Charles University in Prague
Faculty of Science
Department of Zoology

Systematics of oribatid mite families Damaeidae and Gymnodamaeidae (Acari: Oribatida), feeding ecology of selected oribatid species

Systematika pancířníků čeledí Damaeidae a Gymnodamaeidae (Acari: Oribatida), potravní ekologie vybraných druhů pancířníků

Ph.D. Thesis

Mgr. Jan Mourek

Internal supervisor
Prof. RNDr. Jaroslav Smrž, CSc.
Faculty of Science, Charles University, Prague, Czech Republic

External co-supervisor
Doc. RNDr. Ladislav Miko, Ph.D.
European Commission, DG Environment, Brussels, Belgium

Prague, May 2010

Declaration

I hereby declare that I did not previously submit this Ph.D. thesis or its part to fulfil conditions of the same or of another university degree.

I further declare that this Ph.D. thesis as such is not intended as a publication and it must not be considered as a publication in the sense of International Code of Zoological Nomenclature (1999). None of the nomenclatory acts proposed in the attached unpublished manuscripts is available until the works are published in ordinary way. To avoid confusion, I omitted the scientific names of one new species and one new subgenus proposed in *contribution 1.4* (Mourek et al., subm.).

Jan Mourek
Charles University in Prague, Faculty of Science

31. May 2010

Prohlášení

Prohlašuji, že jsem tuto dizertační práci ani její část nepředložil k získání stejného nebo jiného akademického titulu.

Dále prohlašuji, že tato dizertační práce jako taková není zamýšlena jako publikace a nesmí být považována za publikaci ve smyslu Mezinárodních pravidel zoologické nomenklatury (1999). Žádný z nomenklatorických činů navržený v předložených rukopisech není platný, dokud nebudou tyto práce řádně publikovány. Abych předešel nedorozumění, vypustil jsem jména nového druhu a nového podrodu z *příspěvku 1.4* (Mourek et al., subm.).

Jan Mourek
Univerzita Karlova v Praze, Přírodovědecká fakulta

31. května 2010

Content

1 List of contributions included in the thesis 4

2 Acknowledgements 5

3 Introduction 7

3.1 Damaeidae and Gymnodamaeidae in the context of current oribatid classification 8

3.2 Current state of taxonomy of Damaeidae 9

3.3 Current state of taxonomy of Gymnodamaeidae 13

3.4 Trophic interactions between oribatid mites and soil fungi 16

4 Synopsis of the contributions 18

4.1 Problems of taxonomy and morphology of European Damaeidae and Gymnodamaeidae 18

4.2 Feeding preferences of selected oribatid mites inhabiting pine litter and their interactions with saprotrophic ascomycetes 20

5 References 22

6 Aggreements of the co-authors 28

7 Fulltext versions of contributions included in the thesis 31

1 List of contributions included in the thesis

1. Problems of taxonomy and morphology of European Damaeidae and Gymnodamaeidae

Contribution 1.1

Weigmann G., **Mourek J.** (2008) Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari: Oribatida: Gymnodamaeidae). ***Zoosystematics and Evolution*** 84, 255 - 264.

Contribution 1.2

Miko L., **Mourek J.** (2008) Taxonomy of European Damaeidae (Acari: Oribatida) I. *Kunstidamaeus* Miko, 2006, with comments on *Damaeus* sensu lato. ***Zootaxa*** 1820, 1-26.

Contribution 1.3

Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. & Sabelis M. W. (eds.): ***Trends in Acarology*.** Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.

Contribution 1.4

Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species.

Contribution 1.5

Mourek, J., Miko, Skubała, P. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) V. Redescription of *Epidamaeus bituberculatus* (Kulczynski, 1902).

2. Feeding preferences of selected oribatid mites inhabiting pine litter and their interactions with saprotrophic ascomycetes

Contribution 2.1

Koukol O., **Mourek, J.**, Janovský Z., Černá K. (2009) Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? *Soil Biology and Biochemistry*. 1124-1131.

Contribution 2.2

Koukol O., Janovský Z., Černá K., **Mourek J.** (*submitted*) The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes.

2 Acknowledgements

I dedicate this Ph.D. thesis to my dear parents, who had to wait long eight years, before it has been finished. I am grateful for all their love, care, patience and understanding.

Jan

I would like to express my very special thanks to the supervisors, Prof. RNDr. Jaroslav Smrž, CSc. and Doc. RNDr. Ladislav Miko, Ph.D., for their continuous support, advice and tolerance during the whole study. L. Miko directly participated in four contributions included in my thesis as co-author or first author. Prof. Dr. Roy A. Norton (State University of New York, College of Environmental Science & Forestry, Syracuse) helped a lot by reading and commenting most of the manuscripts, offering new ideas and encouraging us during the research. He has been always ready to share his outstanding knowledge and expertise in various fields of acarology.

I am very grateful to Prof. Dr. Gerd Weigmann (Institut für Zoologie, Freie Universität Berlin, Germany) for the possibility to participate in his research of European Gymnodamaeidae. He further hosted me during my study visit in his laboratory (October - December 2003), allowed me to use his extensive library and collection of oribatid mites. During the whole study, he was open for discussion of different problems related with my thesis.

Prof. Fabio Bernini (Department of Evolutionary Biology, University of Siena) and Dr. Piotr Skubała (University of Upper Silesia, Katowice) kindly provided valuable material and faunistic data of Damaeidae and contributed as co-authors to particular studies.

Mgr. Ondřej Koukol, Ph.D. (Dept. of Botany Charles University Prague, Faculty of Science) came with the idea to conduct joint experiments of trophic interactions of oribatid mites and soil saprotrophic fungi. He not only did an important part of the research and preparation of the manuscripts, but also cared for the administration logistic support of the whole project. I am especially grateful to him for his friendly tolerance and understanding for my slow rate of work. Finally, he helped me a lot by making available his favourite laser jet "*Máňa*" for printing this thesis.

Bc. Kristýna Černá (Dept. of Botany) helped a lot with preparing the experiments on oribatid-fungal interactions and with collecting the data. Mgr. Zdeněk Janovský (Dept. of Botany) analysed the data from these experiments and was the essential partner in planning the experimental designs. Moreover, he significantly participated in all phases of preparation of both manuscripts.

Mgr. Ivana Marková (Bohemian Switzerland National Park) kindly assisted during the collection of material on the territory of the National Park.

Assoc. Prof. Konrad Thaler († 11. 7. 2005), Dr. Heinrich Schatz, Dr. Irene Schatz (both Institut für Zoologie und Limnologie, Universität Innsbruck, Austria) and Mechthild Schatz (Innsbruck, Austria) kindly supported me during my short study visit in Innsbruck (November 2004), when I studied the Damaeidae in the collection of Dr. Franz Mihelčič. Heinrich Schatz also kindly provided part of the essential literature and some faunistic data.

Dr. Miroslav Hyliš (Laboratory of Electron Microscopy, Charles University in Prague, Faculty of Science) and the staff of the Laboratory of Electron Microscopy (Institute of Parasitology, Biology Centre, Academy of the Sciences of Czech Republic, v.v.i., České

Budějovice), kindly assisted during the SEM-study and helped me with solving some methodical problems.

RNDr. Peter Ľuptáčik, Ph.D. (Institute of Biology and Ecology, Faculty of Science, University of P. J. Šafárik, Košice, Slovakia), RNDr. