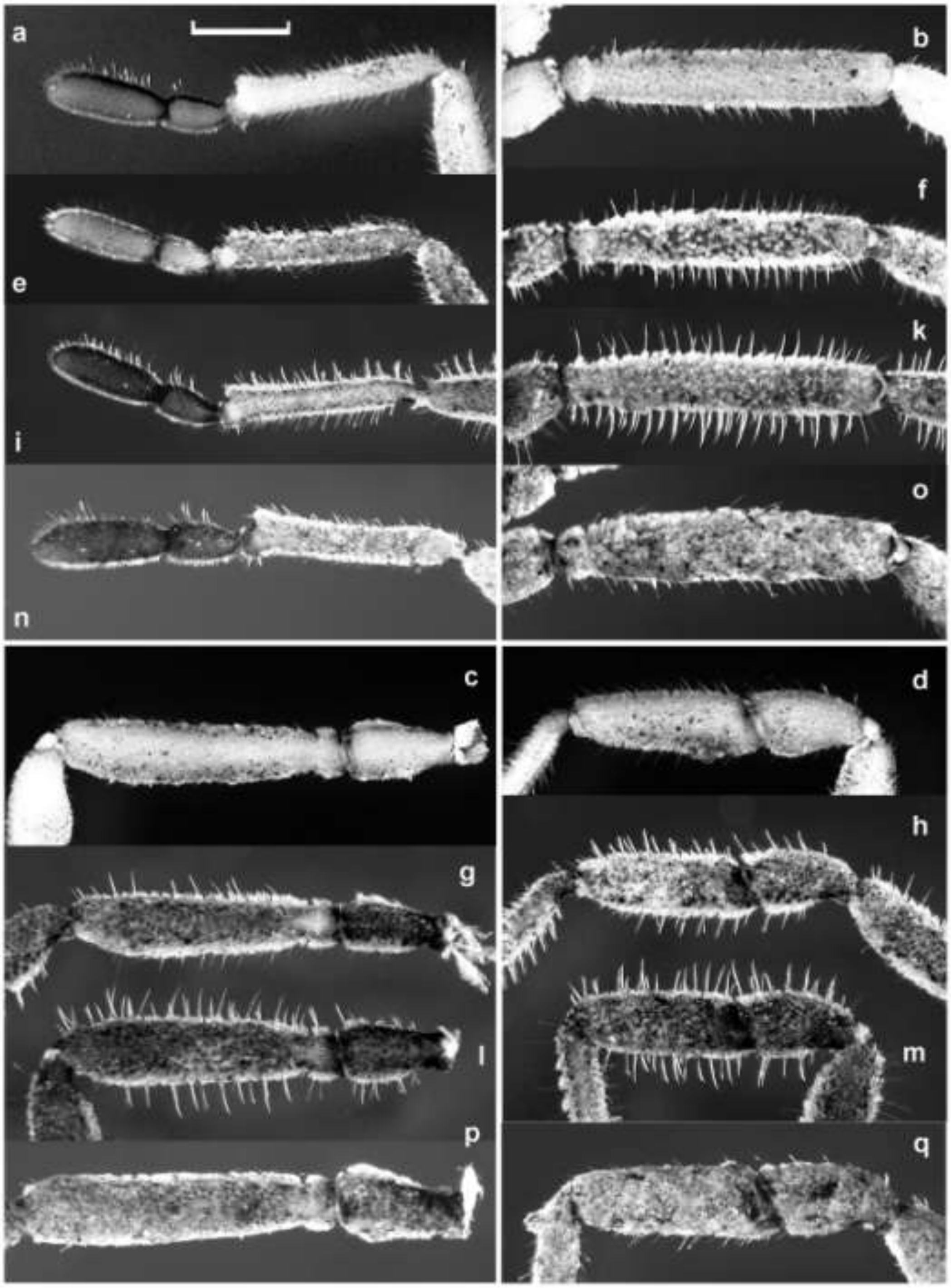


Fig. 4.5. Leg morphology of the species of the *Trogulus hirtus* clade, males (femur II dorso-lateral view, all other lateral view). – *a–d*: *T. pharensis* [man.n.] (Croatia, Hvar, near Sinje Spilje, CJM 4881); – *e–h*: *T. thaleri* [man.n.] (Croatia, Drvenik, CJM 4985); – *i–m*: *T. hirtus* Dahl (Montenegro, Herceg Novi, Monastir Savina, CJM 4969); – *n–q*: *T. melitensis* [man.n.] (Croatia, Mljet, Bjejajka, 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.

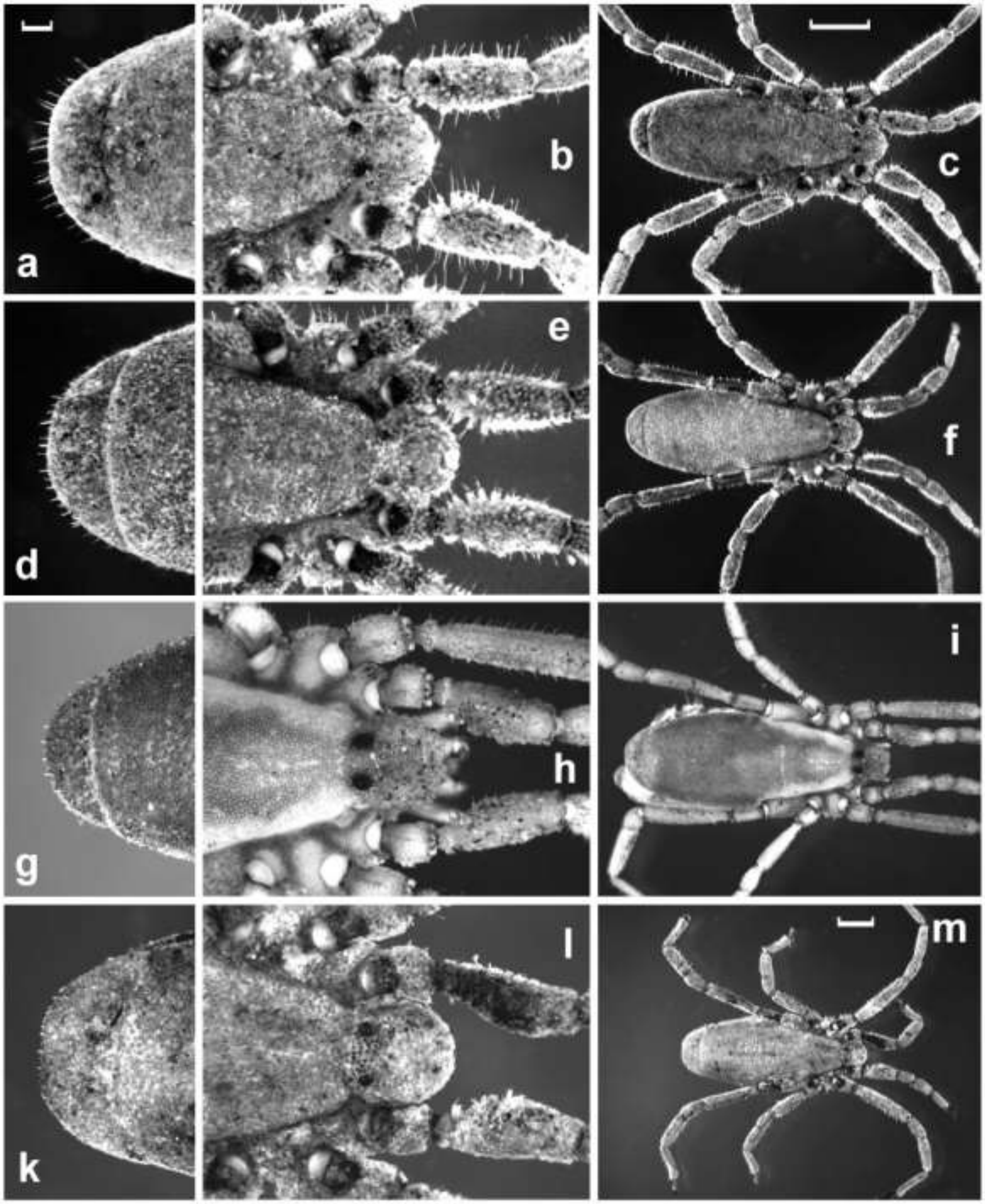


Fig. 4.6. Dorsal side of males of the *Trogulus hirtus* clade. – *a–c*: *T. hirtus* (Montenegro, Herceg Novi, Monastir Savina, CJM 4969); – *d–f*: *T. thaleri* [man.n.] (Croatia, Drvenik, CJM 4985); – *g–i*: *T. pharensis* [man.n.] (Croatia, Hvar, near tunnel to Zavala, CJM 4881); – *k–m*: *T. melitensis* [man.n.] (Croatia, Mljet, Bjejajka, 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*).

evergreen deciduous forest, very dense and dark, litter in stony debris, 1♂, 1juv., I. Karaman leg. 1. 5. 1997 (CIK 1500); ibidem 1♂, 1♀, 1juv., A. Schönhofer leg. 12. 5. 2006 (CJM 4969).

MOLECULAR GENETICS (Fig. 4.1): The only sequenced specimen (CJM 4969) possesses many autapomorphies and cyt*b* distances of 13.8–16.9% to other taxa within the clade. A close relationship to *T. melitensis* [man.n.] 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 "shoulders", along rear end of opisthosoma (Figs. 4.6*a–c*) and on all legs (there very distinct, Figs. 4.5*i–m*). Tips of hairs on legs bent anteriorly, well visible on femur IV (Figs. 4.4*c*, 4.5*l*). Body shape slightly more robust and broader than in *T. karamanorum* [man.n.] (Fig. 4.6*c*).

SIMILAR SPECIES: Due to its hairy appearance *T. hirtus* can be easily told apart from *T. karamanorum* [man.n.], *T. melitensis* [man.n.] and *T. pharensis* [man.n.], 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* [man.n.] but according to current knowledge both live in allopatry and differ in the shape of their hair coat on femur IV.

DESCRIPTION

BODY (Figs. 4.6*a–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. 4.6*b*): 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. 4.4*c*, 4.5*i–m,* 4.6*a–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**: ♂ (n=5) 4.15–4.5 mm; ♀ (n=2) 4.35–4.5 mm, **length of 10 longest hairs on femur IV**: 90–170 µm; **average of 10 longest hairs per individual**: 136–155 µm; – **relation of length of distal to basal segment of tarsus II** : ♂ 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* [man.n.], the central segment therefore quadrangular. Legs of *T. karamanorum* [man.n.] thicker and shorter than in *T. hirtus* and due to heavy incrustations difficult to measure.

GENITAL MORPHOLOGY (Fig. 4.7): 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. 4.7*b*), stylus relatively short and moderately bent. The male holotype was available to us only close to the publication of the present paper. Consequently, not additional drawings could be added. Nevertheless, one can state that the penis of the holotype perfectly matches Figs. 4.7*a–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.

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. 4.4): 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. tricarinatus*. The available type material allowed cor-

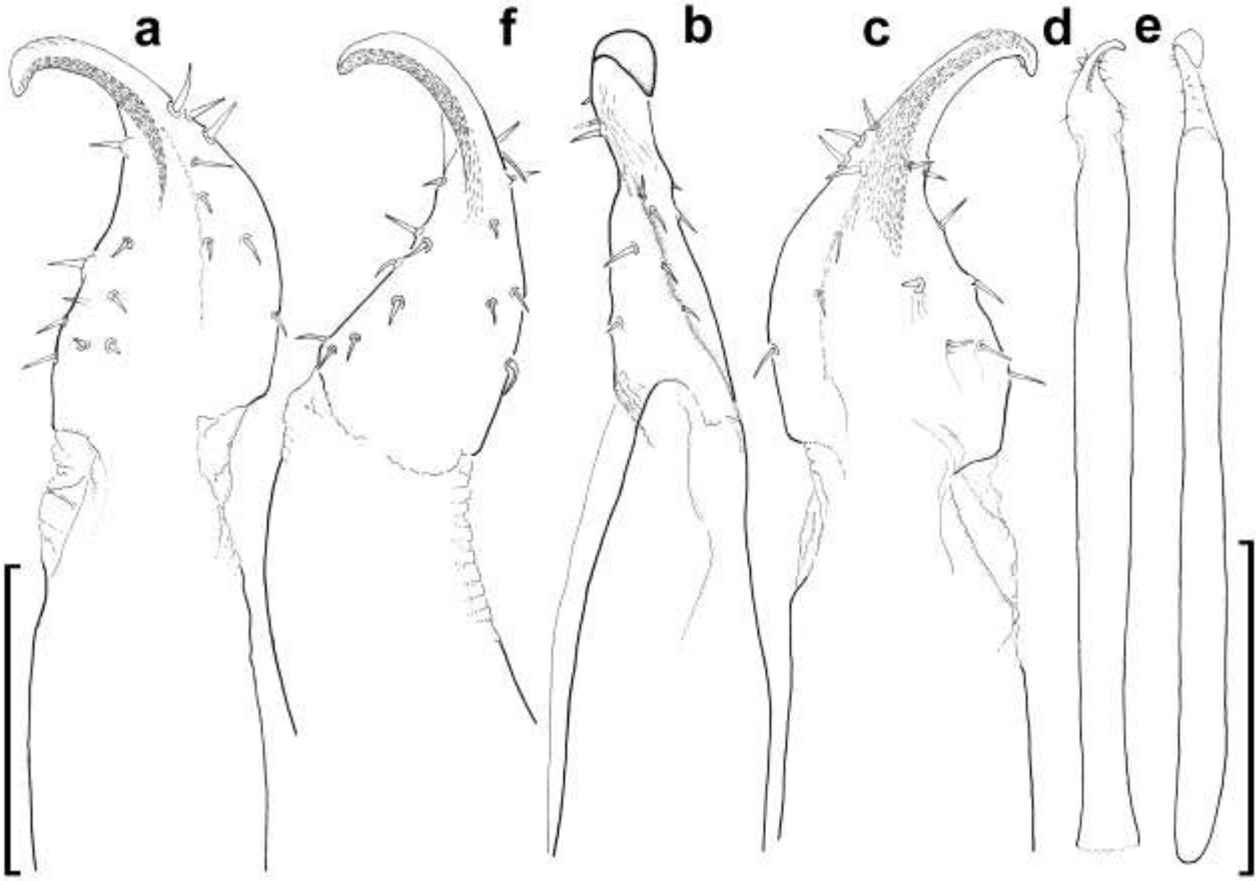


Fig. 4.7. *Trogulus hirtus* Dahl, penis morphology. Glans penis and distal part of truncus (*a–c, f*; *a* and *f* dorsal view; *c* ventral view; *b* lateral view); total penis (*d–e*; d ventral view, e lateral view). – *a–e*: Herceg-Novi (CJM 4969), – *f*: same locality (CIK 1500). Left scale line 0.1 mm (*a–c, f*), right scale line 0.5 mm (*d–e*).

rect identification of new material (CJM 4969; see material examined). 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 the results based on morphology and molecular genetics presented in this study. However, *T. falcipenis* and *T. hirtus* are not closest relatives; instead they belong to different clades within the *T. hirtus* species-group.

Trogulus thaleri [man.n.]

(Figs. 4.3, 4.4*b*, 4.5*e–h*, 4.6*d–f*, 4.8)

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♀, 1juv., A. Schönhofer leg. 14. 5. 2006 (CJM 4938); Dalmatia, Biokovo Mt. (field lable: 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. 4.1): The taxon is supported by all topologies and is close to *T. pharensis* [man.n.] Both species live in close geographic proximity (Fig. 4.4). The distance value between them amounts to only 4.8–5.9% and is relatively low (note the intraspecific distances of *T. karamanorum* [man.n.] populations which amount to 3.5%). However, morphological differences to *T. pharensis* [man.n.] are pronounced and point to species status.

DIAGNOSIS: A very small and slender *Trogulus* conspicuously covered with long hairs (Figs. 4.5*e–h*, 4.6*d–f*), inserted nearly perpendicularly but slightly pointing anteriorly, bristles also on the "shoulders", on the rear end of opisthosoma (Fig. 4.6*d*) and on all legs (Figs. 4.5*e–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. 4.4*b*). Body shape more slender than in *T. hirtus* (Fig. 4.6*f*).

SIMILAR SPECIES: *T. thaleri* [man.n.] (Croatian coast) is similar to *T. pharensis* [man.n.] but clearly allopatric. Both species can easily be told apart by comparison of the hair coat on femur IV. *T. pharensis* [man.n.] is on average larger than *T. thaleri* [man.n.]

DESCRIPTION

BODY (Figs. 4.6*d–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. 4.6*e*): Cap with long lateral papillae, thus without sharp contours, longish to roundish; eye interdistance variable; "shoulders" 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. 4.5*e–h*, 4.6*d–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* [man.n.]; **length of 10 longest hairs on femur IV**: 50–130 µm; **average of 10 longest hairs per individual**: (65–) 78–107 µm; – **relation of length of distal to basal segment of tarsus II**: ♂: 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. melitensi* [man.n.] and *T. pharensis* [man.n.]

GENITAL MORPHOLOGY (Fig. 4.8): 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* species-group.

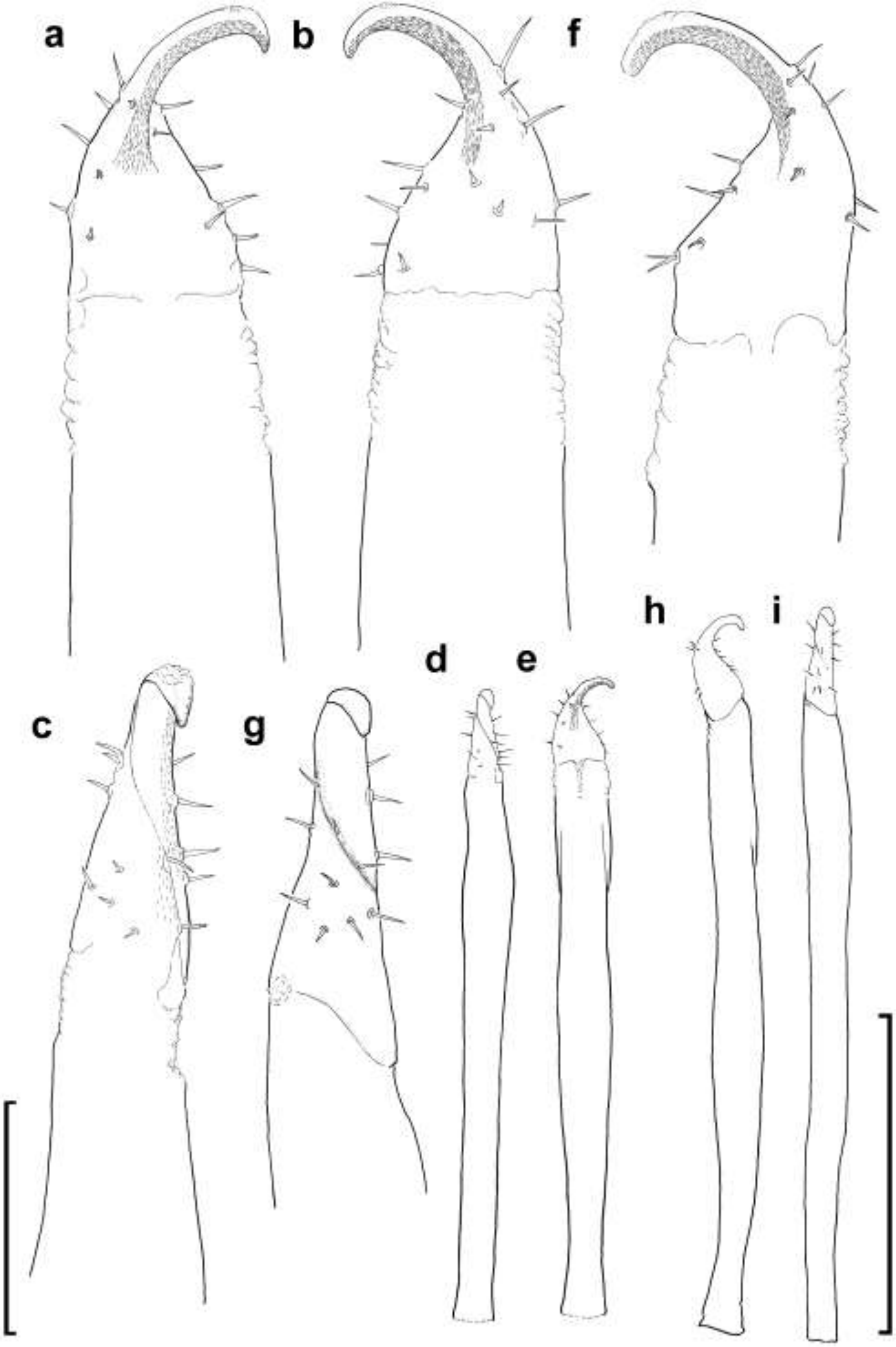


Fig. 4.8. *Trogulus thaleri* [man.n.], penis morphology. Glans penis and distal part of truncus (*a–c*, *f–g*; a ventral view; *b*, *f* dorsal view; *c*, *g* lateral view); total penis (*d–e*, *h–i*; *d*, *i* lateral view; *e*, *h* ventral view). – *a–e*: Drvenik, type locality (CJM 4985), *f–i*: Podaca (CJM 4938). – Left scale 0.1 mm (*a–c*, *f–g*), right scale line 0.5 (*d–e*, *h–i*).

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

DISTRIBUTION (Fig. 4.4): 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 chapter 4.5.3.1, 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 population densities, mostly in association with *Cyphophthalmus* species.

DERIVATIO NOMINIS: The species name honours Konrad Thaler (19. 12. 1940, Innsbruck – 11. 07. 2005, Stubaier Alpen), 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 chapter 4.5.3.1.

***Trogulus pharensis* [man.n.]**

(Figs. 4.3, 4.4*a*, 4.5*a–d*, 4.6*g–i*, 4.9)

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, 1juv.; 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♀, 1juv., A. Schönhofer leg. 14. 5. 2006 (CJM 4881).

MOLECULAR GENETICS (Fig. 4.1): The cyt*b* distance between *T. pharensis* [man.n.] and the most closely related species, *T. thaleri* [man.n.], is only 4.8–5.9%. See details under *T. thaleri* [man.n.]

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. 4.5*b*), inconspicuous on the "shoulders" and along the rear end of the opisthosoma (Fig. 4.6*g*). Hairs on femur IV straight and about one third shorter than in *T. thaleri* [man.n.] (Figs. 4.4*a*, 4.5*c*), body size on average larger than in *T. thaleri* [man.n.] (Fig. 4.6*i*).

SIMILAR SPECIES: See *T. thaleri* [man.n.]

DESCRIPTION

BODY (Figs. 4.6*g*–*i*): Similar to *T. thaleri* [man.n.] in overall appearance. Eye mound and front cap (Fig. 4.6*h*): Similar to *T. thaleri* [man.n.] No specific characters recognized.

HAIR COAT (Figs. 4.5*a*–*d*): Inconspicuous, long hairs especially on leg II (femur II), hairs on femur IV short, pointing anteriorly in an acute angle.

MEASUREMENTS: ♂ (n=2); ♀ (n=3): – **Body length**: ♂: 4.05–4.45 mm; ♀: 4.8–4.85 mm, on averge larger than *T. thaleri* [man.n.]; **length of 10 longest hairs on femur IV**: 30–70 µm; **average of 10 longest hairs per individual**: 49–59 µm; – **relation of length of distal to basal segment of tarsus II** : ♂ 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. 4.9): Truncus quite stout and nearly parallel-sided, 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 massiv, 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,

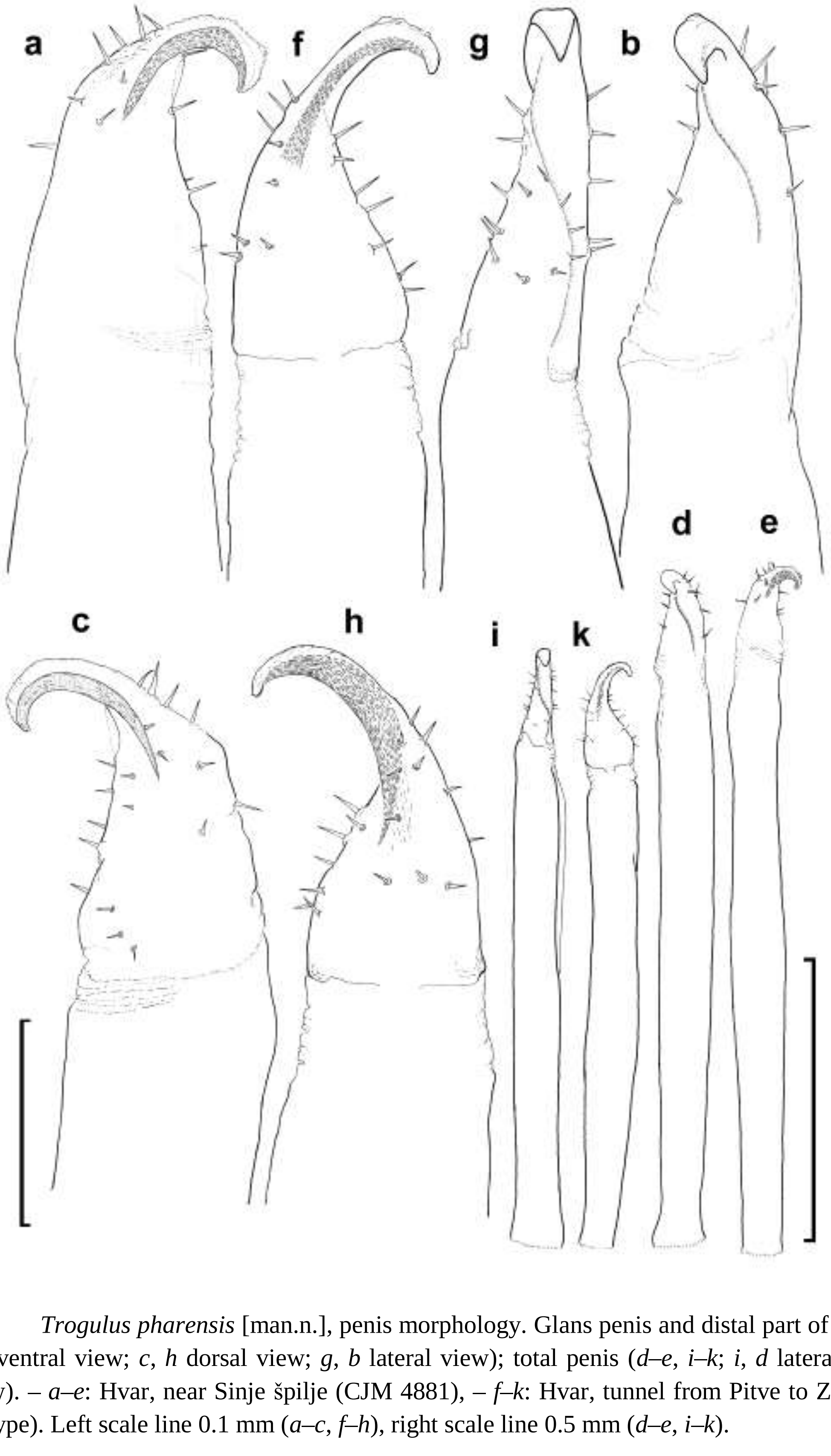


Fig. 4.9. *Trogulus pharensis* [man.n.], penis morphology. Glans penis and distal part of truncus (*a–c*, *f–h*; *a*, *f* ventral view; *c*, *h* dorsal view; *g*, *b* lateral view); total penis (*d–e*, *i–k*; *i*, *d* lateral view; *k*, *e* ventral view). – *a–e*: Hvar, near Sinje špilje (CJM 4881), – *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*).

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. 4.4): 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* [man.n.] and *T. pharensis* [man.n.] is quite low, distinct morphological characters suggest species status of both genetic clusters. The average body size is considerably larger in *T. pharensis* [man.n.] and length and position of hairs on femur IV clearly separate the two species (see Fig. 4.4).

***Trogulus melitensis* [man.n.]**

(Figs. 4.3, 4.4*d*, 4.5*n–q*, 4.6*k–m*, 4.10)

*Trogulus tricarinatus hirtu*s NOVAK 2004a, Nat. Croat. 13: 235, 253 (records).

HOLOTYPE: **Croatia**: Southern Dalmatia, Mljet Island, Soline, Bjejajka, in pit Jama u uvali šume Bjejajka (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. 4.1): 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* [man.n.] is actually restricted to Mljet.

DESCRIPTION

BODY (Figs. 4.6*k–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. 4.6*l*): Front cap oval, eyes about their interdistance away from rear 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. 4.4*d*, 4.5*n–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; – **relation of length of distal to basal segment of tarsus II** : ♂ 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 segment 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. 4.10): 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. 4.4): Croatia, according to present knowledge endemic to Mljet Island.

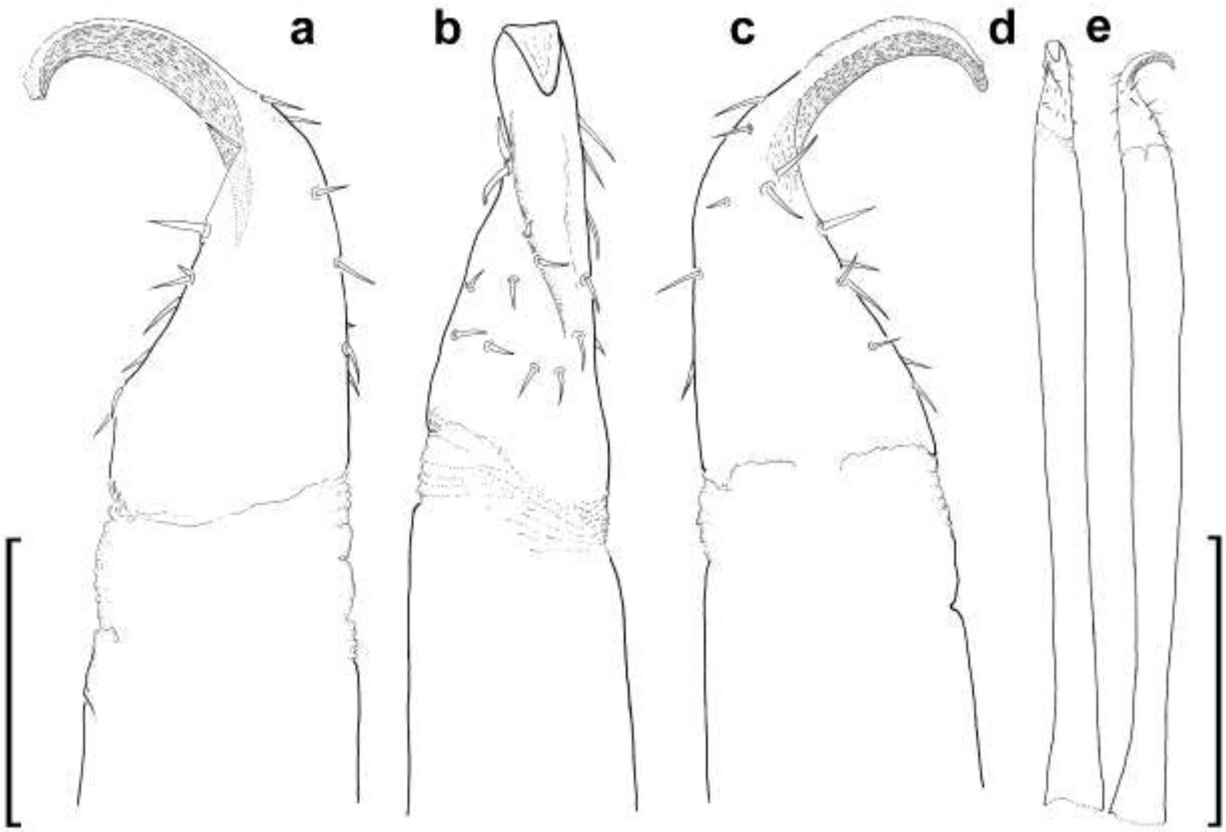


Fig. 4.10. *Trogulus melitensis* [man.n.], penis morphology. Glans penis and distal part of truncus (*a*–*c*; *a* dorsal view; *b* lateral view; *c* ventral view); total penis (*d*–*e*; d lateral view, e ventral view). – *a*–*e*: Mljet Island (CRO 4). Left scale line 0.1 mm (*a*–*c*), right scale line 0.5 mm (*d*–*e*).

DERIVATIO NOMINIS: Derived from Melita, the ancient Latin name for Mljet Island.

DISCUSSION: As *T. melitensis* [man.n.] is asumed to be restricted to Mljet Island, a former record of *T. tricarinatus hirtus* from Mljet is assigned to the paratype series.

4.5.3.2. THE *TROGULUS FALCIPENIS* CLADE

MOLECULAR GENETICS (Fig. 4.1): 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 two species are distinguished, *T. falcipenis* Komposch, 2000 and *T. karamanorum* [man.n.], separated by distance values of 14.9–15.8%. Species differentiation within the clade is further supported by genital morphology (Fig. 4.13) and morphometric characters (Fig. 4.11).

MORPHOLOGICAL CHARACTERS: Morphological characters shared by both species of the clade could not be identified except for the smaller glans penis in comparison to the species of the *T. hirtus* clade.

DISTRIBUTION (Fig. 4.2): 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.

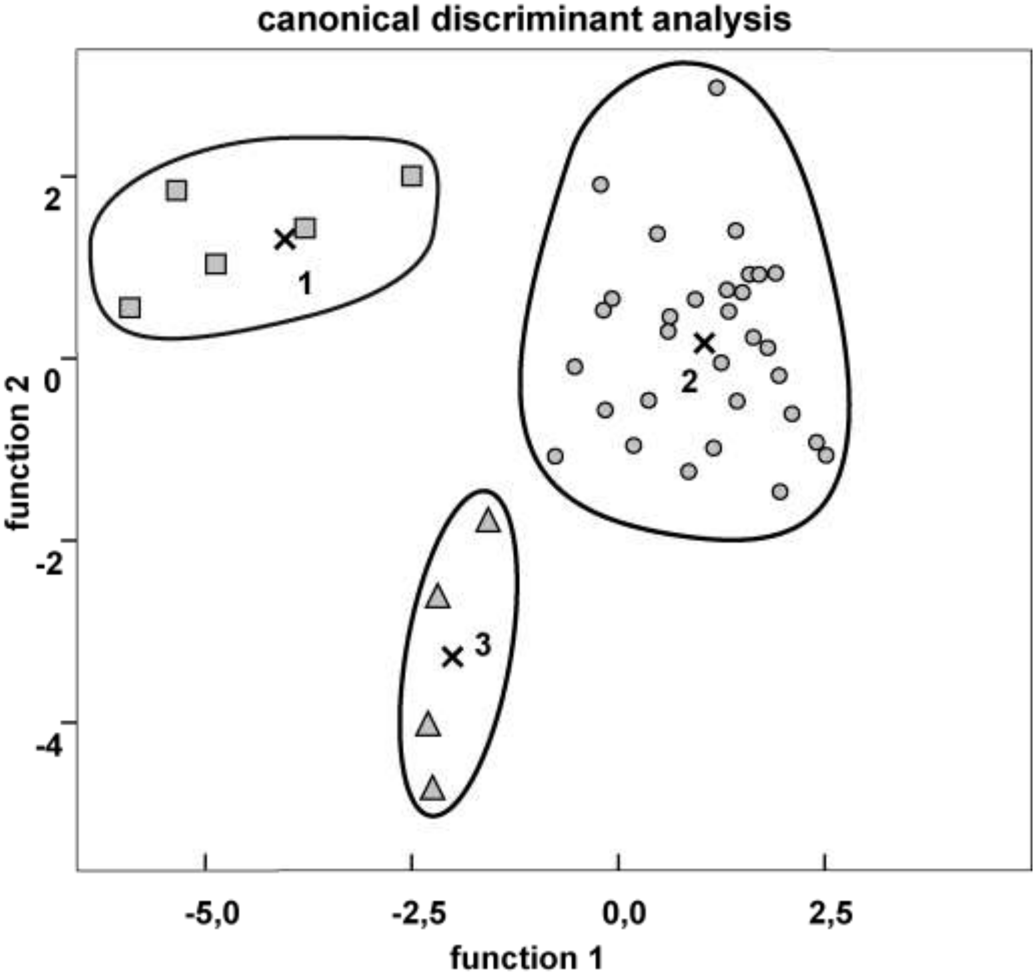


Fig. 4.11. Canonical discriminant analysis to distinguish *Trogulus falcipenis* Komposch, *T. karamanorum* [man.n.] and an unknown *Trogulus* species from Velebit Mts. – 1/squares: *T. falcipenis*; 2/circles: *T. karamanorum* [man.n.] 3/triangles: *Trogulus* sp. from Velebit. Crosses: centroids.

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. 4.11) from *T. falcipenis* and *T. karamanorum* [man.n.] 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. 4. 1986 (CNS 42/1986); Mt. Zecjate (considered 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. 4.2, 4.11, 4.12*a–m*, 4.13*a–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 et al. 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* Komposch leg. 6. 9. 1999

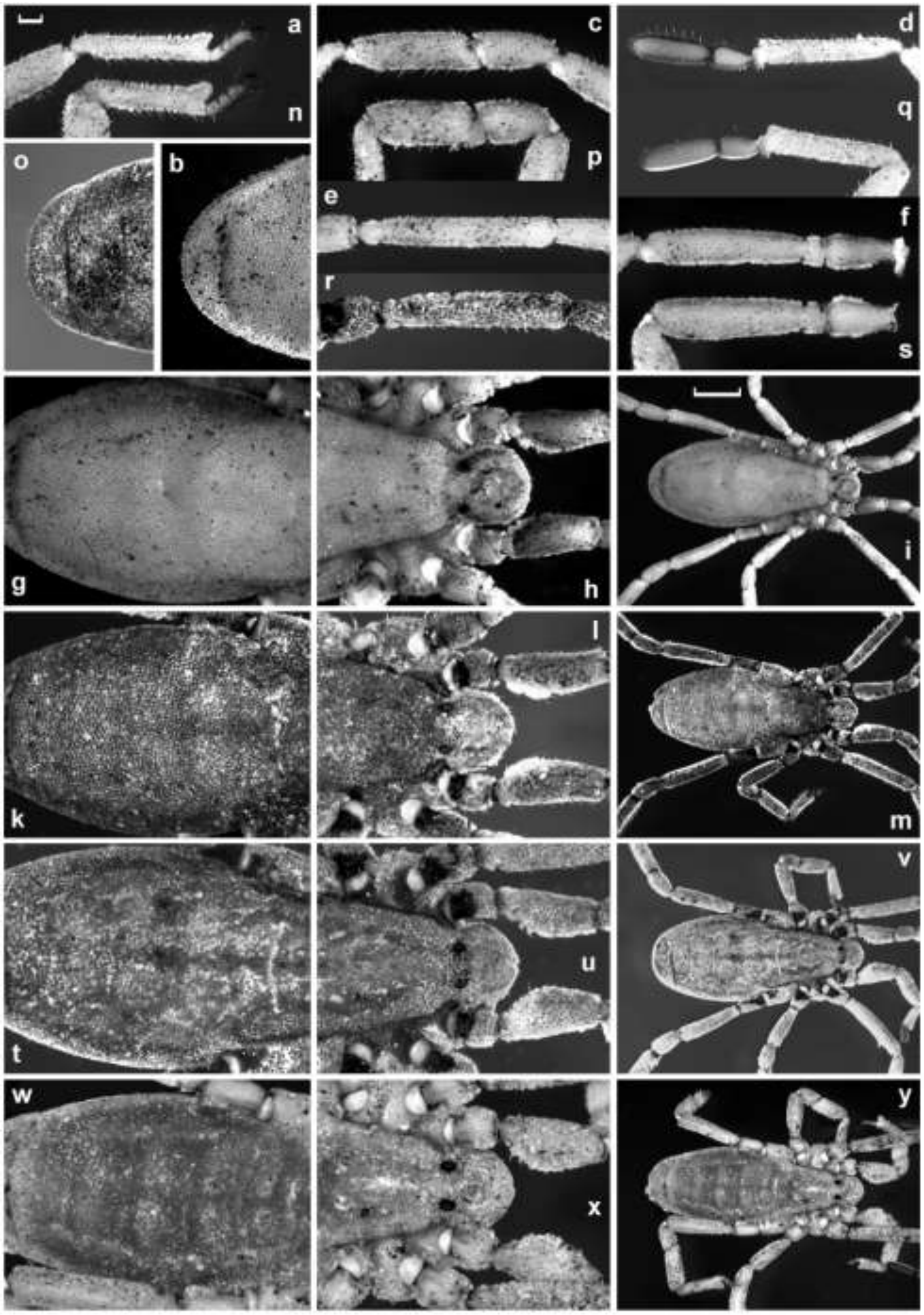


Fig. 4.12. Dorsal side and legs of males of the *Trogulus falcipenis* clade. – *a–m*: *T. falcipenis* (*a–i*: Koschuta, paratype, CJM 3241; – *k–m*: Topla valley, CJM 4952); – *n–y*: *T. karamanorum* [man.n.] (*n–v*: Gjonovitze cave near Gostivar CJM 4889; – *w–y*: Camp Valdanos, N Ulcinj, CJM 4882). – 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.

(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♂, 1juv., 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♂, 1juv., 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♀, 1juv., 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♀, 2juv., 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♀, 1juv., T. Novak leg. 19. 08. 2005 (CNS 98/2005).

MOLECULAR GENETICS (Fig. 4.1): The only sequenced specimen (CJM 4952) shows many autapomorphies and distance values of 14.9–15.8% to the related *T. karamanorum* [man.n.] from the southern and central Balkans. This close relationship is strongly supported by all topologies.

DIAGNOSIS (Figs. 4.12*a–m*): A very small *Trogulus*, the smallest within its geographical range; more slender and with longer legs than *T. karamanorum* [man.n.], eye interdistance larger, coloration 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 chapter 4.5.3.2, doubtfull records). 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. 4.12*g–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 coloration partly reddish, blackish at joints between coxae and trochanters.

EYE MOUND AND FRONT CAP (Figs. 4.12*h*, *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; – **relation of length of distal to basal segment of tarsus II** : ♂ 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. 4.13*a–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. 4.13 *e–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. 4.13 *b–c*).

VARIABILITY: Due to the small material available for investigation 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; 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. 4.2): 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 confined to the southern Alps proper. Records from northern Croatia (Fig. 4.2, questionmarks) at lower altitude likely belong to a similar, yet undescribed taxon (treated here as *Trogulus* sp. "Velebit", see chapter 4.5.3.2, doubtful records). 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. 4.1) 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.

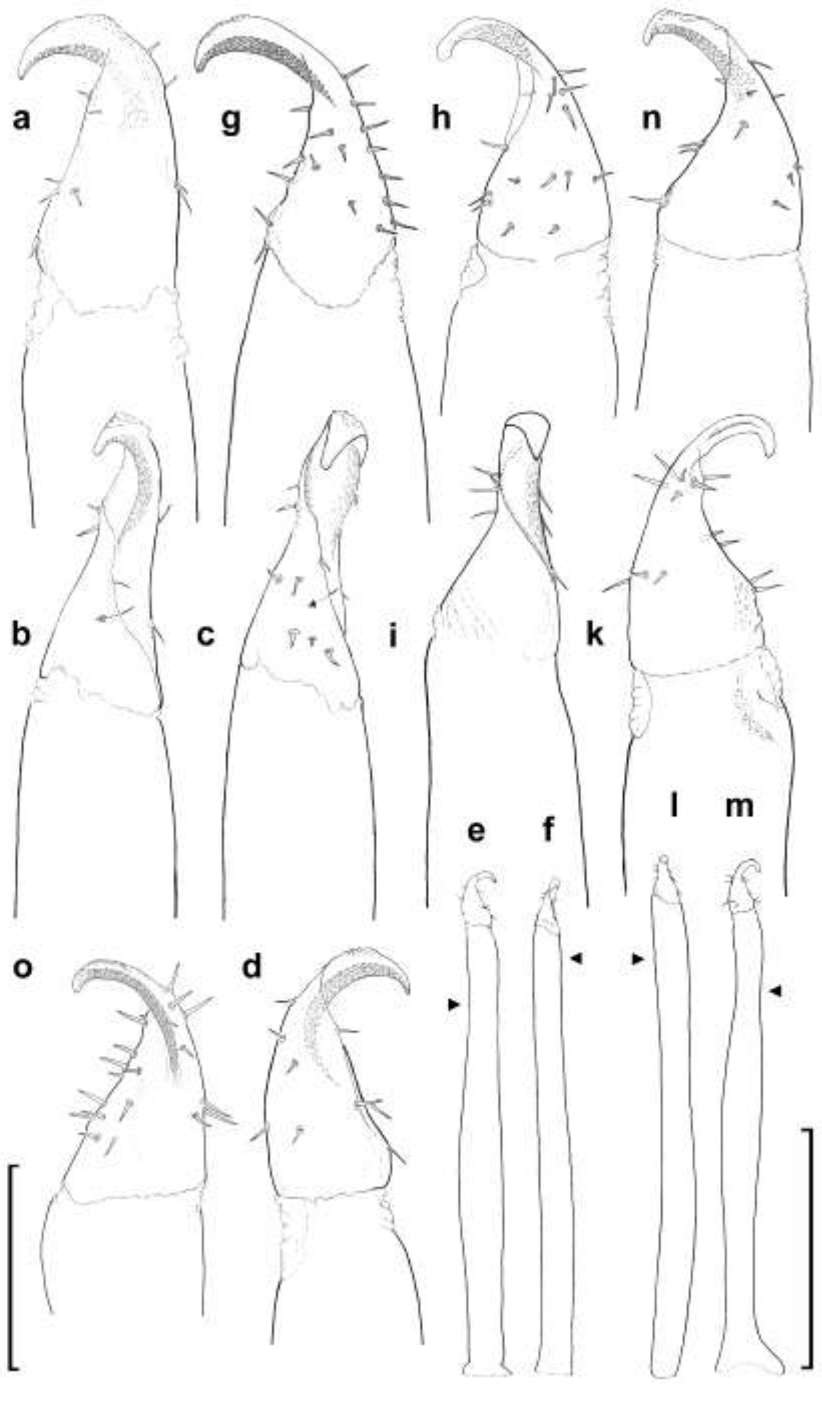


Fig. 4.13. Penis morphology of the species of the *T. falcipenis* clade. Glans penis and distal part of truncus (*a–d*, *g–k*, *n–o*; *a*, *g*, *h*, *n*, *o* dorsal view; *b*, *c*, *i* lateral view; *d*, *k* ventral view); total penis (*e–f*, *l–m*; *f*, *l* lateral view, *e*, *m* ventral view). – *a–i*: *T. falcipenis* Komposch. *a–f*: Topla-Tal, (CJM 4952), *g*: Koschuta, paratype (CJM 3241). – *h–o*: *T. karamanorum* [man.n.] *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.

Trogulus karamanorum [man.n.]

(Figs. 4.2, 4.12*n–y*, 4.13*h–o*, 4.14)

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

HOLOTYPE: **Republic of Macedonia**: 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♂, 3juv., 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♀, 10juv.; 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♀, 4juv., 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♀, 2juv., 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., Smrdliva voda, 736 m (N: 41° 11' 31.7", E: 22° 16' 53.6"), beech forest near stream, sieving leaf litter, 4♂, 3♀, 1juv., 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♂, 1juv., 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♀, 1juv., A. Schönhofer leg. 8. 5. 2006 (CJM 5136); same locality, 1♂, I. Karaman leg. 16. 8. 1985 (CIK 403c); same locality, 1♀, 1juv., 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♀, 1juv., A. Schönhofer leg. 10. and 11. 5. 2006 (CJM 4882); same locality, 1♂, 2♀, 1juv., 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♂, 2juv., H. Schweiger leg. 2. 9. 1957 (NHMW 19712) [paratype of *T. falcipenis*]; Virpazar, 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♀, 1juv., S. Pešic 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. Pešic leg. 30. 5. 1997 (CIK 1438); Bar, Rumija Mt., Sutorman pass (N: 42° 09', E: 19° 06'), 1♀, 1juv., I. Karaman leg. 4. 5. 1997 (CIK 1451); Danilovgrad, S Tunjevo, Milovićka vrela (N: 42° 38', E: 19° 01'), 1♀, 1juv., 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, Milovićka vrela (N: 42° 38', E: 19° 01'), 1♂, I. Karaman leg. 6. 5. 2003 (CIK 1507); same data, 1♀, 1juv., I. Karaman leg. 11. 4. 1997 (CIK 1495); Budva, Prijevor (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♀, 1juv., S. Pešic leg. 25. 5. 1997 (CIK 1472); **Serbia**: 30 km SE Ivanjica, Devići (N: 43° 26', E: 20° 23'), 1♀, 2juv., 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. 4.1): Many autapomorphies and cyt*b* distance values of 14.9–15.8% separate *T. karamanorum* [man.n.] 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. Genetic distances are consequently neglected in this case.

DIAGNOSIS (Fig. 4.12*n*–*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 coloration without reddish tinge. Truncus penis inflated below glans (in lateral view, Fig. 4.13*l*). 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* [man.n.] minute representatives of the *T. tricarinatus* species-group occur. The presence of a sickle-like stylus is always distinctive for *T. karamanorum* [man.n.] (and other possibly still unknown species of the *T. hirtus* species-group). Note that the north-western distributional limit of *T. karamanorum* [man.n.] 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.

DESCRIPTION

BODY (Figs. 3.2, 4.12*t*–*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. 3.2, 4.12*t*, *v*, *w*, *y*); irregular papillation often obscuring the suture between prosoma and opisthosoma; body coloration without reddish tinge, blackish at joints of legs.

EYE MOUND AND FRONT CAP (Figs. 4.12*u*, *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* [man.n.] is very heterogeneous, 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* [man.n.] with certainty. **Body length**: ♂ (*n* = 43) 3.85–4.7 mm, ♀ (*n* = 44) 4.05–5.5 (5.6) mm; all other data referring to 16 ♂ 15 ♀: – **relation of length of distal to basal segment of tarsus II** : ♂ 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.

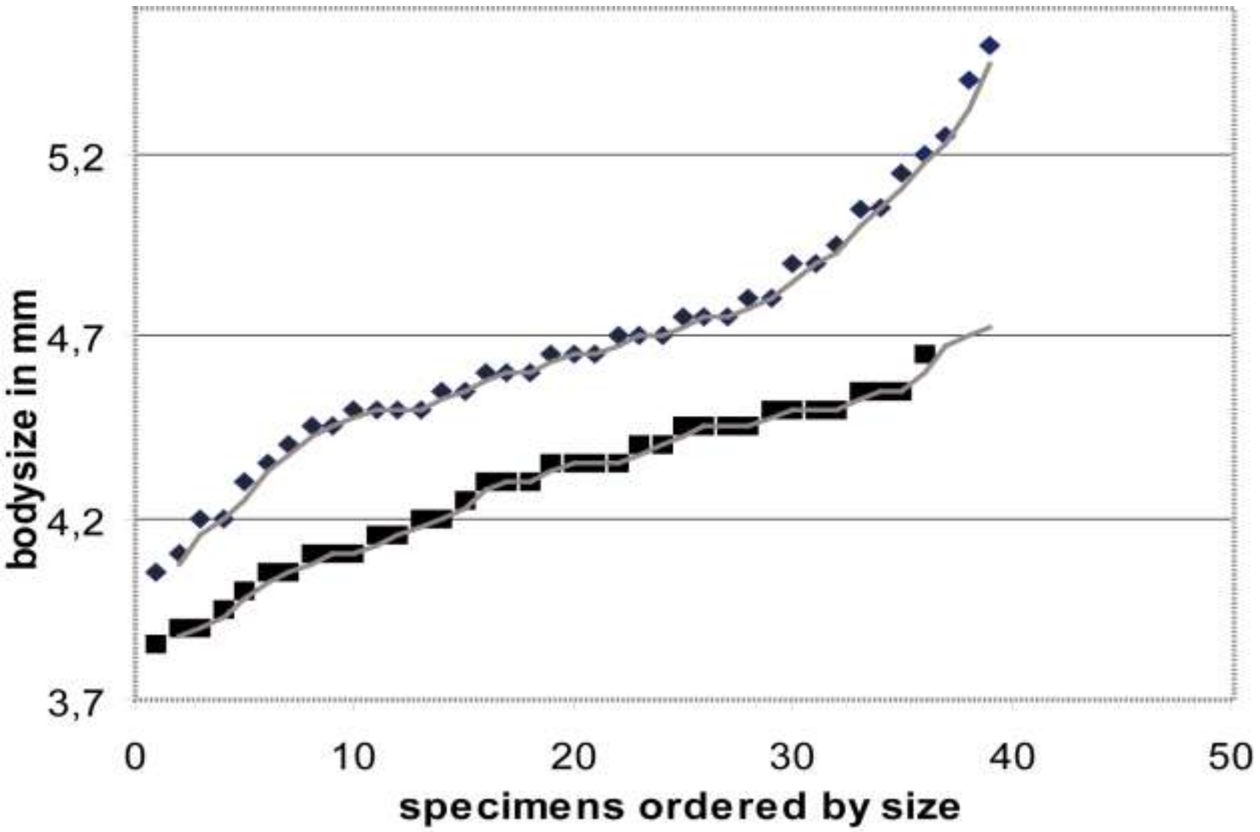


Fig. 4.14. Range of body size within the available sample of *Trogulus karamanorum* [man.n.] specimens. Increase in males (lower curve) is continuous, in females it is so only in the central part (upper curve). Each square refers to one individual.

GENITAL MORPHOLOGY (Figs. 4.13*h*–*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. 4.14), 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. Own data hint at a continuous distribution from sea level to 1500 m without preference of a distinct range except for Greece where *T. karamanorum* [man.n.] seems to be restricted to altitudes around 1000 m.

DISTRIBUTION (Fig. 4.2): 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* [man.n.] 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* [man.n.], 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.*

4.5. Abstract

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 assigned 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 Neretva River), *T. falcipenis* Komposch, 2000 (NW Balkans from SE Carinthia to N Slovenia), *T. karamanorum* [man.n.] (central Balkans from SE Serbia and S Croatia to NE Greece), *T. thaleri* [man.n.] (central Croatian coast, Makarska riviera), *T. pharensis* [man.n.] (central Croatian coast, Hvar Island) and *T. melitensis* [man.n.] (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.

5. Revision of the genus *Trogulus* Latreille: the *Trogulus coriziformis* species-group of the western Mediterranean (Opiliones: Trogulidae)

5.1. Introduction

With respect to the taxonomy of most invertebrate groups, Europe is one of the world's best researched regions. Yet, several groups of organisms remain poorly known owing to their rarity, inconspicuousness and their lack of easily recognizable diagnostic morphological characters. Within the European harvestmen (Opiliones), the family Trogulidae is a showcase of cryptic diversity. No other family has experienced as many recent descriptions as Trogulidae, making a general revision clearly necessary (ROEWER 1950, ŠILHAVÝ 1967, 1968, GRUBER 1968, 1969, AVRAM 1971, CHEMINI 1983, CHEMINI & MARTENS 1988, MARTENS & CHEMINI 1988, KOMPOSCH 2000). The revisions by DAHL (1903) and ROEWER (1923) were mere species listings, providing determination keys that do not reflect phylogenetic relationships.

The combination of uniform appearance and high variability among the few potentially diagnostic characters has inhibited a purely morphological approach to elucidating the systematics of the Trogulidae. Therefore, the use of molecular data is herewith advocated as a major instrument for the reconstruction of phylogenetic relationships within the family. Within the largest genus, *Trogulus* Latreille, 1802, preliminary investigations using molecular data indicated that the number of species exceeds three times the number of currently valid taxa. To investigate this cryptic diversity further, the approach was taken of defining clearly identifiable genetic clades as a first step to evaluate other characters for use in trogulid systematics.

The current study is focusing on the medium- to large-sized *Trogulus* species of the western Mediterranean area, mainly referred to as *T. coriziformis* C. L. Koch, 1839 and *T. aquaticus* Simon, 1879 (e.g. DAHL 1903, ROEWER 1923, 1925, 1950, KRAUS 1959, 1961, RAMBLA 1960, 1967, BRIGNOLI 1968, MARTENS 1978, BRIGNOLI & RAFAELLI 1978, MARCELLINO 1982). This group of species is summarised according to the oldest available name as the *Trogulus coriziformis* species-group. It is confined to Italy, Corsica, the south-western Alps and the Balearic Islands, parts of the Pyrenees and Cantabric Mountains and the

Iberian Peninsula (Fig. 5.1*a*). For more than one and a half centuries the names *Trogulus coriziformis* and *T. aquaticus* have been used as collective terms for specimens with similar body size (>9 mm) and equal length of the tarsus segments of leg II. Although the identity and geographic boundaries of the two taxa remained undefined, new similar species have been described (*T. rossicus* Šilhavý, 1968, *T. banaticus* Avram, 1971) and descriptions of two taxa did not refer to descriptions of the older taxa (*T. salfii* De Lerma, 1948, *T. lusitanicus* Giltay, 1931). Consequently, reliable characters for the delineation of species needed to be found. In chapter 4 genital morphology was shown to be the most useful morphological trait for the determination of members of the *T. hirtus* species-group of the Balkan Peninsula. This holds true also for the material commonly labelled *T. coriziformis* and *T. aquaticus*, but this group of species appears morphologically more heterogeneous in many respects.

To investigate this problematic species-complex, a molecular approach was used (using the mitochondrial cytochrome *b* (cyt*b*) and the nuclear 28S rRNA (28S) genes) to look for distinct genetic lineages and to combine them with morphological characters in order to delineate ‘species’. Investigated was also all available material to delineate characters useful for species recognition and outlined their distributions to find possible geographical boundaries among species.

5.2. Material

Fourteen samples of the *Trogulus coriziformis* species-group were available for molecular analysis (Tab. 5.1). Nineteen additional sequences belonging to other species of *Trogulus* were also included. These were species of similar body size or genital morphology that are often attributed to ‘*T. coriziformis*’, as well as species assigned to other species-groups. For hierarchical outgroup rooting I used sequences obtained from other trogulid genera (*Anelasmocephalus cambridgei* Simon, 1879; *Calathocratus beieri* Gruber, 1968; *Platybessobius* sp. Roewer, 1940; all Tab. 5.1).

In addition to that I was able to study an extensive material from several private and public collections (see chapter 3.1). According data is listed with the respective species in the chapter 5.5.3.

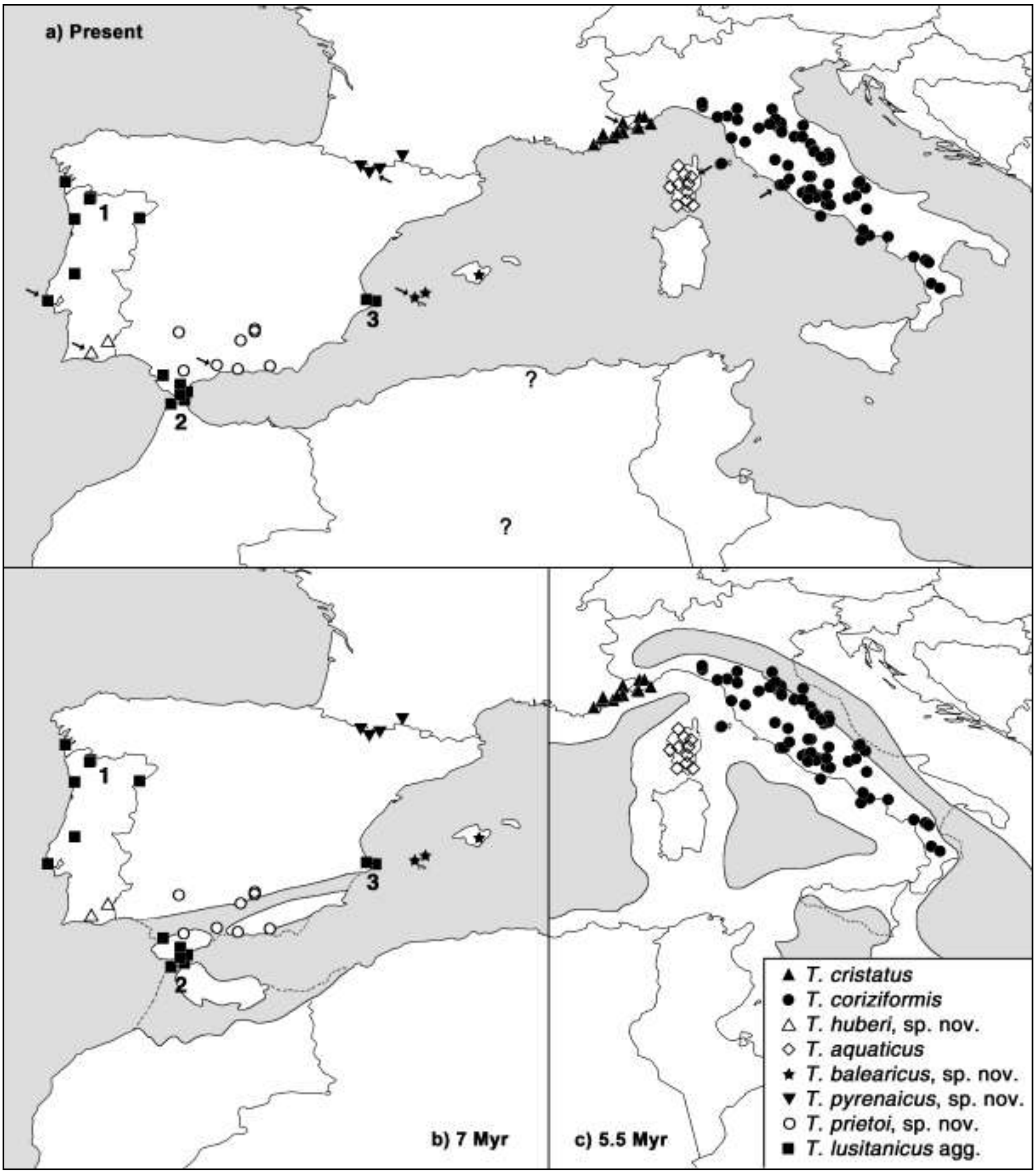


Fig. 5.1. (*a*) Current distribution of the *Trogulus coriziformis* species-group in the western Mediterranean. Arrows indicate (neo-) type localities, numbers indicate populations of *T. lusitanicus* agg. referred to in the text. 1, northern Portugal, Albergaria; 2, southern Spain, Gibraltar, Morocco; 3, south-western Spain, Alicante. Question marks refer to unconfirmed or indeterminable records possibly affiliated to *T. lusitanicus* agg. (*b*) Reconstruction of the western Mediterranean, 7 Mya, late Miocene, overlain with the actual distribution of the *T. coriziformis* species-group (map modified after DE JONG (1998)); (*c*) as in *b* but 5.5 Mya, Messinian.

5.3. Results

According to the Akaike information criterion (POSADA & BUCKLEY 2004) the best fit model for the cyt*b* dataset was the GTR+I+G model with the following likelihood settings: Empirical base frequencies: πA=0.3796, πC=0.2684, πG=0.0325, πT=0.3196; proportion of invariable sites I=0.3501; Ti/Tv ratio=5.9397; gamma shape parameter α =0.5081. For the concatenated 28S/cyt*b*-alignment the SYM+I+G model with the following likelihood settings was used: base frequencies: equal; proportion of invariable sites I=0.3365; Ti/Tv ratio=5.4123; gamma shape parameter α=0.2530 was favoured.

For cyt*b* fourteen sequences assigned to the *T. coriziformis* species-group and nineteen further Trogulidae sequences (in total 33 sequences, Table 5.1) produced an alignment of 552 bp. There were 234 variable sites (42.4%) in the alignment of which 199 (36.1%) were parsimony informative (for ingroup sequences of the *T. coriziformis* species-group only). Seven sequences were obtained for 28S assigned to the *T. coriziformis* species-group and those were grouped with the same assemblage as for the cyt*b* dataset (in total 26 sequences, Table 5.1). They produced an alignment of 1167 bp with 53 variable sites (4.5%) of which 30 (2.6%) were parsimony informative (for ingroup only). Both datasets were combined as partition homogeneity test indicated no heterogeneity (P = 0.289; a value P > 0.01 is not significant [CUNNINGHAM 1997]).

The efficiency of sequence extraction and the phylogenetic resolution is different for the used fragments. Cyt*b* sequences could be obtained from double the number of specimens than in 28S. Cyt*b* exhibits high evolution rates and offered valuable autapomorphies for species recognition and species relationships. In contrast, resolution at higher phylogenetic levels is obscured by repeated reversible mutations. In the case of the 28S data this information bias is opposite to the cyt*b* data and responsible for most of the information for higher phylogenetic levels. To present as much valuable data as possible the taxon rich cyt*b* data and a concatenated 28S/cyt*b* dataset were processed. Bayesian, MP and ML analyses resulted in trees of almost identical topology (variable in respect to few basal splits of the cyt*b* dataset in the outgroups) for the respective dataset (Figs. 5.2, 5.3). Genetic distance values for the cyt*b* dataset are given in Table 2.

Within *Trogulus* two main clades are well supported by 28S/cyt*b* data (Fig. 5.3). A basal clade comprising all specimens associated to the *T. coriziformis* species-group and a

Table 5.1. List of material used for molecular genetic analysis.

Taxon	Voucher	Country	Locality	Acc. no. Cyt b	Acc. no. 28S rRNA
Anelasmocephalus cambridgei	CJM 3846	Germany	Alzey, Nieder-Wiesen	FJ373241	FJ373245
Calathocratus beieri.	CJM 5738	Turkey	Osmaniye Erzin	FJ373243	FJ373246
Platybessobius sp.	CJM 5118	Turkey	Izmir Nif Dagi	FJ373212	FJ373247
Trogulus aquaticus	CJM 3058	France	Corsica	FJ373233	–
T. balearicus sp. nov.	SMF 11816	Spain	Balearic Islands, Ibiza	FJ373231	–
T. balearicus sp. nov.	CCP 3616	Spain	Balearic Islands, Mallorca	FJ373232	FJ373250
T. banaticus	CJM 4927	Romania	Cluj, Closani	FJ373244	FJ373249
T. closanicus	CJM 5154	Croatia	Biokovo Mountain	FJ373242	FJ373251
T. niger	CJM 4945	Romania	Cluj, Closani	FJ373236	FJ373263
T. coriziformis	CJM 1058	Italy	Lazio, Prov. Roma	FJ373239	–
T. coriziformis	CJM 5009	Italy	Tuscany, Prov. Firenze	FJ373221	FJ373253
T. coriziformis	CJM 5051	Italy	Abruzzo, Prov. Chieti	FJ373222	FJ373252
T. coriziformis	CJM 5423	Italy	Tuscany, Prov. Livorno, Elba	FJ373227	–
T. cristatus	CJM 4972	Italy	Liguria, Prov. Imperia	FJ373216	FJ373254
T. graecus	CJM 5083	Greece	N of Igoumenitsa	FJ373223	FJ373255
T. graecus	CMK Igr	Italy	Valencano, Bari	FJ373240	FJ373248
T. gypseus	CJM 4478	Turkey	30 km E Alanya	FJ373218	FJ373256
T. huberi sp. nov.	CJM 5344	Portugal	Algarve, ca. 50 km N Faro	FJ373224	FJ373257
T. karamanorum [m.n.]	CJM 3025	Greece	W Makedonia, Pindos Mts.	FJ373215	FJ373258
T. lusitanicus agg.	BMNH2	Spain	UK, Gibraltar	FJ373229	–
T. lusitanicus agg.	CCP 1966	Spain	Cádiz, Algeciras	FJ373226	–
T. lusitanicus agg.	ZMC ♀	Portugal	Braga, Albergaria	FJ373228	–
T. lusitanicus agg.	ZMC ♂	Portugal	Braga, Albergaria	FJ373225	FJ373259
T. martensi	CJM 4690	Switzerland	Basel	FJ373213	FJ373261
T. nepaeformis	CJM 3832	Slovenia	Idrija	FJ373235	FJ373262
T. oltenicus	CJM 4873	Romania	Cluj, Closani	FJ373237	FJ373264
T. prietoi sp. nov.	CJM 5321	Spain	Andalusia, Prov. Malaga	FJ373230	–
T. setosissimus	CRO 7	Croatia	Biokovo Mountain	FJ373238	FJ373265
Trogulus sp.	CJM 4900	Macedonia	Radika valley	FJ373220	FJ373266
T. squamatus	CJM4831	Montenegro	Monastery Morača	FJ373234	FJ373267
T. tingiformis	CJM 4613	Hungary	35 km W Budapest	FJ373219	FJ373268
T. torosus	CIK 1518	Bosnia-Herzegovina	Trebinje, Matulica pecina	FJ373217	FJ373269
T. tricarinatus	CJM 5312	Germany	Saxony, Dresden city	FJ373214	FJ373270

clade including all other *Trogulus* taxa incorporated in this analysis. The monophyly of the *T. coriziformis* species-group is further supported by cyt*b* data, but with low bootstrap values for MP. The 28S/cyt*b* data further supports the separation of the *T. coriziformis* species-group from all other *Trogulus* by a mean between-group distance of 12.8%, which is considerably larger than the individual within-group distances (9.2% for *T. coriziformis* species-group, 9.0% for all other *Trogulus* taxa). The *T. coriziformis* clade is split into four distal clades with large genetic distances (Figs. 5.2, 5.3). 1, a clade comprising *T. cristatus* and *T. coriziformis* (28S only, unsupported by cyt*b*) and *T. aquaticus* (cyt*b* only); 2, a clade comprising *T. lusitanicus* agg. (southern Spain; ‘agg.’ refers to a composite species, for explanation see chapter 5.5.3, *T. lusitanicus*), *T. prietoi* sp. nov. and *T. huberi* sp. nov.; 3, a clade including the two divergent lineages of *T. balearicus* sp. nov.; 4, the isolated lineage of *T. lusitanicus* agg. (northern Portugal). Within these clades, relations are revealed by the cyt*b* data only (Fig. 5.2). It supports close relation between *T. coriziformis* and *T. aquaticus* and between *T. lusitanicus* agg. (southern Spain) and *T. prietoi* sp. nov. Relationships between the groups remained unresolved.

Table 5.2. Genetic distances within the *Trogulus coriziformis* species group and trogulid outgroups. Distances of 552 bp of the cytochrome *b* gene are given in %; uncorrected p-distances.

no.	Taxon	Voucher	1	2	3	4	5	6	7	8	9	10	11
1	*Anelasmocephalus* cambridgei, Germany	CJM3846											
2	*Calathocratus* beieri, Turkey	CJM5738	29.43										
3	*Platybessobius* sp., Turkey	CJM5118	30.27	26.24									
4	*Trogulus aquaticus,* France, Corsica	CJM3058	33.49	29.15	28.97								
5	*T. balearicus* sp. nov., Spain, Ibiza	SMF11816	31.84	28.15	30.54	17.12							
6	*T. balearicus* sp. nov., Spain, Mallorca	CCP3616	30.98	27.18	28.89	17.17	8.22						
7	*T. banaticus,* Romania	CJM4927	32.57	27.85	31.88	21.66	21.27	19.72					
8	*T. closanicus,* Croatia	CJM5154	28.76	25.52	28.97	21.50	21.42	21.32	22.02				
9	*T. niger,* Romania	CJM4945	29.51	24.80	27.82	21.76	21.16	20.23	20.41	11.55			
10	*T. coriziformis,* Italy, Abruzzo	CJM5051	31.98	28.52	30.20	13.51	19.20	18.07	22.57	21.24	22.21		
11	*T. coriziformis,* Italy, Elba	CJM5423	31.99	28.10	29.71	12.93	18.80	17.98	22.35	21.01	22.16	0.19	
12	*T. coriziformis,* Italy, Lazio	CJM1058	32.09	28.59	30.07	13.08	19.30	18.49	22.47	21.33	22.32	0.37	0.00
13	*T. coriziformis,* Italy, Tuscany	CJM5009	32.27	28.47	30.09	13.24	19.31	18.52	22.29	21.33	22.10	0.55	0.00
14	*T. cristatus,* Italy, Liguria	CJM4972	32.52	27.74	30.25	17.28	17.75	16.60	19.99	19.43	19.38	17.16	17.10
15	*T. graecus,* Greece	CJM5083	29.92	27.65	29.02	21.72	21.65	20.39	20.92	19.85	18.59	23.26	23.40
16	*T. graecus,* Italy	CMKIgr	30.27	27.47	28.78	22.09	21.40	19.75	21.63	19.27	19.33	22.13	22.26
17	*T. gypseus,* Turkey	CJM4478	28.94	26.73	30.39	23.54	21.95	21.35	20.53	20.69	20.17	22.50	22.22
18	*T. huberi* sp. nov., S. Portugal	CJM5344	33.83	28.55	28.02	22.76	20.65	19.50	24.17	23.04	21.85	23.55	23.34
19	*T. karamanorum* [man.n.], Greece	CJM3025	32.70	29.87	28.55	23.62	24.82	24.26	22.51	21.97	21.91	25.72	25.49
20	*T. lusitanicus,* Portugal, Albergaria	ZMC ♂	32.56	28.83	29.94	20.66	19.88	19.21	24.08	24.62	23.13	20.77	20.70
21	*T. lusitanicus,* Spain, Cadiz	CCP1966	33.10	28.90	29.07	22.76	20.47	17.92	23.82	23.78	22.63	21.92	21.39
22	*T. lusitanicus,* UK, Gibraltar	BMNH2	33.10	28.90	28.89	22.58	20.29	17.73	23.82	23.60	22.63	21.74	21.21
23	*T. lusitanicus,* Portugal, Albergaria	ZMC ♀	32.61	28.64	29.40	19.96	19.68	18.83	24.06	23.54	22.79	20.24	20.16
24	*T. martensi*, Switzerland	CJM4690	32.14	26.45	28.52	24.54	20.61	20.01	19.88	16.62	14.22	24.66	24.02
25	*T. nepaeformis,* Slovenia	CJM3832	31.21	24.81	27.97	24.54	20.61	19.63	20.68	17.21	14.60	22.97	22.54
26	*T. oltenicus,* Romania	CJM4873	31.66	26.91	30.05	23.89	21.43	21.64	21.63	18.72	17.17	22.15	22.05
27	*T. prietoi* sp. nov., S. Spain	CJM5321	34.74	29.10	31.50	20.02	19.02	18.02	20.71	23.06	23.42	19.57	19.12
28	*T. setosissimus,* Croatia	CRO7	31.30	27.09	29.83	20.77	20.68	20.19	16.75	18.51	18.23	20.69	20.44
29	*T. squamatus,* Montenegro	CJM4831	31.44	26.20	28.03	22.23	21.38	19.66	20.16	16.17	14.41	22.84	22.80
30	*T. tingiformis,* Hungary	CJM4613	31.38	28.90	29.30	22.12	21.47	21.58	21.14	18.82	18.38	22.41	22.17
31	*T. torosus,* Montenegro	CIK1518	30.58	29.30	28.60	20.39	21.42	21.06	21.30	21.27	20.29	20.86	20.41
32	*T. tricarinatus,* Germany	CJM5312	32.25	26.89	29.23	21.80	21.31	21.96	20.24	19.64	17.62	24.25	24.16
33	*Trogulus* sp., Macedonia	CJM4900	28.73	27.32	30.03	24.46	23.41	21.79	22.17	19.82	18.58	23.94	23.93

no.	Taxon	Coll.-no.	12	13	14	15	16	17	18	19	20	21	22
13	*T. coriziformis,* Italy, Tuscany	CJM5009	0.00										
14	*T. cristatus,* Italy, Liguria	CJM4972	17.24	17.24									
15	*T. graecus,* Greece	CJM5083	23.51	23.56	21.15								
16	*T. graecus,* Italy	CMKIgr	22.39	22.43	20.72	8.40							
17	*T. gypseus,* Turkey	CJM4478	22.36	22.33	20.23	17.80	17.74						
18	*T. huberi* sp. nov., S. Portugal	CJM5344	23.50	23.44	20.68	24.19	25.42	23.74					
19	*T. karamanorum* [man.n.], Greece	CJM3025	25.49	25.64	24.99	24.89	25.21	23.04	26.27				
20	*T. lusitanicus,* Portugal, Albergaria	ZMC ♂	21.05	20.84	21.60	25.78	24.85	22.42	23.32	24.76			
21	*T. lusitanicus,* Spain, Cadiz	CCP1966	22.02	22.03	21.55	25.06	23.97	24.08	19.38	25.54	21.33		
22	*T. lusitanicus,* UK, Gibraltar	BMNH2	21.84	21.85	21.36	24.88	23.79	23.90	19.20	25.36	21.15	0.18	
23	*T. lusitanicus,* Portugal, Albergaria	ZMC ♀	20.52	20.31	20.85	25.58	24.48	22.41	22.99	24.10	0.36	20.98	20.80
24	*T. martensi*, Switzerland	CJM4690	24.39	24.16	19.28	19.96	19.98	17.01	21.71	23.34	21.94	22.41	22.23
25	*T. nepaeformis,* Slovenia	CJM3832	22.90	22.89	19.51	17.22	17.56	18.38	21.51	22.45	23.10	21.49	21.31
26	*T. oltenicus,* Romania	CJM4873	22.40	22.42	20.39	20.05	19.27	19.60	23.24	24.88	24.30	26.69	26.69
27	*T. prietoi* sp. nov., S. Spain	CJM5321	19.48	19.47	19.56	22.70	22.85	25.07	18.12	25.91	22.04	16.67	16.67
28	*T. setosissimus,* Croatia	CRO7	20.81	20.79	18.08	21.08	21.78	18.62	24.34	19.72	20.43	23.06	22.88
29	*T. squamatus,* Montenegro	CJM4831	22.78	22.74	19.22	21.27	21.05	20.98	21.92	23.91	24.99	22.28	22.28
30	*T. tingiformis,* Hungary	CJM4613	22.35	22.51	19.35	20.45	21.53	20.23	22.96	23.14	23.78	24.41	24.23
31	*T. torosus,* Montenegro	CIK1518	20.76	20.74	19.93	22.43	22.52	19.98	23.96	22.49	24.64	22.85	22.85
32	*T. tricarinatus,* Germany	CJM5312	24.15	24.13	20.58	17.60	18.48	19.71	22.42	24.33	25.30	24.27	24.45
33	*Trogulus* sp., Macedonia	CJM4900	24.26	24.23	19.72	22.37	21.81	21.75	25.75	22.49	22.06	22.65	22.65

no.	Taxon	Coll.-no.	23	24	25	26	27	28	29	30	31	32
24	*T. martensi*, Switzerland	CJM4690	21.77									
25	*T. nepaeformis,* Slovenia	CJM3832	22.91	7.29								
26	*T. oltenicus,* Romania	CJM4873	24.14	18.95	18.10							
27	*T. prietoi* sp. nov., S. Spain	CJM5321	21.88	23.74	21.69	23.24						
28	*T. setosissimus,* Croatia	CRO7	19.67	18.17	19.05	18.74	20.54					
29	*T. squamatus,* Montenegro	CJM4831	24.74	17.32	17.16	19.23	21.95	17.61				
30	*T. tingiformis,* Hungary	CJM4613	22.88	13.18	13.24	20.45	23.32	17.83	16.41			
31	*T. torosus,* Montenegro	CIK1518	23.91	20.46	20.43	22.18	21.60	18.76	19.99	21.74		
32	*T. tricarinatus,* Germany	CJM5312	25.65	19.06	18.90	16.89	22.95	21.37	18.25	18.92	21.05	
33	*Trogulus* sp., Macedonia	CJM4900	22.06	19.29	19.57	21.45	24.48	20.14	22.12	21.18	23.45	24.12

The computations using the morphometric dataset with different settings revealed similar results. Although highly similar in morphology, the combination of a few characters enabled separation among the taxa of *T. coriziformis* species-group by 98% (canonical discriminant analysis; Figs. 5.4, 5.14). The respective characters are given in chapter 5.5.3. Members of the two *T. lusitanicus* agg. populations from northern Portugal and southern Spain could not be differentiated even in the two group analysis (see chapter 5.5.3, *T. lusitanicus*).

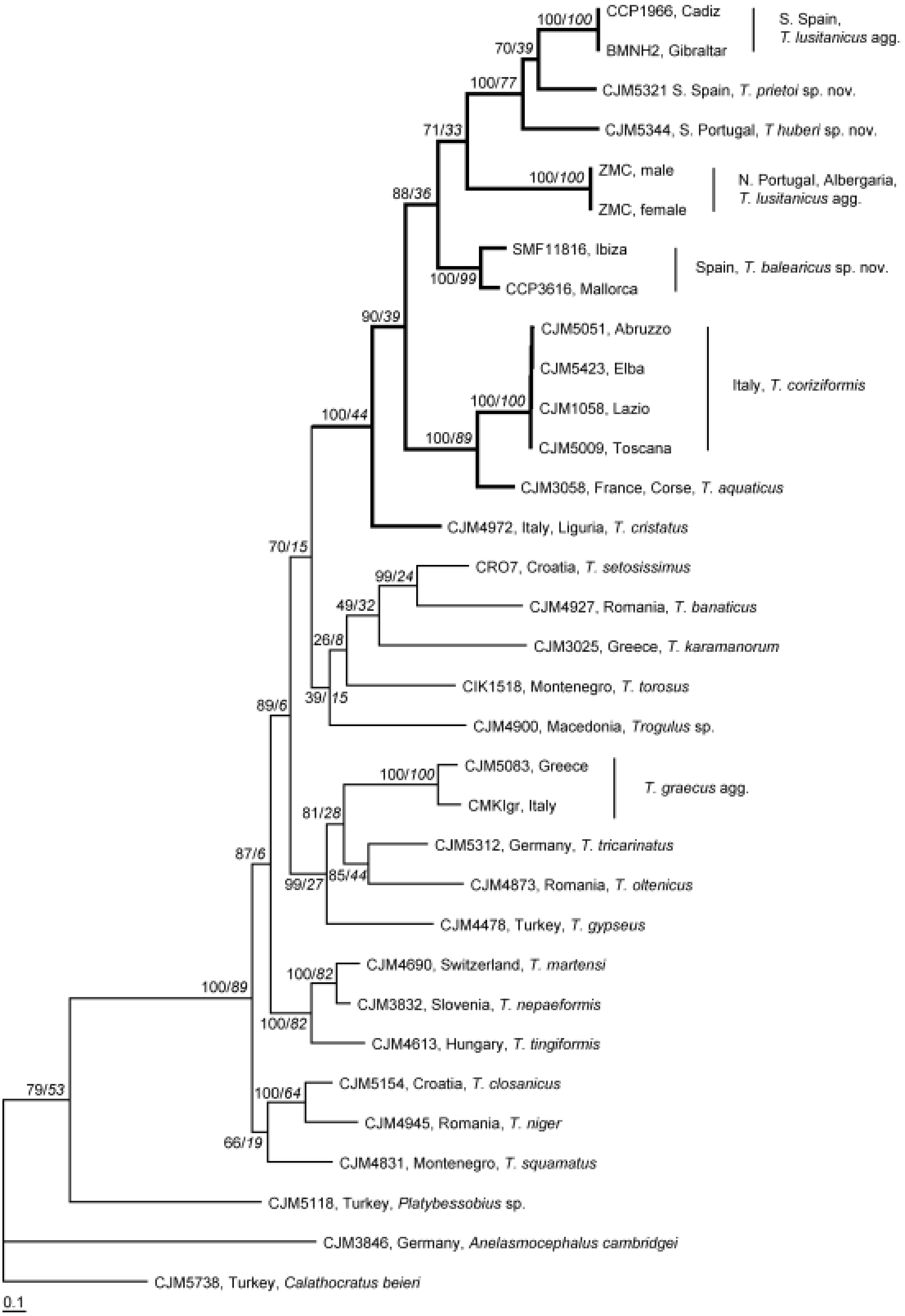


Fig. 5.2. Bayesian phylogram of the *Trogulus coriziformis* species-group and related taxa, 552 bp, cytochrome *b* gene. This topology is consistent with Maximum Likelihood (ML) and Maximum Parsimony (MP) trees (not shown). Support values indicated at nodes represent *a posteriori* probabilities and MP bootstrap support values after 2000 replicates (italics), respectively. The *Trogulus coriziformis* species-group is indicated by bold branches.

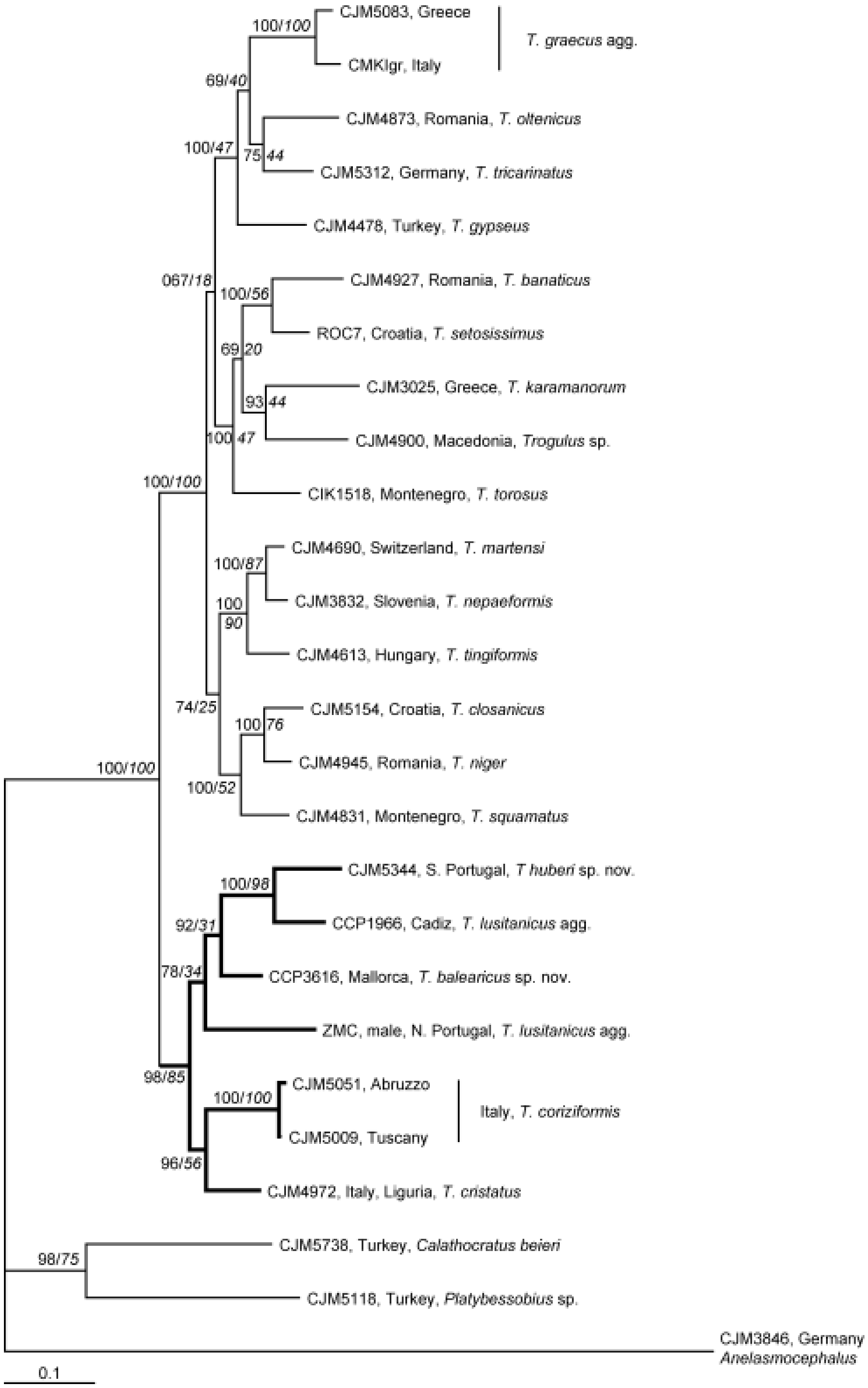


Fig. 5.3. Bayesian phylogram of the *Trogulus coriziformis* species-group and related taxa, combined alignment of 1145 bp 28S rRNA and 552 bp cytochrome *b* gene. This topology is consistent with Maximum Likelihood (ML) and Maximum Parsimony (MP) trees (not shown). Support values indicated at nodes represent *a posteriori* probabilities and MP bootstrap support values after 2000 replicates (italics), respectively. The *Trogulus coriziformis* species-group is indicated by bold branches.

Molecular and morphometric results are highly correlated with the distribution pattern of the *T. coriziformis* species-group (Fig. 5.1). It can be split in an eastern lineage comprising *T. aquaticus*, *T. coriziformis* and *T. cristatus* and a western lineage including *T. lusitanicus* agg. (southern Spain), *T. huberi* sp. nov. and *T. prietoi* sp. nov. Genital morphological characters correlate with these groups, with *T. balearicus* sp. nov. from the eastern lineage having a rounded penial stylus and *T. lusitanicus* agg. (northern Portugal) and *T. pyrenaicus* sp. nov. from the western lineage both having a divided stylus. Despite this, the latter species assignments are not supported with respect to genetics (*Trogulus pyrenaicus* sp. nov. could not be included in the genetic analysis owing to a lack of fresh material).

5.4. Discussion

5.4.1. Delineation of species-groups

The molecular genetic results revealed the *T. coriziformis* species-group as sister-group to all other *Trogulus* taxa. This clade therefore represents a subgeneric division of *Trogulus* rather than a species-group. Its high genetic divergence explains the remarkable degree of male genital morphological variation in the species-group. It was found generally that penial structures are conservative features within *Trogulus* species-groups (chapter 4). Only within single lineages of the *T. coriziformis* clade is this character more uniform, thus resembling the degree of conserved penial structure within other *Trogulus* species-groups.

Consequently, an unambiguous definition of the *T. coriziformis* species-group based on genital morphological characters alone is not possible. Furthermore, the straight penial stylus is not a unique feature within this group but may be considered as plesiomorphic within *Trogulus*. It is present in several unrelated and partly undescribed taxa especially from the Balkan Peninsula (*T. torosus* Simon, 1885, *T. banaticus* Avram, 1971, *T. setosissimus* Roewer, 1940, *Trogulus* sp. Macedonia). These species exhibit various synapomorphies with the *T. coriziformis* species-group and prohibit its clear morphological delineation. However, the geographical distribution clearly defines the *T. coriziformis* species-group. Its members are almost completely allopatric to other *Trogulus* taxa and are restricted to the western Mediterranean area. Only one species of the *T. nepaeformis* species-group in the Pyrenees and another on the Italian Peninsula are sympatric with the *T. coriziformis* species-group. These species are quite distinct in both size and genital morphology.

5.4.2. Phylogenetic relationships within the group

Although genetic distances are considerable between the single taxa of the *T. coriziformis* species-group (Table 5.2), distributional areas of species do not overlap as is common for taxa with comparable genetic distances (Fig. 5.1; see chapter 6.4.4). Despite this, a correlation between immediate geographical neighbourhood and genetic relationship is obvious. This suggests low dispersal ability during and after the speciation processes to trigger the diversification of the species-group. One example is the relationships among *T. coriziformis* from the Italian Peninsula, *T. aquaticus* from Corsica and *T. cristatus* from the south-eastern Alps. *Trogulus coriziformis* and *T. aquaticus* show close genetic affinities and relatively low genetic distance (12.9–13.5%; cyt*b*) and share the unique feature of prominent papillae on the pedipalps (Fig. 5.6). The relationship with *T. cristatus* is revealed by the rounded penial stylus as the common feature (Figs. 5.7, 5.8, 5.12). Another similarly supported clade comprises *T. huberi* sp. nov., *T. prietoi* sp. nov. and *T. lusitanicus* agg. (southern Spain) from the southern Iberian Peninsula with a stylus terminating in a pair of lamellae. This results in a cut-off appearance as common character (Figs. 5.17*a*, *e*, 5.18*i*, 5.21). These specific stylus features suggest bringing the remaining taxa into the group of this general penial scheme (*T. balearicus* sp. nov. (rounded stylus tip) and *T. lusitanicus* agg. (northern Portugal; stylus tip with lamellae)). Although this scheme is maintained in the taxonomic section, molecular data suggest grouping the latter two with the south Iberian clade.

Large genetic distances support the species status of those populations that were sequenced for this study. Intraspecific variability was only investigated for a few species but was considerably low. For *T. coriziformis*, the most widespread taxon of the species-group (Fig. 5.1*a*), sequences from distant localities did not exceed 0.6%. Within populations of *T. lusitanicus* from northern Portugal and southern Spain the intraspecific variation was similarly low (0.2–0.4%). Interspecific distance between these populations is as high as 21.3%, indicating species status. But correlating morphological characters could not be found (see chapter 5.5.3, *T. lusitanicus*). Another example of high intraspecific variation that may indicate the presence of cryptic species refers to *T. balearicus* sp. nov.; specimens of which from Ibiza and Mallorca differ by a genetic distance value of 8.2%.

5.4.3. Biogeography

The distribution pattern of the species and the restriction of the species-group to the western Mediterranean implies its evolution to be connected with the geological history of the area. Different geological scenarios were investigated that might have caused the distributional pattern of the present taxa. Geological processes during the late Tertiary in the western Mediterranean are especially well reflected by the present distribution pattern of several species.

During the Messinian (5.5 Myr), the area of the present Italian Peninsula was divided by a marine transgression covering most of its eastern parts and the Po valley in the North (DE JONG 1998; Fig. 5.1*c*). The area of Puglia in the south-east was then divided from the rest of present Italy and connected with the middle Balkan. The Adriatic Sea was dry. Neither this formerly separated part of Italy nor large parts of the formerly submerged areas were subsequently colonized by the present *T. coriziformis*. Instead, Puglia was colonized by a member of the Balkan *T. graecus* species-group (see *graecus*, chapter 12.3).

Furthermore, the Messinian salinity crisis caused the connection between Corsica and Italy (DE JONG 1998) and resulted in the common distributional area of the present *T. coriziformis* (Italy) and *T. aquaticus* (Corsica). They diverged much later and both are sister to *T. cristatus* (southwestern Alps).

The geological evolution of the southern Iberian Peninsula is still under discussion and speciation processes have to be interpreted carefully. ROSENBAUM et al. (2002) showed that several microplates shifted from eastern Spain southwestwards and collided with the southern margins of the Iberian and northern margin of the African plate (15–10 Myr) where they remained until the present. DE JONG (1998) dated the isolation of these microplates by marine transgression between 18–7 Myr. Consequently, long-lasting geographic isolation of several regions at the southern margin of the Iberian Peninsula is generally assumed (DE JONG 1998; ROSENBAUM et al. 2002). This scenario largely coincides with the distributional areas of the present species of the *T. coriziformis* group (Fig. 5.1*b*). More recent diversification occurred on the Balearic Islands where *T. balearicus* sp. nov. exhibits marked genetic distances between the islands of Ibiza and Mallorca.

The small-scaled distributional areas of the taxa of the *T. coriziformis* species-group in combination with their obviously limited dispersal abilities provide the first example that Trogulidae are an excellent group for zoogeographic studies. Within Opiliones, the suborder Cyphophthalmi have already proven to be a most useful taxon to investigate biogeographic patterns on a worldwide scale (Boyer et al. 2007*b*) as well as in Europe (Boyer et al. 2005, Karaman in press). Nevertheless Cyphophthalmi does not fully cover the geographically highly complex Mediterranean biogeography, whereas Trogulidae are present with a variety of genera, subgroups and species of often small distribution areas in nearly every corner of the Ancient Mediterranean region eastwards to Kyrgyzstan in Central Asia. In most areas more than one representative is present, enabling historic patterns to be determined. Further detailed zoogeographic information can be expected to be obtained through a detailed molecular genetic investigation of Trogulidae.

5.5. Taxonomy

5.5.1. Diagnosis of the *Trogulus coriziformis* species-group

Assignment of specimens to the *T. coriziformis* species-group is possible based on the male genital morphology (straight penial stylus) in combination with their geographical distribution (representatives of this taxon are found on the Iberian and Italian Peninsula, south-western Alps, Corsica and the Balearic Islands) or genetic information. Females can be assigned to the respective species by body size, external morphological traits and geographical information.

Description:

Body: The *T. coriziformis* species-group comprises medium- to large-sized species (♂ 7.90–12.85 mm; 8.60–15.35 mm). Species are quite variable, not fitting into a general scheme. Most characters are species specific and often affected by allometric growth. Papillae on the dorsal side of body are small and regularly spaced (Figs. 5.10*a*, *c*, 5.15*a*, *c*) or form different patterns on the opisthosoma and prosoma that are caused by clearly defined regions of high and low papillae density (Figs. 5.5*a*, *c*, 5.19*a*, *d*, *g*). The papillation on the prosoma can be useful for species identification.

EYE MOUND AND FRONT CAP: The morphology of the eye mound is generally a useful character in *Trogulus* systematics enabling easy species delineation in some cases. Characteristics range from two markedly elevated eye hills separated by a distinct groove to a flat and fused ocularium. Additionally, the distance between the eyes is variable, making this character useful for morphometrics.

LEGS AND PALPI: The length of leg II and its segments are particularly useful for identification of several species. The apophyses on tarsus III and IV are considerably large in several species (Figs. 5.11*c*, *f*, 5.16*c*, *i*, *m*). A crest of elongated papillae on the dorsal femur II is clearly marked in species from the eastern part of the distributional range, whereas it is lacking in the large species from the Iberian Peninsula. In several species a useful character is the sparse but prominent papillation on the palps (Fig. 5.6*a*, *d*, *g*, *k*).

PENIS MORPHOLOGY: The truncus is dorso-ventrally flattened as in most other *Trogulus* species, stout and cuneiform. In smaller species it is nearly parallel-sided, the base drawn out in two short indistinct roots, only exceptionally constricted in midsection, gradually tapering into the elongated and triangular glans (in ventral/dorsal view), continuously merging into the stylus (Figs. 5.12*f*, 5.17*f*, 5.21*b*, *f*, *k*), or with a distinct knob at the intersection (Figs. 5.7*b*, *f*, 5.8*b*, *f*). The stylus is minute, outstretched, straight in line with the truncus, partly long and slender (Figs. 5.12*e*, *f*, 5.13) or short and stout (Figs. 5.7, 5.8). The distal end of the stylus is rounded (Figs. 5.7, 5.8, 5.12, 5.13 in dorsal view) or truncated and divided into a pair of lamellae (Figs. 5.17*a*, *e*, 5.18*i*, 5.21*a*, *e*, *i*, *n*, in dorsal view), the glans is sparsely covered with medium sized setae.

DISTRIBUTION: This species-group is restricted to the western Mediterranean. The distribution is disjunct and species (according to current information) are strictly allopatric (Fig. 5.1). Members of the *T. nepaeformis* species-group are sympatric with those of the *T. coriziformis* species-group but can easily be distinguished by genital morphology or body size. Its range is continuous on the Italian Peninsula excluding the south-eastern part and the Po valley; westwards it is disjunctly distributed along the Mediterranean coast to the Iberian Peninsula. It occurs at the southern border of the western Alps and locally in the central Pyrenees, and on the Balearic Islands and Corsica. On the Iberian Peninsula it is restricted to a narrow belt along the southern and western coast, only in northern Portugal it is recorded

~200 km inland. It most probably occurs along the north-western African coast (females have been reported from Morocco, unconfirmed records exist from Algeria and Tunisia).

COMPOSITION: The *T. coriziformis* species-group currently contains eight species: *T. coriziformis* C. L. Koch, 1839; *T. aquaticus* Simon, 1879; *T. cristatus* Simon, 1879; *T. lusitanicus* Giltay, 1931; *T. balearicus* sp. nov.; *T. huberi* sp. nov.; *T. prietoi* sp. nov. and *T. pyrenaicus* sp. nov. Species have been grouped according to genital morphological characters. The first four species, (*T. coriziformis, T. aquaticus, T. cristatus* and *T. balearicus* sp. nov.) exhibit a rounded stylus tip (Figs. 5.7, 5.8, 5.12, 5.13). *Trogulus huberi* sp. nov., *T. pyrenaicus* sp. nov. and *T. lusitanicus* agg. have distinct lamellae at the stylus tip that give the stylus a cut-off appearance (Figs. 5.17*a*, *e*, 5.18*i*, 5.21*a*, *e*, *i*, *n*). *Trogulus prietoi* sp. nov. is included in the latter group due to genetic relations. This species is quite variable with respect to genital morphology (Fig. 5.18*a*, *b*, *e*, *f*, *i*, *k*).

5.5.2. Key to species of the *Trogulus coriziformis* species-group

1 Stylus of glans penis rounded, no lamella inflating distal end (Figs. 5.7, 5.8, 5.12, 5.13). Balearic Islands, Corsica, south-western Alps, Italian Peninsula **2**

1* Stylus with lamella inflating distal end, truncated (Figs. 5.17*a*, *e*, 5.18*i*, 5.21*a*, *e*, *i*, *n*), if different, body size below 9.5 mm and restricted to Andalusia. Iberian Peninsula including Pyrenees **5**

2 Pedipalps dorsally with large tubercles, metatarsus considerably inflated (Fig. 5.6*a*, *d*, *g*, *k*); rear end of opisthosoma deeply incised (Fig. 5.5*c*, *e*, *g*), stylus short and broad ventral and dorsal view (Figs. 5.7*a*, *b*, *e*, *f*, 5.8*a*, *b*, *e*, *f*). Italian Peninsula and Corsica **3**

2* Pedipalps without large tubercles, metatarsus of pedipalpus smooth, as slender as tarsus (Fig. 5.11*a*, *d*, *g*, *k*); hind end of opisthosoma not or only slightly incised (Fig. 5.10*a*, *c*, *e*, *g*); stylus long and straight (Figs. 5.12*a*, *b*, *e*, *f*, 5.13*a*, *b*, *e*, *f*). South-western Alps, Balearic Islands **4**

3 Large irregular areas on dorsal scute void of papillae, especially close to the suture line between prosoma and opisthosoma, soil incrustation lacking in these parts and dorsal coloration patchy (Fig. 5.5*a*–*d*). Eye lenses projecting over lateral border of ocular tubercle (Fig. 5.5*b*, *d*). Restricted to Corsica .... ***aquaticus***

3* Papillae on dorsal scute regularly spaced without large spots void of papillae (Fig. 5.5*e*–*h*), some populations on the western coast of the Italian Peninsula with few spots lacking papillae. Eye lenses not projecting over lateral border of ocular tubercle (Fig. 5.5*f*, *h*). Restricted to the Italian Peninsula .... ***coriziformis***

4 Body size of males 9.3–10.5 mm, females 10.6–11.9 mm; ratio of length of distal to basal segment of tarsus II medium to large: 1.19–1.62; apophysis on metatarsus IV large (Fig. 5.11*c*, *f*). Restricted to the south-western Alps .... ***cristatus***

4* Body size of males smaller than 8 mm; ratio of length of distal to basal segment of tarsus II large: 1.65–1.8. Endemic to the Balearic Islands.................................... ***balearicus* sp. nov.**

5* Without a prominent Y-shaped median ridge on dorsal prosoma. Southern Coast of the Iberian Peninsula and in the central Pyrenees 6

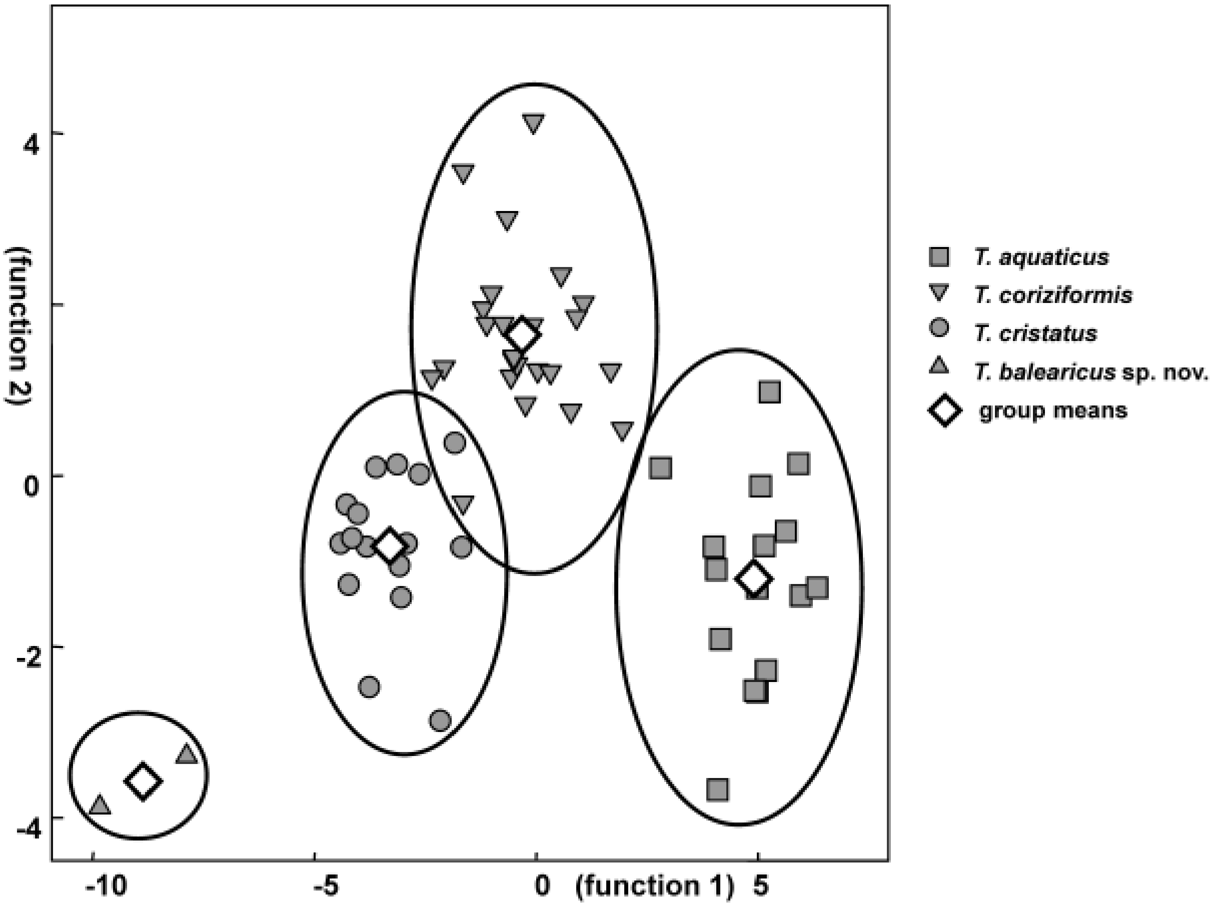


Fig. 5.4. Results of the canonical discriminant analysis to separate four species within the *Trogulus coriziformis* species-group exhibiting a rounded penial stylus. The discriminant functions incorporated eye interdistance, distance between outer border of coxae II, length of femur II and length of basal segment II as the most significant characters to classify 98.3% of all included specimens correctly.

6 Body size of males: 10.45–10.8 mm, females: 11.8 mm; opisthosoma from ventral side slender and elliptic rather than egg-shaped (Fig. 5.19*m*). Restricted to southern Portugal .... ***huberi* sp. nov.**

6* Bodysize of males 8.2–9.9 mm, females: 8.6–10.45 mm; opisthosoma from ventral side egg-shaped. Central Pyrenees and Andalusia, southern Spain **7**

7 Dorsal papillation regular, without pattern (Fig. 5.15*c*, *d*), head cap flat and elongated (Fig. 15*d*), legs slender, apophysis on metatarsus IV small (Fig. 5.16*e*, *f*). Restricted to the central Pyrenees (Prov. Huesca, bordering regions of France) .... ***pyrenaicus* sp. nov.**

7* Dorsal papillation with a distinct median and faint transversal ridges of dense papillae on opisthosoma (Fig. 5.15*e*, *g*), head cap broad rather than elongated (Fig. 5.15*f*, *h*), legs normal, apophysis on metatarsus IV prominent (Fig. 5.16*h*, *i*, *l*, *m*). Restricted to Andalusia, southern Spain .... ***prietoi* sp. nov.**

5.5.3. Species accounts

Trogulus aquaticus Simon, 1879

(Figs. 5.5*a*–*d*, 5.6*a*–*f*, 7)

Trogulus aquaticus SIMON 1879: 306, pl. 24, figs. 22–23 (in part). – DAHL 1903: 285. (in part); ROEWER 1923: 637–639 (in part); ŠILHAVÝ 1969: 25–26, figs. 8–13; NOVAK 2005: 321.

Trogulus coriziformis ROEWER 1923: 639 (in part). – ROEWER 1925: 177 (in part); DI CAPORIACCO 1949: 121; ROEWER 1950: 55; MELLO-LEITÃO 1936: 6 (in part); MARCELLINO 1982: 34, 41, fig. 2 (in part).

Trogulus nepaeformis MARCELLINO 1971: 405–406, fig. 2 (in part).

MATERIAL EXAMINED: SYN-/NEOTYPE: **France, Corsica, Haute Corse:** Corte (N: 42°19’, E: 9°08’), 6♂, 3♀, E. Simon leg. (MNHP 2191), [♂, neotype is separated within the series, the penis is dissected. The vial contains 1♂, *T. graecus* agg which originates most probably not from Corsica].

ADDITIONAL MATERIAL: **France, Corsica**: 1♂, Kahmann leg. 1952 (SMF 9283), det. as *Trogulus nepaeformis*; 1♂, L. Becker leg. 3. 6. 1938 (BRINS), C. F. Roewer det. 1913 (det.No.2449); 1♂ (SMF RII/8654); 1♀, K. Thaler leg. 3. 10. 1974 (CJM 3058); **Dép. Corse-du-Sud:** Sartène (N: 41°37’, E: 8°56’), 1♂ (MNHP, no number); Col de Vergio, 1400 m (N: 42°14’, E: 8°53’), 1♀, Mediterranean-course of the 2. Zool. Inst. leg. 5. 1974 (NHMW 4732), J. Gruber det. *T. coriziformis*; Storage lake of Ospedale, *Pinus* forest, wet riparian zone, under logs, 900 m (N: 41°42, E: 9°08'), 1♀, W. Schawaller leg. 2. 8. 1980 (CJM 3055); Estuary of the river Cavo, N Porto Vecchio, maquis (N: 41°36', E: 9°16'), 1♂, H. Schmalfuß leg. 9. 6. 1977 (CJM 3056); Fiumicicoli-Valley near Bains de Caldane, in litter of *Alnus* and *Rubus*, 300 m (N: 41°41', E: 9°03'), 1juv., W. Schawaller leg. 1. 8. 1980 (CJM 3059); Side valley of Sagone, 6 km SW Vico, litter of *Robinia* and *Fagus*, 300 m (N: 42°07', E: 8°43'), 1juv., W. Schawaller leg. 31. 7. 1980 (CJM 3064); Forest of Coscione, 3 km NE Col de la Vaccla, 7 km SW Zicavo, *Fagus* forest, sieving, 1100 m (N: 41°53', E: 9°05'), 1juv., J. Spelda leg. 3. 10. 1994 (CJM 5434); **Dép. Haute-Corse:** Forêt de Valdo-Niello (N: 42°20', E: 9°00'), 1♂, Inst. Univ. Vienna leg. 22. 5. 1974 (NHMW 8177), J. Gruber det. as *T. coriziformis*; Forêt de Valdo-Niello, 2 km E Col de Vergio, 1250 m (N: 42°17', E: 8°54'), 1♀, J. Spelda leg. 28. 9. 1994 (CJM 5446); Forêt de Tartagine, pitfall traps (N: 42°28', E: 9°00'), 5♂, 1♀, H. G. Müller leg. June 1984 (CJM 3704); 15 km N L´Ile Rousse, near Ostriconi, *Alnus* forest, wet litter (N: 42°37', E: 8°55'), 1♂, H. G. Müller leg. June 1984 (CJM 3705); near Ostriconi, 200–300 m from the sea shore, pitfall-locality (N: 42°37', E: 8°55'), 1♂, H. G. Müller leg. 8. 1982 (CJM 3706); Fontaine de Padula, 8 km SE Venaco, 920 m (N: 42°13', E: 9°10'), 1juv., B. Daams & J. Martens leg. 8. 6. 1982 (CJM 4029).

DIAGNOSIS: Large to very large *Trogulus*, restricted to Corsica. Dorsal papillation irregular, coloration patchy. Interocular distance large; eye lenses reach lateral border of front cap.

DESCRIPTION

BODY: Dorso-median ridge on prosoma faintly indicated, dorsal papillae widely and irregularly spaced (Fig. 5.5*b*, *d*), large irregular patches void of papillae, most frequently around borderline of pro- and opisthosoma, these lack soil incrustation, varying individually without clear pattern, therefore coloration of pro- and opisthosoma patchy (Fig. 5.5*a*–*d*). Regular and dense dorsal papillation at median ridge, on lateral margins of body and cranial part of prosoma. Median dorsal ridge prominent and can be seen with the naked eye. Transversal ridges of opisthosoma faintly elevated, often obscured by the papillation and therefore indistinct (Fig. 5.5*a*, *c*).

EYE MOUND AND FRONT CAP: Eye mound large and elevated, sometimes drawn out distally. Eyes separated by a shallow depression. Distance between eyes large, eye lenses protruding over lateral border of eye mound reaching lateral border of front cap, thereby separating front cap and 'shoulders' (Fig. 5.5*b*, *d*).

LEGS AND PEDIPALPI: Similar to *T. coriziformis*, legs are longer and more slender (Fig. 5.6*a*–*f*).

PENIS MORPHOLOGY: Similar to and nearly indistinguishable from *T. coriziformis*. Differences worth mentioning are: bump on the intersection between glans penis to stylus low, glans narrows to stylus (lateral view, Fig. 5.7*b*, *f*). Stylus slightly longer than in *T. coriziformis*, stylus in distal third not laterally bent as strong as in *T. coriziformis* (Fig. 5.7*a*, *e*, dorsal view).

MEASUREMENTS: **Body length**: ♂(*n* = 10) 9.45–13.1; ♀ (*n* = 6) 11.2–14.1; **body width**: ♂ 3.4–4.7; ♀ 4.4–5.3; **coxa II interdistance**: ♂ 3.9–5.2; ♀ 4.55–5.5; **coxa IV interdistance**: ♂ 4.15–5.6; ♀ 5.1–6.25; **width at coxa II**: ♂ 3.9–5.2; ♀ 4.55–5.5; **width of body at shoulder**: ♂ 1.68–2.23; ♀ 2.05–2.38; **eye interdistance**: ♂ 0.88–1.04; ♀ 1.01–1.17; **interocular distance**: ♂ 0.68–0.79; ♀ 0.82–0.91; **length of head cap**: ♂ 1.18–1.53; ♀ 1.35–1.6; **width of head cap**: ♂ 1.18–1.5; ♀ 1.4–1.65; **length of leg II**: ♂ 12.6–18.5; ♀ 14.9–17.4; **length of metatarsus II**: ♂ 2.53–3.75; ♀ 3.08–3.6; **length of femur II**: ♂ 3.15–5.65; ♀ 4.35–5.55; **length of femur I**: ♂ 2.13–3.2; ♀ 2.63–3.33; **length of tarsus IV**: ♂ 1.08–1.34; ♀

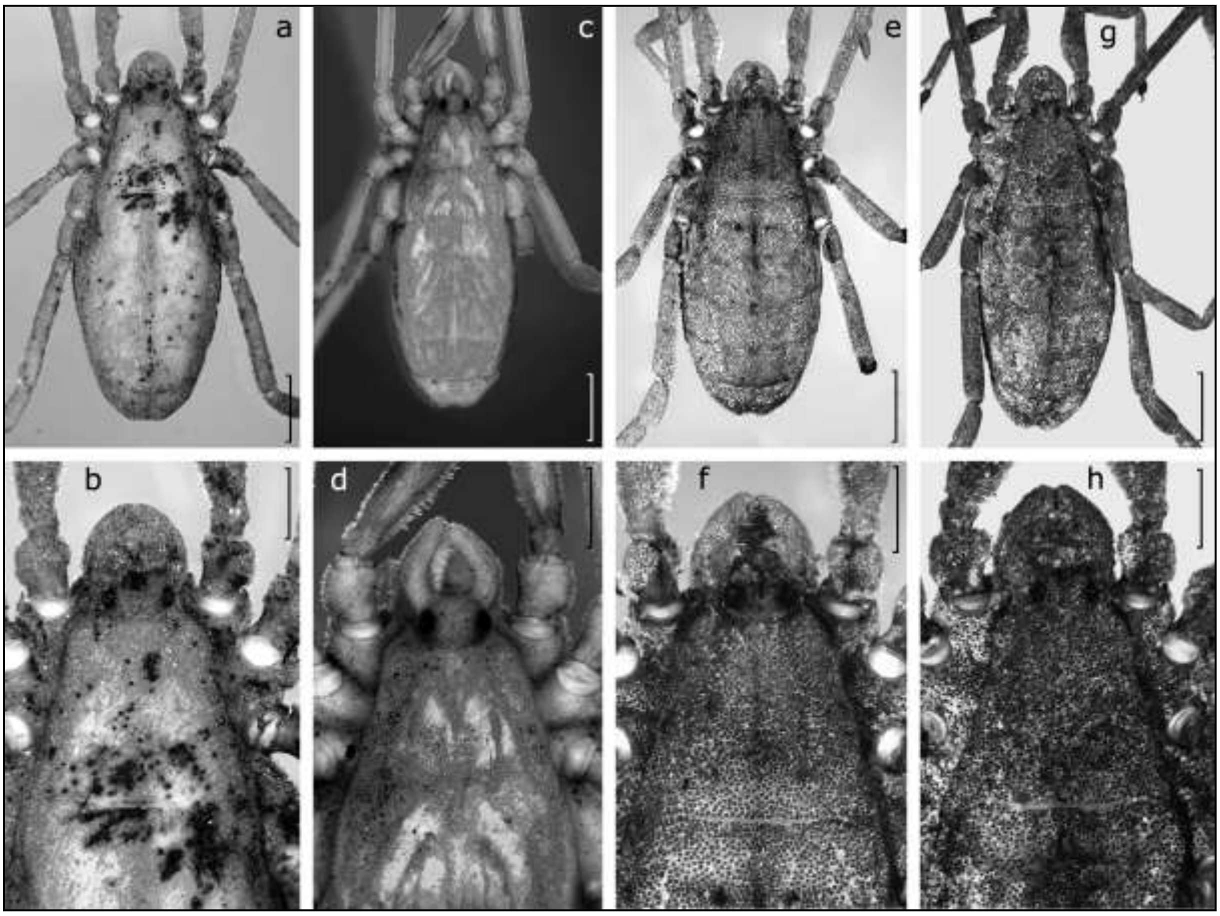


Fig. 5.5. Body of ♂ of *Trogulus aquaticus* Simon and *T. coriziformis* C. L. Koch dorsal view. (*a*–*d*) *T. aquaticus*; (*a*, *b*) neotype, France, Corse, Corte, MHNP 2191; (*c*, *d*) France, Corsica, BRINS; (*e*–*h*) *T. coriziformis*; (*e*, *f*) neotype, Italy, Lazio, Prov. Roma, Monti della Tolfa, SMF, ex CJM 1058; (*g*, *h*) Italy, Abruzzo, Prov. Chieti, Fara Filiorum Petri, CJM 5051. Upper row, scale lines 2.0 mm, bottom row 1.0 mm.

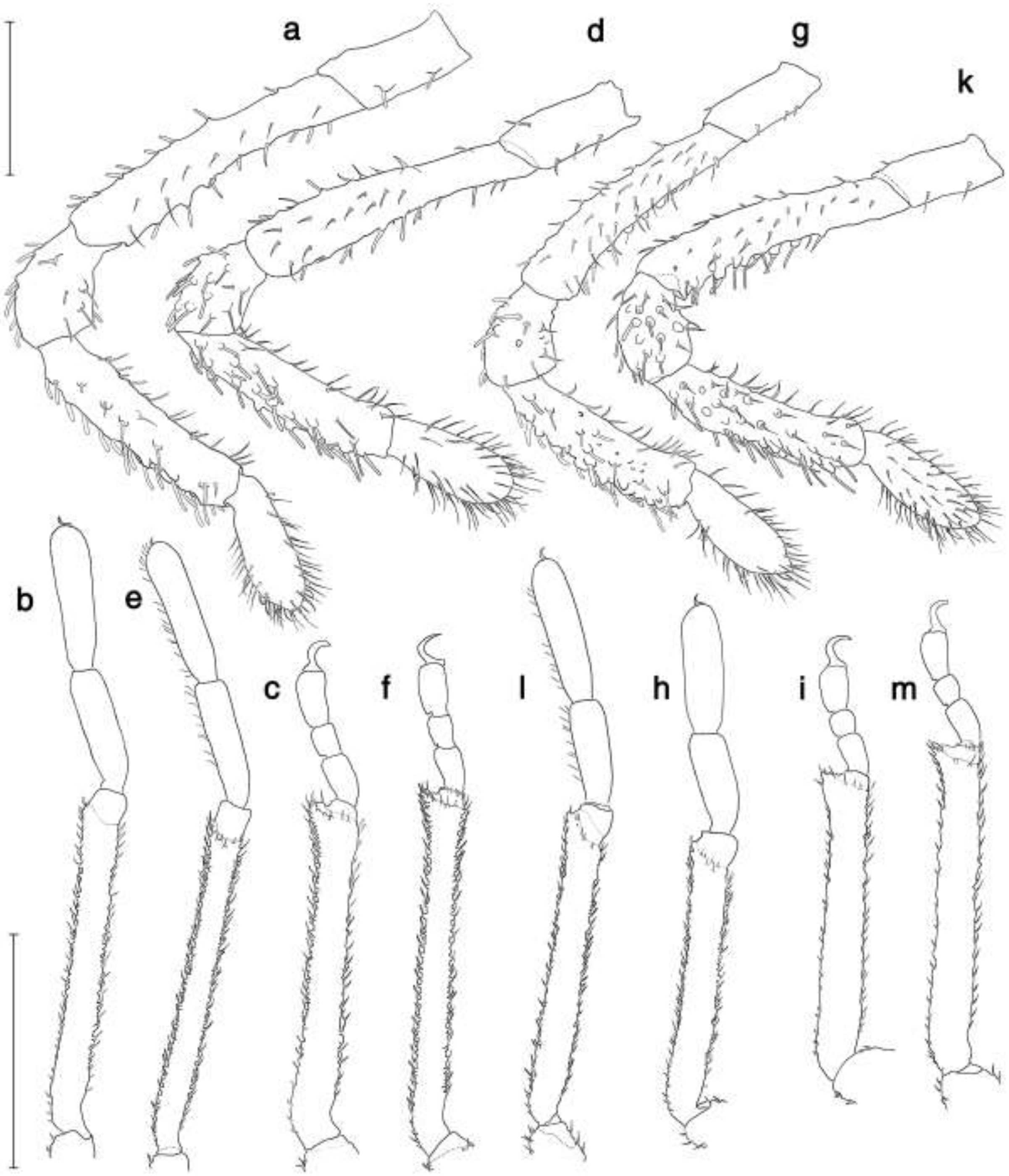


Fig. 5.6. Pedipalps and distal parts of legs of *Trogulus aquaticus* Simon and *T. coriziformis* C. L. Koch, ♂. (*a–f*) *T. aquaticus*; (*a–c*) neotype, France, Corse, Corte, MHNP 2191; (*d–f*) France, Corse (BRINS); (*g–m*) *T. coriziformis*: (*g–i*) neotype, Italy, Lazio, Prov. Roma, Monti della Tolfa, CJM 1058; (*k–m*) Abruzzo, Prov. Chieti, CJM 5051. (*a*, *d*, *g*, *k*) Right pedipalpus; (*b*, *e*, *h*, *l*) metatarsus and tarsus II; (*c*, *f*, *i*, *m*) metatarsus and tarsus IV; all medial view. Upper left, scale line 0.5 mm (*a*, *d*, *g*, *k*), bottom left 2.0 mm (*b*, *c*, *e*, *f*, *h*, *i*, *l*, *m*).

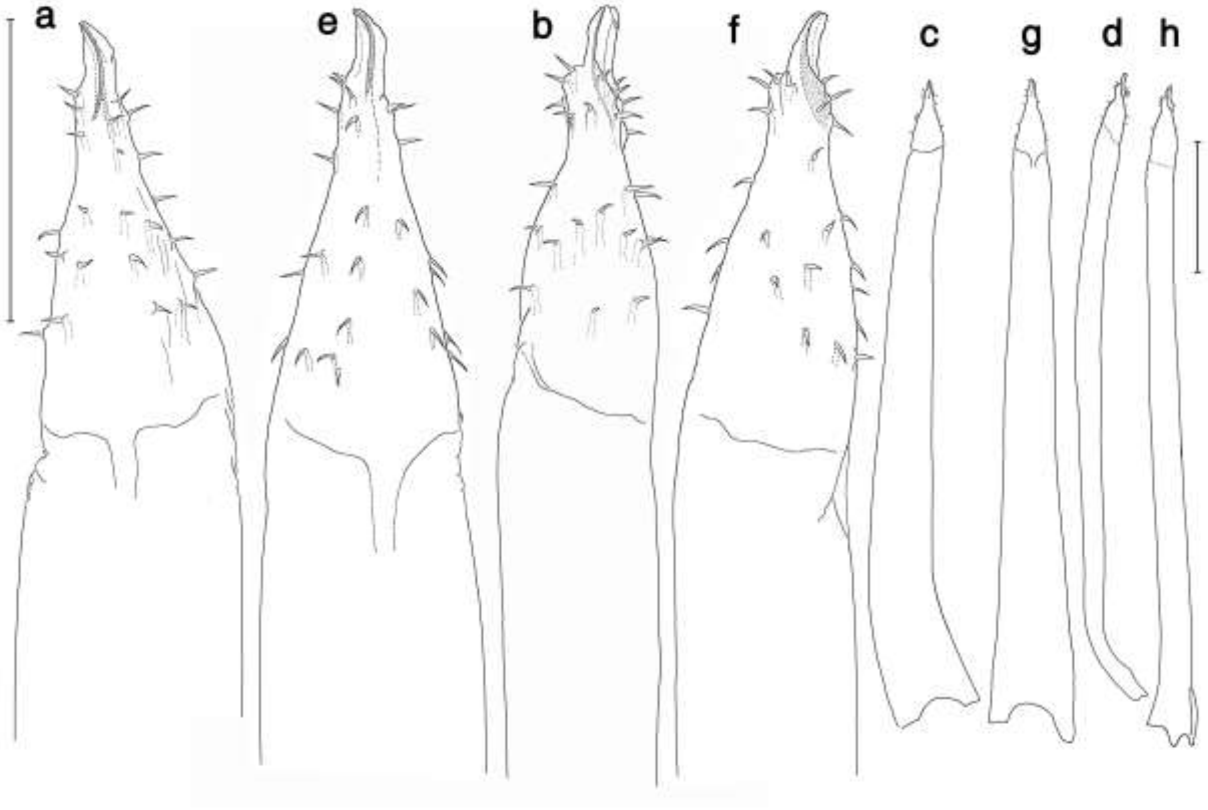


Fig. 5.7. Penes of *Trogulus aquaticus* Simon. (*a–d*) Neotype, France, Corse, Corte, MHNP 2191; (*e–h*) France, Corsica (BRINS). (*a, b, e, f)* Glans and distal part of truncus; (*c, d, g, h*) penis; (*a, c, e, g*) dorsal view; (*b, d, f, h*) lateral view. Scale line on the left 0.2 mm (*a, b, e, f*), on the right 0.5 mm (*c, d, g, h*).

1.24–1.38; **length of metatarsus IV**: ♂ 2.73–3.58; ♀ 3.21–3.93; **length of penis**: 2.4–3.1; **length of basal segment of tarsus II**: ♂ 0.95–1.45; ♀ 1.08–1.19; **length of distal segment of tarsus II**: ♂ 1.08–1.6; ♀ 1.25–1.38; **ratio of length of distal to basal segment of tarsus II**: ♂ 1.11–1.31; ♀ 1.14–1.2; **length of leg II/Body length**: ♂ 1.32–1.48; ♀ 1.07–1.33. – The canonical discriminant analysis (Fig. 5.4) used the length of basal segment of tarsus II and the interocular distance, but also the width of head cap to correctly classify all but one specimen of *T. coriziformis* and *T. aquaticus*.

VARIABILITY: There is a considerable amount of variability in body size and the intensity of papillation.

DISTRIBUTION: This species is restricted to Corsica where it is widely distributed in the central and western parts. No records from eastern Corsica are known to us (Fig. 5.1).

ECOLOGY: SIMON (1879) reported *T. aquaticus* to be common in humid places. W. Schawaller found it on a wet lake shore. It has been collected twice in forests with *Alnus*, probably close to running water, and the need for constant and high humidity is obvious. It

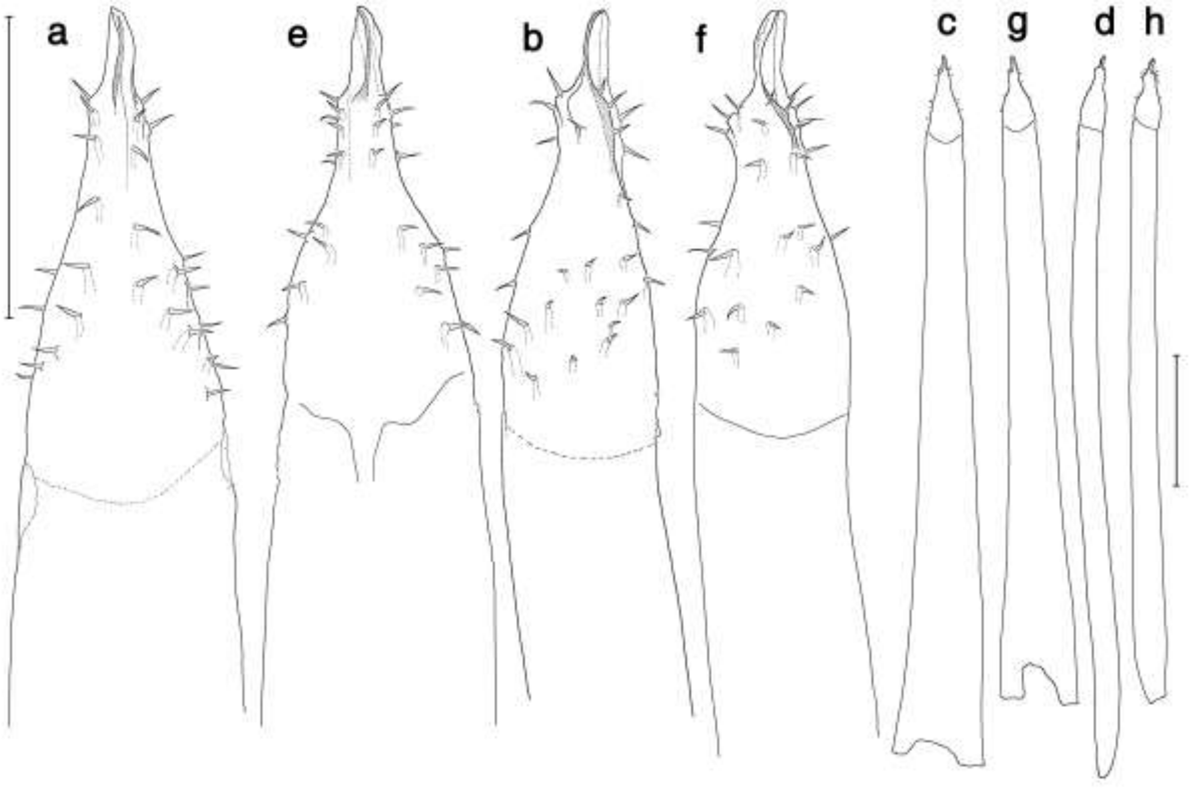


Fig. 5.8. Penes of *Trogulus coriziformis* C. L. Koch. (*a–d*) Neotype, Italy, Lazio, Prov. Roma, Monti della Tolfa, CJM 1058; (*e–h*) Abruzzo, Prov. Chieti, CJM 5051; (*a, b, e, f)* glans and distal part of truncus; (*c*, *d*, *g*, *h*) penis; (*a*, *c*, *e*, *g*) dorsal view; (*b*, *d*, *f*, *h*) lateral view. Scale line on the left 0.2 mm (*a, b, e, f)*, on the right 0.5 mm (*c*, *d*, *g*, *h*).

has also been collected in drier forest communities with *Fagus* and *Robinia*. Records range from sea level up to 1400 m.

REMARKS: There is no doubt regarding the identity of the type series (NHMP 2191), because SIMON (1879) mentioned the nine specimens he found at the type locality. The correct identity of *T. aquaticus* is confirmed by numerous specimens collected from Corsica that are identical to the type material. ŠILHAVÝ (1968) draw one male from this series that is designated here as neotype and that is recognisable in the type series. Neotype designation is important because the type series also contains 1♂ *T. graecus* agg. that is not likely to originate from Corsica and should be excluded. All denominations for *T. aquaticus* outside Corsica refer to other species. *Trogulus aquaticus* is very similar to the related but allopatric *T. coriziformis*.

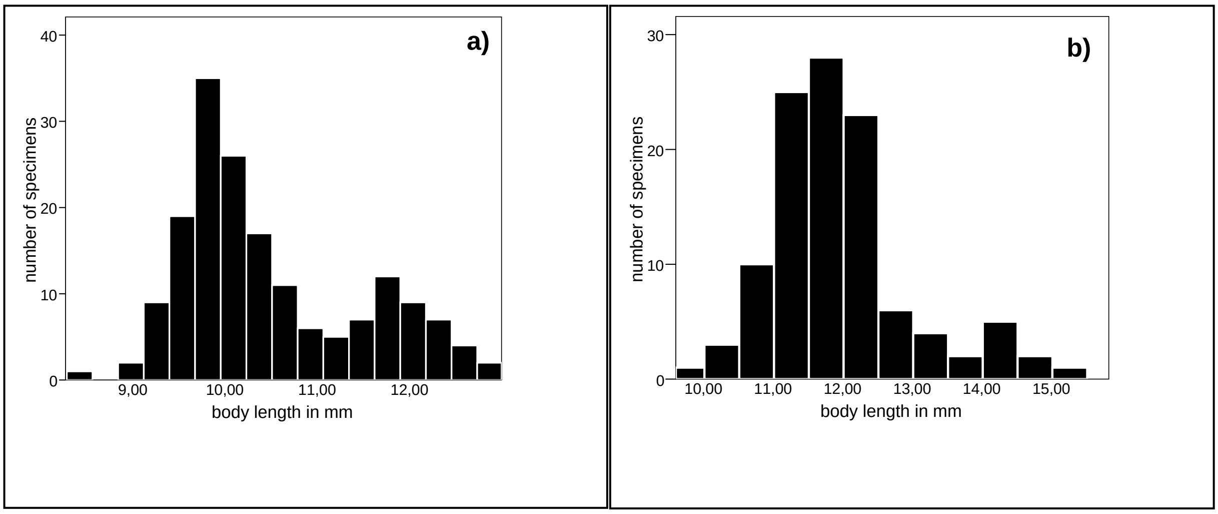


Fig. 5.9. Body size distribution in (*a*) males and (*b*) females of *Trogulus coriziformis* shows two maxima.

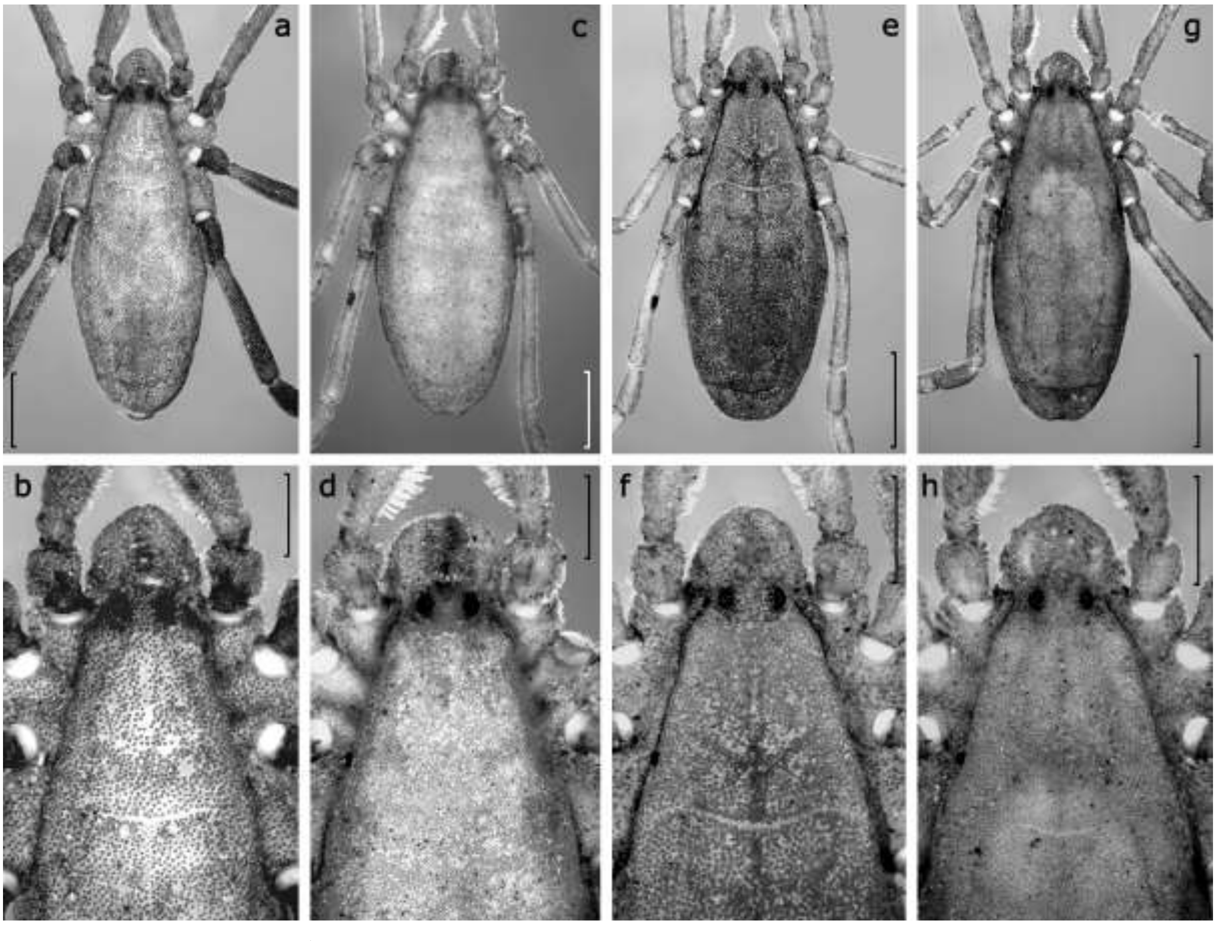


Fig. 5.10. Body of ♂ of *Trogulus cristatus* Simon and *T. balearicus* sp. nov., dorsal view. (*a*–*d*) *T. cristatus*; (*a*–*b*) Italy, Liguria, Prov. Imperia, N San Remo, CJM 4972; (*c*–*d*) holotype, France, Provence, Dép. Alpes-Maritimes, MHNP 2193; (*e*–*h*) *T. balearicus* sp. nov.; (*e*–*f)* holotype, Spain, Balearic Islands, Ibiza, Sierra Grosa, SMF 11816; (*g*–*h*) paratype, Ibiza, NW Santa Eulalia, BMNH. Upper row, scale lines 2.0 mm, bottom row 1.0 mm.

Trogulus balearicus sp. nov.

(Figs. 5.10*e–h*, 5.11 *g–m*, 5.12)

Trogulus nepaeformis KRAUS 1961: 338; – RAMBLA 1972: 90.

MATERIAL EXAMINED: HOLOTYPE: **Spain**: Balearic Islands, Ibiza, Sierra Grosa, valley directing to San José, detritus and litter from *Quercus ilex* and grass (N: 38°55’, E: 1°17’), 1♂, H. Franz leg. 10. 4. 1960 (SMF 11816).

PARATYPES: **Spain**: Balearic Islands, Ibiza, NW Sta Eulalia (N: 38°58’, E: 1°31’), 1♂, J. A. Murphy leg. 31. 12. 1981 (BMNH); El Vidrá, leg. 7. 7. 1936, 2juv. (CMR 801, not seen); Mallorca, Manacor, Cova des Pont, 16C, under stone, 33 m (N: 39°33’, E: 3°12’), 1juv., M. Vadell leg. 8. 4. 2006 (CCP 3616).

DIAGNOSIS: A medium-sized and compact *Trogulus,* the smallest within *T. coriziformis* species-group and the only *Trogulus* on the Balearic Islands. It is further characterised by the slender stylus and large ratio of length of distal to basal segment of tarsus II ratio (1.65–1.8).

DESCRIPTION

BODY: Dorsal papillation regular (Fig. 5.10*e–h*), dorsal median ridge on prosoma faintly indicated, around median and transversal ridges on opisthosoma densely packed, best seen at low magnification. Only median ridge indistinctly elevated, rear end not notched.

EYE MOUND AND FRONT CAP: Front cap broad and circular, eye mound moderately elevated (Fig. 5.10*f, h*), separated by a deep but shallow depression. Eyes about half their diameter from lateral border of front cap.

LEGS AND PEDIPALPI: Legs short, most obviously seen in femur II and IV; distal end of femur IV does not reach suture of opisthosoma and last abdominal segment, median segment of tarsus IV as long as high (Fig. 5.11*i, m*); ridge of elongated papillae on femur II, apophyses on astragalus of metatarsus III and IV small as in *T. coriziformis*. Base of hairs on dorsal metatarsus of pedipalpus thick but not prominent (Fig. 5.11*g, k*). Tarsi II short and broad, ratio of length of distal to basal segment of tarsus II large (Fig. 5.11*h, l*).

PENIS MORPHOLOGY: Truncus almost parallel sided, gradually merging into the glans penis (Fig. 5.12*c, d, g, h*); glans penis regularly narrowing into stylus (Fig. 5.12*a, b, e, f*), slightly bulbous at base, small bump at the intersection glans to stylus (lateral view, Fig. 5.12*b, f*), stylus long and slender, distal third bent slightly dorso-lateral, tip rounded.

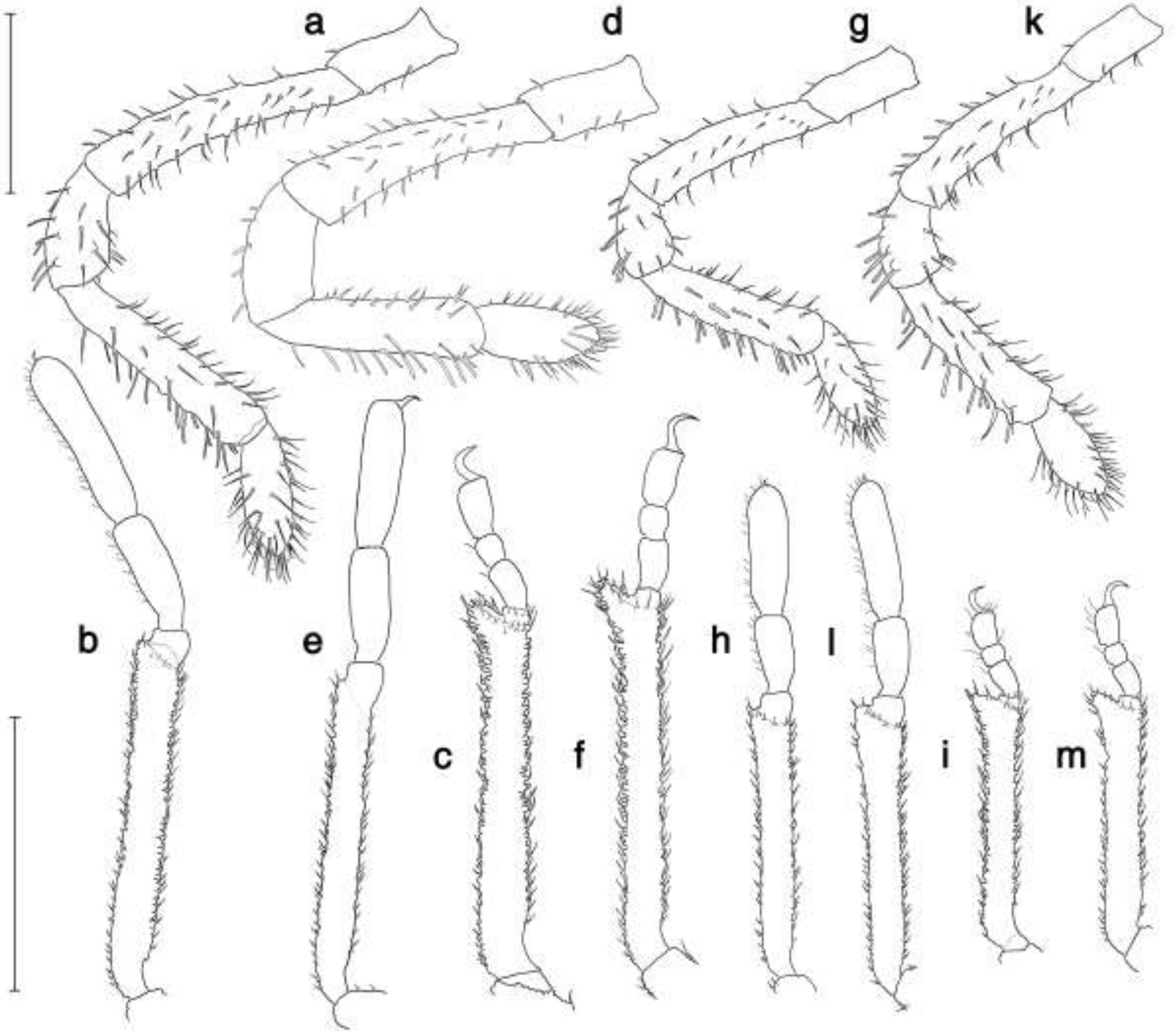


Fig. 5.11. Pedipalps and distal parts of legs of *Trogulus cristatus* Simon and *T. balearicus* sp. nov., ♂. (*a–f) T. cristatus*; (*a–c*) Italy, Liguria, Prov. Imperia, N San Remo, CJM 4972; (*d–f)* holotype, France, Provence, Dép. Alpes-Maritimes, MHNP 2193; (*g–m*) *T. balearicus* sp. nov.; (*g–i*) holotype, Spain, Balearic Islands, Ibiza, Sierra Grosa, SMF 11816; (*k–m*) paratype, Ibiza, northwest Santa Eulalia, BMNH.(*a*, *d*, *g*, *k*) Right pedipalpus; (*b*, *e*, *h, l)* metatarsus and tarsus II; (*c*, *f*, *i*, *m*) metatarsus and tarsus IV; all medial view. Upper left, scale line 0.5 mm (*a*, *d*, *g*, *k*), bottom left 2.0 mm (*b, c*, *e*, *f*, *h*, *i*, *l*, *m*).

MEASUREMENTS: (Only ♂, *n* = 2): **Body length**: 7.7–7.9; **body width**: 2.95–3.0; **coxa II interdistance**: 3.05–3.1; **coxa IV interdistance**: 3.4–3.35; **width at coxa II**: 3.05–3.1; **width of body at shoulder**: 1.25–1.28; **eye interdistance**: 0.58–0.62; **interocular distance**: 0.4–0.45; **length of head cap**: 0.75–0.79; **width of head cap**: 0.9; **length of leg II**: 9.8–10.1; **length of metatarsus II**: 2.08–2.10; **length of femur II**: 2.9–2.95; **length of femur I**: 1.58–1.65; **length of tarsus IV**: 0.68; **length of metatarsus IV**: 0.81–0.88; **length of penis**: 1.6–1.99; **length of basal segment of tarsus II**: 0.56–0.58; **length of distal segment of tarsus II**: 0.95–1.01; **ratio of length of distal to basal segment of tarsus II**: 1.65–1.8; **length of leg**

II/Body length: 1.27–1.28. Due to its small size *T. balearicus* sp. nov. can be separated using morphometric data from all other members of the species-group (Fig. 5.4).

VARIABILITY: No data due to paucity of material.

ECOLOGY: The species was collected from litter and detritus and under stones in valleys with evergreen hard-leafed forest, most probably from low altitudes (the only record at 30 m).

DISTRIBUTION: Recorded from the Balearic Islands Ibiza and Mallorca (Fig. 5.1).

REMARKS: Genetic results (cyt*b*) show distinct differences between the specimen from Ibiza and the juvenile from Mallorca, suggesting further diversification within the Balearic Islands (Fig. 5.2, Table 5.2). For the time being both populations are united under one name. Species of the *T. nepaeformis* species-group are similar in size and external morphology but

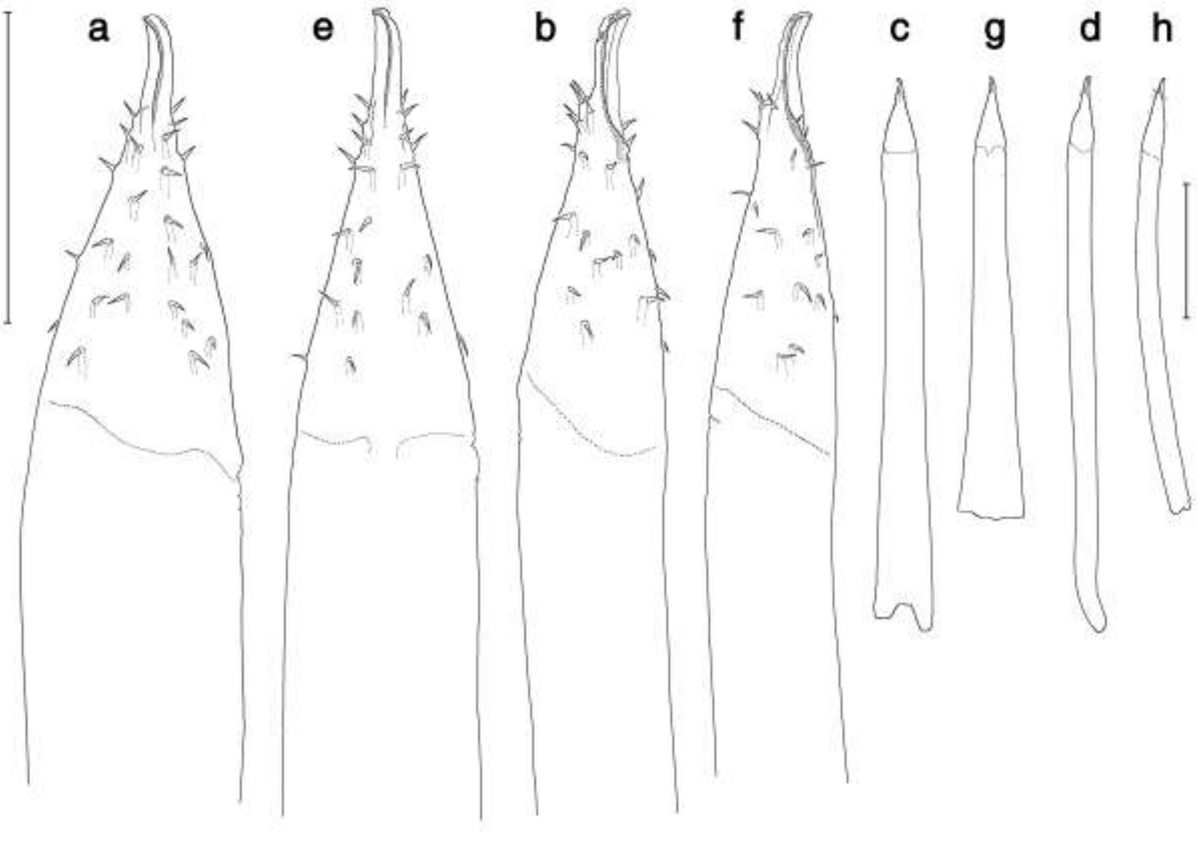


Fig. 5.12. Penes of *Trogulus balearicus* sp. nov. (*a*–*d*) Holotype, Spain, Balearic Islands, Ibiza, Sierra Grosa, SMF 11816; (*e*–*h*) paratype, Ibiza, NWSanta Eulalia, BMNH. (*a, b, e, f)* Glans and distal part of truncus; (*c*, *d*, *g*, *h*) penis; (*a*, *c*, *e*, *g*) dorsal view; (*b*, *d*, *f*, *h*) lateral view. Scale line on the left 0.2 mm(*a*, *b*, *e*, *f*), on the right 0.5 mm(*c*, *d*, *g*, *h*).

are allopatric and differ in genital morphology. The genetic analyses do not reveal any clear relationship within the *T. coriziformis* species-group but stylus morphology is similar to the eastern taxa.

ETYMOLOGY: The species name refers to the distribution of the species.

Trogulus coriziformis C. L. Koch, 1839

(Figs. 5.5*e–h*, 5.6*g–m*, 5.8)

Trogulus coriziformis C. L. KOCH 1839: 128–130, figs. 420*a–c*. – CANESTRINI 1875: 12; SIMON 1879: 308; ROEWER 1923: 635, 639 (in part); ROEWER 1925: 177 (in part); MELLO-LEITÃO 1936: 6 (in part); ZANGHERI 1966: 533; BRIGNOLI 1968: 274–276, figs. 65–68; MARCELLINO 1970: 364–366, figs. 1–6 (in part); MARCELLINO 1971: 402, 404–405; BRIGNOLI & RAFAELLI 1978: 95–96; MARTENS 1978: 174–175. (figs. for *T. cristatus*; in part). MARCELLINO 1982: 36, 41, 43, fig. 2 (in part); NOVAK 2005: 321.

Trogulus aquaticus SIMON 1882: 47. – DAHL 1903: 286–287 (in part); MARCELLINO 1965: 330; BRIGNOLI & RAFAELLI 1978: 95; GOZO 1908: 138; DI CAPORIACCO 1949: 121.

Trogulus nepaeformis TROSSARELLI, 1934: 20.

Trogulus salfii DE LERMA 1948: 160–164. – MARCELLINO 1965: 330; MARCELLINO 1982: 34. **Syn. nov.**

MATERIAL EXAMINED: NEOTYPE: **Italy**: Lazio, Prov. Roma, Monti della Tolfa, between Tolfa und Rota (N: 42°09’, E: 11°57’), 1♂ (from 6♂, 5♀, 3juv.), A. Vigna leg. 16. 3. 1969 (SMF ex CJM 1058).

ADDITIONAL MATERIAL: **Italy, Abruzzo, Prov. Chieti:** Fara Filiorum Petri, riverine forest with nitrophil herb layer, loamy soil, under logs and stones, 211 m (N: 42°14’46,5“, E: 14°11’5,6“), 3♂, 4♀, 1juv., A. Schönhofer, J. Hillen leg. 5. 4. 2006 (CJM 5051); Pretoro, Grotta del Cane, cave (N: 42°12’, E: 14°8’), 1♂, Antonucci leg. 18. 4. 1983 (MSNB); road S652, Departure Bomba, dense Oak forest with understorey, litter and humus, sieving, 169 m (N: 42°3’36,9”, E: 14°20’44,8”), 1juv., A. Schönhofer, J. Hillen leg. 6. 4. 2006 (CJM 5091); **Prov. L'Aquila:** Parco Nazionale d'Abruzzo, Val Fondillo SE Opi (N: 41°45’, E: 13°51’), 1♂, Pasculli & Vigna leg. 28. 5. 1974, P. M. Brignoli det. (MV); Prov.Teramo, 1♂, W. Stoecklin leg. 7. 3. 1905 (NHMB 56-a); **Basilicata, Prov. Potenza:** Chiaromonte, Piano Toscano, 1750 m (N: 39°54’, E: 16°11’), 3♂, 1juv., G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 2. 6. 1991 (MSNB); Lucania, surroundings of Rivello (gia a secco), 600 m (N: 40°04’, E: 15°45’), 1♀, G. Ferro leg. 18. 3. 1967, P. Brignoli det. (CJM 1059, data published in BRIGNOLI 1968); Viggianello, pitfall (N: 39°58’, E: 16°5’), 6♂, 4♀, P. Pantini, M. Valle. leg. July – Aug.1993 (MSNB); dito, 3♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg.

6. 1990 – 6. 1991 (MSNB); dito, 600 m, 3♂, 3♀, M. Valle leg. 6 – 8. 1989 (MSNB); Viggianello, Torno, pitfall, 300 m (N: 39°58’, E: 16°7’), 2♀, M. Valle leg. 9.1989/5.1990 (MSNB); dito, 650 m, 2♂, 1♀, M. Valle leg. 6./8.1989 (MSNB); **Calabria**: 2♂, 2♀, C. F. Roewer det. (SMF RII/11032); **Prov. Cosenza:** Sila Piccola Mountains, Passo di Acquabona near Bocca di Piazza, 1020 m (N: 39°09’, E: 16°30’), 1♂, V. Sbordoni leg. 7. 10. 1967, P. Brignoli det (CJM 1061); near Cosenza (N: 39°17’, E: 16°15’), 1♂ (SMF RII/549) [formerly *T. gypseus*]; **Campania, Prov. Napoli**: Castellammare di Stabia, Pozzano (N: 40°41’, E: 14°27’), 1♂, 1♀ (SMF 1363); Fiumara near Neapel, 1juv., Verhoeff leg., Roewer det. (ZMB 12002); Island Capri (N: 40°33’, E: 14°13’), 1♀ (SMF 1362); Neapel (=Naples) (N: 40°51’, E: 14°16’), 1♀, W. Carl leg. (MHNG), [formerly *T. aquaticus*]; Pozzano, Castellammare di Stabia, stone pits (N: 40°41’, E: 14°27’), 1♀, Verhoeff leg. 20. 4., Roewer det. (ZMB 11998); **Prov. Salerno:** S Montecorvino, Bachaue with *Salix* and *Urtica*, under stones, 116 m (N: 40°38’42,1”, E: 14°59’41,2”), 1♀, A. Schönhofer leg. 8. 4. 2006 (CJM 4995); **Emilia-Romagna, Prov. Modena:** Lago Albert 2 km N Montefiorino (N: 44°22’, E: 10°37’), 1♀, 1juv., J. Spelda leg. 1. 4. 1993 (CJM 5458); **Prov. Parma:** Bedonia, Passo di Montevacà, *Castanea sativa* forest, pitfall, 800 m (N: 44°32, E: 9°36’), 7♂, P. Pantini, M. Valle leg. 6. – 9. 1992 (MSNB14/11); dito, 2♂, leg. 11. 1992 – 4. 1993 (MSNB); dito, 1♀, G. Buttazelli, R. Cerbino, P. Pantini, M. Valle leg. 9. 1991 – 5. 1992 (MSNB); dito, 7♂, R. Cerbino, M. Valle leg. 4. – 8. 1991 (MSNB14); Tornolo, Tarsogno, mixed deciduous forest, moist to fresh, pitfall, 800 m (N: 44°27’, E: 9°36’), 5♂, 2♀, 2juv., P. Pantini, M. Valle leg. 1994 (MSNB); dito, 6♂, 2♀, leg. 6. – 9. 1992 (MSNB); dito, 2♂, 1juv., R. Cerbino, M. Valle leg. 4. – 8. 1991 (MSNB); dito, 3♂, G. Buttazelli, R. Cerbino, P. Pantini, M. Valle leg. 9. 1991 – 5. 1992 (MSNB); **Prov. Bologna:** Imola, Riserva Naturale Bosco della Frattona, pitfall (N: 44°21’, E: 11°38’), 1♂, R. Fabbri leg. 14. 6. – 7. 7. 2000 (MSNB); **Prov. Forlì-Cesena:** Parco Nazionale Foreste Casentinesi, Bagno di Romagna, N di Sasso Fratino, loc. La Seghettina, staz. 25, mixed deciduous forest, 570 m (N: 43°50’, E: 11°48’), 3♂, 1♀, M. Bertozzi leg. 9. 1997 (MSNB); dito., 1♂, 1♀, Scaravelli, M. Bertozzi leg. 26. 8. 1997 (MSNB); dito, San Godenzo, confine regione, pecceta, staz. 30, 880 m (N: 43°55’, E: 11°37’), 2♂, Scaravelli, M. Bertozzi leg. 5. 9. 1997 (MSNB); dito, Tredozio, Lago di Ponte, staz. 10, riparial wood, pitfall, 620 m (N: 44°4, E: 11°44, 1♂, M. Bertozzi leg. 28. 8. 1997 (MSNB29/9); Santa Sofia, loc. Il Sasso, staz. 12, riparial wood, 800 m (N: 43°57’, E: 11°53’), 1♂, M. Bertozzi leg. 21. 7. 1997 (MSNB); dito, 815 m, 1♀, M. Bertozzi leg. 21. 7. 1997 (MSNB); dito. loc. Corniolo, Pian del Grado, staz. 23, *Carpinus betulus* forest, 780 m (N: 43°53’, E: 11°43’), 1♂, 1♀, 2juv., M. Bertozzi leg. 26. 9. 1997 (MSNB); dito, S. Paolo in Alpe, staz. 27, meadow with shrubs, pitfall, 1020 m (N: 43°52’, E: 11°47’), 3♂, M. Bertozzi leg. Aug.1997 (MSNB); dito, Pietrapazza, Felcitino ceduo, staz. 19, pitfall, 600 m (N: 43°50’, E: 11°54’), 1♀, Scaravelli, Bertozzi leg. 22. 8. 1997 (MSNB); **Prov. Rimini:** Gemmano, Riserva Naturale di Onferno, dry deciduous forest, pitfall, 280–400 m (N: 43°52’, E: 12°32’), 1♀, R. Fabbri leg. 24. 8. – 29. 9. 2000 (MSNB); dito, 1♂, leg. 21. 6. – 21. 7. 2000 (MSNB); dito, 1♀, leg. 9. 11. 2000 – 7. 4. 2001 (MSNB); calanco, 280–330 m, 1♀, leg. 9. 11. 2000 – 7. 4. 2001 (MSNB23/12); dito, 1♂, 1♀, leg. 20. 4. – 25. 5. 2000 (MSNB); **Lazio, Prov. Frosinone**: Monti Lepini, near Pozzo l'Arcaro by Ceccano, 340La (cave registry number), 300 m (N: 41°34’, E: 13°19’), 1juv., V. Sbordoni leg. 4. 12. 1966, P. M.

Brignoli det. (CJM 1055, data published in BRIGNOLI 1968); dito, Supino, Grotta Pozzo del Faggeto, 343La (cave registry number), 814 m (N: 41°36’, E: 13°13’), 1♂, V. Sbordoni leg. 26. 11. 1967 P. M. Brignoli det. (CJM 1057, from BRIGNOLI 1968); Comune Trevi nel Lazio, 700 m (N: 41°51’, E: 13°13’), 1♂, 1juv., V. Sbordoni leg. 4. 11. 1967, P. M. Brignoli det. (CJM 1065, from BRIGNOLI 1968); Lazio, Prov. Frosinone, Piglio, 500 m (N: 41°49’, E: 13°7’), 1♂, P. Brignoli leg. 19. 10. 1969, M. Brignoli det. 1978 (MV, from BRIGNOLI & RAFAELLI 1978); **Prov. Latina:** Monte Circeo, evergreen Oak forest, sieved and under stones, 18 m (N: 41°14’48,5“, E: 13°2’16,0“), 1♂, 1♀, A. Schönhofer leg. 9. 4. 2006 (CJM 5055); **Prov. Rieti:** Abruzzi, Riserva Naturale Montagne della Duchessa (Monte Velino), Val Foa ("val fua"), 1500 m (N: 42°10’, E: 13°17’), 1♂, 1juv., A. Vigna leg. 29. 6. 1968 (CJM 1062); Prov. Roma, Altopiano di Arcinazzo, 800 m (N: 41°51’, E: 13°10’), 1♀, 1juv., P. Brignoli leg. 17. 4. 1966 et det. (CJM 1053, from BRIGNOLI 1968), Lago di Albano SE Rom, 300 m (N: 41°44’, E: 12°39’), 1♀, V. Sbordoni leg. 24. 3. 1966 (CJM 1064, from BRIGNOLI 1968); Montesacro N Rom (N: 41°56’, E: 12°31’), 1juv., Gobbi leg. 2. 4. 1967 (MV); Monti della Tolfa, between Tolfa und Rota (N: 42°09’, E: 11°57’), 2♂, 1juv., A. Vigna leg. 16. 3. 1969 (CJM 975); dito, 6♂, 5♀, 3juv., leg. 16. 3. 1969 (CJM 1058, one ♂, **designated as neotypus**, now SMF); dito, 2♀, leg. 2. 3. 1969 (CJM 1060); Pietralata (N: 41°55’, E: 12°31’), 2♀, Turillazzi leg. 27. 4. 1969 (CJM 1076); prope Gennazzano a. cl. Bergsee (N: 41°50’, E: 12°59’, 1♀ (ZMC, formerly *T. nepaeformis*); dito, 1juv. (ZMC); Rome, under stone, 1♂, 1♀, S. Bergsöe leg. 2. 1863 (ZMC, formerly *T. rostratus*); road from Cave to Valmontone, humid valley with forest and *Hedera* under stones, 286 m (N: 41°47’22,0”, E: 12°54’37,2”), 2♂, 2♀, A. Schönhofer leg. 10. 4. 2006 (CJM 4988); Tivoli, Fonte Bologna (N: 42°01’, E: 12°46’), 1♀, V. Sbordoni, R. Argano leg. 6. 2. 1964 (CJM 1066, from BRIGNOLI 1968); dito, Vill. Maria, 250 m (N: 41°59’, E: 12°43’), 1♀, A. Vigna leg. 5. 2. 1964 (CJM 1067, from BRIGNOLI 1968); **Prov. Viterbo:** Lago di Vico, Monte Fogliano E Vetralla (N: 42°19’, E: 12°08’), 1♀, A. Vigna leg. 2. 2. 1969 (CJM 1075); **Liguria, Prov. La Spezia:** Varese Ligure, Passo Centocroci, pasture land, pitfall, 1000 m (N: 44°25’, E: 9°37’), 2♂, 2♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 9. 1991 – 5. 1992 (MSNB); **Marche, Prov. Ascoli Piceno:** Amandola, loc. Vidoni, mixed deciduous forest, pitfall, 680 m (N: 42°59’, E: 13°18’), 4♂, M. Rismondo, R. Fabbri leg. 23. 6. – 27. 7. 2004 (MSNB); dito, prateria stabile, pitfall, 670 m (N: 42°59’, E: 13°18’), 4♂, leg. 23. 6. – 27. 7. 2004 (MSNB); Montemonaco, loc. Isola S. Biagio, pasture land, pitfall, 990 m (N: 42°54’, E: 13°17’), 3♂, 3♀, 2juv., M. Rismondo, R. Fabbri leg. 23. 6. – 27. 7. 2004 (MSNB); dito, *Ostrya carpinifolia* forest, 2♀, leg. 23. 6. – 27. 7. 2004 (MSNB); 2♀, M. Rismondo, F. Taffetani leg. 23. 6. – 27. 7. 2004 (MSNB); dito, *Castanea sativa* forest/meadow, 790 m, 1♂, 2♀, M. Rismondo, R. Fabbri leg. 23. 6. – 27. 7. 2004 (MSNB); Prov. Di Pesaro and Urbino, Monte Nerone (N: 43°33’, E: 12°31’), 4♂, 2♀, Sciasky leg. 18. 9. 1982, Tedeschi det. (MHNG); **Prov. Macerata:** Riserva Naturale di Torricchio, l'Abbeveratoio (N: 42°58’, E: 13°03’), 1♂, C. Chemini leg. 7. 5. 1973 (NHMW), J. Gruber det.; dito, 1♂, leg. 7. 6. 1973 (NHMW); dito, 1♂, leg. 16. 6. 1973 (NHMW); dito, 1♀, leg. 23. 9. 1973 (NHMW); Castelsantangelo sul Nera, Gualdo, pitfall, 900 m (N: 42°53’, E: 13°9’), 1♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); dito, above Rapegna, pitfall, 1200 m (N: 42°51’, E: 13°8’), 1♂, P. Pantini, M. Valle leg. 6 – 9.

1992 (MSNB); Fiuminata, Passo Cornello, pitfall, 800 m (N: 43°7', E: 12°51'), 10♂, 2♀, Pantini P., Valle M. leg. 6 – 9. 1992 (MSNB); dito, 3♂, 1♀, 1. – 6. 1992 (MSNB); dito, 2♂, leg. 9. 1992 – 6. 1993 (MSNB); dito, 4♂, 1♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); Fiuminata, road to Passo Cornello, pitfall, 600 m (N: 43°9', E: 12°52'), 1♂, Pantini P., Valle M. leg. 9. 1992 – 6. 1993 (MSNB); dito, 1♂, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); Sarnano, loc. Colle, mixed deciduous forest, pitfall, 550 m (N: 43°4', E: 13°16'), 1♂, 2♀, M. Rismondo, R. Fabbri leg. 23. 6. – 27. 7. 2004 (MSNB); dito, untiled land, 1♂, leg. 23. 6. – 27. 7. 2004 (MSNB); dito, 2♀, leg. 27. 7. – 1. 9. 2004 (MSNB); Visso, Monte La Bandita, pitfall, 1300 m (N: 42°56', E: 13°5'), 1♂, P. Pantini, M. Valle leg. 9. 1992 – 6. 1993 (MSNB); **Molise, Prov. Campobasso:** Campitello Matese, *Fagus*, 1400 m (N: 41°27', E: 14°23'), 2♀, W. Schawaller leg. 1. 6. 1987 (CJM 2854); **Toscana, Prov. Arezzo:** Chiusi della Verna, Parco Nazionale Foreste Casentinesi, staz. 15, forest, pitfall, 560 m (N: 43°41, E: 11°55), 3♂, Scaravelli, Bertozzi leg. 5. 8. 1997 (MSNB); dito, Rimbocchi Pezza, staz. 16, forest, pitfall, 580 m (N: 43°41, E: 11°55), 2♂, 2♀, Scaravelli, Bertozzi leg. 5. 8. 1997 (MSNB); **Prov. Di Pistoia:** Scesta/Lima (Fluß) (N: 44°02', E: 10°38'), 1♀, K. Bauer leg. 12. 4. 1960, J. Gruber det. (NHMW 3156); **Prov. Di Siena:** 3 km W Radicofani (N: 42°53', E: 11°43'), 2♂, 4♀, H. Zimmer leg. 5. 10. 1967, J. Gruber det. (NHMW 3157); **Prov. Firenze:** Dicomano, riverine forest, under stones and sieving, 223 m (N: 43°54'42,3“, E: 11°33'42,0“), 2♂, 3♀, A. Schönhofer leg. 11. 4. 2006 (CJM 5009); Fiesole near Florenz (N: 43°48°, E: 11°15°, 2♀, Verhoeff leg., Roewer det. (ZMB 11997); **Prov. Livorno:** Elba, S Marciana, valley, station of cabinovia, 320–360 m (N: 42°46', E: 10°10'), 1♂, J. Spelda ded. 5. 10. 2004 (CJM 5423); dito, valley of Pomonte, E Pomonte, under stone near stream (N: 42°45'18,8", E: 10°8'28,2"), 1♀, M. Nickel leg. 5. 4. 1998 (CJM 6007); St. Livorno, Colognole, 400 m (N: 43°31', E: 10°27'), 1♀, W. Schawaller leg. 23. 4. 1979 (CJM 1867); **Prov. Massa-Carrara:** 1♂, 1♀, Verhoeff leg., Roewer det. (ZMB 12001); Alpe Apuane, Campo Cecina, 1200 m (N: 44°07', E: 10°03'), 1♂, I. Löbl leg. 30. 7. 1984, P. Mitov det. (MHNG); **Prov. Pisa:** Volterra (N: 43°24', E: 10°51'), 1♂, P. Brignoli leg. 13. 10. 1969 (CJM 1068); **Umbria, Prov. Perugia:** Nocera Umbra, Colle Aprico, pendici Monte Pennino, pitfall, 700 m (N: 44°9', E: 10°20', 6♂, 3♀, 1juv., G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); dito, 2♂, 1♀, P. Pantini, M. Valle leg. 9. 1992 – 6. 1993 (MSNB); dito, 7♂, 4♀, leg. 6. – 9. 1992 (MSNB); dito, 2♂, leg. 1. – 6. 1992 (MSNB); San Giustino, Monte Moriccio, pitfall, 900 m (N: 43°34', E: 12°18'), 2♂, 1♀, P. Pantini, M. Valle leg. 6. – 9. 1992 (MSNB); dito, 1♂, 1♀, leg. 11. 1992 – 6. 1993 (MSNB); dito, 1♀, leg. 6. – 12. 1991 (MSNB); San Giustino, Parnacciano, pitfall, 700 m (N: 43°33', E: 12°17'), 1♀, P. Pantini, M. Valle leg. 6. – 9. 1992 (MSNB); dito, 3♂, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); Sigillo, above the village, pitfall, 550 m (N: 43°20', E: 12°45', 1♂, 1♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); dito, 1juv., P. Pantini, M. Valle leg. 1. – 6. 1992 (MSNB); Sigillo, verso Monte Cucco, pitfall, 800 m (N: 43°20', E: 12°45'), 1♀, P. Pantini, M. Valle leg. 6. – 9. 1992 (MSNB); dito, 3♂, 2♀, G. Buttarelli, E. Ghilardi, P. Pantini, M. Valle leg. 6. – 12. 1991 (MSNB); dito, 850 m, 1♀, P. Pantini, M. Valle leg. 1. – 6. 1992 (MSNB); **Prov. Terni:** Orvieto (N: 42°43', E: 12°06'), 1♀, 1juv., Verhoeff leg., Roewer det. (ZMB 12000); not localized: Fiume, graveyard, 2♀, Verhoeff leg. 17. 10. (ZMB 12084, formerly *T. rostratus*); Spain: Asturias, Oviedo 1♂, 1♀ (SMF 1364), *T. coriziformis* and not an Iberian species, wrong locality indication by Roewer.

There are many citations from Abruzzi and Lazio (TROSSARELLI 1934, ŠILHAVÝ 1969, MARCELLINO 1970, 1971, BRIGNOLI & RAFAELLI 1978) that could not be investigated but most probably represent this species.

DIAGNOSIS: Large to very large *Trogulus* with a distinct median notch at rear end of opisthosoma. Papillation on dorsal scute dense and regular; pepipalps with prominent papillation. Restricted to the Italian Peninsula.

DESCRIPTION

BODY: Dorsal median ridge on prosoma deeply incised but narrow and sometimes indistinct (Fig. 5.5*f*, *h*). Dorsal median ridge on opisthosoma pronounced, composed of densely-packed papillae. Transverse ridges faintly elevated and best visible to the naked eye. Papillation and coloration regular (Fig. 5.5*e*–*h*). Rear end of opisthosoma with a distinct median notch in most specimens.

EYE MOUND AND FRONT CAP: Front cap elliptic, eye mound elevated, eyes separated by an incision (Fig. 5.5*f*, *h*). Distance between eyes normal, eyes directed sidewards, eye lens not projecting beyond lateral border of eye mound; at least half their diameter from lateral border of front cap.

LEGS AND PEDIPALPI: Apophyses on metatarsi III and IV small and pointed, not drawn out beyond the end of astragalus and without prominent papillae (Fig. 5.6*i*, *m*). Tarsi III and IV shorter than in *T. aquaticus*. Dorsal hairs on pedipalpi thick with blunt end, situated on prominent papillae (Fig. 5.6*g*, *k*), metatarsus therefore appearing more massive than tarsus. Formation of a distinct crest of elongated papillae on femur II is restricted to specimens of large body size. Tarsus II appears more compact than in *T. aquaticus* (Fig. 5.6*l*, *h*).

PENIS MORPHOLOGY: Truncus penis cuneiform, slightly broadened above midsection (dorsal view Fig. 5.8*c*, *d*, *g*, *h*), glans penis short and broad, basal part inflated (lateral view, Fig. 5.8*b*, *f*), narrowing towards the stylus, a prominent bump with setae at the intersection to stylus; stylus short and pointed, slightly bent laterally in distal third (dorsal view, Fig. 5.8*a*, *e*).

MEASUREMENTS: Body length data was obtained from all available individuals: ♂ (*n* = 172): 8.4–12.85; ♀ (*n* = 110): 9.9–15.35; all other measurements are from series CJM 1058, 5009, 5051, 5423 (♂, *n* = 12; ♀ *n* = 12): **Body length**: ♂ 9.4–11.7; ♀ 10.7–12.1; **body width**:

♂ 3.5–4.6; ♀ 4.1–4.9; **coxa II interdistance**: ♂ 4.0–4.9; ♀ 4.2–4.8; **coxa IV interdistance**: ♂ 4.25–5.2; ♀ 4.75–5.65; **width at coxa II**: ♂ 4.0–4.9; ♀ 4.2–4.8; **width of body at shoulder**: ♂ 1.73–2.08; ♀ 1.85–2.85; **eye interdistance**: ♂ 0.76–0.97; ♀ 0.79–0.95; **interocular distance**: ♂ 0.57–0.73; ♀ 0.61–0.76; **length of head cap**: ♂ 1.05–1.33; ♀ 1.03–1.53; **width of head cap**: ♂ 1.15–1.48; ♀ 1.3–1.58; **length of leg II**: ♂ 12.5–15.7; ♀ 12.8–14.9; **length of metatarsus II**: ♂ 2.53–3.21; ♀ 2.68–3.1; **length of femur II**: ♂ 3.6–4.45; ♀ 3.8–4.35; **length of femur I**: ♂ 2.1–2.63; ♀ 2.28–2.65; **length of tarsus IV**: ♂ 0.98–1.14; ♀ 1.05–1.18; **length of metatarsus IV**: ♂ 2.65–3.24; ♀ 2.9–3.38; **length of penis**: 2.18–2.66; **length of basal segment of tarsus II**: ♂ 0.88–1.1; ♀ 0.9–1.03; **length of distal segment of tarsus II**: ♂ 1.13–1.46; ♀ 1.08–1.33; **ratio of length of distal to basal segment of tarsus II**: ♂1.23–1.34; ♀ 1.13–1.34; **length of leg II/Body length**: ♂: 1.25–1.45; ♀ 1.17–1.29. The canonical discriminant analysis included interocular distance, length of basal segment II and width of head cap to correctly classify all but one specimen of *T. coriziformis* and one of *T. aquaticus*. For variation in body size within *T. coriziformis* see Fig. 5.9. Large specimens form a clearly separated peak in the analysis.

VARIABILITY: Specimens from the north-western border of the area (Emilia-Romagna, Prov. Parma, Bedonia; Liguria, Prov. La Spezia, Varese Ligure) are significantly larger than those from all other areas (Fig. 5.9). Single specimens lack papillation on some spots of the dorsal scute and are remarkably similar to *T. aquaticus*. Further intraspecific differentiation of this widespread species is possible but this could not corroborated due to the lack of material available for molecular genetics.

DISTRIBUTION: *Trogulus coriziformis* is restricted to the Italian Peninsula and adjacent islands (Elba, Capri; Fig. 5.1). Its northern extent spans from La Spezia in the west along the northern border of the Apennines but excludes the Po valley. Southwards it occurs continuously to Calabria with a large distributional gap including Apulia, Monte Gargano and parts of Basilicata. It is apparently allopatric with *T. graecus* that inhabits this part of the Italian peninsula.

ECOLOGY: *Trogulus coriziformis* is most frequently encountered in river valleys with permanently humid environments, mostly under stones. It has been recorded from many pitfall traps in different forest communities (evergreen oak forest, mixed deciduous forest with *Carpinus betulus*, *Ostrya carpinifolia*, dry *Castanea sativa* forest) and a few have been found in open communities (for example pasture and meadow). The species has been collected from areas ranging in elevation from sea level to 1750 m, with only few records of specimens occurring above 1000 m.

REMARKS: The type series in the C. L. Koch collection seems to be lost (other *Trogulus* types of KOCH (1839) are located in BMNH). KOCH (1839) was unable to specify the origin of his material, but since CANESTRINI (1875) the name *T. coriziformis* has been used for the large *Trogulus* specimens of the Italian Peninsula. BRIGNOLI (1968) separated the similar-sized *T. graecus* (also from Italy) from *T. coriziformis* based on genital morphology. This was approved by MARTENS (1978) who synonymised *T. cristatus* with *T. coriziformis* and suggested to use the type locality of *T. cristatus* (Alpes-Maritimes, Lantosque) for *T. coriziformis*. Because both species are treated as valid here, a neotype and the type locality for *T. coriziformis* has to be fixed anew. Recommended is the region Lazio, province of Rome (Monti della Tolfa, between Tolfa and Rota, 42°09’N, 11°57’E), from where most available collections of the species originate. As neotypus one male from CJM 1058 is designated now deposited in SMF. In the original description KOCH (1839) mentioned the notched rear end of the opisthosoma and the prominent papillae on the palps and this holds true for the neotype and this species in general. *Trogulus salfii* De Lerma, 1948 (Campania, Salerno, Olevano sul Tusciano, Grotta di S. Michele) could not be investigated but characters are well within the range of *T. coriziformis* and DE LERMA (1948) did not consider this species at all. The type locality is within the range of investigated *T. coriziformis* specimens with low morphological variation. A specimen collected close to the type locality (CJM 4995) genetically emerged as *T. coriziformis*. It therefore is proposed to treat *T. salfii* as synonym of the latter species. Due to the large body size, *T. coriziformis* can be confused with *T. graecus* that is allopatric to the former species (see this chapter, Distribution) and the genital morphology differs. *Trogulus coriziformis* is closely related to the allopatric *T. aquaticus*.

***Trogulus cristatus* Simon, 1879**

(Figs. 5.10*a–d*, 5.11*a–f*, 5.13)

Trogulus cristatus SIMON 1879: 308. – DAHL 1903: 284. (in part); ROEWER 1923: 636.

Trogulus coriziformis (all in part) ROEWER 1923: 636. – MELLO-LEITÃO 1936: 6; MARTENS 1978: 174–175, figs. 254–255, 275; MARCELLINO 1982: 41, 43, fig. 2.

MATERIAL EXAMINED: SYNTYPES: **France, Provence, Dép. Alpes-Maritimes**: 1♂, 1♀, 1juv. (MNHP 2193) [the male is specified as holotype; this series most likely comprises material from localities mentioned in the original description]: Saint-Martin de Lantosque (N: 43°58’, E: 7°18’), Power leg; Mont Boron near Nizza (N: 43°41’, E: 7°18’), Debray leg.

ADDITIONAL MATERIAL: **France, Provence, Dép. Alpes-Maritimes:** Riviera, Beaulieu-sur-Mer near Nizza, Ravine de la Musta (N: 43°42’, E: 7°19’), 1♀, Brölemann leg. 8. 2. 1903 (MNHP 23561), Berland det.; Cagnes (N: 43°40’, E: 7°08’), 1♂, 1♀, Brölemann leg. (MNHP 12675); Villefranche-sur-Mer near Nizza, 1♂, R. Schenkel leg. 4. 1935 (NHMB 56-b), E. Schenkel det. as *T. coriziformis*; Dry valley between Villars-sur-Var and tunnel of Mescla, old stone terrasses in dry decidious forest, under mossy stones, handcollected, 231 m (N: 43.93119, E: 7.13273), 1♀, A. Schönhofer leg. 2. 9. 2008, (CJM 6226); stream Valley Vallon Cervagne near Roquebillière, in stone hump near stream and sieving of humus between these stones, handcollected and sieving, 685 m (N: 44.01562, E: 7.29831), 2♂, A. Schönhofer leg. 2. 9. 2008, (CJM 6227); Col de Turini, Coniferous forest, in stone hump near stream and in humus between these stones, sieving, 1513 m (N: 43.97729, E: 7.38560), 1juv., A. Schönhofer leg. 3. 9. 2008, (CJM 6228); Mercantour National Park, La Minière de Valaura, mixed forest on north facing slope with small streams, 1476 m (N: 44,06917, E: 7,1319), 1♀, 1juv., A. Schönhofer leg. 5. 9. 2008, (MNHP); **Dép. Var:** 15 km NW St. Tropez, Massiv des Maures, Col de Vignon, 360 m (N: 43°20’, E: 6°28’), 1♀, J. Martens leg. 29. 3. 1982 (CJM 2066); Bagnols-en-Forêt (N: 43°31’, E: 6°41’), 1♀, V. Aellen leg. 26. 4. 1999 (MHNG), P. Schwendinger det. *T. coriziformis*; no locality given, 1♂, 1♀ (BRINS), Roewer det. 1913 als *T. tricarinatus* (det. No. 2457), L. Becker rev. as *T. cristatus*; Callian (N: 43°38’, E: 6°44’), 1♂ (MNHP); **Italy**: Riviera, 1♂, 1♀ (SMF 1346), det. as *T. nepaeformis*; **Liguria, Prov. Imperia:** N San Remo, small valley with stream, *Castanea sativa* and oak forest, under stones deep in the soil, 460 m (N: 43°49’34,5“, E: 7°43’23,1“), 1♂, 2♀, 3juv., A. Schönhofer leg. 18. 3. 2006 (CJM 4972); Riviera, San Remo (N: 43°49’, E: 07°46’), 1♀ (SMF 1345), det. as *Trogulus nepaeformis*; **Prov. Savona:** Andora, Marina di Andora, meadow, 40 m (N: 43°56’, E: 8°7’), 1♀, R. Fabbri leg. 23. 9. 2005 (MSNB); **Piemonte, Prov. Cuneo:** T. Negrone, W Ormea, Pt. Nava, 900 m (N: 44°08’, E: 07°56’), 1♂, K. Thaler leg. 2. 10. 1972 (CJM 1589); surroundings of Viozene, Pian Rosso, 1200–1500 m (N: 44°08’, E: 07°47’), 1♀, K. Thaler leg. 4. 10. 1972 (CJM 1590).

MATERIAL NOT EXAMINED: MARTENS (1978) mentioned specimens from Cannes and La Roquette (both Alpes-Maritimes) which likely do represent *T. cristatus* but could not be relocated in MNHP.

DIAGNOSIS: Medium to large *Trogulus* species, restricted to the southwestern Alps. Stylus of glans long and slender. Apophyses on metatarsi III and IV prominent. Pedipalps smooth, without papillae.

DESCRIPTION

BODY: Dorso-median ridge on pro- and opisthosoma indistinct (Fig. 5.10*a–d*), rear end of opisthosoma not incised, dorsal papillation regular, sometimes more widely spaced at the distal part of prosoma, density unchanged on opisthosomal ridges.

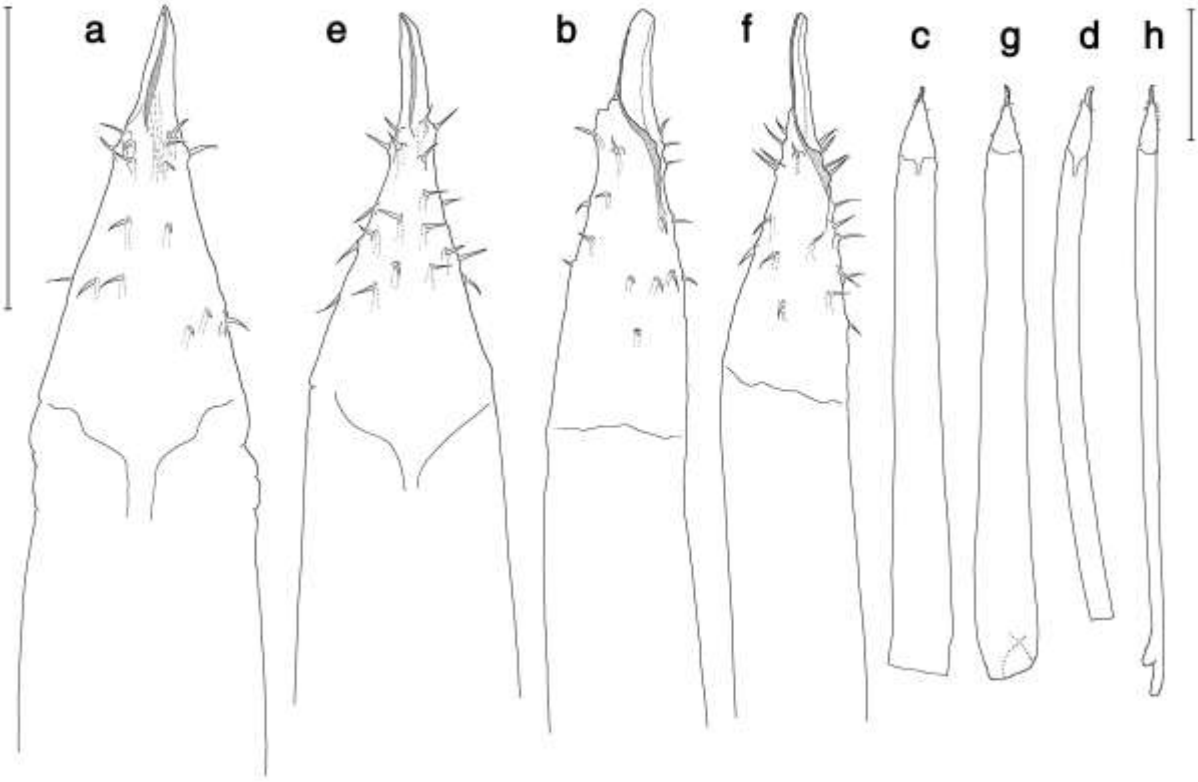


Fig. 5.13. Penes of *Trogulus cristatus* Simon. (*a*–*d*) Holotype, France, Provence, Dép. Alpes-Maritimes, MHNP 2193; (*e*–*h*) Italy, Liguria, Prov. Imperia, northern San Remo, CJM 4972. (*a*, *b*, *e*, *f*) Glans and distal part of truncus; (*c*, *d*, *g*, *h*) penis; (*a*, *c*, *e*, *g*) dorsal view; (*b*, *d*, *f*, *h*) lateral view. Scale line on the left 0.2 mm (*a*, *b*, *e*, *f*), on the right 0.5 mm (*c*, *d*, *g*, *h*).

EYE MOUND AND FRONT CAP: Front cap variable in shape (Fig. 5.10*b*, *d*), mostly circular, eye mound of normal size, only slightly elevated. Eyes separated by a flat depression. Distance between eyes as in *T. coriziformis*, eye directed sidewards, placed about half their diameter from lateral border of eye mound.

LEGS AND PEDIPALPI: Much more slender than in *T. coriziformis*. Distal segment of tarsus II considerably longer than basal segment (Fig. 5.11*b*, *e*). Apophyses of metatarsus III and IV drawn out beyond the end of astragalus (Fig. 5.11*c*, *f*), broad and bluntly ended, with prominent long papillae. Metatarsus of pedipalpi with pointed hairs dorsally (Fig. 5.11*a*, *d*), papillae small and inconspicuous, metatarsus therefore appears smooth and as slender as tarsus; crest of large papillae dorsal on femur II.

PENIS MORPHOLOGY: In most investigated specimens (Fig. 5.13*e*–*h*) truncus parallel-sided (dorsal/ventral view), only at base slightly cuneiform; glans penis relatively short, triangular, not considerably inflated, glans gradually narrowing into the long and slender stylus, no bump at the intersection between glans and stylus, stylus straight, not bent at distal third, tip rounded. Holotype (Fig. 5.13*a–d*) differs in having: shorter and broader stylus, bump at intersection from glans penis to stylus, and a generally broader glans penis (lateral view).

MEASUREMENTS: **Body length**: ♂(*n* = 6) 9.3–10.55; ♀ (*n* = 10) 10.6–11.9; **body width**: ♂3.3–3.9; ♀ 4.2–4.9; **coxa II interdistance**: ♂ 3.8–4.65; ♀ 4.1–4.9; **coxa IV interdistance**: ♂ 4.0–4.6; ♀ 4.7–5.6; **width at coxa II**: ♂ 3.8–4.65; ♀ 4.1–4.9; **width of body at shoulder**: ♂ 1.5–1.78; ♀ 1.75–2.03; **eye interdistance**: ♂ 0.77–0.84; ♀ 0.82–0.96; **interocular distance**: ♂ 0.52–0.65; ♀ 0.61–0.71; **length of head cap**: ♂ 0.95–1.23; ♀ 0.98–1.45; **width of head cap**: ♂ 1.1–1.28; ♀ 1.23–1.53; **length of leg II**: ♂ 12.6–14.1; ♀ 12.8–15.3; **length of metatarsus II**: ♂ 2.53–2.95; ♀ 2.6–3.18; **length of femur II**: ♂ 3.75–4.25; ♀ 3.95–4.7; **length of femur I**: ♂ 2.15–2.4; ♀ 2.3–2.7; **length of tarsus IV**: ♂0.88–1.04; ♀ 0.93–1.13; **length of metatarsus IV**: ♂2.48–2.95; ♀ 2.65–3.2; **length of penis**: 2.13–2.74; **length of basal segment of tarsus II**: ♂0.83–0.91; ♀ 0.78–0.94; **length of distal segment of tarsus II**: ♂1.09–1.38; ♀ 1.15–1.35; **ratio of length of distal to basal segment of tarsus II**: ♂: (type: 1.19) 1.36–1.62; ♀ 1.22–1.56; **length of leg II/Body length**: ♂: 1.33–1.39; ♀ 1.19–1.28. *Trogulus cristatus* tends to a slender opisthosoma, the ratio of length of distal to basal segment of tarsus II being larger than in *T. coriziformis* and *T. aquaticus*. The canonical discriminant analysis (Fig. 5.4) used the lengths of femur II, basal segment II and tarsus IV, width at the shoulder and the distance between the inner borders of coxae II to classify most specimens of *T. coriziformis* and *T. cristatus*. However, these data do not seem sufficient to always correctly assign the two similar species using morphometry. The holotype and one female (Bagnols-en-Forêt) of *T. cristatus* were classified as *T. coriziformis*.

VARIABILITY: The genital morphology and the ratio of length of distal to basal segment of tarsus II of the type specimen is remarkably different from all other investigated males at the vicinity of the type locality (see this chapter, Remarks). Other characters such as body size, the presence of smooth palps and the prominent apophyses on metatarsi III and IV are shared by all specimens.

DISTRIBUTION: This species is restricted to the south-western Alps within a belt of 30–40 km width along the coast between 15 km NW of St Tropez, France and Marina di Andora, Italy (Fig. 5.1). ‘Southern France’ was originally cited by DAHL (1903), ROEWER (1923), and MELLO-LEITÃO (1936) followed this indication.

ECOLOGY: *Trogulus cristatus* is found under stones in valleys with permanent humidity and different forest communities as *Castanea sativa* and *Quercus* or *Fraxinus* or *Larix* dominated woods. Its vertical distribution ranges from sea level to 1500 m.

REMARKS: The male holotype is quite different to other males from the same population. Its stylus is broad and not slender as is usual in *T. cristatus* and the ratio of length

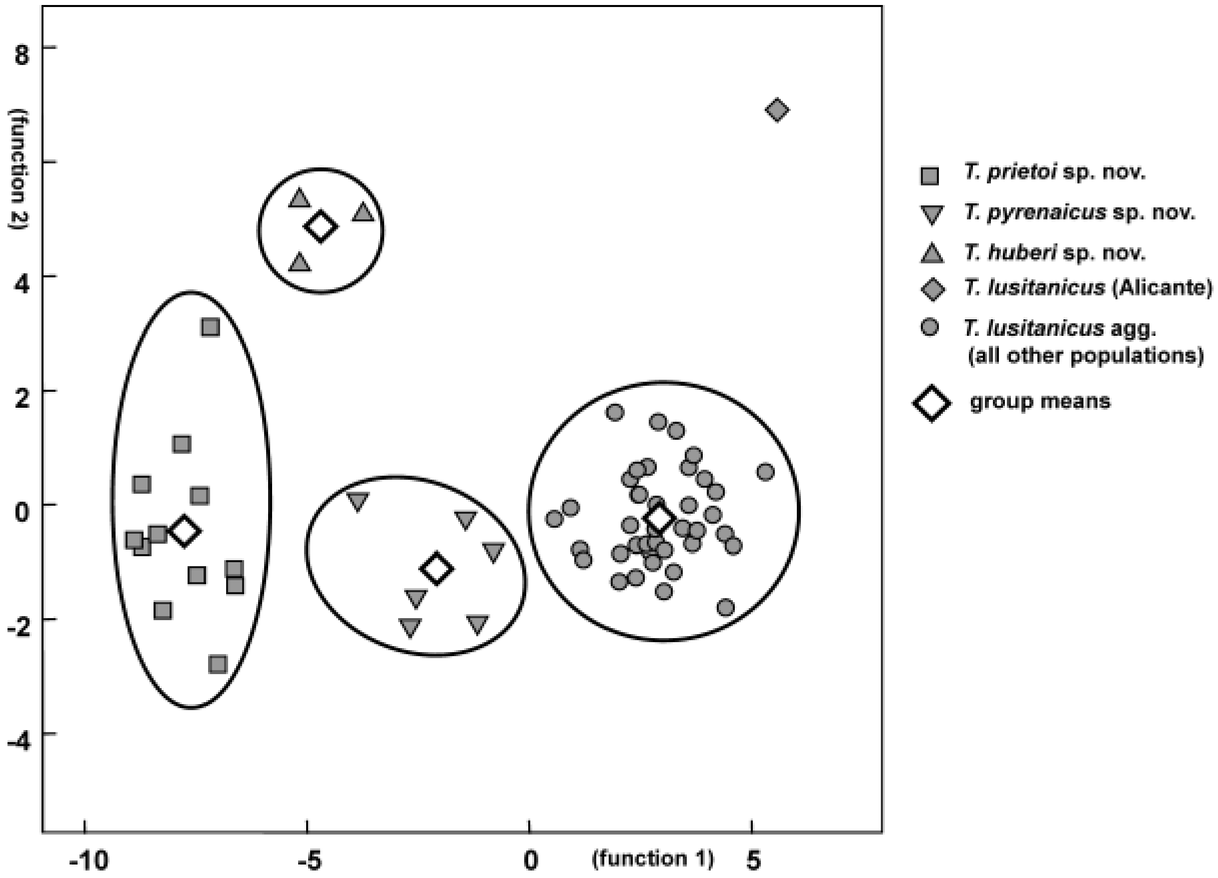


Fig. 5.14. Results of the canonical discriminant analysis to separate species of the *Trogulus coriziformis* species-group from the Iberian Peninsula. The discriminant functions incorporated the distance between the outer borders of the eyes and length of femur I and II as most significant characters to classify 100% of all included specimens correctly.

of distal to basal segment of tarsus II is 1.19, similar to *T. coriziformis*. Canonical discriminant analysis identifies this specimen as *T. coriziformis*. Due to the similarity of the holotype MARTENS (1978) synonymised *T. cristatus* with *T. coriziformis*. Apparently, SIMON (1879) united several series of various origin (see *T. aquaticus*, *T. lusitanicus*). This might apply for the type series of *T. cristatus* as well, because he published in 1879 two localities (Lantosque; Montboron) but the reference series is labelled 'Alpes-Maritimes'. This origin is confirmed in Simon's accession book. *Trogulus cristatus* is genetically, morphologically, and geographically well defined. Because of the large ratio of length of distal to basal segment of tarsus II *T. cristatus* has often been assigned to the *T. nepaeformis* species-group. All taxa of the latter group show a dorsally bent stylus. The presented data confirms that no other *Trogulus* species is sympatric with *T. cristatus*. The closely related sister-species *T. aquaticus* and *T. coriziformis* have prominent papillae on the palps and smaller apophyses on metatarsi III and IV.

Trogulus huberi sp. nov.

(Figs. 5.15*a*, *b*, 5.16*a–c*, 5.17*a–d*, 5.19*m*)

MATERIAL EXAMINED: HOLOTYPE: **Portugal, Algarve:** ca. 50 km N Faro, Alte, near Hotel „Alte“, in crack of a stonewall, at night, 250 m (N: 37°14’16,8“, W: 8°11’6,3“), 1♂, S. Huber leg. 22. 10. 2006 (CJM 5344).

PARATYPES: **Portugal**, **Algarve:** ca. 50 km N Faro, E of Alte, Peña da Rocha, under stone, 330 m (N: 37°15’0“, W: 8°5’52,4“), 1♀, S. Huber leg. 22. 10. 2006 (CJM 5346); Beja, Mértola, surroundings of Mértola, *Pinus pinea* forest, 90 m (N: 37°38’, W: 7°39’), 1♂, P. Cardoso leg. 29. 5. 2003 (CCP 3323).

DIAGNOSIS: A large but slender *Trogulus* with small interocular distance, small eyes and regular papillation without Y-shaped ridge on prosoma. Opisthosoma from ventral view elliptical rather than egg-shaped. Restricted to southern Portugal.

DESCRIPTION

BODY: Ventral scute elliptical (Fig. 5.19*m*) rather than egg-shaped, opisthosoma dorsally with regularly spaced papillae, median and transversal ridges prominent, papillation with the same density (Fig. 5.15*a*, *b*). Median furrow on prosoma indistinct, only few papillae lacking, ending in a transverse zone of weak papillation at caudal third bordered by a zone of dense papillation resulting in an anchor-like appearance (Fig. 5.15*b*).

EYE MOUND AND FRONT CAP: Front cap broad and circular (Fig. 5.15*b*), pointing downwards when seen in lateral view, appearance large because indistinct shoulders of prosoma and intersection of opisthosoma to eye mound narrow, eye mound separated by a shallow depression. Eye interdistance and eyes small compared with *T. lusitanicus* agg.

LEGS AND PEDIPALPI: Legs long and slender, without ridge of elongated papillae on femur II; apophyses on astragalus of metatarsus III and IV broad and prominent (Fig. 5.16*c*). Calcaneus of leg II slightly larger than in *T. lusitanicus* agg (Fig. 5.16*b*). Base of hairs on dorsal part of pedipalpus thickend but not prominent (Fig. 5.16*a*).

PENIS MORPHOLOGY: Truncus cuneiform, slightly constricted in distal third, gradually narrowing into the glans penis (Fig. 5.17*c*, *d*); glans penis triangular and narrow in dorsal view, base of glans bulbous in lateral view (Fig. 5.17*a*, *b*), intersection between stylus and

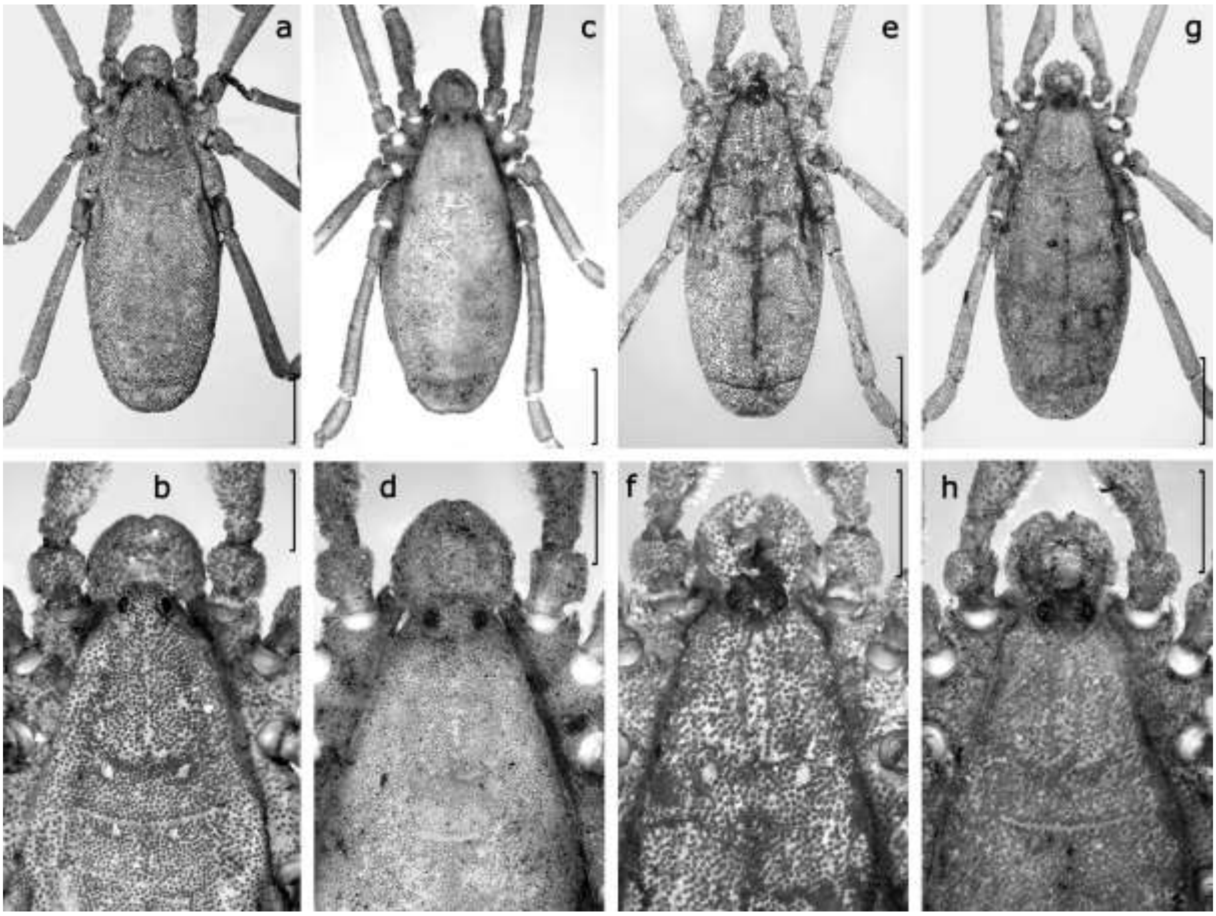


Fig. 5.15. Body of ♂ of *Trogulus huberi* sp. nov., *T. pyrenaicus* sp. nov. and *T. prietoi* sp. nov., dorsal view. (*a*, *b*) *T. huberi* sp. nov., holotype, Portugal: Algarve, Alte, CJM 5344; (*c*, *d*) *T. pyrenaicus* sp. nov., holotype, Spain: Aragón, Prov. Huesca, Monte Perdido, Torla, CJM 1360; (*e*, *h*) *T. prietoi* sp. nov.; (*e*, *f*) holotype, Spain: Andalusia, Prov. Málaga, S of Villanueva de la Concepcion, CJM 5321; (*g*, *h*) paratype, Spain, Prov. Jaen, Valdepeñas de Jaén, Sierra de la Pandera, CCP 1937. Upper row, scale lines 2.0 mm, bottom row 1.0 mm.

glans pronounced by prominent papillae bearing a hair but lack a bump; stylus narrow compared to *T. lusitanicus* specimens (Fig. 5.21*a*, *b*, *e*, *f*, *i*–*k*), distal end of stylus truncated, divided in two lamellae.

MEASUREMENTS: **Body length**: ♂(n = 2) 10.45–10.8; ♀(n = 1) 11.8; **body width**: ♂3.9–4.0; ♀ 4.5; **coxa II interdistance**: ♂ 3.9–4.1; ♀ 4.2; **coxa IV interdistance**: ♂ 4.4–4.5; ♀ 4.9; **width at coxa II**: ♂ 3.9–4.1; ♀ 4.2; **width of body at shoulder**: ♂ 1.68–1.78; ♀ 1.73; **eye interdistance**: ♂ 0.67–0.68; ♀ 0.74; **interocular distance**: ♂ 0.45–0.49; ♀ 0.53; **length of head cap**: ♂ 1.0–1.03; ♀ 1.28; **width of head cap**: ♂ 1.2–1.3; ♀ 1.35; **length of leg II**: ♂ 15.0–15.1; ♀ 15.35; **length of metatarsus II**: ♂ 3.18–3.2; ♀ 3.28; **length of femur II**: ♂ 4.55–4.7; ♀ 4.7; **length of femur I**: ♂ 2.55–2.75; ♀ 2.73; **length of tarsus IV**: ♂ 0.95–0.98; ♀ 1.0; **length of metatarsus IV**: ♂ 3.05–3.08; ♀ 3.1; **length of penis**: 2.25–2.4; **length of basal segment of tarsus II**: ♂ 0.91–1.05; ♀ 1.03; **length of distal segment of tarsus II**: ♂

1.25–1.3; ♀ 1.03; **ratio of length of distal to basal segment of tarsus II**: ♂: 1.24–1.37; ♀ 1.37; **length of leg II/Body length**: ♂: 1.40–1.44; ♀ 1.30. The canonical discriminant analysis (Fig. 5.14) used eye interdistance and length of femur I and II to separate all specimens of *T. huberi* and *T. lusitanicus* agg. Specimens appear quite slender, which is not immediately obvious based on opisthosomal measurements. The ratio of body length to body width within the heterogeneous *T. lusitanicus* agg. extends from 2.30–2.66; for *T. huberi* it is 2.68–2.70.

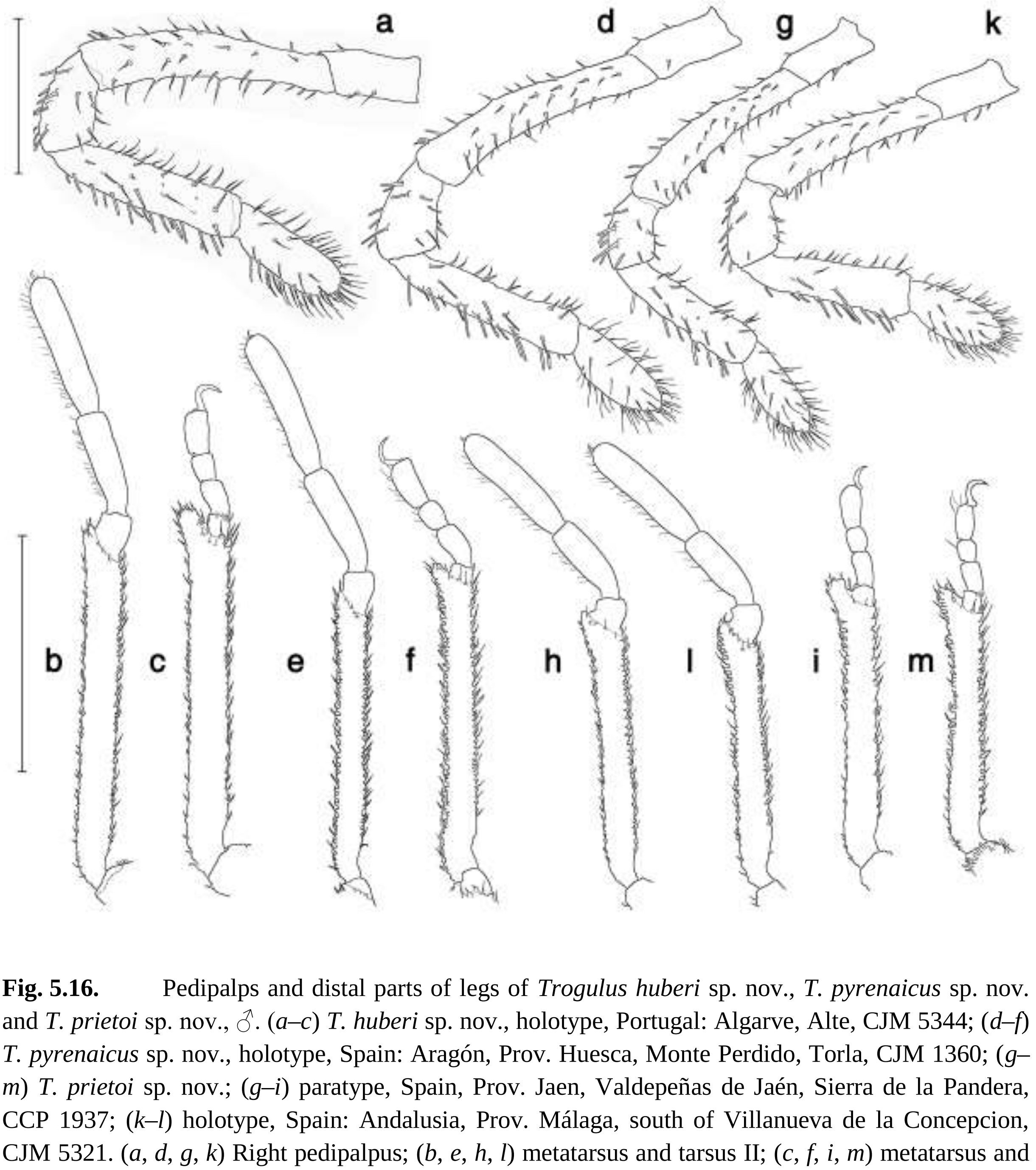


Fig. 5.16. Pedipalps and distal parts of legs of *Trogulus huberi* sp. nov., *T. pyrenaicus* sp. nov. and *T. prietoi* sp. nov., ♂. (*a–c*) *T. huberi* sp. nov., holotype, Portugal: Algarve, Alte, CJM 5344; (*d–f*) *T. pyrenaicus* sp. nov., holotype, Spain: Aragón, Prov. Huesca, Monte Perdido, Torla, CJM 1360; (*g–m*) *T. prietoi* sp. nov.; (*g–i*) paratype, Spain, Prov. Jaen, Valdepeñas de Jaén, Sierra de la Pandera, CCP 1937; (*k–l*) holotype, Spain: Andalusia, Prov. Málaga, south of Villanueva de la Concepcion, CJM 5321. (*a*, *d*, *g*, *k*) Right pedipalpus; (*b*, *e*, *h*, *l*) metatarsus and tarsus II; (*c*, *f*, *i*, *m*) metatarsus and tarsus IV; all medial view. Upper left, scale line 0.5 mm (*a*, *d*, *g*, *k*), bottom left 2.0 mm (*b*, *c*, *e*, *f*, *h*, *i*, *l*, *m*).

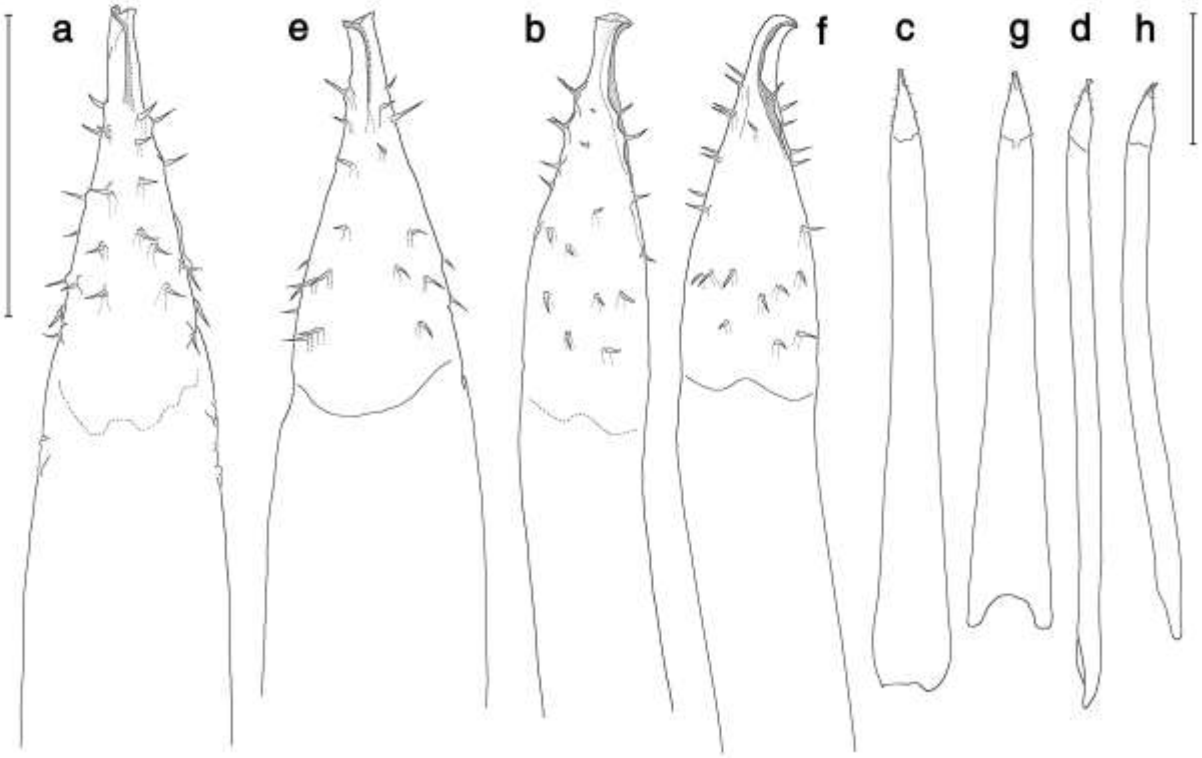


Fig. 5.17. Penes of *Trogulus huberi* sp. nov. and *T. pyrenaicus* sp. nov. (*a–d*) *T. huberi* sp. nov., holotype, Portugal: Algarve, Alte, CJM 5344; (*e–h*) *T. pyrenaicus* sp. nov., holotype, Spain: Aragón, Prov. Huesca, Monte Perdido, Torla, CJM 1360. (*a*, *b*, *e*, *f*) Glans and distal part of truncus; (*c*, *d*, *g*, *h*) penis; (*a*, *c*, *e*, *g*) dorsal view; (*b*, *d*, *f*, *h*) lateral view. Scale line on the left 0.2 mm (*a*, *b*, *e*, *f*), on the right 0.5 mm (*c*, *d*, *g*, *h*).

VARIABILITY: No data due to the small quantity of material.

DISTRIBUTION: Recorded only from two close localities in southern Portugal (Alte, Mertola; Fig. 5.1).

ECOLOGY: The species was collected from dry and open country with few bushes and trees under calcareous rocks (S. Huber, pers. comm.). All records are from low altitudes (90–330 m).

REMARKS: Although *T. huberi* is regarded as closely related to *T. lusitanicus* agg. it is genetically well differentiated and morphologically distinct from the female holotype of *T. lusitanicus*.

ETYMOLOGY: The name honours Siegfried Huber, who has continuously contributed material to the current work on Opiliones, including material of this new species.

Trogulus lusitanicus Giltay

(Figs. 5.19*a*–*l*, 5.20, 5.21)

Trogulus lusitanicus GILTAY 1931: 1–2. – RAMBLA 1967: 5.

Trogulus aquaticus (all in part) SIMON, 1879: 306. – RAMBLA 1960: 5–6; KRAUS 1961: 338–339; PRIETO 2003: 135.

Trogulus coriziformis DAHL 1903: 286–287 (in part). – ROEWER 1923: 639 (in part); ROEWER 1925: 177 (in part); MELLO-LEITÃO 1936: 6. (in part); KRAUS 1961: 338–339 (in part); RAMBLA 1967: 5; MARCELLINO 1982: 41, 43, fig. 2 (in part).

MATERIAL EXAMINED: HOLOTYPE: **Portugal, Lisboa:** Cintra (N: 38°47’, W: 9°23’), 1♀, Camille Van Voixem leg. 17. 7. 1938 (BRINS).

ADDITIONAL MATERIAL: **Portugal, Porto:** Porto (N: 41°09’, W: 8°36’), 1♀ (SMF 1365); **Braganca:** Douro, Freixo de Espada, Lagoaça, PF924628, *Castanea*, *Pinus*, 400 m (N: 41°11’, W: 6°43’), 1♂, 1♀, P. Cardoso leg. 3. 6. 2001 (CCP 3331); dito, 1♂, P. Cardoso leg. 17. 6. 2001 (CCP 3332); **Braga:** Peneda-Gerês Nationalpark (PNPG), Albergaria, dense oak forest (*Quercus robur, Q. pyrenaica*), with dense understorey and deep leaf litter, hand collected and pitfall traps, 600–700 m (N: 41°47’42“, W: 8°8’12“) 115♂, 88♀, 44juv., P. Cardos et al. leg. 1. – 15. 6. 2005 (many series, ZMC); PNPG, Gerêz (N: 41°44’, W: 8°10’), 1♀, K. Pfau leg. 18. 9. 1983 (CJM 2549); **Santarém:** Villa Nova de Ourém, Bairro, ND328798, *Pinus pinea* forest, 320 m (N: 39°34’, W: 8°36’), 1♂, P. Cardoso leg. 23. 4. 2002 (CCP 3321); **Spain, Valencia, Prov. Alicante:** Vall d´Ebo, Pego (N: 38°49’, W: 0°08’), 1♀, 1juv., C. Prieto leg. 04. 10. 1990 (CCP 947); Jávea, Granadella, valley (N: 38°46’, E: 0°08’), 3juv., 17. 4. 1998 (CCP 1807); **Andalucía:** 1♂, Staudinger leg. (ZMB 13962, exclusive record for DAHL 1903, ROEWER 1923, 1925, PRIETO 2003); **Prov. Cádiz:** Jerez (N: 36°37’, W: 6°02’), 1♂, 2♀, 1juv. (MNHP 2197, formerly *T. aquaticus*); Tarifa, Algeciras (GPS not accurate; N: 36°04’, W: 5°32’), 2♂, 1♀ (MNHP 24831, formerly *T. aquaticus*); dito, 1♂, Mazarredo leg. (CCP 3624); Algeciras (N: 36°08’, W: 5°26’), 1♀, C. Prieto leg. 8. 1. 2004 (CCP 1966); Parque Natural de Los Alcornocales, Ojen Valley (N: 36°21’, W: 5°32’), 1♀, J. A. Murphy leg. 17. 4. 1974 (BMNH); **United Kingdom**: Gibraltar, Upper Rock, under stone (N: 36°08’, W: 5°20’), 1♀, A. Santona leg. March 1991 (BMNH); **Morocco**: Tanger (N: 35°47’, W: 5°48’), 2♀, Verhoeff leg. (ZMB 11999), Roewer det. *T. gypseus*; Jbel Moussa near Ceuta, under stones (N: 35°54’, W: 5°25’), 1♀, 1juv., H. Franz leg. 27. 3. 1963 (CJM 3743).

DOUBTFULL RECORDS: Algeria: Grande Kabylie, Yakouren, 730 m (N: 36°44’, E: 4°25’), 1juv., C. Besuchet & I. Löbl & D. H. Burckhardt leg. 12. 5. 1988 (MHNG); 1Ex, Abdul Kerim leg. (Museo di Milano, TROSSARELLI 1934, not examined); Gardaïa (N: 32°29’, E: 3°40’), Martin leg. (record from Simon’s collection book, MNHP 14288, not examined).

MATERIAL NOT EXAMINED: Spain: Prov. Cádiz, Sierra de la Luna, between Algeciras and Tarifa, 300 m (N: 36°4’ W: 5°31’), several ♂, and ♀, Rambla leg. 10. 2. 1957 (CMR 371–380).

DIAGNOSIS: A medium-sized to large *Trogulus* with a broad median furrow on prosoma, bordered by densely papillated ridges. Opisthosoma egg-shaped in ventral view.

DESCRIPTION: The description is based on the female holotype supplemented by the most similar population from Albergaria. Variability among specimens from Gibraltar (G) and Alicante (Alic) is outlined (see this chapter, Remarks).

BODY: Ventral scute egg-shaped (Fig. 5.19*c, f, i*). Median furrow on prosoma without papillae (Fig. 5.19*b, e, h*), well defined by densely papillated ridges (in most specimens); opisthosoma and caudal part of prosoma with widely spaced and irregular papillation, rarely forming a faint pattern; median ridge on opisthosoma densely papillated (Fig. 5.19*a, d, g*);

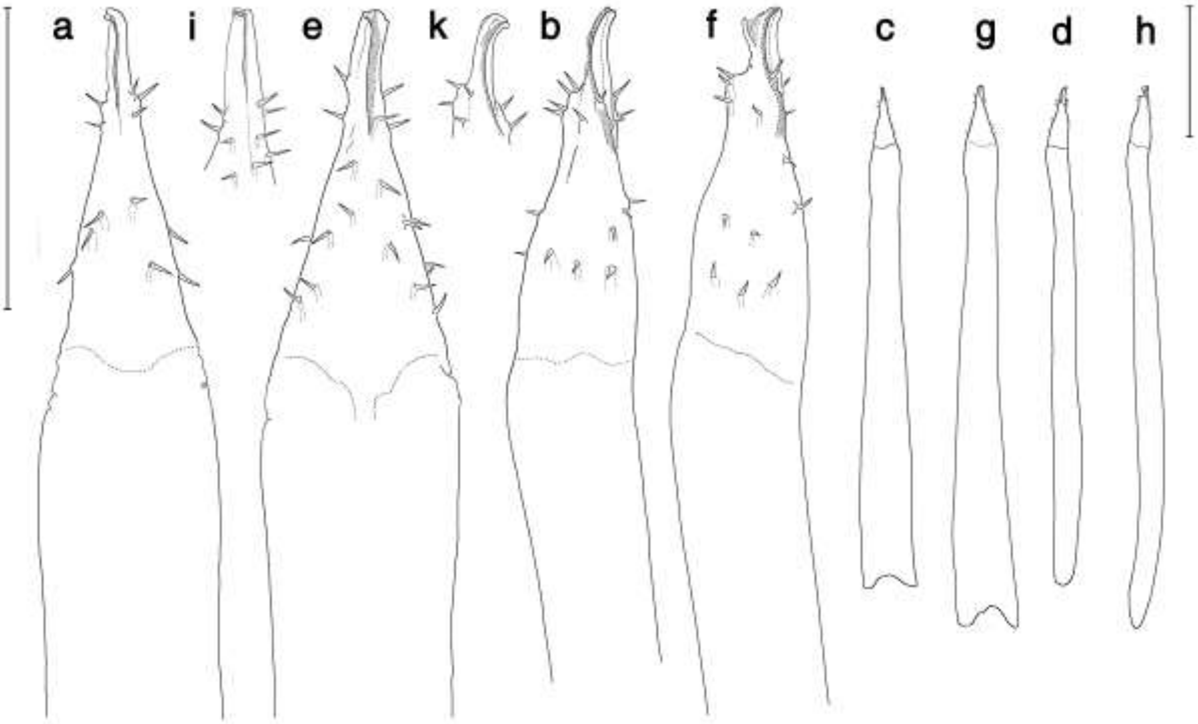


Fig. 5.18. Penes of *Trogulus prietoi* sp. nov., Spain: Andalusia. (*a–d*) Holotype, Prov. Málaga, south of Villanueva de la Concepcion, CJM 5321; (*e, h*) paratype, Prov. Jaen, Valdepeñas de Jaén, Sierra de la Pandera, CCP 1937; (*i*), paratype, Prov. Málaga, Nerja, CJM 2733; (*k*) paratype, Prov. Almería, Sima de Alain, Berja, CCP 1953. (*a, b, e, f*) Glans and distal part of truncus; (*c, d, g, h*) penis; (*i, k*) penial stylus; (*a, c, e, g, i*) dorsal view; (*b, d, f, h, k*) lateral view. Scale line on the left 0.2 mm (*a, b, e, f, i, k*), on the right 0.5 mm (*c, d, g, h*).

dorsal and transverse ridges prominent; rear end of opisthosoma smooth or only faintly notched. G (Fig. 5.19d–f): opisthosomal ridges most prominent, hind end of opisthosomal plate bent dorsally, thereby strongly separating sixth abdominal segment. Alic (Fig. 5.19k–l): with regularly spaced papillae on opisthosoma, medial and transversal ridges not prominent.

EYE MOUND AND FRONT CAP: Eye mound moderately elevated (Fig. 5.19*b*, *e*, *h*), eyes large, eyes separated by a shallow depression, front cap circular, pointing downwards in lateral view. Alic (Fig. 5.19*l*) and G (Fig. 5.19*e*): eye mound broad and high, eyes separated by a broad but shallow depression without papillae.

LEGS AND PEDIPALPI: Femur II smooth, without crest of elongated papillae; considerable variability in length of legs, especially tarsus and metatarsus II (Fig. 5.20*b*, *e*, *h*, *l*); apophyses on metatarsus III and IV indistinct (Fig. 5.20*c*, *f*, *i*, *m*); hairs on pedipalpi on elevated basis but less prominent than in *T. coriziformis* (Fig. 5.20*a*, *d*, *g*, *k*). Alic: legs long and slender, segments of tarsus II nearly equal in length (Fig. 5.20*l*), apophyses on astragalus of metatarsus III an IV broad and prominent.

PENIS MORPHOLOGY: Based on the Albergarian population (Fig. 5.21*a*–*h*): truncus long and slender (lateral view), gradually narrowing to the glans; glans elongated and triangular, gradually narrowing into the broad stylus, only some hairs on prominent papillae indicating intersection from glans to stylus; stylus diverging into two gradually bent and broadly overlapping hyaline lamellae, stylus slightly bent dorso-laterally in distal third, in mid section slightly bent to the opposite direction (dorsal view) thereby distal end of glans with stylus S-bent. Males from Gibraltar area are similar (Fig. 5.21*i*–*m*), despite one differing male (NHMP 24831, Fig. 5.21*n*–*q*). This is most likely to be a composite series and the male illustrated not to originate from the Gibraltar population: Truncus more wedge-shaped, slightly constricted at distal third and slightly inflated below glans; glans shorter and inflated and not elongated (lateral view), intersection to stylus marked with a bump; lamellae in dorsal view straight and not curved.

MEASUREMENTS: Due to the heterogeneity of the material several datasets are provided. Data for the holotype is indicated (H), the population from Albergaria (A), specimens from Gibraltar and the western range as rest are summarised (R) and annotated where the female from Alicante (Alic) exceeds the measurements of R. **Body length**: H: 12.2; A: ♂ (*n* = 115) 9.3–11.0; ♀ (*n* = 88) 10.5–12.5; R: ♂ (*n* = 5) 10.65–12.1; ♀ (*n* = 14) 10.9–14.6; **body width**: H: 5.0; A: ♂ (*n* = 10) 3.8–4.6; ♀ (*n* = 10) 4.5–4.9; R: ♂ 4.15–4.85; ♀ 4.4–6.1; **coxa II interdistance**: H: 4.9; A: ♂ 4.25–4.6; ♀ 4.35–4.8; R: ♂ 4.55–4.9; ♀ 4.5–5.5; **coxa IV**

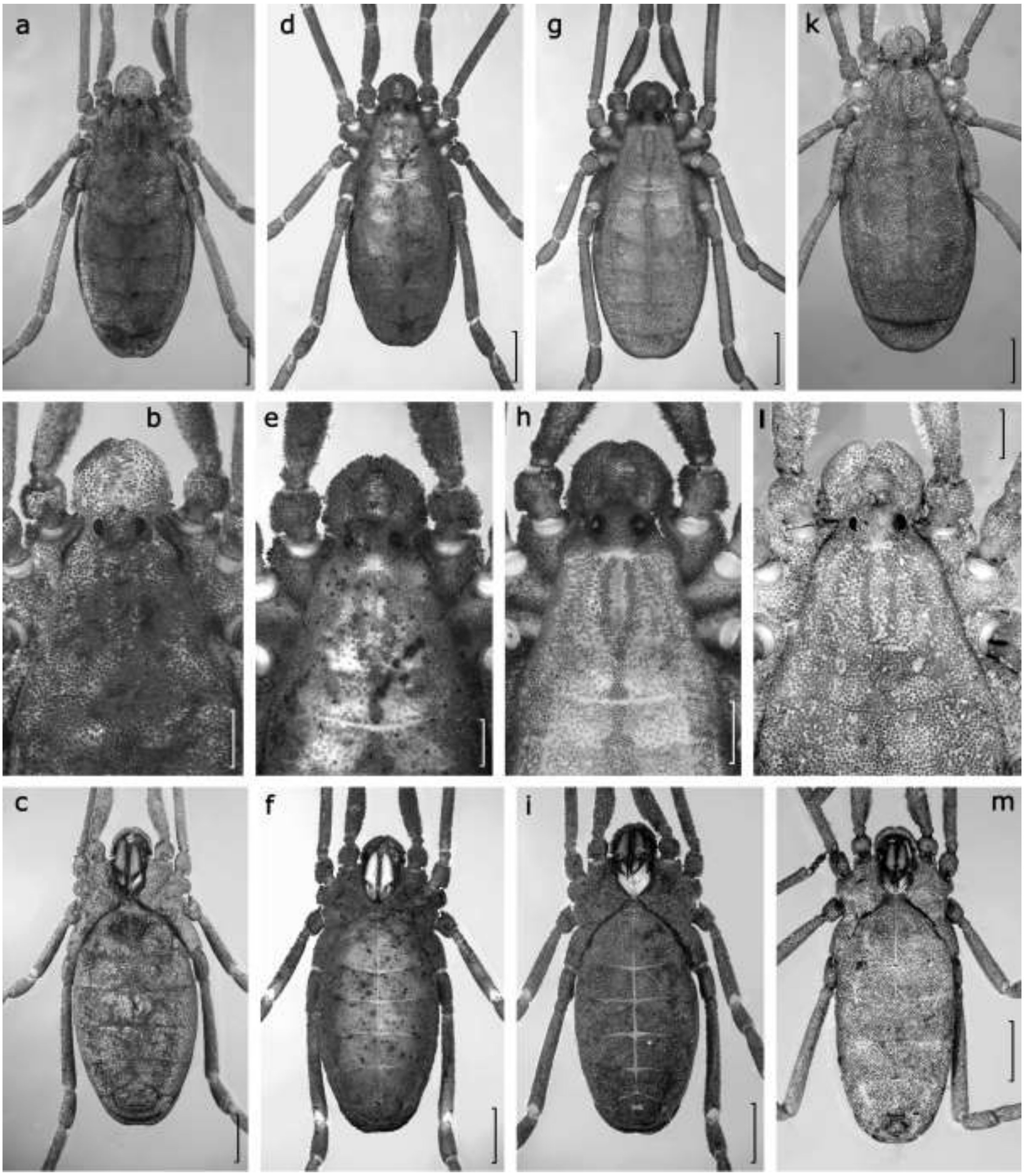


Fig. 5.19. Body of *Trogulus lusitanicus* agg. and *T. huberi* sp. nov., dorsal and ventral view. (*a–c*) *T. lusitanicus* Giltay, holotype, ♀ Portugal, Lisboa, Cintra, BRINS; (*d–l*) *T. lusitanicus* agg; (*d–f*) ♂, Spain, Prov. Cádiz, Jerez, NHMP 2197; (*g–i*) ♂, Portugal, Braga, Albergaria, ZMC; (*k*, *l*) ♀ Spain, Alicante, Vall d'Ebo, CCP 947; (*m*) *T. huberi* sp. nov., Portugal, Algarve, Alte, CJM 5344. Upper and bottom row, scale lines 2.0 mm, median row 1.0 mm.

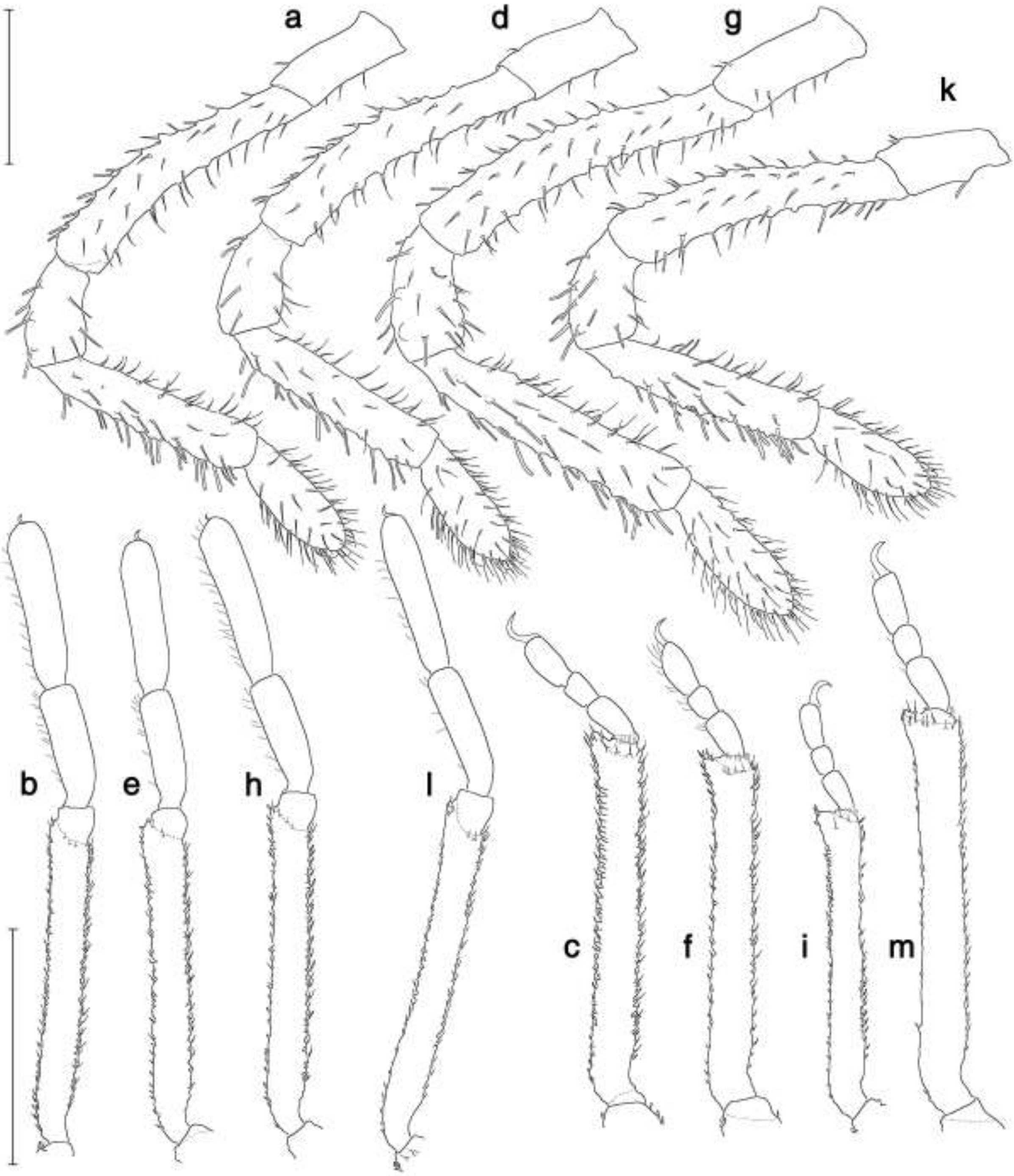


Fig. 5.20. Pedipalps and distal parts of legs of *Trogulus lusitanicus* agg., ♂. (*a–c*) Portugal, Braga, Peneda-Gerês National Park, Albergaria, ZMC; (*d–f*) same locality, different male; (*g–i*) Spain, Prov. Cádiz, Tarifa, Algeciras, MNHP24831; (*k–l*) Spain, Prov. Cádiz, Jerez,MNHP2197. (*a*, *d*, *g*, *k*) Right pedipalpus; (*b*, *e*, *h*, *l*) metatarsus and tarsus II; (*c*, *f*, *i*, *m*) metatarsus and tarsus IV; all medial view. Upper left, scale line 0.5 mm (*a, d, g, k*), bottom left 2.0 mm (*b–c, e, f, h, i, l, m*).

interdistance: H: 5.5; A: ♂ 4.6–4.9; ♀ 4.8–5.3; R: ♂ 4.8–5.5; ♀ 4.8–6.5; **width at coxa II**: H: 4.85; A: ♂ 4.25–4.7; ♀ 4.35–4.9; R: ♂ 4.6–4.9; ♀ 4.5–5.5; **width of body at shoulder**: H: 1.9; A: ♂ 1.65–1.83; ♀ 1.9–1.95; R: ♂ 1.75–1.98; ♀ 1.8–2.38; **eye interdistance**: H: 0.9; A: ♂ 0.79–0.92; ♀ 0.84–0.99; R: ♂ 0.84–0.94; ♀ 0.84–0.99; Alic: 1.08; **interocular distance**: H: 0.65; A: ♂ 0.56–0.76; ♀ 0.63–0.7; R: ♂ 0.65–0.69; ♀ 0.58–0.85; Alic: 0.88; **length of head cap**: H: 1.4; A: ♂ 1.25–1.43; ♀ 1.15–1.4; R: ♂ 1.23–1.45; ♀ 1.13–1.53; Alic: 1.55; **width of head cap**: H: 1.08; A: ♂ 1.25–1.5; ♀ 1.33–1.55; R: ♂ 1.35–1.55; ♀ 1.08–1.63; Alic: 1.78; **length of leg II**: H: 15.1; A: ♂ 13.3–14.7; ♀ 13.7–14.95; R: ♂ 14.5–15.45; ♀ 13.2–16.1; Alic: 19.0; **length of metatarsus II**: H: 3.15; A: ♂ 2.68–2.93; ♀ 2.7–3.1; R: ♂ 2.9–3.3; ♀ 2.8–3.6; Alic: 4.0; **length of femur II**: H: 4.65; A: ♂ 3.95–4.4; ♀ 4.0–4.55; R: ♂ 4.35–4.8; ♀ 4.05–5.1; Alic: 5.8; **length of femur I**: H: 2.73; A: ♂ 2.38–2.68; ♀ 2.5–2.78; R: ♂ 2.55–2.88; ♀ 2.5–2.93; Alic: 3.4; **length of tarsus IV**: H: 1.25; A: ♂ 1.08–1.15; ♀ 1.1–1.2; R: ♂ 1.1–1.2; ♀ 1.1–1.25; Alic: 1.3; **length of metatarsus IV**: H: 3.44; A: ♂ 2.83–3.2; ♀ 2.9–3.28; R: ♂ 3.15–3.38; ♀ 2.93–3.58; Alic: 3.95 **length of penis**: A: 2.25–2.84; R: 2.55–2.91; **length of basal segment of tarsus II**: H: 1.13; A: ♂ 0.95–1.1; ♀ 0.93–1.06; R: ♂ 1.03–1.05; ♀ 0.83–1.13; Alic: 1.43; **length of distal segment of tarsus II**: H: 1.4; A: ♂1.25–1.43; ♀ 1.2–1.35; R: ♂ 1.18–1.43; ♀ 1.09–1.43; Alic: 1.53; **ratio of length of distal to basal segment of tarsus II**: H: 1.24; A: ♂ 1.21–1.42; ♀ 1.17–1.43; R: ♂ 1.12–1.39; ♀ 1.10–1.39; Alic: 1.07; **length of leg II/Body length**: H: 1.24; A: ♂1.33–1.41; ♀ 1.18–1.27;R: ♂1.27–1.36; ♀ 1.10–1.27; Alic: 1.34. It is obvious that the female from Alicante differs in more than one aspect from all other specimens assigned to *T. lusitanicus* here. The canonical discriminant analysis (Fig. 5.14) places it as clearly distinct.

VARIABILITY: High, most probably due to the presence of as yet unrecognised cryptic species.

DISTRIBUTION: The distribution of this species is divided into three sections along the western and southern coast of the Iberian Peninsula (Fig. 5.1). Most localities are in close to the coast, only in northern Portugal do records extend as far as 200 km inland (Freixo de Espada). The three sections are: *i*, north-western Spain (Pobla de Segur) and northern Portugal (Albergaria, Freixo de Espada) to southern Portugal (Sintra), with large gaps in-between, probably due to low sampling activity; *ii*, a small region close to the Strait of Gibraltar, including the area south of a line from Jerez to Gibraltar and few records from Morocco (Tanger, Ceuta, further records along the north-western African coast remain unconfirmed); *iii*, two isolated records are from Alicante.

ECOLOGY: CARDOSO *et al.* (in press) specified xerotherme forest communities with *Pinus* and *Castanea* at 600–700 m as habitat for the Albergaria population where *T. lusitanicus* was abundant. Other records alongside the coast are geographically associated with low altitudes, so the species is probably present from sea level.

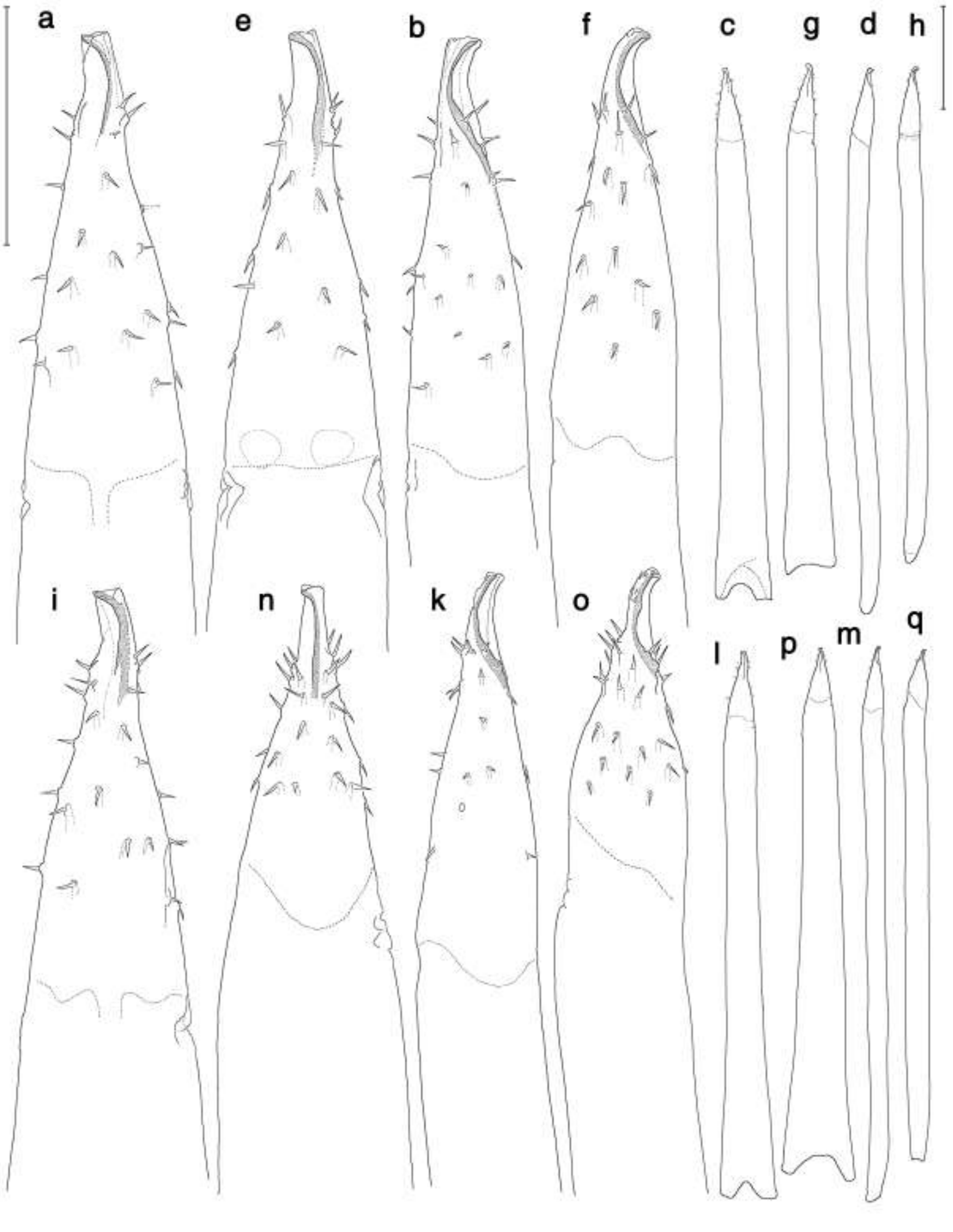


Fig. 5.21. Penes of *Trogulus lusitanicus* agg. (*a*–*d*) Portugal, Braga, Peneda-Gerês National Park, Albergaria, ZMC; (*e*–*h*) same locality, different male; (*i*–*m*) Spain, Prov. Cádiz, Jerez, MNHP 2197; (*n*–*q*) Spain, Prov. Cádiz, Tarifa, Algeciras, MNHP 24831. (*a*, *b*, *e*, *f*, *i*–*k*, *n*, *o*) Glans and distal part of truncus; (*c*, *d*, *g*, *h*, *l*, *m*, *p*, *q*) penis; (*a*, *c*, *e*, *g*, *i*, *l*, *n*, *p*) dorsal view; (*b*, *d*, *f*, *h*, *k*,*m*, *o*, *q*) lateral view. Upper left, scale line 0.2 mm(*a*, *b*, *e*, *f*, *i*, *n*, *k*, *o*), upper right 0.5 mm (*c*, *d*, *g*, *h*, *l*, *m*, *p*, *q*).

REMARKS: The taxonomy of this ‘species’ is difficult and still unresolved. Genetic data indicate that more than one taxon is concerned. Two populations formerly synonymised within *T. lusitanicus* are morphologically so different from the female holotype that they are assigned species rank (*T. huberi* and *T. prietoi* sp. nov.). For the remaining three populations it was not possible to separate them from *T. lusitanicus* by morphology alone. Genetic data revealed large genetic distances between specimens from northern Portugal (Albergaria, ZMC) and southern Spain (near Gibraltar) but the latter material apparently contained mixed material of questionable origin (Collection Simon, NHMP, Fig. 5.21*n–q*). Only females were available for sequencing. For the morphologically outstanding population from Alicante, in southwestern Spain only one female was available. Due to the paucity of material, this study therefore refrains from erecting another species.

Trogulus prietoi sp. nov.

(Figs. 5.15*e–h*, 5.16*g–m*, 5.18)

Trogulus aquaticus RAMBLA 1960: 5–6 (in part).

Trogulus coriziformis (all in part); DAHL 1903: 286–287. – ROEWER 1923: 639; ROEWER 1925: 177; MELLO-LEITÃO 1936: 6; KRAUS 1959: 294; MARCELLINO 1982: 41, 43, fig. 2; PRIETO 2003: 135.

MATERIAL EXAMINED: HOLOTYPE: **Spain, Andalucía:** Prov. Málaga, ruin 6 km S of Villanueva de la Concepcion (N: 36,873, W: 4,513), 1♂, J. Spelda ded., leg. 15. 3. 2004 (CJM 5321).

PARATYPES: **Spain, Andalucía:** 1♂, Staudinger leg. (ZMB 1007, cited by DAHL 1903, ROEWER 1923, 1925, MELLO-LEITÃO 1936); **Prov. Almería:** Berja, Sima de Alain (N: 36°51’, W: 2°56’), 1♂, C. Prieto leg. 31. 7. 2004 (CCP 1953); **Prov. Cádiz**: Parque Natural de la Sierra de Grazalema, Sierra del Pinar, El Bosque (N: 36°45’, W: 5°29’), 1♀, H. Paulus leg. 17. 3. 1980 (CJM 3068); **Prov. Jaén**: Sierra de Cazorla, Los Rajez, dry stoney hillside with occasional pines (N: 37°54’, W: 3°24’), 2♂, 12. 9. 1982 (BMNH); Bedmar (N: 37°49’, W: 3°24’), 1♀, leg 18. 2. 2003 (CCP 1936); Valdepeñas de Jaén, Sierra de la Pandera (N: 37°35’, W: 3°49’), 2♂, 2♀, C. Prieto leg. 6. 4. 2003 (CCP 1937); Parque Natural de Cazorla, Cazorla, sieving near waterfall (N: 37°54’, W: 3°24’), 2juv., H. Franz leg. 11. 4. 1959 (SMF 11121, in KRAUS 1959: 294); **Prov. Málaga:** E Málaga, Nerja (N: 36°45’, W: 3°52’), 1♂, J. Scheuern leg. 19. – 30. 4. 1987 (CJM 2733); **Prov. Sevilla:** Constantina: C. Fuenfría (N: 37°52’, W: 5°37’), 1♀, leg. 21. 2. 2004 (CCP 1923).

Diagnosis: A medium-sized *Trogulus*, the smallest on the southern Iberian Peninsula. Prosoma and opisthosoma dorsal with regular papillation. Truncus penis inflated below glans penis; glans penis slender and triangular. Restricted to Andalusia.

Description

Body: Opisthosoma with regularly spaced papillae in dorsal view (Fig. 5.15*e*, *g*), median and transverse ridges prominently elevated, no changes in papillation density. Median furrow on prosoma indistinct (Fig. 5.15*f*, *h*).

Eye mound and front cap: Front cap broad and shovel-shaped (Fig. 5.15*f*, *h*), widest at distal third, pointing downwards in lateral view.

Legs and pedipalpi: Legs short (Fig. 5.16*h*, *l*), distal end of femur IV surpasses suture of last abdominal segments; without crest of elongated papillae on femur II, apophyses on astragalus of metatarsus III and IV broad and prominent (Fig. 5.16*i*, *m*), median segment of tarsus IV longer than high, distal end of astragalus slightly inflated, accentuating the intersection to the calcaneus; pedipalpi smooth, without prominent papillae (Fig. 5.16*g*, *k*).

Penis morphology: Truncus cuneiform (Fig. 5.18*c*, *d*, *g*, *h*), gradually narrowing from base but markedly inflated below glans penis (dorsal view, Fig. 5.18*a*, *c*, *e*, *g*); glans penis slender and triangular in dorsal view (Fig. 5.18*a*, *e*), bulbous in lateral view (Fig. 5.18*b*, *f*), intersection from glans to stylus with a distinct and prominent bump; stylus variable, narrow to rather broad, straight to laterally bent, tip rounded or divided, slightly hooked or with

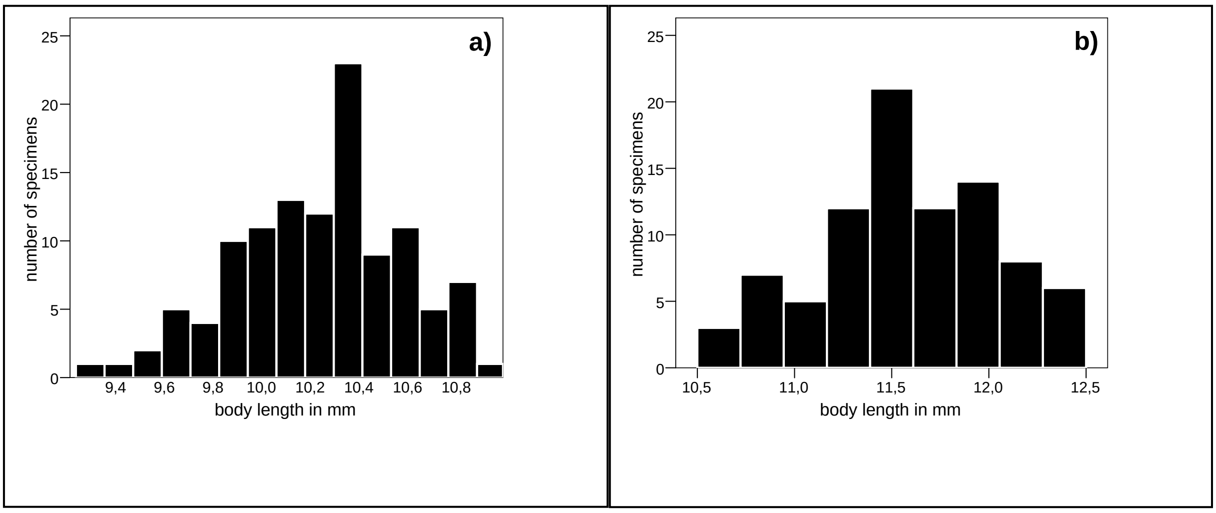


Fig. 5.22. Size distribution in (*a*) males and (*b*) females of *Trogulus lusitanicus* agg. from the Albergaria population, northern Portugal.

an additional lateral lamella (Fig. 5.18*a*, *b*, *e*, *f*, *i*, *k*).

MEASUREMENTS: **Body length**: ♂ (*n* = 7) 8.2–9.3; ♀ (*n* = 5) 8.6–9.85; **body width**: ♂ 3.1–3.65; ♀ 3.5–3.8; **coxa II interdistance**: ♂ 3.2–3.55; ♀ 3.35–3.75; **coxa IV interdistance**: ♂ 3.5–4.05; ♀ 3.8–4.2; **width at coxa II**: ♂ 3.2–3.55; ♀ 3.35–3.75; **width of body at shoulder**: ♂ 1.2–1.4; ♀ 1.4–1.5; **eye interdistance**: ♂ 0.36–0.54; ♀ 0.39–0.49; **interocular distance**: ♂ 0.36–0.54; ♀ 0.39–0.49; **length of head cap**: ♂ 0.86–1.0; ♀ 0.88–1.03; **width of head cap**: ♂ 1.0–1.1; ♀ 1.03–1.18; **length of leg II**: ♂ 10.4–13.95; ♀ 11.2–12.5; **length of metatarsus II**: ♂ 2.08–2.83; ♀ 2.33–2.8; **length of femur II**: ♂ 3.15–4.1; ♀ 3.3–3.9; **length of femur I**: ♂ 1.8–2.23; ♀ 1.88–2.15; **length of tarsus IV**: ♂ 0.71–0.93; ♀ 0.81–0.9; **length of metatarsus IV**: ♂ 2.03–2.63; ♀ 2.2–2.56; **length of penis**: 1.98–2.48; **length of basal segment of tarsus II**: ♂ 0.65–1.1; ♀ 0.9–1.2; **length of distal segment of tarsus II**: ♂ 0.9–1.2; ♀ 1.06–1.1; **ratio of length of distal to basal segment of tarsus II**: ♂: (1.09) 1.27–1.5; ♀ 1.29–1.46; **length of leg II/Body length**: ♂: 1.24–1.5; ♀ 1.22–1.30. See also *T. pyrenaicus* sp. nov.

VARIABILITY: Body size variable. The male from Sima de Alain has a large body size (9.3 mm) coupled with small ratio of length of distal to basal segment of tarsus II (1.09). A male of similar body size (Nerja, 9.25 mm) has the second smallest ratio of length of distal to basal segment of tarsus II (1.27). Maybe this character follows allometric growth within this species.

DISTRIBUTION: This species is restricted to Andalusia in southern Spain (Fig. 5.1). Records are from an approximately 130 km wide coastal belt from Berja–Los Rajez in the east to Sierra del Pinar–Constantina in the west. This species possibly has a wider distribution and is sympatric with *T. lusitanicus* agg. at its western limit.

ECOLOGY: The collection labels cite ‘dry stony hillsides’ or ‘near waterfall’. This may point to a broad ecological spectrum, but no further data available. No indication is available of the vertical distribution of this species.

REMARKS: Cyt*b* analysis suggests there may be a close relationship between *T. prietoi* and *T. lusitanicus* agg. *T. huberi* is sister to both. *Trogulus prietoi* does not display a distinct diverging lamella at the distal tip of the penial stylus as is the case in these related species (Fig. 5.18). This structure was found to be present, but it is minute in at least half of the specimens investigated (e.g. Fig. 5.18*i*) and strongly reduced in another individual (Fig. 5.18*f*). As the stylus structures are generally variable within this species (Fig. 5.18*a*, *b*, *e*, *f*, *i*–*k*) the partial loss of the second lamella may represent an autapomorphy.

ETYMOLOGY: The name honours my Spanish colleague, the arachnologist Carlos Prieto, who presented us with most of the specimens of this new taxon for this investigation.

***Trogulus pyrenaicus* sp. nov.**

(Figs. 5.15*c*, *d*, 5.16*d–f*, 5.17*e–h*)

Trogulus coriziformis (all in part) MARTENS 1978: 175. – MARCELLINO 1982: 41, 43, fig. 2.

MATERIAL EXAMINED: HOLOTYPE: **Spain, Aragón, Prov. Huesca**: Pyrenees, Parque Nacional de Ordesa-Monte Perdido, Monte Perdido, Torla, beech forest, 1000 m (N: 42°38', W: 0°06'), 1♂, J. Niethammer leg. 29. 5. 1972 (CJM 1360).

PARATYPES: **France, Pyrenees, Haute-Garonne:** SW St. Gaudens, Bas Nistos, surroundings of Grotte de l´Eglise, 560 m (N: 43°01', E: 0°56'), 1♀, J. Martens leg. 21. 8. 1978 (CJM 1694); **Spain**, **Aragón, Prov. Huesca:** Bielsa, Embalse de Pineta, 1300 m (N: 42°37', E: 0°13'), 1♀, C. Prieto leg. 25. 9. 1987 (CCP 732); Pueyo de Jaca, 1100 m (N: 42°43', W: 0°17'), 2♀, leg. 8. 8. 1985 (CCP 561); same data as holotype: 1♀ (CJM 1360).

DIAGNOSIS: Medium-sized to large *Trogulus* with regular dorsal papillation. Body compact, legs slender, head cap large and elongated. Glans penis bulbous without a bump at intersection to stylus. Restricted to the central Pyrenees.

DESCRIPTION

BODY: Dorsal median ridge on prosoma faintly indicated by few missing papillae (Fig. 5.15*d*), dorsal papillation otherwise regular, without variation in density (Fig. 5.15*c*). Median ridge distinctly elevated, less so transversal ridges but well to be seen without magnification. Hind end of opisthosoma with an indistinct incision.

EYE MOUND AND FRONT CAP: Head cap large and elongated, especially when compared to body length (Fig. 5.15*c*, *d*); head cap broadest in midsection; interocular distance moderate, eyes about their diameter from lateral border of head cap, eye mound similar to that of *T. prietoi*.

LEGS AND PEDIPALPI: Legs long and slender, well to be seen at femur II and IV and tibia II and IV (Fig. 5.16*e*, *f*); distal end of femur IV surpassing dorsal suture between last opisthosomal segments when stretched backwards; a ridge of elongated papillae on basal part of femur II, apophyses on astragalus of metatarsus III and IV small (like in *T. coriziformis*); dorsal hairs on pedipalpi on slightly elevated bases (Fig. 5.16*d*).

PENIS MORPHOLOGY: Truncus cuneiform, slightly constricted in distal third (Fig. 5.17*g*, *h*), gradually narrowing to glans; glans penis short (Fig. 5.17*e*, *f*), base bulbous, intersection to stylus without a bump; stylus short and broad, distal end broadly truncated, divided in two lamellae.

MEASUREMENTS: **Body length**: ♂ (*n* = 1) 8.95; ♀ (*n* = 5) 9.5–10.45; **body width**: ♂ 3.6; ♀ 3.9–4.2; **coxa II interdistance**: ♂ 3.9; ♀ 3.95–4.3; **coxa IV interdistance**: ♂ 4.2; ♀ 4.5–4.8; **width at coxa II**: ♂ 3.9; ♀ 3.95–4.3; **width of body at shoulder**: ♂ 1.45; ♀ 1.53–1.8; **eye interdistance**: ♂ 0.45; ♀ 0.49–0.67; **interocular distance**: ♂ 0.45; ♀ 0.49–0.67; **length of head cap**: ♂ 1.2; ♀ 1.13–1.23; **width of head cap**: ♂ 1.18; ♀ 1.23–1.35; **length of leg II**: ♂ 11.6; ♀ 11.6–13.5; **length of metatarsus II**: ♂ 2.58; ♀ 2.38–2.9; **length of femur II**: ♂ 3.7; ♀ 3.7–4.25; **length of femur I**: ♂ 2.18; ♀ 2.03–2.43 m; **length of tarsus IV**: ♂ 1.04; ♀ 0.95–1.11; **length of metatarsus IV**: ♂ 2.68; ♀ 2.5–2.95; **length of penis**: 2.08; **length of basal segment of tarsus II**: ♂ 0.93; ♀ 0.78–1.03; **length of distal segment of tarsus II**: ♂ 1.23; ♀ 1.05–1.23; **ratio of length of distal to basal segment of tarsus II**: ♂ 1.32; ♀ 1.19–1.39; **length of leg II Body length**: ♂ 1.30; ♀ 1.17–1.33. The canonical discriminant analysis (Fig. 5.14) includes body length and coxa II interdistance to classify all specimens of the similar *T. pyrenaicus* and *T. prietoi* correctly. To separate *T. pyrenaicus* from *T. cristatus* the length of leg II, metatarsus II and tarsus IV were included. *Trogulus pyrenaicus* is more slender at the opisthosoma than *T. prietoi* and the legs and tarsal segments are more elongated as in *T. cristatus*.

VARIABILITY: Due to the paucity of material available for study, little is known about variation in this species.

DISTRIBUTION: *Trogulus pyrenaicus* is restricted to the central Pyrenees (Fig. 5.1). It has been reported from France, Prov. Haute-Garonne and Spain, Prov. Huesca.

ECOLOGY: Most records are from mountain valleys. *Fagus* forest is cited on one record. It has been collected from 560–1100 m, although most records are around 1000 m.

REMARKS: Although only one male was available and sequence data are hitherto lacking, genital morphology, morphometrics and geographic separation enable easy differentiation from other members of the species-group. Characters of the penial stylus suggest a relationship with the Iberian taxa of the *T. coriziformis* species-group. A closer relationship with *T. lusitanicus* agg. from northern Portugal (Albergaria) may be apparent from molecular genetics.

In the description of *Metopoctea exarata* SIMON (1879) gave 'Pyrenées' as the type locality (Haute-Garonne, Luchon, sur les bords de la Piqua). The genus *Metopoctea* was synonymised with *Trogulus* by DAHL (1903). The original description of *exarata* also mentions localities on Corsica (Porto-Vecchio, Calvi, Ajaccio). Two juveniles of the type series most probably do indeed belong to *T. aquaticus* owing to their large body size. The other two juveniles may belong to the *T. nepaeformis* species-group that is present in the Pyrenees. While juveniles in *Trogulus* are always difficult to determine, it is suggested to discontinue use of the name *T. exarata*.

A female from Lérida, Spain (Cataluña, Prov. Lleida, Pobla de Segur, border of river Flamisell (N: 42°14', W: 8°52'), 1♀, F. Haas leg. 16.4.1918 det. as *T. coriziformis* (SMF 1784, ROEWER 1925, MARCELLINO 1982)) differs in body size (12.3 mm) and other characteristics from *T. pyrenaicus*. Recollecting males from that locality is recommended to clarify the status of these taxa.

Species of the *T. nepaeformis* species-group are considerably smaller and different in genital morphology. *Trogulus pyrenaicus* is quite similar in body size to *T. cristatus* and *T. prietoi* but different in genital morphology, proportions of the body, head cap and legs, and its distribution.

ETYMOLOGY: The species name refers to its distribution in the Pyrenees.

5.6. Abstract

Within the well researched European fauna of harvestmen, the genus *Trogulus* Latreille exhibits unexpectedly high cryptic diversity. The species' uniform morphology hinders an exclusively morphological approach to their systematics and taxonomy, and a preliminary molecular study estimated the number of species to be three times higher than currently known. The current study focuses on a clearly defined species-group within *Trogulus*, combining molecular (~1700 bp 28S rRNA and the cytochrome *b* gene), distributional, morphometric and morphological data. Relationships are reconstructed using Bayesian inference, maximum parsimony and maximum likelihood and this information is subsequently used to evaluate morphological characters for systematic usability and to identify biogeographical processes leading to speciation events. The *Trogulus coriziformis* species-group is defined and diagnosed and includes eight species. Three species are

redefined: *T. coriziformis* C. L. Koch, 1839, for which a neotype is designated, and *T. aquaticus* Simon, 1879 and *T. cristatus* Simon, 1879 for which lectotypes are designated. Four species are described as new: *T. balearicus* sp. nov. from the Balearic Islands, *T. huberi* sp. nov. from southern Portugal, *T. prietoi* sp. nov. from Andalusia, Spain, and *T. pyrenaicus* sp. nov. from the central Pyrenees. *Trogulus lusitanicus* Giltay, 1931 is used as collective name and probably refers to a composite of species presently difficult to tell apart. *Trogulus salfii* De Lerma, 1948 is proposed as a synonym for *T. coriziformis*. Within *Trogulus*, the molecular genetic data support monophyly and basal placement of the *Trogulus coriziformis* species-group. The species to differ in external morphology (size, papillation of palps, apophyses of legs, pattern of body papillation, morphometric data), 28S and cyt*b* autapomorphies, and to a lesser degree by male genital morphology. The species-group is confined to the western Mediterranean area and its species are allopatrically distributed. Their present distribution corresponds to geological processes in the Miocene and Pliocene indicating that this group of organisms may be of considerable value for further biogeographic studies.

6. Hidden Mediterranean diversity: assessing species taxa by molecular phylogeny within the opilionid family Trogulidae (Arachnida, Opiliones)

6.1. Introduction

For taxa that lack informative morphological characters, molecular genetic data can give insight into lineage diversity and ameliorate the stagnation in revisionary approaches to many difficult-to-access groups. Especially within the European fauna, well researched through centuries of biological investigation, this procedure is especially appealing, and may reveal hitherto undetected new species. In this study molecular genetic data is used to examine the phylogenetics and systematics of the opilionid family Trogulidae Sundevall, 1833, which has long demanded revision on every taxonomic level. Based on a taxon-rich dataset, combining sequence information regarding the nuclear 28S rRNA (28S) and the mitochondrial cytochrome *b* gene (cyt*b*), as well as on expertise acquired from revisions of two species-groups of *Trogulus* (chapter 4, 5), a taxonomic framework for the Trogulidae is presented and supported with morphological and geographical evidence and guidance is given for additional revisions within this delicate group of arthropods. Furthermore, an evaluation of relationships within the superfamily Troguloidea is tried (i.e., Trogulidae, Nemastomatidae and Dicranolasmatidae) within the western palearctic fauna.

6.1.1. Present family-level systematics

According to the most recent phylogenetic studies of the order Opiliones, the family Trogulidae Sundevall, 1833 is positioned within the suborder Dyspnoi Hansen & Sørensen, 1904 (SHULTZ 1998; SHULTZ & REGIER 2001, GIRIBET et al. 2002) as a member of the Troguloidea (SHULTZ 1998, SHULTZ & REGIER 2001). This is in agreement with older evolutionary concepts derived from morphological characters, and this study is based on this concept (Dyspnoi: HANSEN & SØRENSEN 1904, Troguloidea: MARTENS 1976, summary in GRUBER 2007).

Relationship of *Dicranolasma* Sørensen, 1873 to Trogulidae is often discussed, and this genus is traditionally included within the latter due to its bifurcate head cap and soil incrustation of the body. Other authors united *Dicranolasma* with Nemastomatidae Simon, 1872, e.g. because of the presence of complex clavate hairs in juveniles. But this and other characters apparently supporting monophyly have now been identified as symplesiomorphic within the Dyspnoi. Actually, *Dicranolasma* is generally raised to family level and placed at same level as Trogulidae and Nemastomatidae (summary in GRUBER 2007). Placement of *Dicranolasma* as sister to *Trogulus* Latreille, 1802 is suggested by morphological and molecular data (SHULTZ 1998, SHULTZ & REGIER 2001, GIRIBET et al. 2002), but is weakly supported in most analyses. Family status may not be validated upon single representatives of either group. Only a species-rich taxon set comprising all three families may evaluate and support systematic status and relationship of *Dicranolasma*.

6.1.2. Present systematics of Trogulidae

Within Trogulidae the number of tarsal articles (tarsal formula) was the main character used to establish the generic system (ROEWER 1950, ŠILHAVÝ 1967), which was not altered since then. Only when opilionid systematics emerged from the half-century of domination by the views of C. F. Roewer was there a growing demand for reorganisation of his artificial system (summary in BRIGNOLI & RAFFAELI 1978). The most radical account claimed to unite all the trogulid genera within a sole genus *Trogulus* to enable an unbiased approach to systematics (BRIGNOLI & RAFFAELI 1978). But these proclamations remained unacknowledged due to the uncertainties in a reorganisation of the family based upon the few available morphological characters. Consequently, the Roewerian system is still in use today. Acknowledging earlier criticism of Roewer's superficial systematic treatment, molecular data provides an opportunity to realise an unbiased revision and finally to verify morphological characters for use in systematics within Trogulidae.

6.1.3. Species delineation and cryptic diversity

The nominate genus *Trogulus* includes the largest number of species, and they are particularly abundant in Central and Southern Europe. Yet *Trogulus* has never been subject to any serious revision, particularly due to its homogeneous morphology. Species delineations have never been stable, because external morphology usually varies so widely. The revisions of clear-cut species-groups showed that morphological characters alone are inadequate to correctly outline species boundaries and reliably contribute to species systematics (chapter 4 and 5).

Another challenging model group is a complex of the genera *Calathocratus* Simon, 1879, *Platybessobius* Roewer, 1940 and *Trogulocratus* Roewer, 1940 (subsequently referred to as CPT complex), the systematics of which have long been discussed on genus as well as on species level (summary in BRIGNOLI & RAFFAELI 1978). This data set here is more limited than that for *Trogulus,* because species and specimens are rare and difficult to collect. Still far from understanding species boundaries within the CPT complex, we glance at the amount of cryptic diversity, far beyond expectation for the European and Near East fauna.

6.2. Material

Sixty-four samples of Trogulidae, eight of Dicranolasmatidae Simon, 1879 and sixteen of Nemastomatidae were included as ingroup taxa. For hierarchical outgroup rooting two species of the family Ischyropsalididae were used, resulting in a total of ninety samples (Table 6.1). The sample set was chosen for availability of suitable material for genetic study, but includes as many genera, representatives of known and unknown species and morphotypes as possible. Six of the seven Trogulidae genera could be included (fresh material of the monotypic genus *Anarthrotarsus* Šilhavý, 1967 could not be obtained), representing all major lineages. For *Dicranolasma* representatives of the Western and Eastern lineages were included, as well as the morphologically outstanding *D. mladeni* Karaman, 1990. The Nemastomatidae set includes eight genera, which represent nearly all major European lineages.

To illustrate cryptic diversity within Trogulidae, a total of eighty-seven haplotypes were selected from a larger cyt*b* phylogeny (182 of cyt*b* sequences, not shown) according to a threshold of 5% minimum uncorrected p-distance from neighbouring lineages. Evidence that this threshold indicates the possibility of species level is given in chapter 6.4.4. For voucher specimens, their depository and GenBank accession numbers see Table 6.1.

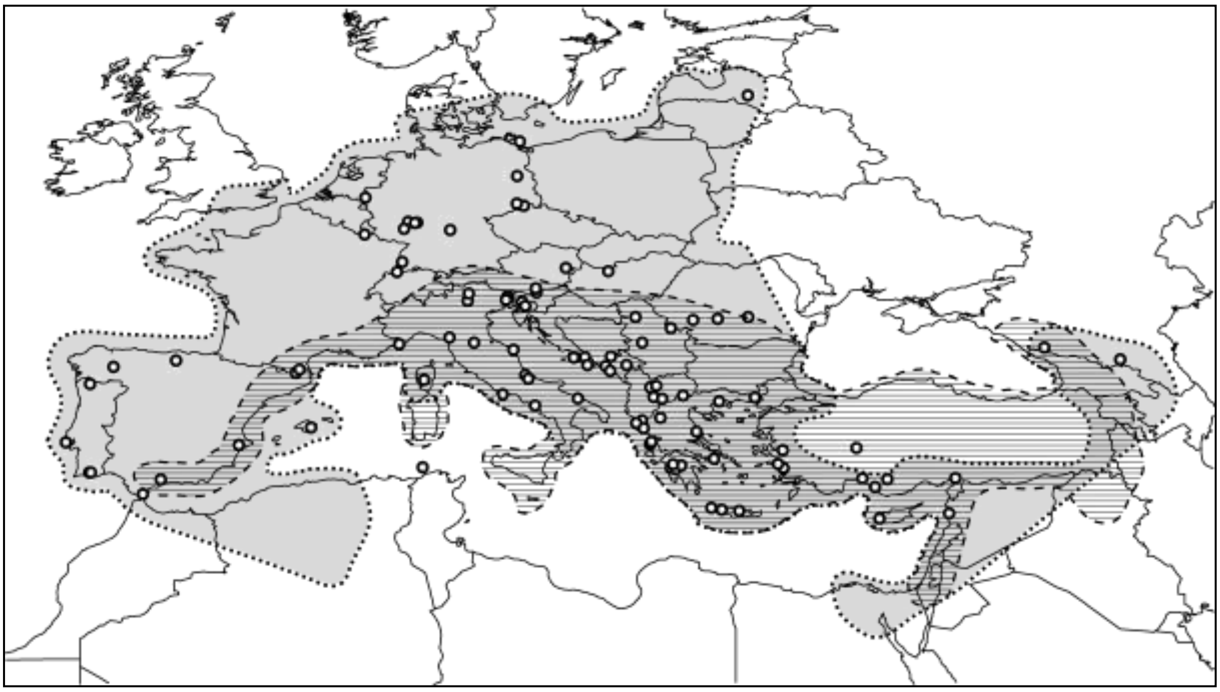


Fig. 6.1. Distribution map showing sampling sites (circles) for all sequenced individuals included in this study. Outlined are main distribution areas of *Trogulus* (dotted line, grey) and *Dicranolasma* (dashed line, horizontal fill).

6.3. Results

The best fit model for both partitions was the GTR+I+G model with the following individual likelihood settings: cyt*b*: empirical base frequencies: $\pi A = 0.3380$, $\pi C = 0.2664$, $\pi G = 0.0316$, $\pi T = 0.3640$; proportion of invariable sites I = 0.2835; Ti/Tv ratio = 3.4373; gamma shape parameter $\alpha = 0.6684$; 28S: empirical base frequencies: $\pi A = 0.1966$, $\pi C = 0.2390$, $\pi G = 0.3256$, $\pi T = 0.2388$; proportion of invariable sites I = 0.4692; Ti/Tv ratio = 5.6369; gamma shape parameter $\alpha = 0.6461$.

The alignment of the cyt*b* partition was 555 bp in length and contained two gaps, resulting from deletion/insertion of 1-2 amino acids. Computation of the complete cyt*b* partition versus a dataset excluding the 3rd position did not change topology nor did it strongly influence bootstrap values. This indicated the restriction of phylogenetic information to the 1st and 2nd codon position and almost complete saturation of the 3rd position on this taxonomic level. The 28S partition alignment was 1165 bp in length and naturally contained a number of gaps, two of which were too variable to align. Computations including and excluding these regions resulted in no conflicting topologies due to the lack of parsimony informative characters. Therefore both data partitions were used untrimmed.

Table 6.1. List of specimen, vouchers, locality information and GenBank accession number for taxa used in this study

Taxon	Voucher	Locality information	Latitude/Longitude	GenBank Accession Nos.	
				28S rRNA	Cyt b
Anelasmocephalus cambridgei (Westwood, 1847)	CJM 3846	Germany: Alzey	N 49.7491/E 7.9602	FJ373245[a]	FJ373241[a]
Anelasmocephalus hadzii Martens, 1978	CJM 4920	Slovenia: Postojna	N 45.7948/E 14.1988	#	#
Calathocratus africanus (Lucas, 1845)	NHMW Tu15	Tunisia: Island Galita	N 37.5167/E 8.9167	_	#
Calathocratus beieri Gruber, 1968	CJM 5738	Turkey: Erzin	N 36.9661/E 36.2602	FJ373246[a]	FJ373243[a]
Carinostoma carinatum (Roewer, 1914)	CJM 4853	Italy: Lusevera, Micottis	N 46.2742/E 13.2836	#	#
Carinostoma elegans (Sørensen, 1894)	CJM 5195	Romania: Gorj, Closani	N 45.0677/E 22.8000	#	#
Dicranolasma cretaeum Gruber, 1998	CJM 5533	Greece: Crete, Agia Irini	N 35.2819/E 25.1651	#	#
Dicranolasma mladeni Karaman, 1990	CJM 4901	Republic of Macedonia: Rostuše, Sveti Jovan Bigorski	N 41.6187/E 20.6096	#	#
Dicranolasma scabrum (Herbst, 1799)	CJM 4928	Romania: Gorj, Closani	N 45.0528/E 22.7746	#	#
Dicranolasma scabrum (Herbst, 1799)	CJM 4123	Slovenia: Breginj	N 46.25/E 13.417	#	#
Dicranolasma soerenseni (Thorell, 1876)	CJM 5001	Italy: Ancona	N 43.5519/E 13.5857	#	#
Dicranolasma soerenseni (Thorell, 1876)	CJM 5056	Italy: Lazio, Monte Circeo	N 41.2468/E 13.0377	#	#
Dicranolasma soerenseni (Thorell, 1876)	CJM 5330	Spain: La Rioja	N 42.3571/E 2.4041	#	#
Dicranolasma sp.	CJM 4160	Greece: Peloponnese, Vitína, Trípoli	N 37.6166/E 22.2	#	#
Histricostoma argenteolunulatum (Canestrini, 1875)	CJM 5254	Italy: Tuscany, Dicomano	N 43.9117/E 11.5616	#	#
Histricostoma dentipalpe (Ausserer, 1867)	CJM 4658	Italy: Tyrol, Montiggler Lake	N 46.4229/E 11.2899	#	#
Histricostoma dentipalpe (Ausserer, 1867)	CJM 4918	Slovenia: Postojna	N 45.7948/E 14.1988	#	#
Ischyropsalis luteipes Simon, 1872	CJM 5336	France: Pyrenees, betw. St.-Marsal and Taulis	N 42.5292/E 2.6111	#	#
Ischyropsalis robusta Simon, 1872	CJM 5474	Portugal: Lisbon, Sintres	N 38.79325/W 9.3928	#	#
Kofiniotis creticus Roewer, 1940	CJM 4997	Greece: Levkada, Frini	N 38.8321/E 20.6666	#	#
Mediostoma vitynae (Roewer, 1927)	CJM 5529	Greece: Crete, Kournas	N 35.3271/E 24.2789	#	#
Mediostoma sp.	CJM 5121	Turkey: Aydin Dilek Dagi Canyon	N 37.6913/E 27.1591	#	#
Mitostoma chrysomelas (Hermann, 1804)	CJM 6108	Germany: Frankfurt am Main	N 50.0677/E 8.6325	#	#
Nemastoma bidentatum Roewer, 1914	CJM 5303	Germany: Saxony, Bad Schandau	N 50.9273/E 14.1218	#	#
Nemastoma bimaculatum (Fabricius, 1775)	CJM 6113	The Netherlands: Limburg, Königslust	N 51.35/E 5.983	#	#
Nemastoma lugubre (Müller, 1776)	CJM 5967	Germany: Greifswalder Oie	N 54.2333/E 13.9166	#	#
Nemastomella hankiewiczii (Kulczynski, 1909)	CJM 5473	Portugal: Algarve, Pena da Rocha, Alte	N 37.2502/W 8.0978	#	#
Paranemastoma quadripunctatum (Perty, 1833)	CJM 6151	Germany: Wiesbaden-Kolheck	N 50.114/E 8.182	#	#
Paranemastoma silli (Herman, 1871)	CJM 4930	Romania: Gorj, Closani	N 45.0528/E 22.7746	#	#
Paranemastoma sp.	CJM 5140	Greece: Corfu, Loutses	N 39.7771/E 19.8903	#	#
Platybessobius caucasicus Šilhavý, 1966	CJM 3044	Russia: Caucasus, Stavropol Prov., Kurdjinov	N 43.67/E 40.83	_	#
Platybessobius singularis Roewer, 1940	CJM 5521	Greece: Crete, Deliana	N 35.4361/E 23.7349	#	#

Taxon	Voucher	Locality information	Latitude/Longitude	GenBank Accession Nos.	
				28S rRNA	Cyt b
Platybessobius cf. *singularis* Roewer, 1940	CJM 5095	Greece: Corfu, Portes	N 39.8020/E 19.8425	_	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 4998	Greece: Levkada, Frini	N 38.8321/E 20.6665	#	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 4189	Greece: Peloponnese, Andrítsaina, Messinia	N 37.4166/E 21.9	_	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 4190	Greece: Peloponnese, Lálas, Ilia	N 37.6666/E 21.7833	#	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 2921	Greece: Thrace, Nomós Rodópi, E Néa Sanda	N 41.1/E 25.9833	_	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 6142	Turkey: Antalya, Kösekbasi	N 36.9/E 32.767	#	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 6145	Turkey: Antalya, Yaylaalan	N 36.943/E 31.499	#	#
Platybessobius cf. *singularis* Roewer, 1940	CJM 5118	Turkey: Izmir Nif Dagi	N 38.3916/E 27.4002	_	FJ373212$_a$
Platybessobius cf. *singularis* Roewer, 1940	CJM 6138	Turkey: Sultandagi, Konya Sultan Dag	N 38.496/E 31.194	#	#
Pyza bosnica (Roewer, 1916)	CJM 5138	Republic of Macedonia: Pelister Mountain, Kopanki	N 41.0333/E 21.2191	#	#
Trogulocratus apenninicus Marcellino, 1965	CJM 3073	Italy: Tuscany, Piazza al Serchio	N 44.1833/E 10.3	_	#
Trogulocratus sinuosus (Soerensen, 1873)	CJM 5090	Italy: Abruzzo, Prov.Chieti, Bomba	N 42.0602/E 14.3457	#	FJ664886$_b$
Trogulocratus sinuosus (Soerensen, 1873)	CJM 5036	Italy: Campania, Prov. Salerno, Cava de Tirreni	N 40.6743/E 14.6987	_	#
Trogulocratus sp.	CCP 3753	Spain: Alicante, Alcoy, Font Rotja, Santuario	N 38.65/W 0.5166	#	#
Trogulus aquaticus Simon, 1879	CJM 3058	France: Corsica	N 42.0/E 9.0	_	FJ373233$_a$
Trogulus balearicus Schönhofer & Martens, 2008	CCP 3616	Spain: Majorca, Manacor, Cova des Pont	N 39.55/E 3.2	FJ373250$_a$	FJ373232$_a$
Trogulus banaticus Avram, 1971	CJM 4927	Romania: Gorj, Closani	N 45.0528/E 22.7746	FJ373249$_a$	FJ373244$_a$
Trogulus banaticus Avram, 1971	CJM 4317	Romania: Prahova, Comarnic	N 45.2333/E 25.6333	_	#
Trogulus banaticus Avram, 1971	CJM 4840	Serbia: Ovcar Banija, Monastere Preobrazenje	N 43.9023/E 20.1961	#	#
Trogulus cf. *cisalpinus* Chemini & Martens, 1988	CJM 4966	Italy: Friuli-Venezia Giulia, Udine	N 46.1042/E 13.1978	#	#
Trogulus closanicus Avram, 1971	CJM 4497	Germany: Feiburg, Gundelfingen	N 48.05/E 7.8666	#	#
Trogulus closanicus Avram, 1971	CJM 4496	Germany: Frankfurt am Main, Kelsterbach	N 50.05/E 8.5166	#	#
Trogulus closanicus Avram, 1971	CJM 4945	Romania: Gorj, Closani	N 45.0676/E 22.8000	FJ373263$_a$	FJ373236$_a$
Trogulus closanicus Avram, 1971	CJM 3826	Slovenia: Runarsko	N 45.7711/E 14.5438	#	#
Trogulus cf. *closanicus* Avram, 1971	CJM 5154	Bosnia and Herzegovina: Gacko, Dramešina	N 43.2/E 18.5833	FJ373251$_a$	FJ373242$_a$
Trogulus coriziformis C. L. Koch, 1839	CJM 5051	Italy: Abruzzo, Prov. Chieti, Fara Filiorum Petri	N 42.2462/E 14.1848	FJ373252$_a$	FJ373222$_a$
Trogulus coriziformis C. L. Koch, 1839	CJM 5009	Italy: Tuscany, Dicomano	N 43.9117/E 11.5616	FJ373253$_a$	FJ373221$_a$
Trogulus cristatus Simon, 1879	CJM 4972	Italy: Liguria, Prov. Imperia, San Remo	N 43.8262/E 7.7230	FJ373254$_a$	FJ373216$_a$
Trogulus falcipenis Komposch, 2000	CJM 4952	Slovenia: Topla, Črna	N 46.4810/E 14.7687	_	FJ664887$_b$
Trogulus graecus Dahl, 1904	CJM 5519	Greece: Athens, Koropion	N 37.95/E 23.8666	_	#
Trogulus graecus Dahl, 1904	CJM 4992	Greece: Levkada, betw. Hortata and Agios Petros	N 38.6992/E 20.5953	_	#
Trogulus graecus Dahl, 1904	CJM 4187	Greece: Peloponnese, Zakháro, Néa Figalía	N 37.4666/E 21.65	_	#

Taxon	Voucher	Locality information	Latitude/Longitude	GenBank Accession Nos.	
				28S rRNA	Cyt b
Trogulus graecus Dahl, 1904	CJM 4875	Greece: Volos	N 39.3514/E 22.9748	_	#
Trogulus graecus Dahl, 1904	CJM 4891	Republic of Macedonia: Kozuf Mountain, Smrdlina voda	N 41.1921/E 22.2815	_	#
Trogulus cf. *graecus* Dahl, 1904	HNHM DL 106	Albania: Delvinë county, Muzinë, Syri i Kaltër	N 39.9246/E 20.1925	#	#
Trogulus cf. *graecus* Dahl, 1904	CJM 5042	Greece: Corfu, Loutses	N 39.7771/E 19.8903	_	#
Trogulus cf. *graecus* Dahl, 1904	CJM 5083	Greece: N Igoumenitsa	N 39.5217/E 20.2691	FJ373255$_{a}$	FJ373223$_{a}$
Trogulus cf. *graecus* Dahl, 1904	CMK Igr	Italy: Valencano, Bari	N 41.0453/E 16.8850	FJ373248$_{a}$	FJ373240$_{a}$
Trogulus gypseus Simon, 1879	CJM 3950	Syria: Qualcat al-Marqab	N 35.15/E 35.95	_	#
Trogulus cf. *gypseus* Simon, 1879	CJM 5520	Greece: Crete, Deliana	N 35.4361/E 23.7349	_	#
Trogulus cf. *gypseus* Simon, 1879	CJM 2840	Greece: Cyprus, Peyia	N 34.88/E 32.38	#	#
Trogulus cf. *gypseus* Simon, 1879	CJM 4478	Turkey: E Alanya	N 36.5026/E 32.1513	FJ373256$_{a}$	FJ373218$_{a}$
Trogulus cf. *gypseus* Simon, 1879	CJM 5103	Turkey: Vilayat Muğla, Bafa-lake, Milas	N 37.4666/E 27.45	#	#
Trogulus hirtus (Dahl, 1904)	CJM 4969	Montenegro: Herceg-Novi, Monastir Savina	N 42.452/E 18.5534	_	FJ664888$_{b}$
Trogulus huberi Schönhofer & Martens, 2008	CJM 5344	Portugal: Algarve, Faro, Alte	N 37.238/W 8.1850	FJ373257$_{a}$	FJ373224$_{a}$
Trogulus karamanorum [man.n]	CJM 3025	Greece: Macedonien, Pindos Mts., Grevena, Smixi	N 40.05/E 21.1166	FJ373258$_{a}$	FJ373215$_{a}$
Trogulus karamanorum [man.n]	CJM 4889	Republic of Macedonia: Gjonovitze Cave near Gostivar	N 41.7011/E 20.9171	#	FJ664890$_{b}$
Trogulus cf. *lusitanicus* Giltay, 1931	ZMC Alb ♂	Portugal: Braga, Peneda-Gerês Nat.-park, Albergaria	N 41.795/W 8.1366	FJ373259$_{a}$	FJ373225$_{a}$
Trogulus cf. *lusitanicus* Giltay, 1931	CCP 1966	Spain: Andalucía, Prov. Cádiz, Algeciras	N 36.1333/W 5.4333	FJ373260$_{a}$	FJ373226$_{a}$
Trogulus martensi Chemini, 1983	CJM 4643	Italy: Prov. Trento, Pérgine Valsugana	N 46.065/E 11.24	#	#
Trogulus martensi Chemini, 1983	CJM 5008	Italy: Tuscany, Dicomano	N 43.9117/E 11.5616	#	#
Trogulus martensi Chemini, 1983	CJM 4690	Switzerland: Basel	N 47.5364/E 7.6025	FJ373261$_{a}$	FJ373213$_{a}$
Trogulus cf. *martensi* Chemini, 1983	CJM 5053	Italy: Abruzzo, Prov. Chieti, Fara Filiorum Petri	N 42.2462/E 14.1848	#	#
Trogulus melitensis [man.n]	CRO 4	Croatia: Dalmatia, Mljet island, Soline, Bjejajka	N 42.7667/E 17.3833	_	FJ664894$_{b}$
Trogulus nepaeformis (Scopoli, 1763)	CRO 16	Croatia: Gorski kotar, V. Kapela Mt., S. Sušica	N 45.3666/E 14.9833	#	#
Trogulus nepaeformis (Scopoli, 1763)	CJM 3852	Serbia: Novi Sad, Sremska Kamenica Glavica	N 45.22/E 19.84	#	#
Trogulus nepaeformis (Scopoli, 1763)	CJM 3832	Slovenia: Idrija	N 46.0027/E 14.0305	FJ373262$_{a}$	FJ373235$_{a}$
Trogulus cf. *nepaeformis* (Scopoli, 1763)	CJM 3834	Austria: Rosaliengebirge, Ramsbachtal	N 47.7461/E 16.2711	#	#
Trogulus cf. *nepaeformis* (Scopoli, 1763)	CEI F23-2	France: Dép. Moselle, Audun-le-Tiche	N 49.4666/E 5.95	#	#
Trogulus cf. *nepaeformis* (Scopoli, 1763)	CCP 3271	Spain: Castilla y León, Prov. Burgos, Pedrosa	N 43.0/W 3.7333	#	#
Trogulus cf. *nepaeformis* (Scopoli, 1763)	CJM 5061	Spain: Prov. León, Vega de Valcarce	N 42.6630/W 6.9491	#	#
Trogulus oltenicus Avram, 1971	CJM 4873	Romania: Vîlcea, Horezu	N 45.1373/E 24.0681	FJ373264$_{a}$	FJ373237$_{a}$

Taxon	Voucher	Locality information	Latitude/Longitude	GenBank Accession Nos.	
				28S rRNA	Cyt b
Trogulus pharensis [man.n]	CJM 5155	Croatia: Hvar, between Plitve and Zavala	N 43.1403/E 16.6738	_	FJ664896[b]
Trogulus prietoi Schönhofer & Martens, 2008	CJM 5321	Spain: Andalucía, Villanueva de la Concepcion	N 36.873/W 4.513	_	FJ373230[a]
Trogulus rossicus Šilhavý, 1968	CJM 3034	Russia: Caucasus, N.Osetia, Fiagdon basin	N 43.05/E 44.73	_	#
Trogulus setosissimus Roewer, 1940	CRO 7	Croatia: Dalmatia, Biokovo Mt., Sv. Jure	N 43.4833/E 16.7000	FJ373265[a]	FJ373238[a]
Trogulus squamatus C. L. Koch, 1839	CJM 4831	Montenegro: Monastery Morača, Morača-Tal	N 42.7646/E 19.3930	FJ373267[a]	FJ373234[a]
Trogulus thaleri [man.n]	CJM 4985	Croatia: Dalmatia, Biokovo Mt., Drvenik	N 43.1586/E 17.2491	#	FJ664898[b]
Trogulus tingiformis C. L. Koch, 1848	CJM 3842	Austria: Völkermarkt, Griffen,	N 46.7055/E 14.7263	#	#
Trogulus tingiformis C. L. Koch, 1848	CJM 4613	Hungary: W Budapest, Tatabanya-Ovaros	N 47.5750/E 18.4576	FJ373268[a]	FJ373219[a]
Trogulus torosus Simon, 1885	CIK 1518	Bosnia and Herzegovina: Trebinje, Matulica pecina	N 42.7086/E 18.3213	FJ373269[a]	FJ373217[a]
Trogulus tricarinatus (Linné, 1767)	CJM 5312	Germany: Saxony, Dresden	N 51.0417/E 13.754	FJ373270[a]	FJ373214[a]
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4824	Germany: Bavaria, Kitzingen	N 49.686/E 10.344	_	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4751	Germany: Berlin, Rüdersdorf	N 52.4720/E 13.7821	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4749	Germany: Saxony, Pirna	N 50.95/E 13.9166	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 5096	Greece: Corfu, Portes	N 39.8020/E 19.8425	#	FJ664900[b]
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 2915	Greece: Macedonien, Nomós Kavala Pangéo	N 40.9/E 24.15	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4810	Latvia: Aizkraukles raj, Stúkmaņi	N 56.6/E 25.6166	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 5246	Republic of Macedonia: Gjonovitze Cave near Gostivar	N 41.7011/E 20.9171	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4971	Republic of Macedonia: Ohrid	N 41.1133/E 20.7884	#	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4899	Republic of Macedonia: Radika valley, Sveti Jovan Bigorski	N 41.6187/E 20.6096	_	#
Trogulus cf. *tricarinatus* (Linné, 1767)	HNHM DL180	Serbia: Golubac, near Danube	N 44.6584/E 21.6625	_	#
Trogulus cf. *tricarinatus* (Linné, 1767)	CJM 4916	Slovenia: Postojna	N 45.7948/E 14.1988	#	#
Trogulus sp.	CRO 14	Croatia: Dalmatia, Dubrovnik, Gromača	N 42.7283/E 18.0153	#	#
Trogulus sp.	CJM 4832	Montenegro: Monastery Morača, Morača-Tal	N 42.7646/E 19.3930	#	#
Trogulus sp.	CJM 4900	Republic of Macedonia: Radika valley, Sveti Jovan Bigorski	N 41.6187/E 20.6096	FJ373266[a]	FJ373220[a]

[a] GenBank accession numbers refer to SCHÖNHOFER & MARTENS 2008 (chapter 5). [b] GenBank accession numbers refer to SCHÖNHOFER & MARTENS in press (chapter 4). “#” indicates sequences were obtained for this chapter but GenBank accession numbers are not yet acquired. “–“ indicate that no sequence was obtained.

The result of the partition homogeneity test just missed the cut-off value to allow combination of 28S and cyt*b* data (P=0.01; a value P>0.01 is not significant [CUNNINGHAM 1997]). Incongruence between 28S and mitochondrial genes is frequently reported without conflicting topologies, when the surveyed taxonomic level does include taxa of different families (e.g., HOU et al. 2007). As the topologies for different genes show no strongly conflicting nodes but differ in resolution and support of comparable taxa, detected incongruence is likely to be caused by the cumulative effect of homoplasy rather than by actual incongruence. Other reasons for erroneously rejecting congruence of combined data partitions are differences in size (DOWTON & AUSTIN 2002), substitution rate, tree topology and evolutionary conditions (DARLU & LECOINTRE 2002), all of which are present in this study system. Therefore the analysis of combined genes proceeded, regarding the fact that combination of loci under different selective pressures will assess evolutionary history more comprehensively for supporting different taxonomic levels.

The combined data set of 28S and cyt*b* includes 1748 bp and comprises 740 parsimony informative sites. The phylogram of the Bayesian analysis strongly supports monophyly of Trogulidae and Nemastomatidae (Fig. 6.2). *Dicranolasma* is included in Trogulidae. Within Trogulidae the genera *Anelasmocephalus*, *Dicranolasma*, *Kofiniotis* and *Trogulus* are strongly supported as monophyletic entities. The genera *Calathocratus*, *Platybessobius* and *Trogulocratus* (CPT complex) were grouped together as monophyletic with a single Turkish *Calathocratus* sequence as sister to the paraphyletic *Platybessobius* and polyphyletic *Trogulocratus* assemblages. High Bayesian support is given for close relationship of the CPT complex and *Trogulus*. Further intergeneric support is low to missing. There is only weak support for a relation of *Anelasmocephalus* and *Kofiniotis*.

The taxon-rich genus *Trogulus* is split into two main lineages covering A) a small group that diversified in the western Mediterranean (*T. coriziformis* species-group, see chapter 5) and B) all remaining taxa which are split into multiple lineages and species-groups, all centred in the eastern Mediterranean. Within the latter group support is low, but several clades are backed by neat geographical circumscription and the structure of male genital morphology (see chapter 6.4.3).

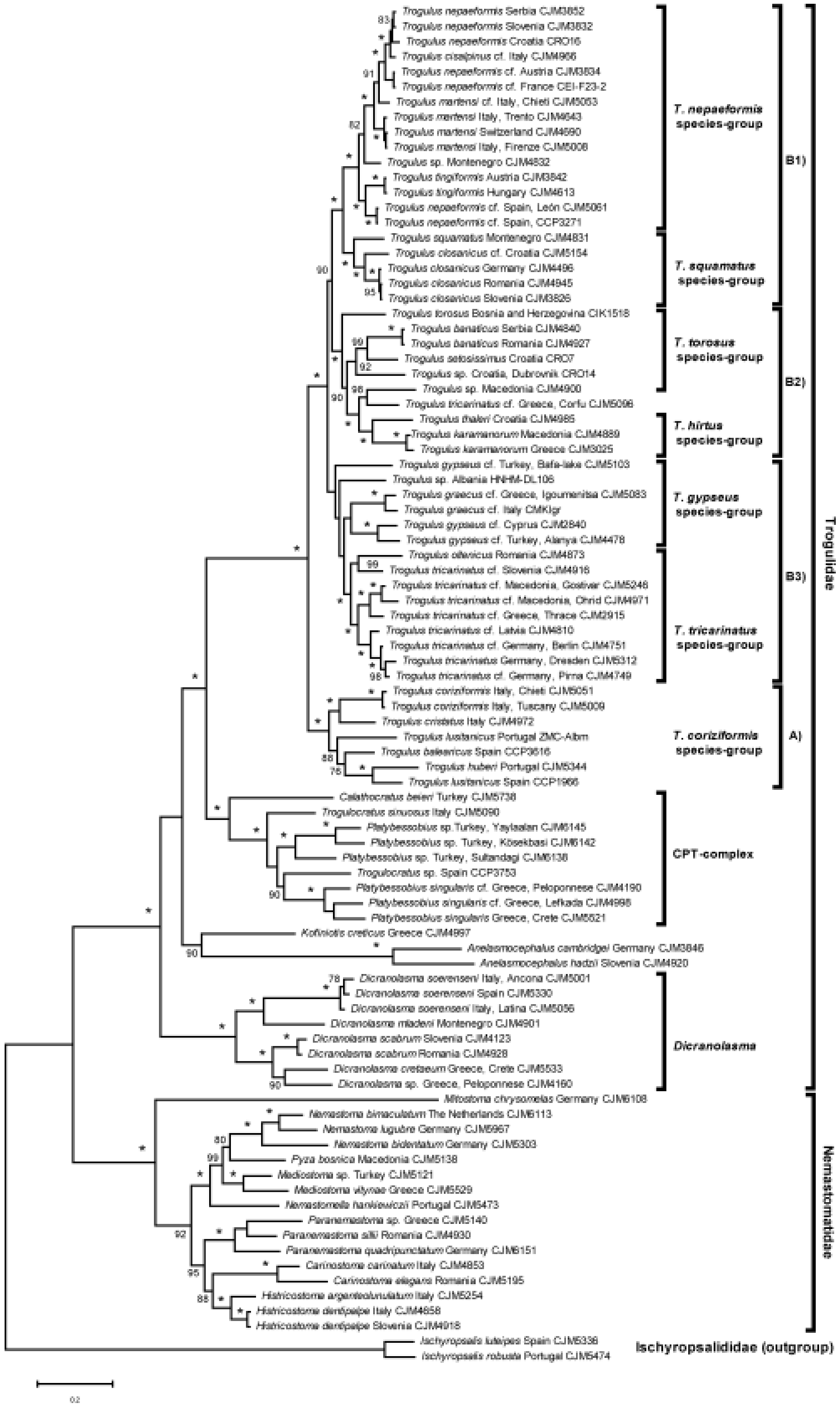


Fig. 6.2. Phylogram of Bayesian analysis combining 28S and cyt*b* data. Bayesian posterior probabilities are indicated at the corresponding nodes, asterisks indicate values of 100, values below 80 are not shown; vertical bars on the right indicate families, genera and species-groups; CPT-complex: genera *Calathocratus, Platybessobius* and *Trogulocratus* (see chapter 6.4, for sequence information see Table 6.1). Depository numbers of voucher specimens are indicated.

The Nemastomatidae are deeply split, showing *Mitostoma* Roewer, 1951 as the sister to all other sequenced members of the family. The latter are further divided into two main groups, which is in accordance with penis morphology. All surveyed genera are clearly backed by molecular data. MP analysis of the combined genes resulted in 56 most parsimonious trees, 6255 steps in length with a consistency index of 0.2267 and a retention index of 0.6541. The bootstrap tree is given in Fig. 6.3. MP shows a tree topology almost identical to the Bayesian analysis but with generally lower bootstrap support. Although genera are supported according to Bayesian values, MP failed to reconstruct any intergeneric relationships. Nemastomatidae are supported with lower values, and only topology backs the clade comprising taxa with bifurcate glans of penis. This is most possibly due to the small taxon set included in this study. As bootstrapping in every case abbreviates the original data and MP does not strongly conflict with Bayesian results, the results of the Bayesian analysis are preferred to be further discussed, especially regarding its consistency with morphological characters and previous sound taxonomic views.

When a threshold of 5% minimum cytb-distance is applied to a data set of 182 of trogulid sequences established for the thesis (not shown), 80 haplotypes are retained, signifying the possibility of a level of cryptic species (Fig. 6.4). This compilation does indicate a large amount of cryptic diversity within the CPT complex, including 17 deeply split lineages presently assignable to 5 valid species-level taxa (3 not included in the analysis). The genus Trogulus, presently encompassing 17 valid species of which 15 are included in the analysis, exhibits 55 species-worthy lineages. According to these data the number of species within the CPT complex rates at least 1.5, within Trogulus 2.4 times higher than known to-date. Results concerning the CPT complex are further presented in Fig. 6.8. Localities are mapped and genetic distances of sequenced individuals are indicated with respect to species and genera concerned. Although the phylogeny shown in Fig. 6.4 reflects most of the previously discussed nodes (Fig. 6.2, 6.3) it was compiled to visualize the amount of cryptic diversity within the Trogulidae.

The cyt*b* gene is not able to resolve early evolutionary events. For example, long-branch attraction is obvious (*Mitostoma*) as well as low bootstrap support in several cases (e.g., Nemastomatidae).

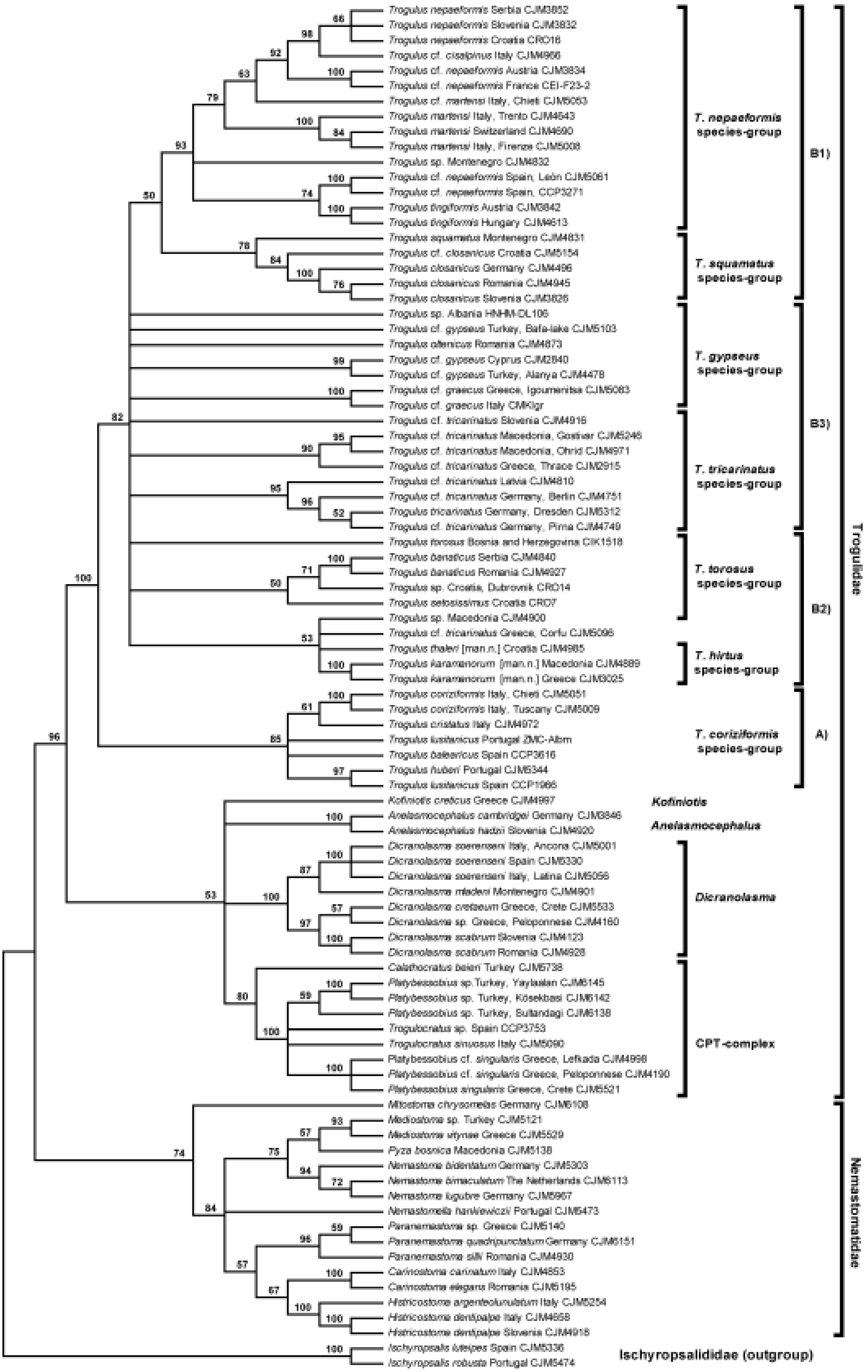


Fig. 6.3. Maximum Parsimony tree combining 28S and cyt*b* data. The tree is condensed, using a cut-off value of 50% bootstrap support. Bootstrap percentages from 1000 iterations are indicated at the according nodes; vertical bars on the right indicate families, genera and species-groups; CPT-complex: genera *Calathocratus*, *Platybessobius* and *Trogulocratus* (see chapter 6.4, for sequence information see Tab. 6.1). Depository numbers of voucher specimens are indicated.

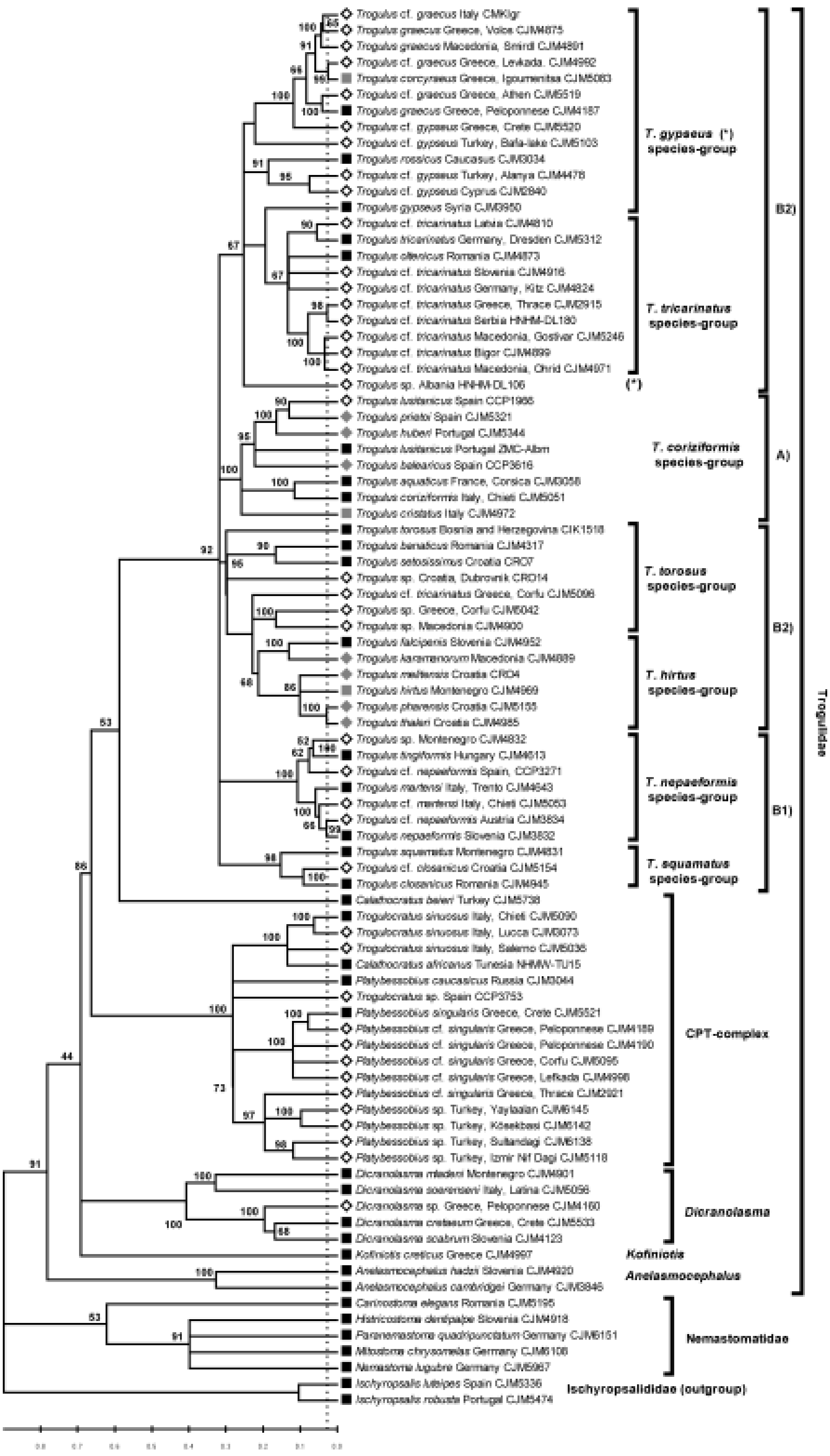


Fig. 6.4. Linearized Neighbor-Joining tree based on cyt*b* sequences representing all haplotypes worthy of species rank. Dotted line indicates 5% sequence distance, assumed here to indicate possible cryptic species level (see chapter 6.4.4 and 6.4.5). Symbols indicate actual taxonomic status of species: black square: valid species; grey squares: formerly synonymised but valid species; grey rhombi: recently described species (see chapter 4, 5); empty rhombi: species awaiting formal description. Vertical bars on the right indicate families, genera and species-groups; CPT-complex: genera *Calathocratus*, *Platybessobius* and *Trogulocratus* (see chapter 6.4; for sequence information see Table 6.1). Depository numbers of voucher specimens are indicated.

6.4. Discussion

6.4.1. Taxonomic inference on family level

Dicranolasma is sister to Trogulidae in Fig. 6.2 but a condensation of the Bayesian tree does place it at similar phylogenetic level of other major lineages within Trogulidae (similar to MP, Fig. 6.3) and this does not emphasize its current family status. We suggest including *Dicranolasma* in Trogulidae to support the stability of this genetic cluster as a taxonomic unit of family level. The placement of *Dicranolasma* within Trogulidae is further corroborated by genital morphology, specialized foraging behaviour on molluscs, and the bifurcate head cap (GRUBER 2007). Features like soil-incrustation mimicry (recently also reported for two species of Nemastomatidae from the Caucasus, MARTENS 2006), specialized clavate hairs in juvenile *Dicranolasma* and the overall nemastomatid habitat inferred from elongated legs and rounded body are to be considered symplesiomorphies within the Troguloidea and Dyspnoi (summary in GRUBER 2007).

6.4.2. Trogulidae: Taxonomic inference on genus and subfamily level

Within the Trogulidae, the genera *Anelasmocephalus*, *Dicranolasma*, *Kofiniotis* and *Trogulus* are well supported as monophyletic entities. Their many distinct autapomorphies suggest that they should be readily accepted as morphologically and phylogenetically distinct taxa. However, *Platybessobius* und *Trogulocratus* appear to be para- or polyphyletic and should be summarized under one genus name. As a combined entity they form a monophyletic sister group to the single *Calathocratus* sequence from eastern Turkey available to us (Fig. 6.2, 6.3). This sequence does not cluster with a second cyt*b* sequence of *Calathocratus* (Fig. 6.4) from North Africa/Tunisia and therefore the two are probably unrelated. Consequently, *Calathocratus* appears to be polyphyletic as well. Taking into account that all three genera are para- or polyphyletic and that the type species of *Calathocratus* and *Trogulocratus* have doubtful and unconfirmed type localities (only the type locality of the type species of *Platybessobius* has been confirmed: Crete, CJM 5521, Table 6.1), their generic status should be reconsidered. Therefore the three poly- and partly paraphyletic genera (CPT complex) are united within the oldest available name, *Calathocratus* Simon, 1879, to create a monophyletic group. This is in agreement with STARĘGA (1966) and BRIGNOLI & RAFFAELI (1978), who proposed unification based on characters such as genital morphology and tarsus I structure (tarsus I with only one segment). Further characteristics of this group are the elongated and constricted head cap and crests of elongated papillae surpassing joints of femora and tibia (GRUBER 1968), present in most species. Other evidence to combine this assemblage under a single genus name may be derived from the distribution of the related genera *Dicranolasma* and *Trogulus* (Fig. 6.1). Both encompass a large area within the Mediterranean region, and eastwards they reach as far as the Caucasus. In contrast, genera of the CPT complex considered within their traditional genus limits show a disjunct distribution, with species of the three "genera" excluding each other. Combining the areas of the CPT species, these genera exhibit a continuous distribution area with few internal areal overlap (Fig. 6.5) and, in addition, match the core area of *Dicranolasma* and *Trogulus*. This fact may underline the parallel evolution of the three groups. Within the CPT complex, the status of the isolated *Calathocratus* sequence from Turkey should be considered further, as well as the closely related genus *Anarthrotarsus* Šilhavý, 1967, which was unavailable for this study.

6.4.3. Systematics of *Trogulus*

Although this integrative approach proved to be effective, the delineation of the two investigated species-groups around *T. coriziformis* C. L. Koch, 1839 and *T. hirtus* Dahl, 1903 could not be accomplished by means of the same character combinations (chapter 4, 5). This is reasonable in view of the different phylogenetic levels of the species-groups involved.

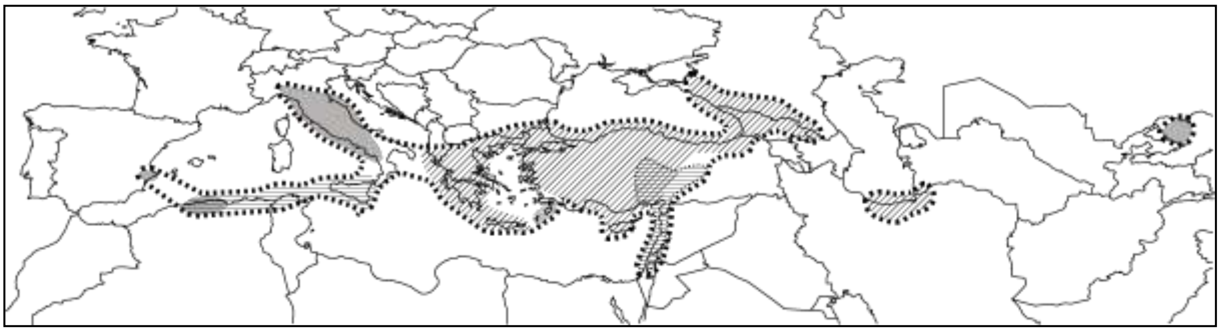


Fig. 6.5. Disjunct allopatric distribution of genera *Calathocratus* (horizontal fill), *Platybessobius* (diagonal fill) and *Trogulocratus* (grey). Black dotted line suggests border of a combined distribution area of the three genera.

Especially the diagnostic value of genital morphological characters does change with respect to the phylogenetic level. Glans morphology is highly conservative within phylogenetically young taxa (e.g., *T. hirtus* species-group and most subsequently defined species-groups, see below). In phylogenetically old taxa (e.g., *T. coriziformis* species-group and subsequently defined lineages, see below) glans morphology is considerably more variable. The systematic value of penial characters is further obscured by the presence of similar characters in taxa which are not closely related. These lineages are only to be defined by molecular monophyly and geographical restriction (e.g., *T. coriziformis* species-group). According to this line of thought one can provide a proposal for *Trogulus* systematics based on the Bayesian analysis (Fig. 6.2) and combine the results with morphological and geographical information (Fig. 6.6). Inserted is the oldest valid species taxon to name the respective species-group.

The genus *Trogulus* is split into two main lineages: Lineage A) comprises species from the western Mediterranean area; lineage B) comprises all other *Trogulus* taxa inhabiting Central, southern and southeastern Europe. The latter group is highly diversified and a clear view of its systematics has not yet been achieved, possibly due to early, rapid and long-lasting diversification. Bayesian analysis does indicate geographical separation in several sub-lineages: Sub-lineage B1), a Central European and North Balkan group; sub-lineage B2) a Central and North Balkan group; sub-lineage B3), a South Balkan and southeastern European group (Fig. 6.6).

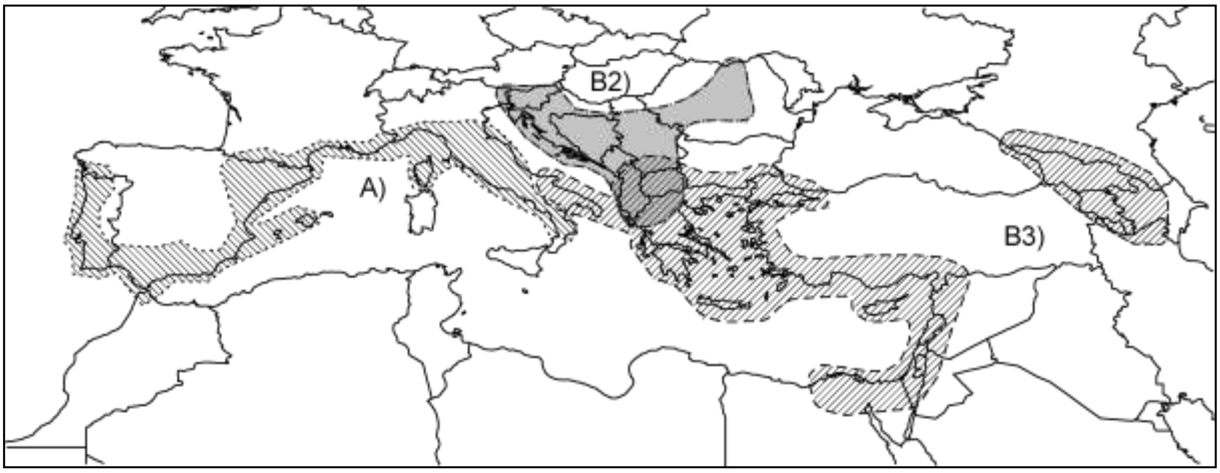


Fig. 6.6. Distribution areas of main radiations within *Trogulus* comprising lineages A and B, the latter subdivided into sub-lineages B1, B2 and B3 (for sub-lineage B1 and the *T. tricarinatus* species-group see Fig. 6.7; see Discussion). Most species within the genus are concentrated in the northern and eastern Mediterranean.

Lineage A) *T. coriziformis* species-group: This well-supported group comprises at present eight species from the eastern Mediterranean (Fig. 6.6) and represents the sister group to all other *Trogulus* taxa. This assemblage shares a straight penial stylus that, however, is present also in several unrelated species from the Balkan Peninsula. This suggests this kind of penial morphology to be symplesiomorphic. The definition of the *T. coriziformis* species-group was based entirely on molecular monophyly and geographical restriction (chapter 5).

Sub-lineage B1). Two species-groups represented by *T. squamatus* and *T. nepaeformis*: These species-groups are well supported and closely related. Their unique and unambiguous character is the dorsally bent stylus of the glans penis (figs. 5, 10 in CHEMINI 1983, figs. 4, 8, 12, 16 in CHEMINI 1984, figs. 268-272 in MARTENS 1978). Separation of these species-groups is to be based on genital morphology and differences in inter-ocular distance (WEISS 1978, CHEMINI 1983, 1984, unpublished data). At present the species-level taxonomy of both groups, which are widespread in Central Europe (Fig. 6.7), is less than clear. Distributional areas of species largely overlap and members of the two groups are superficially similar, especially in external morphology. The *T. squamatus* species-group is composed of *T. squamatus* C. L. Koch, 1839, a yet undescribed Dalmatian species and its most popular representative *T. closanicus* Avram, 1971. The *T. nepaeformis* species-group consists of *T. cisalpinus* Chemini & Martens, 1988, *T. martensi* Chemini, 1983, *T. nepaeformis* (Scopoli, 1763), *T. tingiformis* C. L. Koch, 1848 and of at least 3 undescribed species. Both species-groups are relatively young, and the distribution pattern of several species in the southern Alps suggests their diversification to be connected with the glacial cycles.

Sub-lineage B2). Two species-groups are involved; they are represented by *T. torosus* and *T. hirtus*. The entire sub-lineage comprises morphologically most contrasting taxa. Species are either large to very large, including the opilionid species with the longest body worldwide (*T. torosus* Simon, 1885) or extremely small ones. Bayesian analysis does not support grouping of species according to body size, but also genital morphology suggests that the grouping according to molecular genetic data is useful. The *T. hirtus* species-group encompasses a clear-cut group of closely related species characterised by small body size, sickle-shaped glans penis bent to the right side in dorsal view (see chapter 4). It is restricted to the western Balkan Peninsula (KOMPOSCH 2000, see chapter 4, Fig. 4.2). Species delineation is difficult owing to quite homogeneous penis morphology but it is possible by allopatrically distributed species. The South Balkan forms hitherto assigned to *T. tricarinatus* Linnaeus, 1758 are possibly to be affiliated with the *T. hirtus* species-group (chapter 4, MARTENS 1978). The *T. torosus* species-group comprises large to very large species (*T. banaticus* Avram,

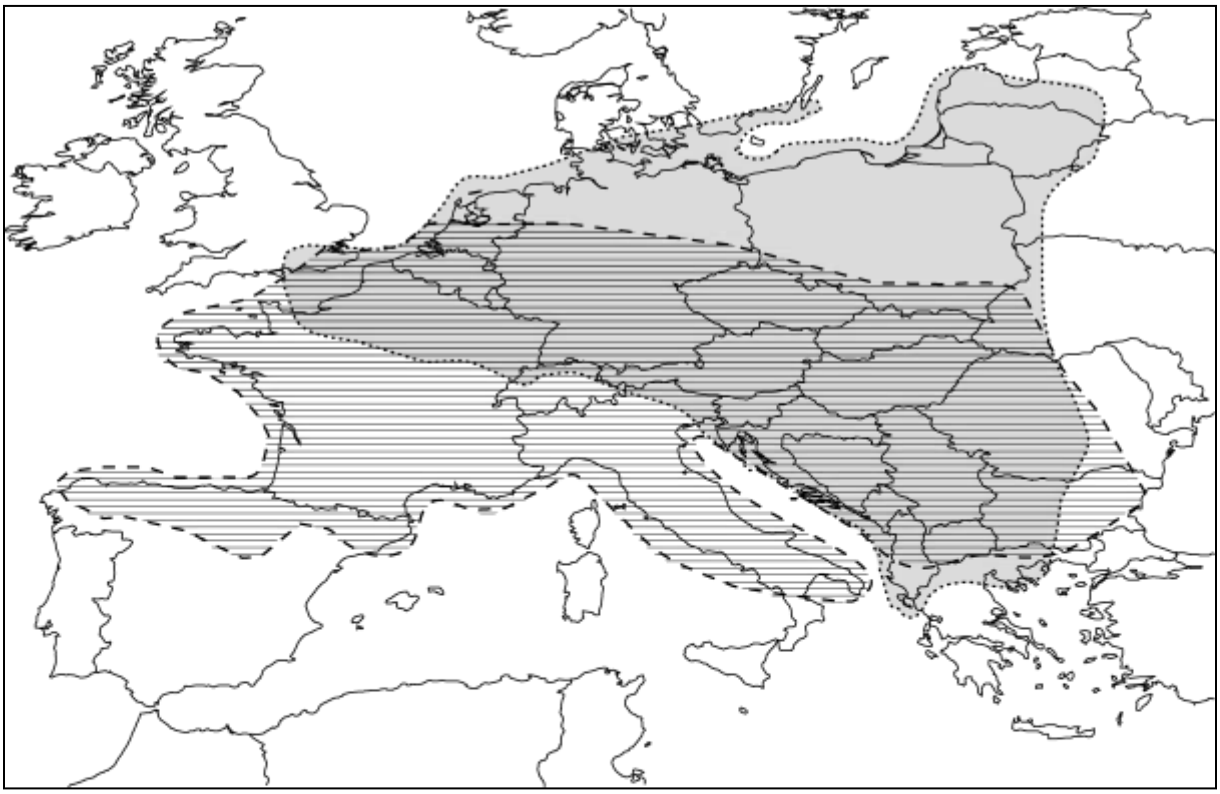


Fig. 6.7. Distribution areas of *Trogulus nepaeformis* species-group and *T. closanicus* species-group (sub-lineage B1; dashed borderline, horizontal fill) and *T. tricarinatus* species-group (part of sub-lineage B3, dotted borderline, grey). Within-group diversification is highest in the Alps and on the Balkans.

1971, *T. torosus*, *T. setosissimus* Roewer, 1940 and three undescribed species). This group is in need of further investigation and it may turn out to be polyphyletic.

Members are characterised by an outstretched stylus, similar to those of the *T. coriziformis* species-group (unpublished), but in some species the stylus is bent in distal third. All species are distinct with respect to morphology and molecular data. The group includes four troglobionts, a feature otherwise absent in *Trogulus.*

Sub-lineage B3). Two species-groups represented by *T. gypseus* and *T. tricarinatus*. Like the previous sub-lineage, this monophylum comprises two groups with contrasting body size, genital morphology and distributional area. Species of both groups have in common a stylus bent to the left in dorsal view (*T. tricarinatus*, fig. 4 in MUČALICA 1988/89; *T. gypseus* species-group: *graecus*, fig. 57 in BRIGNOLI & RAFAELLI 1968; *gypseus*, fig. 1 in MARTENS 1965). This group probably originated in the eastern Mediterranean (Fig. 6.6) because the oldest lineages inhabit this region (Fig. 6.2). The *T. gypseus* species-group (*T. gypseus* Simon, 1879, *T. graecus* Dahl, 1903, both to be split into several species-level lineages) does form a paraphyletic group. However, prior to further investigations It is suggested to treat it as taxonomic unity in need of revision. The affiliation of *T. rossicus* Šilhavý, 1968 (cyt*b* evidence, Fig. 6.4) and *T. uncinatus* Gruber, 1969 (similar genital morphology; GRUBER 1969) with the *T. gypseus* species-group needs to be re-evaluated. The *T. tricarinatus* species-group (including *T. oltenicus* Avram, 1971) represents one distinct lineage within sub-lineage B3). Its species are characterised by small body size and can be separated from species of similar body size belonging to other groups by genital morphology. This young radiation is rich though difficult to access and represents a yet unresolved species swarm which is distributed from the Balkans to the southeastern Alps. At least one parthenogenetic lineage invaded Central Europe (Fig. 6.7) and expanded its area in the north to southern Sweden and Latvia.

6.4.4. Species delineation in *Trogulus*

Delineation of species upon molecular data alone has been criticized, and even poses problems with respect to bar-coding techniques as well (FRÉZAL & LEBLOIS 2008). FRÉZAL & LEBLOIS (2008) suggested using a synergistic approach and complementing genetic species delineation by further independent lines of evidence. This was accomplished in two revisions (chapter 4, 5), where molecular species delineation based upon cyt*b* data was backed up by morphometric analysis, morphological characters and distributional data.

Within *Trogulus* the traditional approach to recognizing species failed with respect to closely related species mainly due to their low level of morphological diversification. Recently described *Trogulus* species have been delineated by comparison of sympatric and even syntopic species (e.g., *T. martensi*: CHEMINI 1983; *T. closanicus*: AVRAM 1971, but see WEISS 1978). Nevertheless, syntopic species were found not to be closely related; instead, they belong in most cases to different species-groups or distinct clades (lowest cyt*b* value distances: e.g., *closanicus* vs. *martensi*: 14.1-15.0%; *closanicus* vs. *nepaeformis*: 13.3-15.1; *nepaeformis* vs. *tingiformis*: 12.2-13.4%). Coincidently, these species pairs are well recognizable by male genital morphology and external characters. In general, *Trogulus* male genital morphology is highly conservative in closely related species (see chapter 4, Figs. 4.7-4.10, chapter 5, Figs. 5.7, 5.8) and, according to experience acquired within this thesis, differences start to become recognizable at an approximate cyt*b* distance of 15% (no distinct differences discernable: *aquaticus*-*coriziformis*: 12.9-13.5% (Figs. 5.7, 5.8); within the *hirtus* clade: 4.8-16.9% (Figs. 4.7-4.10); obvious differences: *coriziformis-cristatus*: 17.1-17.3% (Figs 5.8, 5.13); *falcipenis-karamanorum*[man.n.]: 14.9-15.8% (Fig. 4.13; all chapter 4, 5).

Such sympatric occurrences provide unmistakable evidence for species under the “biological species concept” sensu MAYR (1963). However, species boundaries are present also at considerably lower genetic distance values. For example *T. pharensis* [man.n.] and *T. thaleri* [man.n.] show a distance of 4.8-5.9%, the lowest value found for valid species. These species are further to be told apart by distribution, minute but clearly recognizable morphological characters and morphometric discrimination (chapter 4.5.3.1, Figs. 4.3-4.6). Likewise, separable allopatric sister species are present in the *T. nepaeformis* species-group (*martensi* vs. *nepaeformis* from Austria/France: 6.7-7.4%; *martensi* vs. *nepaeformis* from Croatia/Serbia/Slovenia: 6.2-7.6%; cf. *nepaeformis* from Austria and France vs. *nepaeformis* from Croatia/Serbia/Slovenia: 4.6-6.0%; cf. *nepaeformis* from Spain vs. *tingiformis*: 9.0-9.3%). These data suggest using the lowest cyt*b* cut-off distance value of 5% to propose a minimum distance value for the cyt*b* gene to be indicative for lineages worth to be investigated for the existence of possible cryptic species within *Trogulus*. However, we do not intend to identify species solely upon this genetic distance. Species validation needs to incorporate further evidence as morphometric discrimination, morphological characters or distinct geographic information to be truly acceptable as a complete and full species description. To verify the possible amount of cryptic diversity upon an easy to apply genetic distance is the primary aim of the definition of this 5% “cut-off” value in our study. It is further remarkable that such closely related *Trogulus* species pairs are exclusively allopatric in distribution, which may be related to their young age. These data define them at least as “phylogenetic species” (CRACRAFT 1983, but see species discussion in HAFFER, 1997). Their ‘diagnosibility’, an important trait under the phylogenetic species concept, is given by their molecular characters and also by morphological differences. At present their validity under the biological species concept is impossible to ascertain due to allopatry and a general lack of biological information about the free-living populations.

Proposed as a key feature in Opiliones systematics as early as ŠILHAVÝ (1938), however, in many cases *Trogulus* penis morphology is not capable of resolving species-level taxonomy. Furthermore, there is evidence that glans morphology may be affected by allometric growth, which makes this character controversial for species delineation in *Trogulus* in general (*T. closanicus*; unpublished data). Likewise the same may be true in other groups of Opiliones with a conservative genital morphology (e.g.; *Leiobunum*, see discussion in SCHÖNHOFER & HILLEN 2008). A combination of molecular, geographical, morphological and morphometrical data is suggested to reveal cryptic diversity within many other groups of Opiliones (THOMAS & HEDIN 2008; BOYER et al. 2007*a*).

6.4.5. Cryptic diversity within Trogulidae.

The amount of cryptic diversity found within the Trogulidae is remarkable because the European arthropod fauna is quite well researched. Within Trogulidae only *Anelasmocephalus* was subject to thorough revision by MARTENS (1978) and MARTENS & CHEMINI (1988), who described a number of new species by morphological and distributional data alone, doubling the number of valid species. Although *Trogulus* has always been attractive due to their considerable size, a revision of the genus seemed tedious in view of their homogeneous morphology. Nevertheless, within the last 50 years seven valid species have been described on the basis of morphological characters (3: AVRAM 1971; 1: GRUBER 1969; 1: CHEMINI & MARTENS 1988; 1: CHEMINI 1983; 1: KOMPOSCH 2000; those of chapter 4 and 5 excluded). Enforcing the proposed minimum value of 5% cyt*b* distance (chapter 6.4.4) upon the present data set to consider the possibility of species level (Fig. 6.4), a cryptic diversity of at least 235% is revealed for *Trogulus*. Most of these lineages can be confirmed to represent morphologically distinguishable species, as well. To put a figure on this, about 40 species await formal description. This extraordinary amount is further substantiated by two revisions of *Trogulus* species-groups. Within the *Trogulus coriziformis* species-group four existing species have been accepted, four have been described as new (i. e. 100%) but two further cryptic species were outlined but not described due to the lack of material (i. e. 150%). Within the *Trogulus hirtus* species-group two species were accepted, four described as new (i. e. 200%) and two further species were outlined but not described (i. e. 250%).

Within the CPT complex of genera a value of 150% (12 new lineages, 8 described species) is impressive but is by far underestimated due to low sampling activity, especially in Turkey (Fig. 6.8). This is made still more obvious by the lack of matching haplotypes within any of the deeply split lineages (Fig. 6.4). In other words, distributional areas of haplotype clusters are extremely small and represent small-range species. Several of these clusters were investigated more closely and found that they could readily be distinguished by morphological differences as well. A similar diversification clearly exists in *Trogulus graecus*/*gypseus* (Fig. 6.4), outlining the southern Balkan Peninsula and parts of Anatolia as a major centre of diversification for Trogulidae in general. Obviously, this study so far only touched a major cryptic diversity within the CPT complex. Species' dispersal ability is apparently even lower than in *Trogulus*, hence the remarkable diversity. A similar diversification associated with small-scale distribution was recently revealed for Cyphophthalmi on the Balkan Peninsula, suggesting both groups to be of major interest for the investigation of biogeographical processes (BOYER et al. 2005, KARAMAN 2008, in press).

6.4.6. Nemastomatidae: Implications from a reduced taxon sampling

The molecular phylogeny of the eight nemastomatid genera included in this study (out of 16 generally accepted ones; HALLAN 2003, MARTENS 2006) closely reflects the current generic classification of the western palearctic representatives of the family. *Mitostoma* as sister to all other genera (Figs. 6.2, 6.3) is known for its extremely complicated male genital morphology, which is not matched by any other known nemastomatid genus. The distal three-dimensionally structured part of the penis is similar to a male spider bulb but seems to lack expandable parts (figs. 214-216, 222-224, 229-231 in MARTENS 1978; fig. 35 in MARTENS

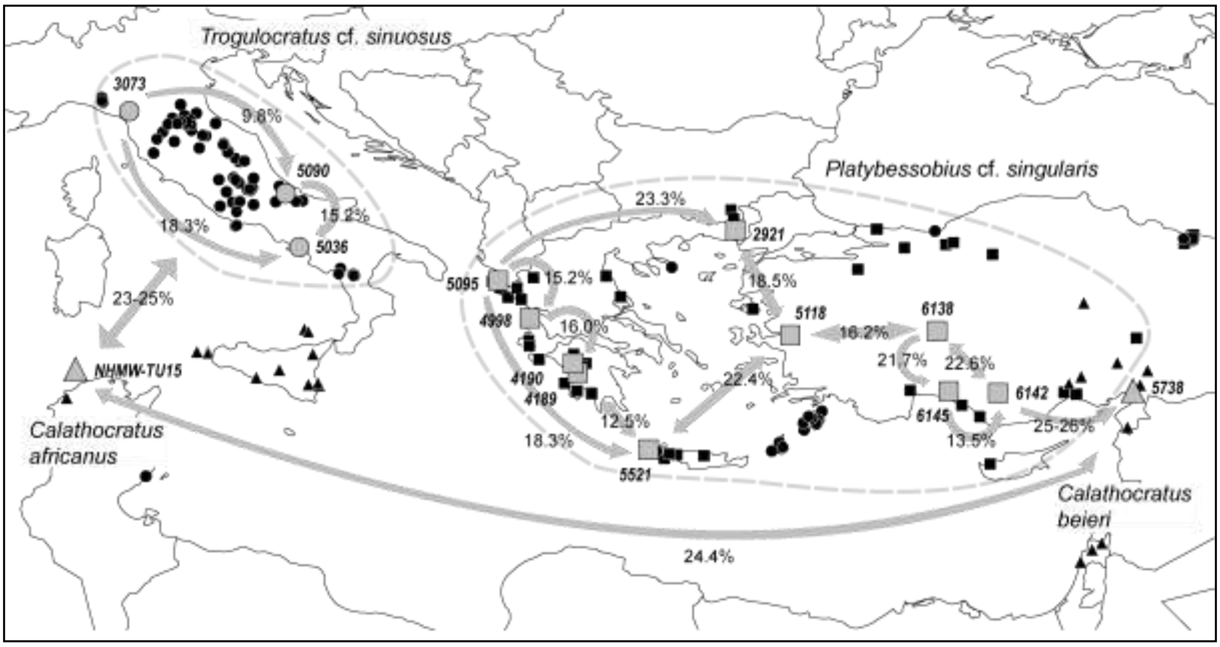


Fig. 6.8. Examples of distribution and cryptic diversity in the genera *Calathocratus* (triangles), *Platybessobius* (squares) and *Trogulocratus* (circles). Grey symbols indicate sequenced specimens. Percentage values of sequence distances between samples (near or on grey arrows) indicate uncorrected p-distance of cyt*b* sequences. Numbers (in italics) indicate depository numbers of sequenced specimens from the J. Martens collection (CJM).

2006). Subfamily status was proposed earlier (KRATOCHVÍL 1958) but is not accepted in current taxonomy. Possible subfamilial status of *Mitostoma* is reasonable and needs further investigation. The remaining genera segregate into two deeply split clusters. One of them, which includes *Carinostoma*, *Histricostoma* and *Paranemastoma*, shares as common feature a bifid distal part of penis. The larger stylus part surmounts and at a distance covers the more slender truncus part (e.g. figs. 155, 184, 195 in MARTENS 1978; fig. 4.16.L in GRUBER 2007). In the species of these genera the secretion of the male cheliceral gland is collected in a common long channel and extruded by a single large pore on or at the base of the cheliceral apophysis (MARTENS & SCHAWALLER 1977). Part of the channel and some of the glandular cells are deeply intruded into the prosoma. Spination of distal part of penis and glans is always inconspicuous.

The taxa of the sister branch represented by the genera *Mediostoma*, *Nemastoma*, *Nemastomella* and *Pyza* are less specialized with respect to genital and cheliceral gland morphology and they represent an array of various diversification levels. Distal parts of penis and glans are always strait, never bifid, sometimes slightly alate. Spination of glans part may be profound or inconspicuous. Male cheliceral gland is present in all genera but is rather unspecialized. It opens to the surface by a multitude of minute pores without a common collective channel. The glandular cells are confined to the basal member of the chelicera and to the cheliceral apophysis proper (MARTENS 1973, MARTENS & SCHAWALLER 1977). In all species incorporated here the molecular analysis correctly joins species to respective genera according to current generic classification.

6.5. Abstract

This is the first comprehensive study to evaluate the relationships between the western palearctic harvestman families Dicranolasmatidae, Trogulidae and Nemastomatidae with focus on the phylogeny and systematics of Trogulidae, using combined sequence data of the nuclear 28S rRNA and the mitochondrial cytochrome *b* gene. Bayesian analysis and Maximum Parsimony do not resolve *Dicranolasma* as distinct family but on similar phylogenetic level as other lineages in Trogulidae. Nemastomatidae and Trogulidae turned out to be monophyletic, as did genera *Anelasmocephalus*, *Kofiniotis* and *Trogulus* within the Trogulidae. The genera *Calathocratus*, *Platybessobius* and *Trogulocratus* each appeared paraphyletic and are synonymised with *Calathocratus*. This study shows molecular data to be

in general concordance with taxa characterised by morphology. Molecular data are especially useful to calibrate morphological characters for systematic purposes within homogeneous taxa. We show the level of genetic distance in most closely related species to be as low as 5% on the basis of the cytochrome *b* distance as low as 5%. Lineages possibly representing cryptic species are reflected by this threshold. By this threshold an estimated number of species 1.5-2.4 times higher in terms of traditionally accepted species than previously believed arise. Cryptic diversity in Trogulidae is thereby demonstrated to be extraordinarily high with respect to European fauna.

7. Distinctive features of Trogulidae genetics

7.1. Introduction

For a number of years molecular systematic has focused on the use of short mitochondrial fragments to identify species and to define species-level to quantify the amount of cryptic diversity (HEBERT et al. 2003). Furthermore this data has been used to establish phylogenies of the respective groups. Thus barcoding techniques have been subject of debate outlining their technical drawbacks when proposed as stand-alone methods. FREZAL & LEBLOIS (2008) provided a comprehensive summary on problems associated with mitochondrial markers, e.g. heteroplasmy, symbiont infections and interspecific hybridization, numts and finally the certainty of species delimitation itself. They proposed not to defend molecular data for its own sake by increasing methods and statistics, but to include further independent data to support the total evidence of a given taxonomic situation.

I have discussed and outlined species limits in chapters 4 to 6 as proposed by FREZAL & LEBLOIS (2008) and have shown general congruence between molecular data and other characters to exclude most of the aforesaid problems. Nevertheless, this approach on systematics of Trogulidae has not only been difficult because of the traditional way of elaborating morphological characters for species delineation, but also considering the working with molecular markers for phylogenetic analysis. Due to limitations in time, material and focus on the main task of systematic investigation of Trogulidae, it has not been possible to elucidate all features. This chapter intends to give an overview on molecular genetic characteristics associated with the investigated taxa and applied molecular methods and attempts to provide reasonable explanations.

7.2. Material

Table 7.1 lists materials explicitly mentioned in this chapter. Accession numbers do not exist for ND1 and 16S sequences and for cyt*b* sequences only in part (if they are referred to in previous chapters). Vouchers are deposited in Collection Jochen Martens (CJM; Johannes Gutenberg-University Mainz, Germany). Fresh material of *Rilaena triangularis* and *Nemastoma dentigerum* was used from whole specimens, voucher numbers were not assigned. Material of these two species was collected in the vicinity of Mainz, Germany in spring 2004.

Table 7.1. List of materials used in this chapter. CJM and number: vouchers from Coll. J. Martens, Mainz, Germany.

Taxon	CJM	Locality information	Coordinates	Collector	Date
Trogulus martensi Chemini, 1983	4690	Switzerland: Basel	N 47.5364/E 7.6025	A. Schönhofer	13.9.2005
Trogulus squamatus C. L. Koch, 1839	4831	Montenegro: Monastery Morača, Morača Valleyl	N 42.7646/E 19.3930	A. Schönhofer	8.5.2006
Trogulus closanicus Avram, 1971	4945	Romania: Gorj, Closani	N 45.0676/E 22.8000	A. Schönhofer & R. Plăiasu	4.-6.5.2006
Trogulus closanicus Avram, 1971	5150	Croatia, Cajetina Canyon, Kučiće	N 43.43/ E 16.83	A. Schönhofer	13.5.2006
Trogulus cf. *closanicus* Avram, 1971	5154	Bosnia and Herzegovina: Gacko, Dramešina	N 43.2/E 18.5833	M. Komnenov	11.9.2006
Trogulus martensi Chemini, 1983	4068	Germany, Bad Kreuznach	N 7.84/E 49.81	A. Schönhofer	7.9.2004
Trogulus martensi Chemini, 1983	4481	Germany, Unteruhldingen	N 9.25/E 47.73	S. Huber	3. 2005
Trogulus martensi Chemini, 1983	4694	Switzerland, Basel, Oberwill	N 47.53/E 7.55	A. Schönhofer	16.9.2005
Trogulus *martensi* Chemini, 1983	4234	Italy, Friuli, Clauzetto	N 46.25/E 12.89	W. Schawaller	2.10.1995
Trogulus tricarinatus (Linné, 1767)	3839	Austria, Carinthia, Ruden	N 46°39’01“/E 14°46’07“	C. & B. Komposch	11.6.2004
Trogulus tricarinatus (Linné, 1767)	3847	Germany, Alzey, Nieder-Wiesen	N 49.75/ E 7.96	A. Schönhofer	13.5.2004

7.3. Results

7.3.1. Overlay of sequences

In around 80% of all individuals treated with the primer combination Cytb-for and Cytb-rev-deg the expected fragment of 630 bp cyt*b* was amplified exclusively. The remaining 20% of the individuals exhibited an additional 70 bp fragment (Fig. 7.1*a*) which overlaid the chromatogram of the 630 bp fragment when sequenced directly (Fig. 7.1*b*, 1th, 2nd and 4th row starting from the left hand side). Furthermore, an increase of the amplification of the 70 bp fragment seemed correlated with a decreased amplification of 630 bp fragment amplifications. Because low numbers of 70 bp copies hindered the analysis of the cyt*b* sequence, the fragment was excluded by agarose gel extraction of the 630 bp lane. However, the first 70 bp of sequences of the extracted fragments were still overlaid and the additional fragment was still present. In contrast, when sequencing the extracted 630 bp fragments with the internal primers Cytb-for int and Cytb-rev int, sequences were not overlaid. These primers were also used successfully to obtain two smaller cyt*b* fragments. In this case, the 630 bp fragment was not amplified due to the dominant 70 bp fragment. For further discussion see chapter 7.4.4.

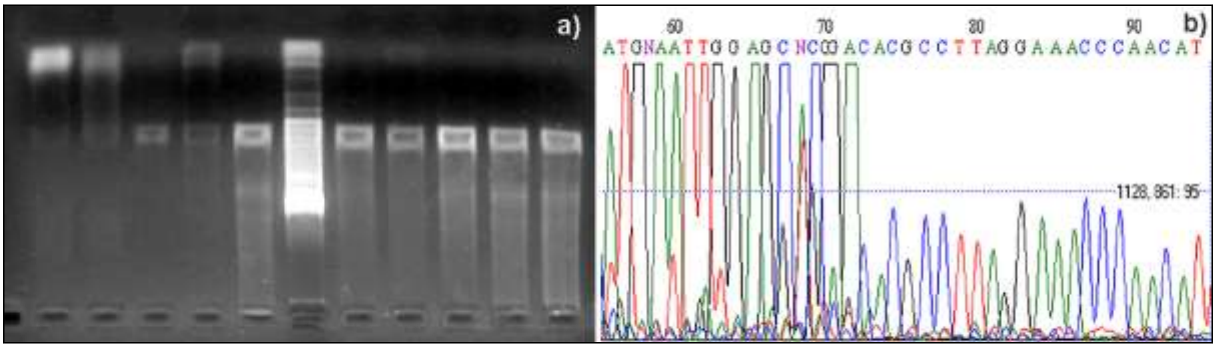
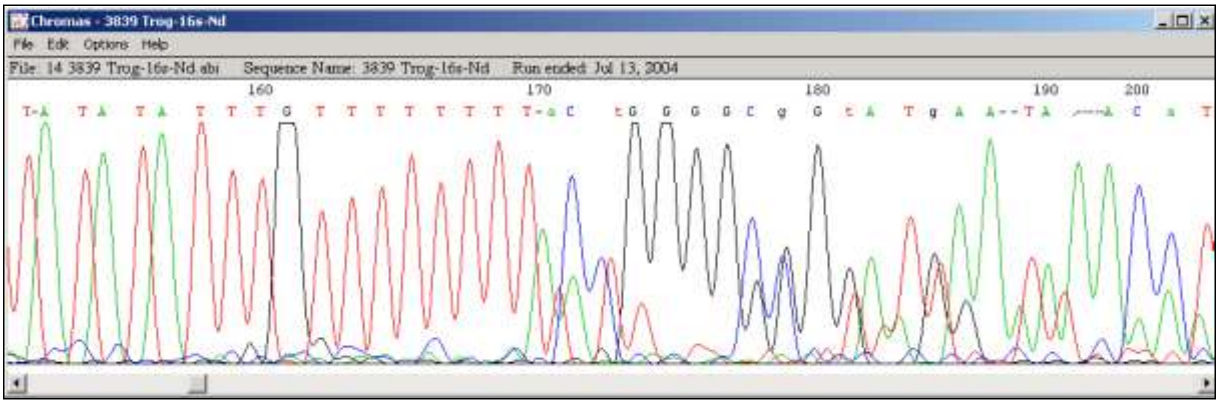


Fig. 7.1. (*a*) Digital image of cytochrome *b* gene-PCR products of different *Trogulus* species separated by agarose gel electrophoresis. Expected fragment of 630 bp is seen in horizontal mid-lane. Upper lane shows a smaller fragment of 70 bp. The quantity of the 630 bp fragment is depleted when the 70 bp fragment is amplified. (*b*) Chromatogram of partial cytochrome *b* gene sequence showing the end of overlay of the 70 bp fragment with the 630 bp fragment.



File: 14 3839 Trog-16s-Nd.abi Sequence Name: 3839 Trog-16s-Nd Run ended: Jul 13, 2004

Fig. 7.2. Chromatogram of two length-variable fragments of 16S rRNA amplified simultaneously from one individual of *Trogulus tricarinatus* (CJM 3839). The lack/superfluity of one base at position ~170 bp causes overlay of chromatographic script and complicates the analysis of the sequences.

Amplification of the 16S rRNA using different primer combinations resulted in the successful amplification of various fragments of the 16S gene. Unfortunately it was not possible to edit a number of sequence chromatograms (Fig. 7.2) and closer investigation revealed the overlay of two sequences differing in at least one base in length. Interpretation of the sequences was thus possible but required difficult and time consuming manual editing. Since only cloning yielded sequences that were easy to read, 16S was not considered for further use in phylogenetic analysis (see chapter 7.4.1 and 7.4.4).

7.3.2. Ambiguous base positions

Ambiguous positions are defined by exhibiting more than one peak for a distinct base at one position of a chromatogram. Investigating 192 cyt*b*-sequences I found in average 5-6 positions (about 1%) of the total 555 bp long fragment to be ambiguous and not assignable to a distinct base (Fig. 7.3*a*). Re-sequencing of the same individual changed the ratio of the individual base but could not exclude the ambiguity of the positions (Fig. 7.4). Furthermore, in closely related taxa and within species these „ambiguities“ were often located at identical positions in the alignment and were considered homologous. Further investigation showed most ambiguous positions to be restricted to the 3rd codon position and the identity of the coded amino acids was not modified (silent mutations). Finally using PAUP and MEGA analyses most of these positions were specified as parsimony uninformative, even when the ambiguous sequences were excluded.

The amount of ambiguities per sequence appeared to some degree taxon-dependent. Especially in *Trogulus closanicus* and *T. martensi* most sequences showed 6 to 20 ambiguities (Fig. 7.5). *Dicranolasma*, the CPT-complex, the *Trogulus torosus* species-group and the *T. tricarinatus* species-group were more heterogeneous but the higher proportion of ambiguity-rich sequences is still obvious (Fig. 7.5). Groups with low values of ambiguities and ambiguity-rich sequences comprise the Nemastomatidae, *Trogulus nepaeformis*, the *T. coriziformis* species-group and the *T. hirtus* species-group.

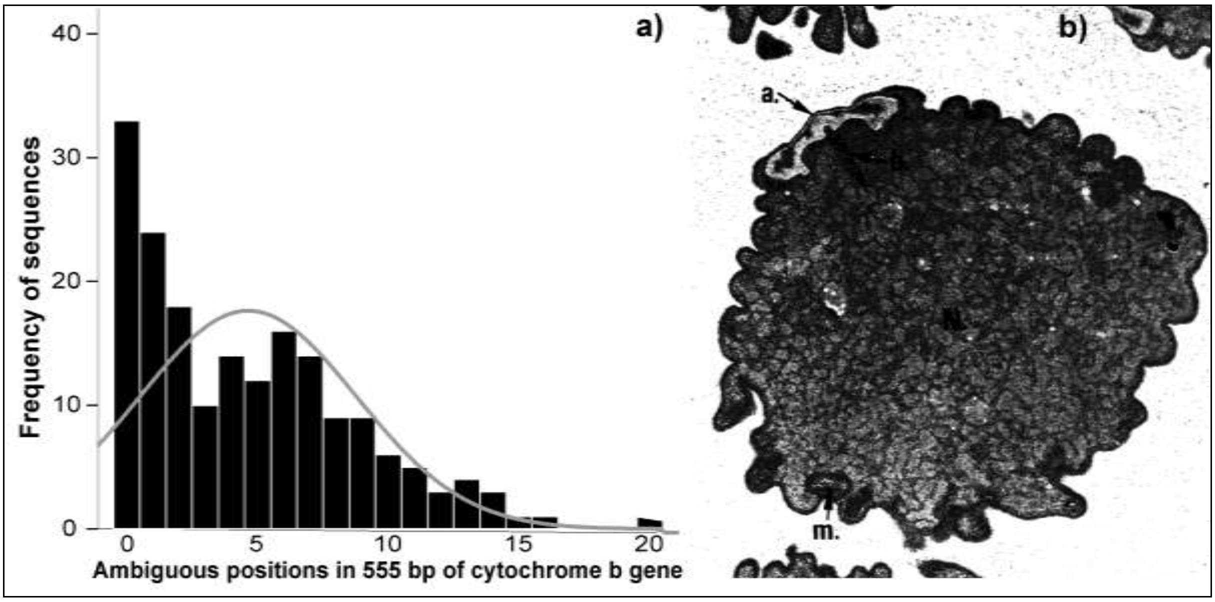


Fig. 7.3. (*a*) Histogram of distribution of ambiguous positions per sequence. 190 sequences of cytochrome *b* gene were included; (*b*) Mature spermatozoon in the testical lumen of *Trogulus nepaeformis*, a: acrosomal rod; m: mitochondrion, magnification 20.000; from JUBERTHIE & MANIER (1977*b*).

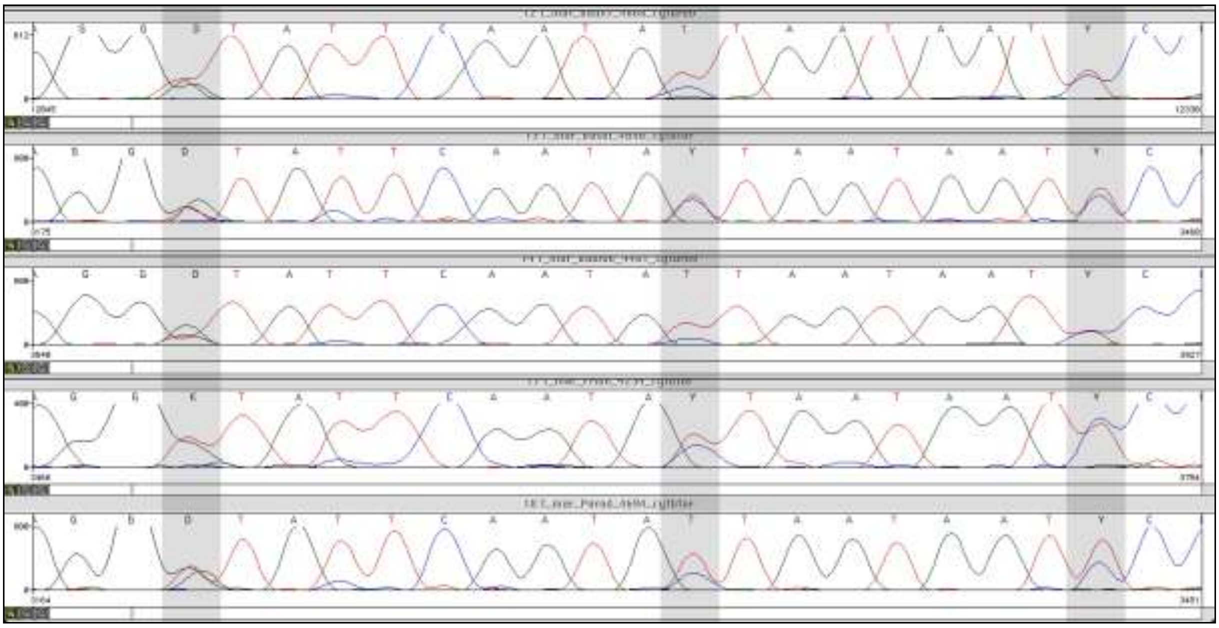


Fig. 7.4. Sequence chromatograms of 254-276 bp (555 bp cytochrome *b* gene alignment) showing ambiguities at homologous positions (greyed out). All sequences derived from *Trogulus martensi*, accessions all CJM: (from top to bottom) 4068, 4690, 4481, 4234 and 4694.

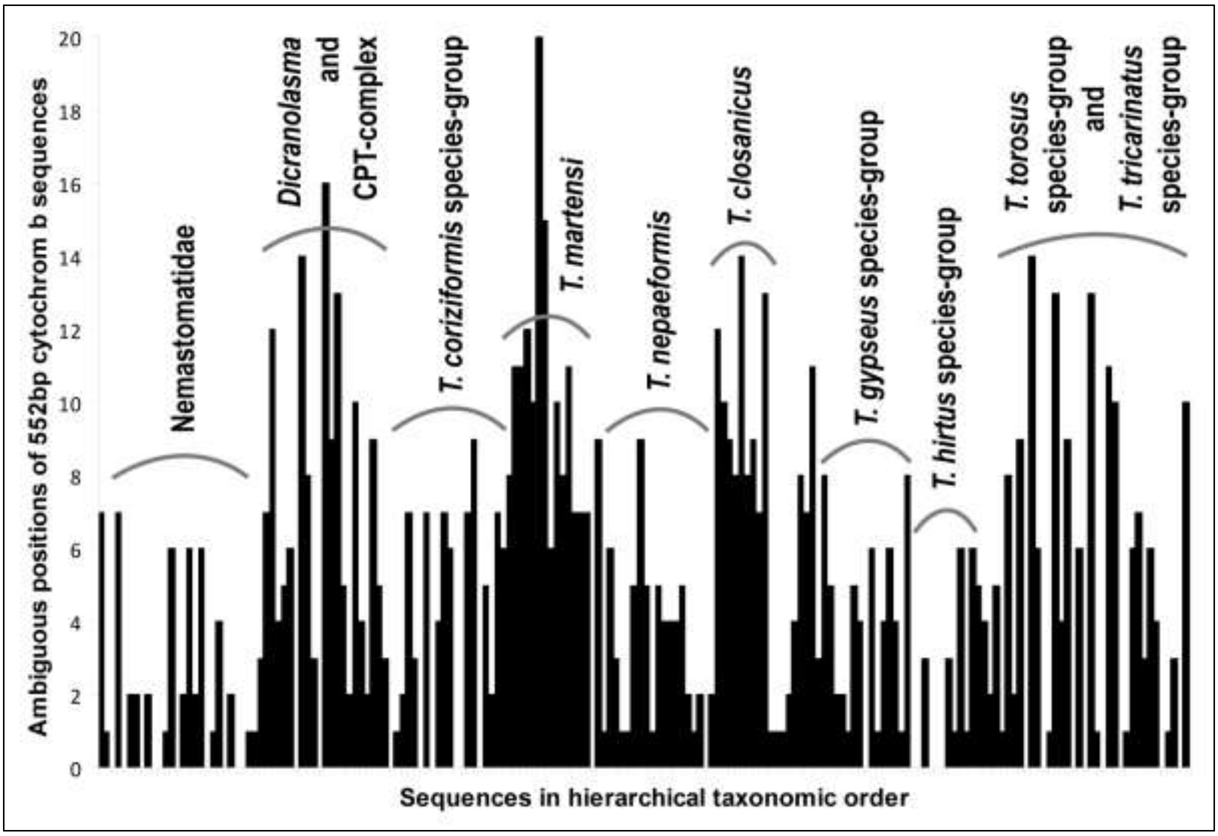


Fig. 7.5. Amount of ambiguous positions of 190 sequences of 555 bp of cytochrome *b* gene. Sequences are arranged from left to right in 1) hierarchical order of taxa (e.g. family, genus, species-group, species), 2) alphabetically within taxa (e.g. genera within Trogulidae: *Anelasmocephalus*, *Calathocratus*, *Dicranolasma*,...). Discussed taxa are named.

7.3.3. Diversity in clones from single individuals

In one case (*T. closanicus*, CJM 5150) the amount of ambiguous positions in the amplified cyt*b* fragment exceeded a value of 5%. Re-sequencing the specimen with a fresh PCR kit did not change this result and excluded polymerase failure. As this amount of ambiguity is in conflict with the proposed species-possibility level (chapter 6.4.4) this unique case was further investigated. Cloning the amplified fragments yielded sequences of 11 clones, each representing its own haplotype. A UPGMA analysis, including *T. squamatus* (CJM 4831, Montenegro), and specimens of *T. closanicus* of two distinct phylogenetic lineages (CJM 4945, Romania; CJM 5154, Bosnia) resulted in a deeply split and highly differentiated tree, assigning different clones to different lineages of *T. closanicus* (Fig. 7.6, see chapter 7.4.2).

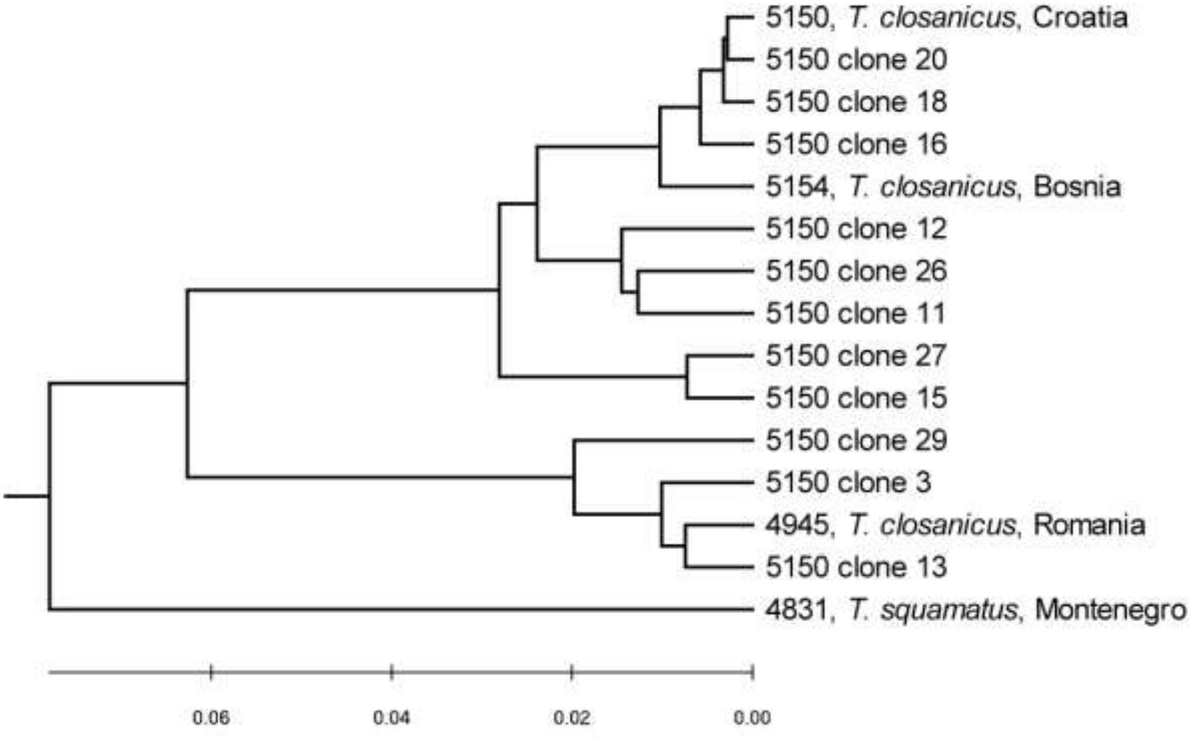


Fig. 7.6. UPGMA tree of cytochrome *b* gene sequences derived from clones of a single individual of *Trogulus closanicus* from Croatia (Cajetina-Canyon, Kučiće, CJM 5150). Above-noted sequence was acquired via direct sequencing and includes about 5% ambiguous positions. All specimens belong to *T. squamatus* species-group. All numbers refer to CJM.

7.3.4. Unexpected long fragments of ND1 PCR

When using the primer combination ND1-N and ND1-J, the size of the amplified opilionid fragment was 2-3 times larger than expected for arachnids (e.g. 548 bp in *Eresus*; JOHANNESEN 2001, Fig. 7.7). Although only few samples were sequenced it appeared that the fragment had a specific length according to family rank of the investigated taxon (~1600 bp for *Trogulus tricarinatus*, CJM 3847, Trogulidae; ~1400 bp for *Rilaena triangularis*, Phalangiidae; ~1800 bp for *Nemastoma dentigerum*, Nemastomatidae). When sequencing the 1631 bp long fragment of *Trogulus tricarinatus* I found the expected genes positioned at both ends of the fragment (partial NADH dehydrogenase subunit 1 gene, 1-489 bp and partial 16S rRNA, ~1372-1631 bp; identified by reference sequence *Phalangium opilio* (EU523757, MASTA & BOORE 2008; Fig. 7.8). Between these were located the NADH dehydrogenase subunit 3 gene (ND3) and a number of tRNAs commonly situated in the vicinity of this gene were located (Fig. 7.8). They were identified by NCBI-Blast as follows: ND3 (590-931 bp) upon *Phalangium opilio* (EU523757, MASTA & BOORE 2008); tRNA Arginin (990-1052 bp) upon *Dermacentor variabilis* (AY059254), *Rhipicephalus pulchellus* (AY059228) and *Hyalomma aegyptium* (AY059264, all MURRELL et al. 2003); tRNA Asparagin (1073-1139 bp) and tRNA Serin (1140-1196 bp) upon *Varroa destructor* (AJ493124, NAVAJAS et al.

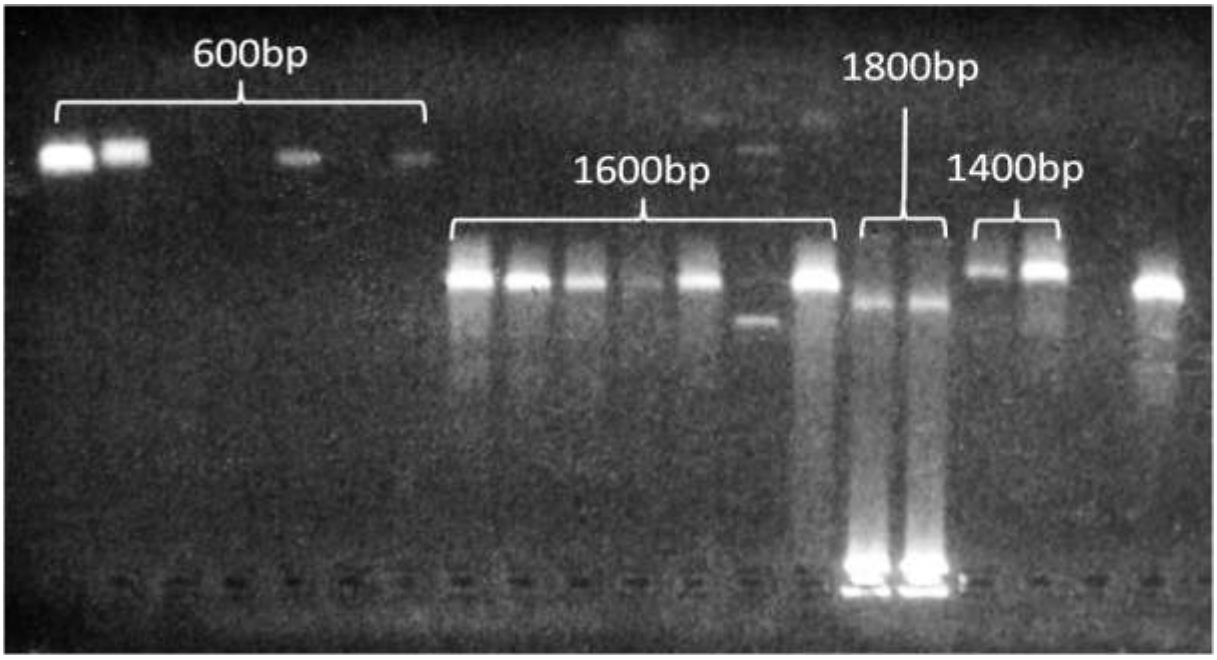


Fig. 7.7. Amplified DNA fragments using primer-combination ND1-N and ND1-J. For spiders (left, unspecified Heteropodidae: Araneae) a fragment length of 600 bp is usual. Fragments of 1600 bp were specific for *Trogulus* (CJM 3847), 1800 bp for *Nemastoma dentigerum* (no accession no.) and 1400 bp for *Rilaena triangularis* (no accession no.).

2002). Not all regions of the fragment could be identified but the tRNA Alanin can be supposed to fill the gap of 60 bp between the ND3 gene and the tRNA Arginin (Fig. 7.8). This gene order is present in most available mitochondrial genomes of arachnids (NCBI). The gap between the tRNAs and 16S is the result of the inability to trace the end of the 16S sequence and even though further tRNAs may be present, the NCBI-Blast was unavailable to identify them (see chapter 7.4.2).

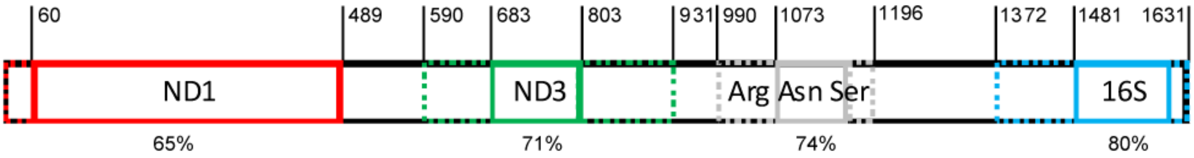


Fig. 7.8. Mitochondrial gene map of PCR fragment expected to include ND1 gene and 16S rRNA, only (*Trogulus tricarinatus*, CJM 3847). Box with black background indicates the obtained sequence (1631 bp), coloured solid boxes indicate BLAST matches with reference sequences, percentages below indicate the accuracy of BLAST matches; dashed boxes show actual size of the respective fragment, according numbers indicate positions on the fragment in amount of base pairs.

7.4. Discussion

7.4.1. Heteroplasmy

A possible cause for ambiguous base positions in a sequence is the presence of simultaneously amplified fragments differing at their respective sites. One explanation for different fragments being amplified in a single PCR is the presence of different lineages of mitochondria in an individual, a genetic feature termed heteroplasmy. While heteroplasmy is a rare case in plant and animal taxa where mitochondria are maternally inherited (e.g. PEARL et al. 2009, KVIST et al. 2003), it can be assumed a common feature in several invertebrate groups. For *Trogulus* (JUBERTHIE & MANIER 1977*b*) as well as for other Opiliones (JONES & COKENDOLPHER 1985, JUBERTHIE & MANIER 1976, 1977a, 1977c, 1978, JUBERTHIE et al. 1976, MOYA et al. 2006, REGER 1969) the incorporation of mitochondria into the mature spermatozoa was shown to be a general trait (e.g. JUBERTHIE 1977*b*, Fig. 7.3*b*). Thereby offspring inherit paternal and maternal mitochondria and are likely to exhibit some degree of heteroplasmy. It is difficult and not the focus of this study to technically prove heteroplasmy. Evidence for the existence of different fragments is derived from the overlay of sequences outlined in chapters 7.3.1 and 7.3.2.

Although the amount of ambiguities of the investigated cyt*b* gene was on average only 1% per sequence, this did not diminish the use of the sequence data for phylogenetic analysis. Neither the species-possibility level applying a threshold of at least 5% genetic distance was affected nor the phylogenetic analysis, because ambiguities were mainly restricted to parsimony uninformative positions. However, while the determination of ambiguities upon sequence chromatograms is likely to be highly subjective, the interpretation of genetic distances should assume an error of 1% in Trogulidae in the case of cyt*b*. Applying "pairwise deletion" of ambiguous sites, as featured by most phylogenetic programs, is necessary when calculating genetic distances. Population studies using mitochondrial genes for haplotype quantification via direct sequencing may not be suitable for this group of organisms.

7.4.2. Possibility of gene rearrangements

The insertion of the ND3 gene and several tRNAs between ND1 and 16S (see chapter 7.3.4) in *Trogulus tricarinatus* seems to be a case of major gene re-arangement. Within Arachnida many cases have been revealed within the last 10 years (BLACK & ROEHRDANZ 1998, QIU et al. 2005, FAHREIN et al. 2007, DOWTON et al. 2002, MASTA et al. 2008) and Opiliones seem to be another arachnid order worth investigating. This task is very promising, especially in view of the differences in length of the amplified fragments of the three investigated families (Fig. 7.7).

It is worthwhile to mention that only a few of the many investigated primer combinations were able to amplify fragments at all (unsuccessful combinations have not been mentioned in the material and methods section). This was especially conspicuous when smaller fragments had been sequenced that were thought to be neighbours on the mitochondrial genome but primer combinations designed to simultaneously amplify both fragments failed.

The applied methods did not discriminate between mitochondrial fragments and nuclear copies of mitochondrial DNA (numts). In *Trogulus closanicus* (CJM 5150; see chapter 7.3.3) several duplications of mtDNA may have caused the high percentage of different copies exhibited in the cloned sequences. In both cases, either mitochondrial re-arrangement or numts, an isolation of mitochondrial DNA will be necessary prior to further investigations.

7.4.3. Effects of micro-organisms on mtDNA

Infections by micro-organisms, whether causing diseases or living as symbionts, have been shown to influence mtDNA identity of host species in arthropods (references in HURST & JIGGINS 2005). Therefore undetected influence of possible mtDNA-shifts following microbial invasion can misdirect population genetic studies derived from solely mitochondrial-oriented phylogenies. The same holds true for mtDNA constitution of sister taxa influenced by introgression of mitochondria via hybridisation events (JIGGINS 2003). The influence of mtDNA alteration by microbial infection on phylogenetic studies solely derived from mtDNA cannot be neglected. The infection with *Wolbachia* bacteria for example, can influence 20% of all insects at any point in time (references in HURST & JIGGINS 2005) and infection levels in spiders are reported to reach levels even as high as 80-100% throughout different taxonomic levels (BALDO et al. 2008). Despite these alarming facts bacterial infections do not presuppose replacement of mtDNA, and subsequent evidence of an infection does not necessarily imply mtDNA to be useless for phylogenetic or biogeographic interpretations (BALDO et al. 2008). It is simply indispensable to validate mtDNA markers for correct barcoding, phylogenetic, biogeographic or systematic studies of any taxonomic level (JIGGINS 2003, BALDO et al. 2008, see chapters 4, 5 and 6).

In summary, the influence of mtDNA alteration via micro-organisms in Trogulidae at present seems to be negligible as no incongruence between morphological characters and phylogenetic results could be detected. The *Trogulus tricarinatus* species-group may represent one exception comprising a number of cryptic species as well as several morphologically indiscernible but genetically diversified lineages. Furthermore, the majority of the Central European lineages of this group are parthenogenetic but sexual populations are interspersed. This is suspicious as the micro-organisms mentioned often enforce feminisation of their hosts (HURST & JIGGINS 2005). Although parthenogenesis was shown not to be obligatorily linked with *Wolbachia* bacteria (GRAPUTTO et al. 2005), the degree of genetic diversification found in these lineages is in need of further investigation.

7.4.4. Usability of the cytochrome *b* gene as molecular marker for Opiliones

This study revealed cyt*b* as very useful for phylogenetic analysis on a species to species-group level within Opiliones (see chapters 4, 5 and 6). Nevertheless this gene has some drawbacks that could not be eliminated when refining the generally applied methods. At first it was not possible to design a reverse primer upon a completely conservative region. The final primer sequence, as listed in the methods section is the result of the usual trial-and-error method to be applied on any organism without matching reference sequences in GenBank. The primer therefore incorporates a large number of ambiguous positions, reducing its stringency. For this reason the annealing temperature had to be reduced, increasing the risk of mispriming. In about 20% of all sequenced specimens this resulted in the amplification of an additional 70 bp fragment (Fig. 7.1*a*) that could not be removed by gel extraction. The explanation is a possible reverse-primer binding site about 70 bp from the forward-primer site. In cases where this site matched the sequence of the reverse primer more adequately than for the designated site the amplification of the 70 bp fragment dominated that of the expected 630 bp fragment. Nevertheless, sequences from most individuals could be obtained and sequencing of low amounts of 630 bp fragments is possible via cloning or amplifying two smaller fragments of cyt*b*, thereby excluding the 70 bp-primer site. For obtaining better results I suggest to design a new reverse primer for cyt*b* when additional information on mitochondrial sequences and on the organisation of the mitochondrial genome of Opiliones becomes available.

Although cyt*b* is particularly informative on species-level, it is very rich in adenine and thymine and quickly saturates at the third codon position with increasing phylogenetic distance of compared taxa (see also GIMENO et al. 1997, CROZIER & CROZIER 1993, SIMON et al. 1994). Cyt*b* becomes particularly uninformative at genus- to subfamily-level and may be expected to cause a higher level of homoplasy with substitutions being dominated by adenine-thymine transversions (GIMENO et al. 1997). Further problems concerning mitochondrial genes in general are discussed by MUELLER (2006).

8. General conclusions

This study has shows the necessity of a revision of the western Palearctic harvestmen family Trogulidae in taxonomic, systematic and evolutionary terms. The traditional system of seven genera and approximately 40 species turned out to be artificial and was neither phylogenetically organised nor was the value of morphological characters for delineation of taxa on different phylogenetic levels correctly understood.

It could be demonstrated that a combination of molecular genetic, morphological, morphometrical and distributional data is sufficient to enable the delineation of species and species-groups within Trogulidae. A combination of evidences from all these different character sets is necessary to verify their congruent results and thereby sound taxonomic conclusions can be obtained.

Taxonomic achievements presented in this thesis comprise the evaluation of the generic system of Trogulidae and two exemplary revisions of species-groups within the genus *Trogulus* (chapter 4 to 6). Of the fourteen species treated within these species-groups eight are described as new and four additional cryptic species are annotated (chapter 4 to 5). This extraordinary amount of cryptic diversity is corroborated by the overall phylogenetic analysis of Trogulidae, rating the number of yet undescribed species by 150-235%, especially in *Trogulus* and the enlarged genus *Calathocratus* (chapter 6). With respect to the current biodiversity debate the Trogulidae seem to be a leading group for further taxonomic and systematic investigation within the European harvestmen fauna.

Despite group-specific conclusions it appears advisable to examine some results in other groups of Opiliones. The revision of Trogulidae showed penial morphology to be only partially informative on species level but well suitable for the delineation of higher phylogenetic levels (chapter 6.4.4). Although penial morphology is advocated as key character for species delineation in Opiliones this may not be the case in all taxa. In families that lack expandable parts of the penial glans in combination with generally uniform penial morphology (e.g. Phalangiidae, Sclerosomatidae, Trogulidae) there might be less possibility to diversify genital characters. Speciation in these groups might not be outlined by modification of the penis. A lack of characters needed for species diagnosis may be inherent.

By investigating historical geographic scenarios the evolution of the considered species became plausible and apparently their history is connected with the paleogeography of the respective area. Consequently, in respect to their recorded species richness and their small scaled distribution areas, the Trogulidae are outlined as a model group for biogeographic investigations within the western Palearctic fauna (chapter 5.4.3).

Genetic features of the study object are discussed in detail (chapter 7). Heteroplasmy is assumed to influence the evaluation of sequences and to infer a 1% error on genetic distances but this does not seriously hinder the use of sequence data for molecular phylogenetic investigations. Heteroplasmy restricts the use of mitochondrial rRNA genes as molecular markers usable for molecular genetics as they may be difficult or even impossible to edit. For ND1 a major gene re-arrangement is assumed, apparently dependent on the family status of the investigated Opiliones. Furthermore, the usability of cyt*b* for phylogenetic studies in Trogulidae and the influence of feminising bacteria are discussed.

Finally, all species-level names used within *Trogulus* are listed and annotated in Appendix 12.3 to give some guidance for further taxonomic treatment. A preliminary key is added for the genera of Trogulidae (Appendix 12.1) and for all valid species within *Trogulus* (Appendix 12.2).

9. Acknowledgements

10. Zusammenfassung

Die Phylogenie und Verwandtschaft der west-paläarktischen Weberknecht-Familie Trogulidae wird dargestellt. Das traditionelle System aus sieben Gattungen und etwa 40 Arten erschien bisher künstlich, und ein phylogenetischer Ansatz ebenso wie eine umfassende Revision wurden seit langem gefordert. Die Arten sind aufgrund ihrer einförmigen Morphologie nur ungenügend charakterisierbar, und ihre zuverlässige Abgrenzung ist durch die Variabilität der wenigen bestimmungsrelevanten Merkmale zusätzlich erschwert. Um Artgrenzen aufzuzeigen, wurden das mitochondriale Cytochrom-*b*-Gen und das nukleäre 28S rRNS-Gen analysiert. Die meisten Gattungen und Arten der Trogulidae wurden einbezogen; als Außengruppe dienten die Nemastomatidae mit acht Gattungen und die monotypische Familie Dicranolasmatidae. Phylogenetische Ergebnisse mit Berechnungen mittels Bayesian analysis, Maximum Parsimony, Maximum Likelihood und Neighbor Joining werden mit Verbreitungsdaten, morphologischen Merkmalen und Diskriminanz-Analysen morphometrischer Werte verglichen. Alle Datensätze kommen generell zu übereinstimmenden Aussagen. Um die Eignung dieser Methodik zu demonstrieren, werden zwei Artengruppen exemplarisch revidiert; die *Trogulus hirtus*-Artengruppe und die *Trogulus coriziformis*-Artengruppe. Erstere ist auf dem mittleren bis nordwestlichen Balkan verbreitet. Innerhalb dieser Artengruppe wird *T. tricarinatus* ssp. *hirtus* in den Artrang erhoben, und vier neue Arten werden beschrieben (*T. karamanorum* [manuscript name], *T. melitensis* [man.n.], *T. pharensis* [man.n] und *T. thaleri* [man.n.]). Die *Trogulus coriziformis*-Artengruppe ist auf den westlichen Mittelmeerraum beschränkt. In dieser Artengruppe werden *T. coriziformis* und *T. aquaticus* neu definiert, *T. cristatus* und *T. lusitanicus* werden revalidiert und vier Arten als neu beschrieben (*T. balearicus*, *T. huberi*, *T. prietoi*, *T. pyrenaicus*). In beiden Artengruppen existieren möglicherweise weitere kryptische Arten, die hier aber nicht beschrieben werden. Das unterschiedliche relative phylogenetische Niveau der Artengruppen wird dargestellt. Diese Ergebnisse werden sowohl für die Artengruppen-Revision der Gattung *Trogulus* als auch für die des Gattungssystems der Familie Trogulidae herangezogen. Der Familienrang der monotypischen Dicranolasmatidae wird abgelehnt, und es wird vorgeschlagen, *Dicranolasma* in die Trogulidae zu integrieren. Die nahe verwandten Gattungen *Calathocratus*, *Platybessobius* und *Trogulocratus* erwiesen sich als para- bzw. polyphyletisch. Sie werden unter dem ältesten Namen *Calathocratus* zusammengefaßt. Die kryptische Diversität innerhalb der Trogulidae ist hoch. Sie wird über morphologische, chorologische und, an diesen Merkmalen geeicht, auch über genetische Daten ermittelt. Diese Diversität erreicht bei *Trogulus* und in der Gattung *Calathocratus* sensu lato 150-235%. Für eine Organismengruppe innerhalb der gut untersuchten europäischen Fauna ist das ein bemerkenswert hoher Wert. Genetische Besonderheiten der Trogulidae (Heteroplasmie, mögliche Änderungen der Genordnung auf dem Mitochondrium) und die Verwendbarkeit des Cytochrom-*b*-Gens für phylogenetische Untersuchungen an Opiliones werden diskutiert.

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12. Appendices

12.1. Preliminary key to the genera of Trogulidae

Key to genera of Trogulidae (according to chapters 6.4.1 and 6.4.2).

1 Body globular, head cap either small and branches not drawn out distally (except papillae) or prominent bifurcate with eyes situated on its branches **2**

1* Body dorsoventrally flattened and elongated, head cap prominent, eyes situated on the prosoma **4**

2 Branches of head cap small, prominent papillae only at the outside pointing distally, body size small (2-6 mm) **3**

2* Branches of head cap prominent, papillae pointing inwards, eyes situated on the branches .... ***Dicranolasma***

3 Body size 2 mm, tibia of legs with two ventral rows of elongated papillae to conceal tarsus and tibia if legs are tucked up. Tarsal formula 3-6-3-3. Only north-western Greece and southern Albania .... ***Kofiniotis***

3* Body size 2-6 mm, tibia without elongated papillae, number of segments of tarsus II 2-4, of tarsus III and IV 3-4. Disjunct distribution from the north-western Balkan Peninsula and Italy throughout Central Europe to the northern Iberian Peninsula and on the north-western African Coast .... ***Anelasmocephalus***

4 Tarsus II with two segments .... ***Trogulus***

4* Tarsus II with one segment **5**

5 Tarsi I-IV all with one segment. Restricted to eastern Crete .... ***Anarthrotarsus***

5* Tarsus III or IV with more than one segment. Disjunct distribution throughout the Mediterranean area, the Near East, Caucasus and Kyrgyzstan

.... ***Calathocratus* (including *Platybessobius* and *Trogulocratus*)**

12.2. Preliminary key to the genus *Trogulus*

This preliminary key is designated to enable determination of species-groups and species of *Trogulus* accepted in this thesis. For figures please refer to the original publication of the respective species (listed in chapter 12.3). Species-groups are further delineated in chapter 6.4.3. Yet undescribed taxa are excluded. About 40 new taxa are in need of description thus this key will change progressively. Use the key only with males, determine the position of the penial stylus. Subsequent determination of correct dorsal and ventral side of penis is crucial. In some taxa (e.g. *T. cristatus*, *T. tingiformis*) the long and slender penial stylus easily breaks off.

1 Penial stylus straight, a simple prolongation of the truncus **2**

1* Penial stylus bent off the axis of the penis truncus, at least in distal third **3**

2 Distal segment of tarsus II as long as or longer than basal segment. Distribution disjunct from the Italian to the Iberian Peninsula, adjacent islands and north-western African Coast .... ***T. coriziformis* species-group**, key to species see chapter 5.5.2

2* Distal segment of tarsus II shorter than basal segment, troglobitic, body size >15 (-24) mm. Localised distribution in the central western Balkan Peninsula .... ***torosus***

3 Penial stylus bent towards lateral side **9**

3* Penial stylus bent towards dorsal side **4**

4 Truncus penis with a distinct black dot below glans, often with a distinct bump at intersection of glans to stylus, interocular distance large, thickness of metatarsus II irregular, *T. squamatus* species-group (see chapter 6.4.3) **5**

4* Truncus penis without a distinct black dot below glans, intersection of glans to stylus rounded and regular, interocular distance small, thickness of metatarsus II regular, *T. nepaeformis* species-group (see chapter 6.4.3) **6**

5 Calcaneus of tarsus II about as long as basal segment of tarsus. body size 8-11 mm. Restricted to southern Croatia and Montenegro .... ***squamatus***

5* Calcaneus of tarsus II much shorter than basal segment of tarsus. Widespread from the northern Balkan Peninsula to Central Europe, body size 6-9 mm .... ***closanicus***

6 Segments of tarsus II equal in length, body size of males 7.0-9.5 mm, of females 7.7-11.5 mm, suture between pro- and opisthosoma not curved. Restricted to the Carpathians, central and eastern Alps and adjacent areas .... ***tingiformis***

6* Distal segments of tarsus II at least 1/3 longer than basal segment. Widespread in Central Europe and on the northern Balkan Peninsula **7**

7 Body size small, males 5.2-5.8 mm, of females 5.8-6.9 mm, Restricted to southern central Alps .... ***cisalpinus***

7* Body size larger in both sexes, species aggregate of morphologically similar species in need of revision, preliminary to be separated by geographical restriction **8**

8 Restricted to Italy (Po Valley and southern to central Italian Peninsula) and to low altitudes in northern Switzerland and south-western Germany .... ***martensi***

8* Widespread in Central Europe and on the northern Balkan Peninsula, apparently excluding the distribution area of *T. martensi* .... ***nepaeformis***

9 Stylus bent to the right in dorsal view, penial stylus pronounced and sickle-shaped. Restricted to the central and northern Balkan Peninsula

.... ***T. hirtus*** **species-group**, key to species see chapter 4.5.2

9* Stylus bent to the left in dorsal view, several varying forms of penial stylus **10**

10 Stylus short, not markedly separated from the elongated triangular glans **11**

10* Stylus long, well differentiated from the glans **15**

11 Stylus small and inconspicuous, body size 7-8 mm. Restricted to the Caucasus ... ***rossicus***

11* Stylus a rounded lobe or short hook bent to the left, body size 9.8-16.5 mm **12**

12 Stylus a short hook. Distribution from Montenegro and northern Macedonia to Slovenia, Serbia and Romania **13**

12* Stylus a rounded lobe. Distribution from the southern Balkan Peninsula to Turkey and the Near East **14**

13 Segments of tarsus II equal in length, body and legs covered with long hairs, endogean. Distribution from northern Macedonia to southern Slovenia and southern Romania .... ***banaticus***

13* Segment of tarsus II shorter than basal segment, body and legs covered with long hairs, troglobitic. Distribution along Dalmatian Coast from southern Croatia to Montenegro .... ***setosissimus***

14 From the southern Balkan Peninsula (southern Macedonia and Bulgaria) to Crete .... ***graecus***

14* Asian part of Turkey (Rhodes Island and Kos Island) and Near East, mainly close to Mediterranean coast .... ***gypseus***

15 Stylus bent in right angle from glans. Localised in the Marmara and Black Sea Region of Turkey .... **uncinatus**

15* Stylus bent to the left in dorsal view, body size in males 4.7-6.0 mm, in females 5.0-6.2 mm. From central Balkan to central Europe **16**

16 Stylus massive, body slender. Restricted to Romania .... ***oltenicus***

16* Stylus more narrow, body more compact, variable in most characters. Widespread on the central Balkan Peninsula and Central Europe .... ***tricarinatus***

12.3. Comments on the validity of available *Trogulus*-species names

This list comments on the validity of all available species-taxa names used in combination with the generic name *Trogulus*. It is supposed to give an overview and to propose treatment of names within *Trogulus* but does not replace necessary revisions of species-groups and re-descriptions of species as exemplified in chapters 4 and 5.

Although I investigated a vast amount of specimens and have seen most type material of the subsequently listed taxa, some important collections and types remained inaccessible or could not be traced. The important type collection of C. L. Koch has been split and deposited at three different institutions (Jason Dunlop, pers. comm.), but only the BMNH housed few

Trogulus assignable to the C. L. Koch Collection. Specimens of the collection of J. Sturm, from which KOCH (1839) described several species, were not included. It is most likely that this material is lost, especially as KOCH (1839) mentioned this as dried material and it is unlikely that it persisted till now.

Several types of the Collection E. Simon housed in MHNP are missing. Some reappeared due to erroneous labelling while researching the collection. I believe more types to be relocated in Paris when more detailed studies are possible on the Collection. The Museum in Bucharest, housing the important Collection of S. Avram (CIS), seemed not interested in loaning specimens for scientific research.

Trogulus africanus **H. Lucas, 1849**

1849 is the original date of description (LUCAS 1849). SIMON (1879) cited 1845. The epithet *africanus* was originally assigned to *Trogulus*. When SIMON (1879) described *Calathocratus* based on this species, he used a specimen with different tarsal formula and doubtful geographic origin (BMNH: Label with Simons handwriting „Corsica“; this specimen matches Simons generic description; it probably was loaned to C. L. Koch, after who’s death his collection was forwarded to BMNH; it is not listed in Simon’s collection book). Till now no recollections are known from Corsica and material of the Simon Collection from north-western Africa, Spain and Corsica frequently comprises doubtful locality information (SCHÖNHOFER & MARTENS 2008).

When Simon specified *africanus* to be generotype of *Calathocratus* he used material he thought belonged to *africanus*. But this belongs to a yet undescribed species (tarsal formula 2-1-2-2) not conspecific with *africanus* (tarsal formula 2-1-3-3) and is thereby invalid as generotype of *Calathocratus*. Fortunately *africanus* can be clearly identified by the original drawings of LUCAS (1849) and is confirmed by new material from Algeria (MHNG). The type material of *Trogulus africanus* Lucas, 1849, unlike his other types, is not labeled as “type”, but a vial with Simon’s handwriting (“*Calathocratus africanus*, env. alg. alger”, 2♂, 3♀, 1juv., MHNP 2201) most likely represents Lucas’ original material. LUCAS (1849) cites *africanus* as an abundant species from five localities. This material should be designated as syntype series for *Trogulus africanus*, thereby representing the generotype of *Calathocratus*, as well. Simon frequently united series or replaced original labels according to his actual systematic view and this is likely to be the same in this case.

Calathocratus africanus, by this definition, has a tarsal formula 2-1-3-3, identical with the genus *Trogulocratus* Roewer, 1940. The type species of *Trogulocratus*, *intermedius* Roewer, 1940 apparently is a junior synonym of *Calathocratus*.

In this context I investigated specimens assigned to *Trogulocratus tunetanus* Roewer, 1950 from Tunisia and Algeria and found them conspecific with *Calathocratus africanus* as previously defined. Consequently *Trogulocratus tunetanus* should be a synonym of *Calathocratus africanus*, as well.

Material from Sicily and adjacent islands (MARCELLINO 1965, 1970, 1972), as well as from the Tunisian coast (NHMW) assigned to *Calathocratus africanus*, is very different from the above mentioned material and represents at least one more undescribed species.

TYPES: As aforesaid material of *Trogulus africanus* from MHNP is not labeled as type. 1♂ (BMNH) used by Simon to describe *Calathocratus* is not a valid type. I propose to designate a neotype for *africanus* and subsequently *Calathocratus* using a male of Lucas series MHNP 2201.

***Trogulus albicerus* Sørensen, 1873**

DAHL (1903) specified *T. albicerus* as 1. juvenile stage of *T. nepaeformis*. HANSEN & SØRENSEN (1904) confirmed *albicerus* as valid species, disregarding DAHL'S (1903) annotation that juvenile *Metopoctea* and adult *Trogulus* may represent the same species. Although CHEMINI & GRUBER (1976) approved species status of *Trogulocratus sinuous*, collected at the same type locality as *albicerus* ("Italia media; prope Gennazzano a. cl. Bergsee captus"), they did not comment on the latter taxon. I have seen the types of both species and confirm *Trogulus albicerus* to represent juveniles of *Trogulocratus sinuosus*. As *T. sinuosus* has page priority over *T. albicerus* the latter is to be synonymised with *T. sinuosus*.

TYPES: Syntypes (8 juv.) are located in ZMC.

Trogulus annulipes Lucas, 1849

1849 is the original date of description. SIMON (1879) cited 1845 which has been copied by ROEWER (1923) and MARTENS & CHEMINI (1988). SIMON (1879) placed his juvenile specimen within his new genus *Metopoctea* Simon, 1879. ROEWER (1923) assigned it to *Anelasmocepalus crassipes* Lucas, 1849, which was approved by MARTENS & CHEMINI (1988).

TYPES: 1 juv. is located in MHNP (the number assigned to this series is probably a misinterpretation of the date of description, 1849. The vial has No. 7849).

Trogulus aquaticus Simon, 1879

The taxon is valid and described in chapter 5.5.3.

Trogulus asperatus C. L. Koch, 1839

MARTENS (1978) placed it in synonymy of *T. tricarinatus*. DAHL (1903), however without examining the type, specified it as 3. juvenile stage of *T. nepaeformis*. The type is a disintegrated juvenile that cannot be further assigned, but it belongs to the *T. nepaeformis* or *T. squamatus* species-group. At the type locality (south-western Germany, Zweibrücken) *T. closanicus* was present (CJM 5341) and *T. asperatus* would be best placed in the synonymy of this species.

TYPES: Holotype (1 juvenile) is located in BMNH.

Trogulus balearicus Schönhofer & Martens, 2008

The taxon is described in chapter 5.5.3.

Trogulus banaticus Avram, 1971

AVRAM (1971) compared *T. banaticus* with *T. tingiformis*. Because of her poor drawings MARTENS (1978) synonymised this species with *T. tingiformis* and the name *T. banaticus* was not used any further. I collected material (Romania, Cluij, Closani, CJM 4927) about 50 km from the type locality (Romania: Monts du Banat: Vallée de Scorila, Poiana Mărului) and investigated rich material from Romania and the northern and central Balkan Peninsula to state that *T. banaticus* is a valid and distinct species. It is not related to *T. tingiformis* but to the central Balkan *T. torosus* species-group (chapter 6.4.3, Fig. 6.2). Adult *T. banaticus* can be told apart from *T. tingiformis* by its dark to blackish coloration, markedly massive head and body with a prominent ocularium, suturline between pro- and opisthosoma forms a double-S curvature and stylus of glans penis is different. Both species are sympatric in Romania (north-eastern Transylvania) and probably in the northern Dinaric Alps. In southern Serbia, Montenegro and Macedonia *T. banaticus* is the only one of these two species. Records of *T. tingiformis* from this area refer to *T. banaticus*. In any case a re-description is necessary.

TYPES: Holotype (1♂) is located in CIS.

Trogulus cambridgei Westwood, 1874

Described as *Trogulus cambridgei* Westwood, 1874, SIMON (1979) placed it in its new genus *Anelasmocephalus*. Revised and re-described in MARTENS (1978) and MARTENS & CHEMINI (1988).

TYPES: Depository not specified in MARTENS (1978) or MARTENS & CHEMINI (1988). The material has not been traced.

Phalangium carinatum Linné, *1768*

According to DAHL (1903) this is an erroneous citation of *Phalangium tricarinatum* in Herbst (1799).

Trogulus cisalpinus Chemini & Martens, 1988

Although closely related to *T. nepaeformis T. cisalpinus* is to be separated from that species by its smaller body size and mensural differences (CHEMINI & MARTENS 1988). Material for molecular investigation is still unavailable, but this is a valid species, restricted to the central southern Alps.

TYPES: Holotype (1♂) is located in ZMB (28940), paratypes (17♂, 17♀) in ZMB, CJM, MTSN, MV, NHMW and MSNB.

***Trogulus closanicus* Avram, 1971**

Synonymised with *T. nepaeformis* by MARTENS (1978). WEISS (1978) pointed to syntopic occurrence of *T. "nepaeformis"* in Romania and *T. closanicus* and separated both forms according to morphometric differences. Characteristics were redrawn by CHEMINI (1984) and thence the species is accepted as valid (but see *T. niger*).

TYPES: Holotype (1♂) is located in CIS.

***Trogulus corcyraeus* Dahl, 1903**

DAHL (1903) specified Greece, Corfu as locus typicus for *T. corcyraeus* and separated the species for its prominent calcaneus of leg II from *T. graecus*. He was disapproved by STARĘGA (1976) who united both species within *T. graecus*. Cyt*b* data showed high distance values between various populations assigned to *T. graecus* and a lineage comprising material from Corfu (CJM 5042) and Igoumenitsa from the adjacent mainland (CJM 5083) was clearly separated (Fig. 6.4, only CJM 5083 shown). *T. corcyraeus* should be redefined within a revision of the composite species *T. "graecus"*.

TYPES: Syntypes (4♂, 5♀, 1juv) are located in ZMB (12003, 12004).

***Trogulus coreiformis* C. L. Koch 1839**

KOCH (1839) did not specify the origin of his material. AUSSERER (1867) assigned specimens from Tyrol (Paschberg, Mühlau) to *T. coreiformis* but the species is not recognizable by the data presented there. In respect to Koch's uninformative drawings and the lack of type and type locality this name should not be used any further.

TYPES: Material is lost (Coll J. Sturm, Nürnberg).

***Trogulus coriziformis* C. L. Koch, 1839**

The taxon is valid and described in chapter 5.5.3.

Trogulus crassipes Lucas, 1849

1849 is the original date of description. SIMON (1879) cited 1845 which has been copied by ROEWER (1923) and MARTENS & CHEMINI (1988). ROEWER (1923) assigned this species to *Anelasmocephalus*. This was approved by MARTENS & CHEMINI (1988) who re-described the species in detail.

TYPES: 3♂, 5♀ are located in MHNP (the number assigned to this series is probably a misinterpretation of the date of description, 1849. The vial has No. 7849).

Trogulus cristatus Simon, 1879

The taxon is valid and described in chapter 5.5.3.

Metopoctea exarata Simon, 1879

The use of this name is disapproved and discussed in chapter 5.5.3 (see *T. pyrenaicus*).

TYPES: Syntypes (6 juv. of 2 different species) are located in MHNP (2198).

Trogulus falcipenis Komposch, 2000

The taxon is valid and described in chapter 4.5.3.2.

Trogulus galasensis Avram, 1971

AVRAM (1971) describes the species upon a single male and female. WEISS (1978) doubts its species status and points to the similarity with *T. nepaeformis* (WEISS 1978) and *T. martensi* (WEISS 1998). The penis morphology drawn by AVRAM (1971) suggests the stylus was broken off and this damaged specimen may show misleading characters. Until the species is recollected at the type locality (Romania, Apuseni Mts., Vallée du Criş Repede) and these characteristics are confirmed, the name should not be used.

TYPES: Holotype (1♂) and paratype (1♀) are located in CIS.

Trogulus graecus Dahl, 1903

This name is commonly used for the large *Trogulus* from the southern Balkan Peninsula (e.g. DAHL 1903, ROEWER 1923, ROEWER 1959, STARĘGA 1976). According to molecular data specimens presently assigned to *T. graecus* split into multiple species-worthy lineages (Fig. 6.4). While the locus typicus in the original description of *T. graecus* is simply "Greece" (DAHL 1903), which is the centre of diversity for this composite species, a redefinition of *T. graecus* and fixation of its type locality is necessary. This may be accompanied by fixation of a lectotypes from the seven syntype series. Of these one male (ZMB 12006) was dissected by Dahl and all appendages and the penis are united on a microscopical slide. This male should be designated as lectotype and the respective locality (Greece, Peloponnese, Patras) specified as locus typicus for *T. graecus*. This is further important because the syntype material most likely comprises more than one species (see *T. corcyraeus*).

Trogulus from southern Italy assigned to *T. graecus* (BRIGNOLI 1968, CJM 2467, CMK Igr) belong to a separate lineage within the composite species *T.* "*graecus*".

TYPES: Syntypes (2♂, 6♀, 2 juv.) are located in ZMB (12005-12011).

Trogulus gruberi Avram, 1971

This is an erroneous description comparing males of *T. tingiformis* with undamaged (*T. gruberi*) and an broken-off penial stylus specimen (AVRAM 1971, ŠHILHAVÝ 1968). Subsequently *T. gruberi* has been synonymised by MARTENS (1978) under the previously described *T. tingiformis*.

TYPES: Depository was not specified for all types, neither was a holotype designated in the publication. Most material for the Avram novelties is located in CIS and NHMW.

Trogulus gypseus Simon, 1879

This name is in use for the medium-sized to large *Trogulus* populations from Turkey and the Near East. The locus typicus is Jerusalem (SIMON 1879) and ŠILHAVÝ (1968) redraw standard diagnostic characters of the male from the type series. Molecular data gained from specimens from western Turkey to Syria shows strong diversification of populations assigned to this epithet (Figs. 6.2-6.4). In some cases clear morphological differences are obvious, but with respect to the sparse material a delineation of single lineages is difficult. Further collections are necessary to access this species complex.

TYPES: Syntypes (1♂, 1♀) are located in MHNP (2192).

Trogulus huberi Schönhofer & Martens, 2008

The taxon is described in chapter 5.5.3.

Trogulus tricarinatus var. *hirta* Dahl, 1903

The taxon is now accepted as *T. hirtus* Dahl, 1903 and described in chapter 4.5.3.1.

Siro inaequipes Karsch, 1884

DAHL (1903) re-specified *Siro inaequipes* (or *S. iniquipes*) as first juvenile stage of *T. nepaeformis* which is reasonable to accept in case of juvenile *Trogulus* types.

TYPES: Material has not been traced.

Trogulus karamanorum [man.n.]

The description of this species is accepted for printing. A preliminary view of this description is given in chapter 4.5.3.2.

Trogulus longipes Haupt, 1956

Fossil from Eocene strata (HAUPT 1956). Affiliation is doubtful and may not represent *Trogulus* at all.

TYPES: Material was not traced.

***Trogulus lusitanicus* Giltay, 1931**

The name *Trogulus lusitanicus* is used for several yet morphologically difficult to delineate genetic clades from the Iberian Peninsula and Morocco. Boundaries of these populations are outlined in chapter 5.5.3.

***Trogulus lygaeiformis* C. L. Koch, 1839**

DAHL (1903) synonymised *T. lygaeiformis* within *T. nepaeformis* without examining any material. KOCH (1839) compared *T. lygaeiformis* with *T. nepaeformis*, but erroneously re-described *T. nepaeformis* upon specimen much larger than *T. nepaeformis* as presently accepted. Thereby *T. lygaeiformis* now has to be compared with species of body size as *T. coriziformis* or *T. graecus*. As KOCH'S (1939) description of *T. lygaeiformis* is insufficient, the type lost and its origin has not been cleared, it is suggested not to use this epithet any further.

TYPES: Material is lost.

***Trogulus martensi* Chemini, 1983**

Described by CHEMINI (1983) from the southern Italian Alps. Molecular data proved it as a distinct species, closely related to *T. nepaeformis* (Figs. 6.2-6.4). Both are difficult to tell apart by genital morphology alone but distribution areas do not seem to overlap. A careful revision of the species of the *T. nepaeformis* species-group is needed to define this taxon even better.

TYPES: Holotype (1♂) is located MTSN (No. 3100)

***Trogulus melitensis* [man.n.]**

The description of this species is accepted for printing. A preliminary view of this description is given in chapter 4.5.3.1.

Phalangium melanotarsum Hermann, 1804

DAHL (1903) determined this species as juvenile of *T. nepaeformis*. He was approved by MARTENS (1978). I do simply neglect former discussions of this epithet (e.g. KOCH 1839, SIMON 1879, AUSSERER 1867, KRAEPLIN 1895) as these authors compare juveniles of different species, and most material is not available for reinvestigation. Although the locus typicus is known (Strasbourg, France) HERMANN's (1804) drawings show a juvenile of the first stages not to be assigned to any other genus than to *Trogulus*. As the name never played a role in systematic literature it is suggested not to reuse the epithet for *Trogulus*.

TYPES: Material seems to be lost.

Acarus nepaeformis Scopoli, 1763

Originally published as *Acarus nepeformis* (*nepiformis* in HAHN 1834), the epithet *nepaeformis* is used as a collective name for a multitude of European *Trogulus* of medium body size and relation of distal segment/basal segment of tarsus II of approximately 1.5. Although several newly described species have been separated compared with *T. nepaeformis*, a delineation and re-description of the original species is still missing. Neglecting older attempts, often referring to different taxa (e.g. KOCH 1839; LATREILLE 1804; HAHN 1834), material from the type locality is to be used for re-description (Slovenia, Idrija). A re-description requires simultaneous delineation of related taxa, like *T. martensi*, *T. closanicus*, and a number of yet undescribed species from Central Europe and the Balkans.

TYPES: Material is definitely lost.

Trogulus niger C. L. Koch, 1839

DAHL (1903) synonymised *T. niger* from Italy (Triest) with *T. nepaeformis* but the type (BMNH) is within the morphological range of the variable *T. closanicus*. Because *T. closanicus* is confirmed for the area near the type locality (Italy, Triest, ZMB 12129) the older name *niger* has priority and replace *closanicus*. Preliminary conservation of *closanicus* is advisable because the delineation of yet undescribed species close to *closanicus* is expected and both may be preserved for valid taxa in the future.

TYPES: Holotype (1♂) is located in BMNH.

Trogulus oltenicus Avram, 1971

MARTENS (1978) synonymised *T. oltenicus* with *T. tricarinatus* but WEISS (1978) approved *T. oltenicus* within his morphometric investigations of *Trogulus* at Podu Olt, Romania. My molecular data show *T. oltenicus* as distinct species within the *T. tricarinatus* species-group (Figs. 6.2-6.4). The species is easy recognizable for its slender body and massive penial stylus (AVRAM 1971) but a re-description is necessary.

TYPES: Holotype (1♂) and paratypes (2♀) are located in CIS.

Trogulus opilionoides L. Koch, 1867

Discussed in SØRENSEN (1873) in combination with *Dicranolasma* and *Amopaum* ROEWER (1923) placed it within *Dicranolasma* which was approved by GRUBER (1998).

TYPES: Material has not been traced.

Trogulus pharensis [man.n.]

The description of this species is accepted for printing. A preliminary view of this description is given in chapter 4.5.3.1.

Trogulus perforaticeps Ausserer, 1867

DAHL (1903) specified it as second juvenile stage of *T. nepaeformis* and AUSSERER's description (1867) seems to refer to *T. nepaeformis* as well (relation of distal segment/basal segment of tarsus II 1.5). His drawing further suggests a juvenile specimen. The locus typicus (Tyrol, Höttinger Berg) is well within the range of *T. nepaeformis* but the type is an indeterminable juvenile it is suggested to follow DAHL (1903) and placing *T. perforaticeps* in the synonymy of *T. nepaeformis*. The name *perforaticeps* never played a role in taxonomic literature.

TYPES: Holotype (1 juv.) is located in NHMW.

Trogulus prietoi Schönhofer & Martens, 2008

The taxon is described in chapter 5.5.3.

Trogulus pyrenaicus Schönhofer & Martens, 2008

The taxon is described in chapter 5.5.3.

Trogulus roeweri Avram, 1971

AVRAM (1971) described *T. roeweri* upon specimen of *T. aquaticus* from Bosnia (SMF 24976). Actually, his series contains three disintegrated females, but the label states eight specimens. Despite this misdirecting circumstance Avram's drawings of the penis suggest the penial stylus to be broken off. WEISS (1978) therefore denied species status of *T. roeweri* and compared it with *T. nepaeformis*. Regarding the shortcomings of the description and type information it is impossible to decide upon the validity of this taxon. It is suggested not to use this epithet in combination with *Trogulus*.

TYPES: Syntypes (1♂, 1♀) should be located in SMF but the relevant series (24976) contains 3♀.

Trogulus rossicus Šilhavý, 1968

The species is the only *Trogulus* in the Caucasus. Medium body size in combination with tarsal segments of equal length and specific genital morphology (ŠILHAVÝ 1968) are distinct characteristics.

TYPES: Holotype (1♂, 321306) and paratype (1♀, 321308) in CVS.

Phalangium rostratum Latreille, 1798

LATREILLE (1798) first placed *rostratum* in *Phalangium* but established *Trogulus* for this species in 1802. Simon did accept and describe *T. rostratus* upon many specimens from France. DAHL (1903) put it in synonymy of *T. nepaeformis*. The name *rostratus* may apply to a species of the *T. nepaeformis* species-group actually present in France and localities correspond to many localities mentioned by SIMON (1879).

TYPES: Material is probably lost.

Trogulus salfii De Lerma, 1948

The name is synonymised within *T. coriziformis* (see chapter 5.5.3).

Trogulus setosissimus Roewer, 1940

This is a distinct and unmistakable species, characterized by dense hair coat giving it an appearance like a *Tegenaria* spider. The distribution area is remarkably small, restricted to the central Dalmatian Coast in Croatia. Specimens were collected from Biokovo Mountain, Hvar Island (type locality) and some mountains near Split. It seems to be a troglobitic species.

TYPES: Syntypes (1♂, 1♀) are located in SMF (9902148).

Trogulus sinuosus Sørensen, 1873

DAHL (1903) specified *T. sinuosus* as 3. juvenile stage of *T. nepaeformis*. CHEMINI & GRUBER (1976) affirmed the validity of the species sinuous but transferred it to *Trogulocratus*.

TYPES: Syntypes (2♂, 3♀) are located in ZMC.

Trogulus squalidus C. L. Koch, 1839

KOCH (1839) separated *T. squalidus* and *T. tricarinatus* by the curvature and perforation of the limbs of the front legs, only. Regarding these minor differences, the locus typicus to be specified with ‘Germany’, only, and the type material probably lost, I approve DAHL (1903) who synonymised *T. squalidus* with *T. tricarinatus*. The name never played a role in taxonomic literature.

TYPES: Material is lost

Trogulus squamatus C. L. Koch, 1839

A distinct and unmistakable *Trogulus* species of the western central Balkan Coast characterised by the calcaneus of leg II equal in length with the basal segment of the tarsus.

TYPES: Type material is lost (Coll. J. Sturm, Nuremberg), material for a re-description is present in ZMB.

Trogulus thaleri [man.n.]

The description of this species is accepted for printing. A preliminary view of this description is given in chapter 4.5.3.1.

Trogulus tingiformis C. L. Koch, 1848

It is clearly defined by representing the only species at its type locality (Upper Bavaria) with tarsal segments II equal in length. Nevertheless, due to the fragility of the penial stylus, easily broken off in preparation, the species was frequently confused and re-described under additional names (e.g. AVRAM 1971, ŠILHAVÝ 1968) till it was re-characterised by MARTENS (1978). Molecular data do not suggest a distinct differentiation between the populations in the Alps and the Carpathians (not shown). The species is often confused with *T. banaticus* (see there).

TYPES: Type material lost, adequate material from the type locality for a re-description is still lacking.

Trogulus torosus Simon, 1885

A distinct and unmistakable *Trogulus* species, characterized by large body size up to 23 mm, lack of hairs on body and legs and the basal article of tarsus II to be longer as the distal one. It seems to be a troglobitic species.

TYPES: Holotype (1♀) is located in MHNP (7781).

Phalangium tricarinatum Linné, 1767

There has been some confusion about the date of description of this species when SIMON (1879) specified 1758. According to HULTH (1907) the 11th edition of Linné's Systema Naturae does not exist (probably a reprint of the 10th edition) and in the 10th edition *tricarinatum* is not listed. Subsequently the description date of this species is 1767, as for the 12th edition.

Within *Trogulus* the correct definition of the name *T. tricarinatus* is by far the most difficult case. It is presently assigned to several nearly inseparable species none of which can be clearly assigned to that name. Although material from the type locality (Dresden, Germany) is present this belongs to one of the many parthenogenetic lineages that invaded Central Europe. Within these lineages molecular systematic revealed a multitude of different, mostly young lineages that is in need of further investigation (see chapter 6.4.3. and 7.4.3, Figs. 6.2-6.4).

MAJCEN (2006) separated 3 distinct forms within Slovenian *T. tricarinatus* by genital morphology. Molecular genetics showed further distinct species to be present on the central Balkan Peninsula. Specimens from Greece differ from these forms by smaller body size (MARTENS 1978) and may represent further species (CJM 2915, 5096). Revision of this species-group is dependent on comprehensive material to delineation the species *T. tricarinatus* itself, to define the multitude of similar species summarised within this epithet and to clarify the relationship and species status of sexual and parthenogenetic lineages widely interspersed in Central Europe.

TYPES: Possibly located in the Linnean Collection, but an inquiry to the Linnean Society has not been answered yet.

***Trogulus tuberculatus* Canestrini, 1876**

According to ROEWER (1923) *T. tuberculatus* is a synonym for *T. nepaeformis*. I have not seen the original description or the type material. According to CHEMINI (1986) no material assigned to *T. tuberculatus* is located in the collection of Canestrini and therefore probably lost. SIMON (1879) stated that Canestrini described *T. tuberculatus* from Italy. This taxon is in need of further investigation.

TYPES: Material is probably lost.

***Trogulus uncinatus* Gruber, 1969**

A valid and distinct taxon from Turkey, easily recognisable by a stylus bent to the left in right angle from truncus (dorsal view).

TYPES: Holotype (1♂) is located in NHMW, paratypes (6♂, 3♀) are located in MG, NHMW and ZIUV.

Trogulus violaceus **Gervais, 1844**

I have not seen the original description (GERVAIS 1844). SIMON (1879) specified it as juvenile *Trogulus*, but does not relate it to any further species. PABST (1953) mentioned the reddish to violet coloration of juvenile *Anelasmocephalus cambridgei* and I would admit to place this name in the synonymy of *Anelasmocephalus*.

TYPES: According to DAHL (1903) located in MNHP, but missing there.

12.4. Morphometric data matrices of Chapter 4 and 5

Data set for morphometric analysis of chapter 5 (Figs. 5.4, 5.14). Discriminant analysis can be accomplished with data corrected and uncorrected by magnification factors. Species: 1=*aquaticus*; 2=*coriziformis*; 3=*cristatus*; 4=*balearicus* sp. nov; 5=*prietoi* sp. nov; 6=*pyrenaicus* sp. nov.; 7=*huberi* sp. nov.; 8=*lusitanicus* agg. Alicante; 9=*lusitanicus* agg. Portugal; 10=*lusitanicus* agg. Gibraltar; 11=*lusitanicus* agg. Albergaria. Sex: m=1; f=2; all in mm.

Serie	**species**	**sex**	**BL**	**BW**	**CoxII**	**WcoxII**	**CoxIV**	**Eyeout**	**Eyein**	**Wcap**	**Lcap**	**Should**	**MtII**	**BSII**	**DSII**	**LegII**	**TaIV**	**FemI**	**FemII**	**MtIV**	**Penis**
Magnification (x)			*1*	*1*	*4*	*1*	*1*	*10*	*10*	*4*	*4*	*4*	*4*	*4*	*4*	*1*	*4*	*4*	*1*	*4*	*4*
NHMW	1	1	9.45	3.4	10.1	3.9	4.15	6.9	9	4.8	4.8	6.7	10.1	3.8	4.3	12.6	4.3	8.5	3.15	10.9	9.6
BRINS	1	1	10	3.6	10.3	4.1	4.2	6.8	8.8	4.7	4.7	7.1	12.4	4.55	5.1	14.6	4.5	9.5	4.3	12.6	10
NHMP 2191	1	1	10.85	4.1	11.7	4.5	4.8	7.4	10	5.3	5.1	7.9	12.1	4.45	5.1	14.7	4.7	10.5	4.4	11.9	10.9
NHMP 2191	1	1	11.4	4.2	11.6	4.4	4.9	7.1	9.3	5.1	5.4	7.4	12.3	4.2	5.1	15.1	4.2	10.8	5.5	12	11.55
NHMP 2191	1	1	11.65	4.6	12.3	4.85	5.35	7.4	10	5.3	5.6	8.3	13.5	4.65	5.4	16.1	4.9	11.6	5	13.3	10.95
NHMP 2191	1	1	11.7	4.4	12.3	4.9	5.4	7.9	9.5	6	6.1	8.1	13.6	4.85	5.45	16.7	4.9	12.3	5.1	13.25	11
CJM 3056	1	1	11.9	4.25	12	4.85	5.2	7.3	9.5	5.7	5.8	8	14.2	4.7	5.7	17.3	5	12.4	5.5	14.3	10.5
MNHP Nov.5	1	1	12.1	4.55	12.3	4.8	5.25	7.4	9.85	5.6	6	8.3	13.45	4.35	5.7	16.1	5.2	11.4	4.7	13.2	10.8
NHMP 2191	1	1	12.45	4.6	13.2	5.2	5.4	7.7	10.4	5.8	5.8	8.9	15	5	6.1	18.5	5.35	12.8	5.65	14.25	11.6
NHMP 2191	1	1	13.1	4.7	12.8	5.1	5.6	7.1	9.7	5.7	5.5	8.2	13.9	5.8	6.4	17.9	4.8	11.1	5.4	14	12.4
CJM 3058	1	2	11.2	4.4	11.8	4.55	5.1	8.2	10.1	5.6	5.6	8.2	12.3	4.3	5.1	14.9	5.1	10.5	4.35	12.85	
NHMP 2191	1	2	12.4	4.9	12.2	4.8	5.4	8.7	11.1	5.9	5.4	9.1	13.4	4.3	5	15.9	4.95	11.9	4.8	13.7	
NHMW	1	2	12.8	5	12.9	4.95	5.5	8.5	10.9	6.4	6	9.2	14.4	4.6	5.5	17	5.5	12.1	5.1	14.8	
CJM 5446	1	2	12.9	5.1	12.8	4.9	5.4	8.6	11	6.3	6.2	9.2	13.5	4.7	5.4	15.8	5.4	11.7	4.7	13.8	
NHMP 2191	1	2	13.7	5.3	13.6	5.15	6.25	9.1	11.2	6.6	5.9	9.5	14.4	4.5	5.4	14.6	4.9	12.4	5.3	14.7	
NHMP 2191	1	2	14.1	5.1	13.9	5.5	6.2	8.9	11.7	6.6	6.4	9.5	14.3	4.75	5.4	17.4	5.5	13.3	5.55	15.7	
CJM 1058	2	1	9.4	3.8	10.9	4.35	4.65	6.7	8.5	5.2	5	7.5	11.35	3.8	4.9	13.7	4.3	9.5	4	11.9	10.65
CJM 1058	2	1	9.45	3.5	10.3	4	4.25	5.7	8.2	4.6	4.3	7.1	10.3	3.9	4.9	12.6	4.05	8.7	3.6	10.7	8.7
CJM 1058	2	1	9.45	3.8	10.6	4.1	4.6	5.7	7.8	4.7	4.2	7	10.5	3.8	5.1	13	4.2	8.8	3.7	11.7	9.5

Serie	**species**	**sex**	**BL**	**BW**	**CoxII**	**WcoxII**	**CoxIV**	**Eyeout**	**Eyein**	**Wcap**	**Lcap**	**Should**	**MtII**	**BSII**	**DSII**	**LegII**	**TaIV**	**FemI**	**FemII**	**MtIV**	**Penis**
Magnification (x)			*1*	*1*	*4*	*1*	*1*	*10*	*10*	*4*	*4*	*4*	*4*	*4*	*4*	*1*	*4*	*4*	*1*	*4*	*4*
CJM 1058	2	1	9.75	3.9	10.3	4.05	4.45	5.7	8.1	5.1	4.9	7.4	10.1	3.5	4.5	12.6	3.9	8.4	3.6	10.6	9.2
CJM 1058	2	1	9.75	3.7	10.7	4.15	4.45	6.1	8.4	5	4.5	7.1	10.1	3.95	4.9	12.5	4.2	9.1	3.7	10.85	10.1
CJM 1058	2	1	9.8	3.6	10.2	4.1	4.4	5.7	7.6	5	4.4	6.9	10.7	4.05	5	13.1	4.25	9.1	3.85	11.15	10
CJM 5009	2	1	9.9	3.75	10.8	4.2	4.5	5.85	8.15	5	5.3	7	11.1	4.05	5.25	13.7	4.25	9.2	4.15	11.4	9.8
CJM 5009	2	1	10.15	3.95	11.2	4.4	4.6	6.3	8.6	5.9	5.2	7.7	12.15	4.4	5.85	14.6	4.3	9.9	4.3	12.8	10.4
CJM 5051	2	1	10.15	4	10.5	4.15	4.575	6	8.3	5.2	4.7	7.2	10.4	3.65	4.8	12.7	4	9.1	3.8	10.85	9.85
CJM 5051	2	1	10.25	3.9	10.6	4.15	4.65	5.9	8.2	5.2	4.6	7.1	11.2	3.9	5.05	13.6	4.1	9.5	3.95	11.5	10.1
CJM 5051	2	1	10.9	4.25	11.2	4.4	4.8	6.2	8.5	5.1	5	7.45	11.8	3.95	5.05	15.3	4.55	10	4.2	12.2	10.6
CJM 5423	2	1	11.7	4.6	12.8	4.9	5.2	7.3	9.7	5.9	5.3	8.3	12.85	4.4	5.4	15.7	4.55	10.5	4.45	12.95	10.15
CJM 5051	2	2	10.7	4.1	10.8	4.2	5	6.4	8.6	5.4	5.1	7.4	10.7	3.7	4.55	12.8	4.3	9.1	3.8	11.7	
CJM 1058	2	2	10.75	4.25	10.9	4.3	4.75	6.1	7.9	5.6	5.1	7.8	11	3.6	4.7	13.4	4.35	9.6	4.05	11.9	
CJM 1058	2	2	11.1	4.6	11.6	4.55	5.05	6.45	8.95	5.2	5.8	8.4	11.5	3.7	4.8	13.8	4.6	10	4.1	12.6	
CJM 5009	2	2	11.2	4.1	11.2	4.4	4.9	6.6	8.6	5.6	4.5	7.9	12.25	3.95	5.3	14.5	4.4	9.6	4.25	12.55	
CJM 5009	2	2	11.35	4.7	11.3	4.4	5.05	6.25	8.5	5.8	5	7.7	12	3.6	5.1	14.3	4.3	9.9	4.25	12.5	
CJM 5051	2	2	11.45	4.55	11.3	4.45	5.65	6.2	8.3	5.7	5.1	8	11.4	3.8	4.3	13.4	4.2	9.6	3.95	11.6	
CJM 5051	2	2	11.6	4.75	12.7	4.55	5.05	6.7	9.3	6.1	4.1	8.3	12	3.7	4.9	14.1	4.6	10.1	4.2	12.6	
CJM 5051	2	2	11.6	4.5	12	4.6	5.1	7.1	9.5	5.8	4.8	8.4	11.7	3.65	4.9	13.7	4.5	9.2	4	12.5	
CJM 1058	2	2	11.85	4.9	12.1	4.8	5.4	6.4	8.9	5.3	5.9	8.5	12.05	3.9	4.65	14	4.45	9.9	4.2	12.7	
CJM 1058	2	2	11.85	4.85	12	4.8	5.2	7.4	9.4	6.1	6.1	8.6	11.9	3.75	4.6	14.3	4.35	10.3	4.2	13.1	
CJM 1058	2	2	12.05	4.6	11.9	4.6	5.2	6.8	9.3	5.7	5.4	8.3	12.05	4.1	5.2	14.2	4.4	10.1	4.3	12.9	
CJM 5009	2	2	12.1	4.7	12.1	4.6	5.2	7.6	10	6.3	5.7	8.3	12.4	4.05	5.15	14.9	4.7	10.6	4.35	13.5	
SMF 1346	3	1	9.3	3.3	9.6	3.8	4.2	5.7	7.7	4.4	4.5	6.3	10.4	3.3	5.1	12.6	3.5	8.6	3.75	9.9	10
NHMP 2193	3	1	9.45	3.6	9.8	3.9	4.3	5.6	7.3	4.8	4.3	6.4	10.1	3.65	4.35	13.1	4.1	9.3	4.9	11.2	
CJM 4972	3	1	9.55	3.4	9.9	3.95	4.1	5.2	7.3	4.6	4.3	6	10.8	3.3	5.35	13.3	4	9.1	3.9	11.1	9.25
CJM 1589	3	1	9.75	3.5	10.2	3.9	4	5.3	7.3	5.1	4.9	6	10.25	3.5	5.5	13.1	4.15	8.8	3.85	10.4	8.5

Serie	**species**	**sex**	**BL**	**BW**	**CoxII**	**WcoxII**	**CoxIV**	**Eyeout**	**Eyein**	**Wcap**	**Lcap**	**Should**	**MtII**	**BSII**	**DSII**	**LegII**	**TaIV**	**FemI**	**FemII**	**MtIV**	**Penis**
Magnification (x)			*1*	*1*	*4*	*1*	*1*	*10*	*10*	*4*	*4*	*4*	*4*	*4*	*4*	*1*	*4*	*4*	*1*	*4*	*4*
NHMB 56-b	3	1	10.3	3.9	10.9	4.65	4.25	6.5	8.4	5	4	7	11.75	3.65	5.25	14.1	4.1	9.4	4.2	11.2	10.95
NHMP 12675	3	1	10.55	3.8	11	4.3	4.6	5.6	7.9	4.8	3.8	7.1	11.8	3.6	4.9	14.1	4.1	9.6	4.25	11.8	10.35
SMF 1346	3	2	10.6	4.4	11	4.35	4.8	6.6	8.8	4.9	3.9	7.2	10.4	3.35	5.2	13.2	3.7	9.6	4.05	10.6	
SMF 1345	3	2	10.8	4.2	11.5	4.1	4.85	6.4	8.6	5	4.6	7	10.6	3.2	4.6	12.8	3.8	9.2	3.95	10.8	
CJM 1590	3	2	10.95	4.3	10.6	4.2	4.7	6.1	8.2	5	4.5	7.1	11.1	3.3	4.95	13.4	4.05	9.2	4.1	11.7	
CJM 4972	3	2	11.15	4.45	11.6	4.55	5.1	6.5	8.5	5.1	4.2	7.8	11.5	3.4	5.2	14.2	4.2	10.2	4.25	11.5	
CJM 2066	3	2	11.3	4.6	11.2	4.35	4.85	6.2	8.5	5.7	4.8	7.2	12.1	3.2	4.7	14.5	4.1	9.5	4.3	12.2	
MHNG	3	2	11.55	4.2	11.9	4.5	4.8	6.6	8.9	6	5.1	8	12.7	3.75	4.6	14.7	4.4	9.8	4.5	12	
CJM 4972	3	2	11.8	4.7	11.4	4.55	5.2	6.1	8.7	5.4	4.9	7.2	12.45	3.5	5.4	14.8	4.5	10.4	4.55	12.55	
NHMP 12675	3	2	11.9	4.7	11.9	4.5	5.3	6.6	8.6	5.8	5.3	7.6	12.4	3.5	4.7	14.6	4.4	9.9	4.5	12.3	
NHMP 23561	3	2	11.9	4.5	12.4	4.7	5.55	6.65	9	5.8	5.8	7.6	12.25	3.1	4.85	14.5	4.2	9.9	4.6	11.9	
NHMP 2193	3	2	12.8	4.9	12.8	4.9	5.6	7.1	9.6	6.1	5.3	8.1	12.6	3.5	5.2	15.3	4.4	10.8	4.7	12.8	
SMF 11816	4	1	7.7	3	7.8	3.1	3.4	4.5	6.2	3.6	3	5	8.3	2.3	3.8	9.8	2.7	6.3	2.9	7.25	
BMNH	4	1	7.9	2.95	7.9	3.05	3.35	4	5.8	3.6	3.15	5.1	8.7	2.25	4.05	10.1	2.7	6.6	2.95	7.5	
CCP 1937	5	1	8.2	3.1	7.9	3.2	3.5	3.9	5.6	4.1	3.5	5	9.7	3.1	4.4	11.2	3.6	7.3	3.3	9.4	
BMNH	5	1	8.35	3.1	8.6	3.4	3.7	4.4	6.5	4.3	3.6	5.4	8.3	2.6	3.6	10.4	2.85	7.3	3.15	8.1	7.9
BMNH	5	1	8.35	3.45	8.7	3.4	3.75	3.6	5.4	4.1	3.45	5	9.6	2.6	3.9	11.1	3.1	7.2	3.25	9.4	8.4
CJM 5321	5	1	8.35	3.13	8.2	3.3	3.6	4.2	5.65	4	4	5.2	9.6	3.1	4.4	11.5	3.3	7.6	3.55	8.9	7.95
CCP 1937	5	1	8.55	3.1	8	3.25	3.55	4.2	5.9	4.1	3.5	4.8	9.8	3.1	4.4	12	3.6	7.7	3.6	9.65	8.15
CJM 2733	5	1	9.25	3.65	8.5	3.5	3.9	4.6	6.1	4.4	3.9	5.6	10.75	3.3	4.2	12.6	3.4	8.9	3.95	10.1	8.45
CCP 1953	5	1	9.3	3.6	9.25	3.55	4.05	5.35	6.8	4.3	4	5.5	11.3	4.4	4.8	14	3.7	8.9	4.1	10.5	9.9
CCP 1923	5	2	8.6	3.5	8.6	3.35	3.8	4.5	6.1	4.1	3.85	5.7	9.5	3	4.25	11.2	3.25	7.5	3.3	9.15	
CJM 3068	5	2	9.15	3.5	8.85	3.5	3.9	4.9	6.8	4.5	3.8	6	9.3	3.4	4.4	11.4	3.3	7.5	3.3	8.8	
CCP 1937	5	2	9.25	3.65	9	3.45	3.9	4.05	5.6	4.3	3.5	5.6	10.5	2.95	4.3	11.3	3.5	7.7	3.6	10.1	
CCP 1936	5	2	9.4	3.7	9.2	3.65	4	3.9	5.9	4.3	3.5	5.8	11.2	3.2	4.3	11.8	3.6	8.6	3.9	10.25	

Serie	**species**	**sex**	**BL**	**BW**	**CoxII**	**WcoxII**	**CoxIV**	**Eyeout**	**Eyein**	**Wcap**	**Lcap**	**Should**	**MtII**	**BSII**	**DSII**	**LegII**	**TaIV**	**FemI**	**FemII**	**MtIV**	**Penis**
Magnification (x)			*1*	*1*	*4*	*1*	*1*	*10*	*10*	*4*	*4*	*4*	*4*	*4*	*4*	*1*	*4*	*4*	*1*	*4*	*4*
CCP 1937	5	2	9.85	3.8	9.6	3.75	4.2	4.4	6	4.7	4.1	6	10.3	3.1	4.3	12.5	3.6	8.1	3.7	9.9	
CJM 1360	6	1	8.95	3.6	9.8	3.9	4.2	4.5	6.6	4.7	4.8	5.8	10.3	3.7	4.9	11.6	4.15	8.7	3.7	10.7	
CJM 1360	6	2	9.5	4	10.6	4.2	4.6	4.9	7	4.9	4.7	6.1	10.9	3.6	4.5	12.6	4.1	8.8	3.7	11.4	
CCP 561	6	2	9.85	4.1	10	3.95	4.55	5.3	7.2	5	4.5	6.4	11.3	3.45	4.8	13.1	4.3	9.7	3.7	11.5	
CJM 1694	6	2	9.95	3.9	10.3	4	4.5	6.7	8.4	5.1	4.9	7.2	9.5	3.1	4.2	11.6	3.8	8.1	4.25	10	
CCP 561	6	2	10.4	4.15	9.5	4.1	4.7	5.3	7	5.4	4.7	6.9	11.5	3.65	4.6	13.1	3.8	9.1	3.9	11.8	
CCP 732	6	2	10.45	4.2	10.8	4.3	4.8	5.6	7.55	5.2	4.8	6.8	11.6	4.1	4.9	13.5	4.45	9.4	4	11.5	
CJM 5344	7	1	10.45	3.9	10	3.9	4.4	4.5	6.7	5.2	4	6.7	12.8	3.65	5	15	3.9	11	4.7	12.2	9.6
CCP 3323	7	1	10.8	4	10.4	4.1	4.5	4.9	6.8	4.8	4.1	7.1	12.7	4.2	5.2	15.1	3.8	10.2	4.55	12.3	9
CJM 5346	7	2	11.8	4.5	10.5	4.2	4.9	5.3	7.4	5.4	5.1	6.9	13.1	4.1	5.6	15.4	4	10.9	4.7	12.4	
CCP 947	8	2	14.15	5.8	13.8	5.35	6.3	8.8	10.8	7.1	6.2	9.5	16	5.7	6.1	19	5.2	13.6	5.8	15.8	
CCP 3321	9	1	11.3	4.35	12.4	4.9	5.25	6.9	9.3	6	5.8	7.5	11.9	4.15	5.4	14.8	4.4	11.5	4.6	13.1	11.65
CJM 2549	9	2	11.35	4.8	11.7	4.6	5.1	6.2	8.7	5.8	5.4	7.2	11.6	4	5.2	13.2	4.6	10	4.15	12.2	
BRINS	9	2	12.2	5	12.1	4.85	5.5	6.5	9.1	4.3	5.6	7.6	12.6	4.5	5.6	15.1	5	10.9	4.65	13.75	
SMF 1784	9	2	12.3	4.95	12.5	4.8	5.45	6.9	9.1	6	4.5	8.4	12.5	4	5.2	14.2	4.8	10.2	4.3	12.8	
SMF 1365	9	2	12.5	4.95	12.3	4.95	5.5	7.1	9.3	5.4	6.1	7.9	12.6	4.1	5.7	14.7	4.7	10.9	4.6	13.2	
NHMP 2197	10	1	10.7	4.35	12	4.6	4.8	6.5	8.8	5.4	4.9	7	11.6	4.1	5.7	14.6	4.8	10.3	4.35	12.6	
CCP 3624	10	1	12.1	4.85	12.7	4.9	5.5	6.9	9.4	6.2	5.5	7.9	13.1	4.2	4.7	15.4	4.5	10.2	4.5	12.8	10.2
NHMP 2197	10	2	10.9	4.4	11.8	4.5	4.8	6.7	8.9	5.5	5.3	7.2	11.1	4	5.1	13.9	4.7	10.1	4.05	12	
BMNH	10	2	11.95	5	12.8	5	5.8	6.9	9.1	5.8	5.6	7.8	12.6	4.1	4.8	14.6	4.7	10.2	4.35	11.7	
NHMP 2197	10	2	12.35	4.9	12.6	4.9	5.4	7.3	9.6	6	5.8	8.4	11.7	4	5.3	14.6	4.65	10.9	4.5	13.1	
ZMB 11999	10	2	12.7	5.3	12.4	4.9	5.9	5.8	8.4	5.7	5.4	8.1	12.7	3.7	4.6	14.4	4.4	10	4.2	12.5	
BMNH	10	2	12.9	5.4	12.6	4.95	5.7	7.2	9.3	5.5	4.5	9.1	13	4	4.7	15.3	4.9	10.3	4.4	13.1	
CJM 3743	10	2	13.55	5.9	13.3	5.3	6.45	7.3	9.6	6.5	5.3	9.2	14	3.5	4.35	16	4.4	11.1	4.8	14.1	
CCP1966	10	2	13.6	5.7	12.8	5	6.5	6.8	9.2	6.1	5.5	8.5	12.85	3.3	4.6	15.3	4.5	10.9	4.5	13.2	

Serie	**species**	**sex**	**BL**	**BW**	**CoxII**	**WcoxII**	**CoxIV**	**Eyeout**	**Eyein**	**Wcap**	**Lcap**	**Should**	**MtII**	**BSII**	**DSII**	**LegII**	**TaIV**	**FemI**	**FemII**	**MtIV**	**Penis**
Magnification (x)			*1*	*1*	*4*	*1*	*1*	*10*	*10*	*4*	*4*	*4*	*4*	*4*	*4*	*1*	*4*	*4*	*1*	*4*	*4*
ZMB 11999	10	2	13.7	5.85	13	5.3	6.2	6.9	9.5	6.3	5.9	8.5	13.3	3.6	4.6	15.6		10.4	4.6		
NHMP 24831	10	2	14.6	6.1	13.9	5.5	6.4	8.5	9.9	6.5	5.7	9.5	14.4	4.3	4.75	16.1	4.95	11.7	5.1	14.3	
ZMC Alb PF G3	11	1	9.7	4	10.7	4.25	4.6	6.4	8.2	5	5	6.6	10.7	3.8	5.2	13.3	4.4	9.5	3.95	11.4	9.5
ZMC Alb PJ2 2.m	11	1	9.9	4	11.3	4.5	4.7	5.9	8	5.5	5.4	6.8	11.2	4	5.2	14	4.3	9.9	4.2	12	9.9
ZMC Alb PF N3	11	1	10	3.9	11.2	4.4	4.65	6.6	8.6	5.2	5	6.9	11	4	5.3	13.8	4.4	9.8	4.1	11.8	1015
ZMC Alb A1	11	1	10.05	3.85	10.9	4.45	4.6	5.8	8.2	5.7	5.3	7	11.1	4.25	5.7	14	4.3	10	4.15	11.7	9
ZMC Alb PFK1	11	1	10.1	3.8	10.9	4.3	4.6	5.6	7.9	5.3	5.2	6.8	10.9	3.85	5	13.5	4.4	10	4.15	11.8	9.8
ZMC Alb PJ2 3.m	11	1	10.35	4.1	11.4	4.5	4.75	6.5	8.5	5.7	5	6.9	11.2	4.2	5.25	14.1	4.5	10.3	4.25	11.9	10
ZMC Alb PF G1	11	1	10.5	4.2	11.3	4.5	4.8	6.3	8.4	5.3	5.4	6.9	11.3	3.8	5.4	14.1	4.4	10	4.2	11.3	10.55
ZMC Alb PFK1	11	1	10.6	4.6	11.4	4.55	4.6	6.7	9.2	5.3	5.2	7	11.3	4.4	5.35	14.2	4.5	10.2	4.25	12.1	11.35
ZMC Alb PJ2 1.m	11	1	10.6	4.4	11.6	4.6	4.8	6.3	8.5	5.8	5.7	7.1	11.6	4.25	5.7	14.4	4.6	10.4	4.4	12.5	10.4
CCP 3332	11	1	10.65	4.15	11.8	4.55	5	7.6	8.4	6	5.1	7.1	12	4	5.3	14.5	4.6	10.6	4.4	13.1	11.4
ZMC Alb A1	11	1	10.8	4.25	11.9	4.6	4.9	6.6	8.8	5.5	5.1	7.3	11.7	4.2	5.6	14.7	4.6	10.7	4.4	12.8	10.2
CCP 3331	11	1	11.7	4.5	12.2	4.7	4.9	6.9	8.8	5.8	5.3	7.3	12.6	4.2	5.6	15.5	4.8	11.4	4.8	13.5	10.9
ZMC Alb day 3 N2	11	2	10.9	4.5	11.2	4.35	4.8	6.5	8.5	5.3	4.6	7.3	10.9	3.8	5.25	13.7	4.4	10.2	4	11.6	
ZMC Alb PFK1	11	2	11.2	4.7	11.5	4.5	4.9	7	9	5.7	5.1	7.4	11.7	4	5.1	14.2	4.6	10.3	4.3	12.6	
ZMC Alb day 6 J5	11	2	11.25	4.55	11.6	4.5	4.9	6.7	8.9	5.8	5.1	7.7	11.3	4.1	4.8	13.7	4.55	10	4.2	12.4	
ZMC Alb day 8 D1	11	2	11.25	4.7	11.5	4.55	5.1	6.7	8.8	5.7	5.1	7.2	11.25	3.7	5.3	14.1	4.4	10.7	4.2	12.3	
ZMC Alb sequ. day 6	11	2	11.5	4.65	11.9	4.5	5	6.6	8.4	5.5	5.2	7.4	11.7	4.05	5	14.1	4.6	10.7	4.35	13.1	
ZMC Alb PFK1	11	2	11.6	4.8	11.8	4.75	5.25	6.5	8.5	5.7	5.6	7.7	11.55	4.1	5.3	14.2	4.5	10.5	4.25	12.4	
ZMC Alb A1	11	2	11.75	4.8	11.9	4.65	5.2	6.8	9	5.8	5.3	7.6	11.8	4.1	5.3	14.4	4.5	10.7	4.25	12.7	
ZMC Alb PJ2 1.f	11	2	11.85	4.7	12	4.7	5.25	6.3	8.7	5.9	5.5	7.6	12.1	4.2	5.4	15	4.7	10.6	4.4	12.7	
ZMC Alb PJ2 2.f	11	2	12.1	4.9	12.1	4.8	5.3	6.6	9.5	5.6	5.3	7.7	11.9	4	5.1	14.3	4.6	10.7	4.25	12.6	
ZMC Alb A1	11	2	12.4	4.9	12.6	4.8	5.3	6.8	9.9	5.8	5.6	7.8	12.2	4.25	5.3	14.6	4.8	11.1	4.55	12.8	
CCP 3331	11	2	12.75	5.1	12.8	4.9	5.4	6.9	9	6.2	5.6	7.6	13.2	4	5.2	15.5	4.5	11.3	4.85	14.1	

Data set for morphometric analysis of chapter 4 (Fig. 4.3*a*). Discriminant analysis can be accomplished with data corrected and uncorrected by magnification factors. Species: 1=*hirtus*; 2=*pharensis* [manuscript name]; 3=*thaleri* [man.n.]; 4=*melitensis* [man.n.]; 5=*hirtus* agg. Sex: m=1; f=2; all in mm.

Serie	**species**	**Sex**	**BL**	**BW**	**Eyeout**	**LegII**	**DSII**	**BSII**	**MtII**	**MtIV**	**WMtIV**	**DSIV**	**MSIV**	**length dorsal hairs FemIV**					**length ventral hairs FemIV**				
Magnification (x)			*1*	*1*	*10*	*1*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*
CJM 4969	1	1	4.15	6.25	3.6	5.3	5.5	3.43	10.05	9.53	1.3	1.55	0.85	1.5	1.45	1.7	1.3	1.3	1.3	1.8	1.4	1.7	1.5
CIK 1500	1	1	4.2	6.1	3.55	5.5	6	3.28	10.45	9.6	1.33	1.58	0.8	1.6	1.65	1.7	1.5	1.6	1	0.9	1.3	1.35	1
ZMB 11697	1	1				0	3.1	1.7	5.5	10.1	1.33	1.6	0.9	1.5	1.45	1.4	1.45	1.2	1.45	1.25	1.3	1.3	1.4
CJM 4969	1	2	4.35	7.2	3.6	5.35	5.25	2.93	10.58	9.8	1.35	1.43	0.73	1.5	1.55	1.6	1.7	1.7	1.4	1.4	1.5	1.7	1.4
CJM 4881	2	1	4.45	5.8	3.65	5.6	5.88	3.4	11.05	9.83	1.28	1.35	0.83	0.8	0.6	0.6	0.5	0.5	0.5	0.5	0.4	0.5	0.3
CJM 5155	2	1	4.05	5.9	3.5	5.1	5.75	3.2	10.1	9.2	1.2	1.35	0.75	0.6	0.5	0.5	0.5	0.4	0.7	0.6	0.5	0.4	0.6
CJM 4881	2	2	4.8	7.15	4.1	5.6	5.5	3.1	11.35	10.6	1.33	1.5	0.78	0.7	0.7	0.6	0.5	0.5	0.7	0.6	0.6	0.5	0.5
CJM 4881	2	2	4.85	6.65	3.9	5.45	5.33	3.13	11.05	10	1.28	1.45	0.85	0.5	0.5	0.5	0.5	0.6	0.8	0.7	0.6	0.5	0.5
CJM 4881	2	2	4.8	6.6	3.8	5.43	5.08	3.05	10.8	10.1	1.38	1.4	0.7	0.6	0.5	0.4	0.5	0.5	0.5	0.5	0.5	0.4	0.5
CJM 4985	3	1	4.1	5.7	3.65	5.43	5.8	3.25	10.75	9.55	1.2	1.3	0.7	1.1	1.1	1	0.7	0.8	0.9	0.9	0.8	0.7	0.7
CJM 4985	3	1	3.8	5.5	3.55	5.2	5.5	3.2	10.45	9.4	0.63	1.23	0.7	1	1	0.9	0.8	0.9	1.1	0.9	1	1.1	0.7
CJM 4985	3	1	4.2	6.1	3.55	5.68	6.05	3.6	11.35	10.2	1.2	1.38	0.7	0.9	1.2	0.6	1	0.8	1.2	1.1	1.1	0.9	0.8
CJM 4985	3	1	3.95	5.9	3.3	5.2	5.48	3.33	10.4	9.95	1.05	1.2	0.7	1	1	0.9	1.1	1.1	1.1	1.1	1.1	1	0.7
MHNG hairs	3	1	4	5.8	3.55	5.3	5.3	3.28	10.73	9.65	1.2	1.33	0.7	1	0.9	0.8	0.8	0.7	0.8	0.8	0.7	0.7	0.6
CJM 4938	3	1	4.25	6	3.7	5.35	5.4	3.33	10.8	9.4	1.2	1.3	0.7	1.1	1.1	1.1	1.15	1.1	1.2	1	0.7	0.6	0.7
CJM 4938	3	1	3.95	5.8	3.6	5.08	5.2	3.25	10.18	9.1	1.18	1.28	0.6	1	1.3	1.3	1.2	1.2	1	0.9	1.2	0.8	0.8
CJM 4985	3	2	4.55	6.85	3.6	5.5	5.05	3.18	10.9	9.95	1.2	1.25	0.7	0.9	1.1	1.1	1	0.9	1	0.8	0.8	0.9	0.7
CJM 4985	3	2	4.55	6.85	3.6	5.7	5.4	3.25	11.45	10	1.2	1.23	0.73	1.2	1.2	0.9	1	0.9	1	1	1.1	1	1.1
CJM 4985	3	2	4.25	6.6	3.5	5.2	4.85	3.05	10.55	9.73	1.15	1.3	0.7	1	1.1	0.8	0.8	1.2	1	1	1.1	0.9	0.8
CJM 4985	3	2	4.4	6.6	3.8	5.38	5.1	3.28	10.88	10	1.2	1.3	0.7	1	1	0.9	0.9	0.9	1.1	1.1	0.6	0.9	1.1
CJM 4867	3	2	4.25	6.3	3.6	5.25	5.2	3.1	10.75	9.7	1.2	1.28	0.68	0.6	0.7	0.7	0.6	0.8	0.8	0.6	0.5	0.5	0.7
CJM 4938	3	2	4.35	6.4	3.5	5.4	5.15	3.08	10.65	10.7	1.2	1.18	0.63	1	0.9	0.7	1	1	1.1	0.9	0.7	0.9	0.8
CJM 4938	3	2	4.55	6.7	3.9	5.5	5.35	3.1	11.05	10.1	1.2	1.3	0.68	1.2	1.1	1.1	1	1.2	0.8	1	1	0.8	0.8

Serie	**species**	**Sex**	**BL**	**BW**	**Eyeout**	**LegII**	**DSII**	**BSII**	**MtII**	**MtIV**	**WMtIV**	**DSIV**	**MSIV**	**length dorsal hairs FemIV**					**length ventral hairs FemIV**				
Magnification (x)			*1*	*1*	*10*	*1*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*	*10*
CRO 4	4	1	5.05	7.1	4.1	6.18	6.55	3.8	11.6	11.2	1.55	1.75	1	0.6	0.6	0.6	0.5	0.4	0.4	0.6	0.4	0.4	0.7
MHNG no hairs	5	1	4.35	6.1	3.8	5.45	5.95	3.5	10.73	10	1.3	1.4	0.8										

Data set for morphometric analysis of chapter 4 (Fig. 4.11). Discriminant analysis can be accomplished with data corrected and uncorrected by magnification factors. Species: 1=*falcipenis*; 2=*karamanorum* [man.n.]; 3=sp. “Velebit”. Sex: m=1; f=2; all in mm.

Serie	**Species**	**sex**	**BL**	**BW**	**WCoxIV**	**WCoxII**	**LegII**	**Eyeout**	**BSII**	**DSII**	**MtII**	**MtIV**
Magnification (x)			*1*	*4*	*10*	*10*	*1*	*10*	*10*	*10*	*10*	*10*
CJM 3241	1	1	19.9	3.15	4.10	1.37	34	0.18	0.14	0.41	1.43	1.22
CJM 4952	1	1	19.2	2.84	3.95	1.34	36	0.17	0.14	0.43	1.4	1.27
NHMW 19105	1	1	18.9	2.64	3.80	1.27	35	0.16	0.11	0.37	1.43	1.29
NHMW 19711	1	1	20	2.6	3.80	1.32	39	0.16	0.11	0.47	1.66	1.48
CJM 3242	1	2	4.7	7.2	20.38	11.75	6.1	4.55	3.2	6.3	12.4	12.1
CJM 4796	1	2	21.2	3.24	4.18	1.39	35	0.19	0.12	0.38	1.46	1.31
CJM 3025	2	1	20.2	3.14	4.10	1.41	29	0.17	0.11	0.36	1.12	1.03
CJM 3025	2	1	19.6	2.97	3.92	1.44	29	0.16	0.12	0.37	1.14	1.05
CJM 4877	2	1	20.9	2.88	4.18	1.47	31	0.16	0.13	0.36	1.27	1.1
CJM 4877	2	1	21.9	2.68	4.15	1.46	34	0.15	0.14	0.35	1.29	1.09
CJM 4882	2	1	21.2	2.56	3.90	1.40	34	0.16	0.14	0.37	1.31	1.07
CJM 4882	2	1	19.3	2.48	3.75	1.30	31	0.16	0.13	0.38	1.3	1.06
CJM 4889	2	1	18.3	2.84	3.80	1.32	30	0.14	0.13	0.4	1.22	1.08
CJM 4933	2	1	18.9	3.2	4.10	1.43	32	0.15	0.13	0.43	1.36	1.12
CJM 4933	2	1	18.9	3.06	4.12	1.39	32	0.16	0.13	0.42	1.34	1.1
CJM 4889	2	1	19.1	2.89	4.02	1.39	32	0.15	0.13	0.42	1.2	1.08

Serie	**Species**	**sex**	**BL**	**BW**	**WCoxIV**	**WCoxII**	**LegII**	**Eyeout**	**BSII**	**DSII**	**MtII**	**MtIV**
Magnification (x)			*1*	*4*	*10*	*10*	*1*	*10*	*10*	*10*	*10*	*10*
CJM 2817	2	1	15	1.95	2.70	1.02	28	0.12	0.1	0.3	1.11	0.91
CJM 5355	2	1	20.7	2.91	4.00	1.32	32	0.15	0.13	0.34	1.37	1.14
CJM 5032	2	1	19.7	2.72	3.90	1.29	32	0.14	0.13	0.37	1.25	1.1
CJM 5032	2	1	16.8	2.52	3.56	1.21	27	0.13	0.12	0.35	1.08	0.97
CJM 5350	2	1	18.7	2.71	3.75	1.35	27	0.16	0.11	0.33	1.06	0.97
CJM 5034	2	1	18.1	2.6	3.73	1.41	29	0.18	0.14	0.42	1.16	1.02
CJM 4877	2	2	23.9	3.2	4.44	1.53	40	0.17	0.14	0.46	1.63	1.46
CJM 4877	2	2	29.1	4.3	5.60	1.72	37	0.20	0.14	0.33	1.46	1.38
CJM 4877	2	2	30.2	4.3	5.60	1.76	37	0.22	0.13	0.34	1.42	1.42
CJM 4882	2	2	24.8	3.6	4.44	1.50	32	0.18	0.12	0.33	1.29	1.18
CJM 4882	2	2	21.6	3.33	4.10	1.37	30	0.15	0.13	0.31	1.24	1.1
CJM 4882	2	2	20.7	3.24	4.25	1.38	29	0.14	0.11	0.31	1.15	1.06
CJM 4889	2	2	20.7	3.41	4.46	1.42	30	0.16	0.11	0.32	1.11	1.05
CJM 4889	2	2	20.7	3.41	4.19	1.43	30	0.17	0.12	0.3	1.08	1.1
CJM 4889	2	2	20.9	3.15	3.99	1.40	29	0.15	0.12	0.31	1.05	1.1
CJM 4889	2	2	21.4	3.33	4.31	1.43	30	0.16	0.12	0.35	1.22	1.12
CJM 4889	2	2	20.7	3.47	4.36	1.43	29	0.17	0.12	0.35	1.24	1.08
CJM 2817	2	2	17.2	2.53	3.34	1.16	29	0.14	0.12	0.38	1.28	1.04
CJM 5032	2	2	18.2	2.92	3.73	1.32	28	0.14	0.13	0.34	1.12	1.01
CJM 5032	2	2	20.2	3.19	3.93	1.35	28	0.15	0.11	0.31	1.11	1.05
CJM 5034	2	2	20.9	3.06	4.17	1.50	32	0.20	0.14	0.41	1.27	1.13
CCD Cres	3	1	17.4	2.17	3.29	1.21	29	0.14	0.1	0.31	1.1	0.98
CCD Velebit	3	1	14.8	1.89	2.95	0.96	27	0.12	0.08	0.27	0.99	0.85
NHMW Nemila	3	2	15	1.85	3.05	0.99	26	0.13	0.08	0.28	0.98	0.86
SMF 1355	3	2	22.6	3.24	3.93	1.53	33	0.19	0.13	0.38	1.34	1.21

13. Erklärung

Hiermit erkläre ich, dass ich diese Arbeit selbständig angefertigt habe. Es wurden keine anderen als die angegebenen Hilfsmittel verwendet.

Mainz, den 17. April 2009

Axel Schönhofer

14. Curriculum Vitae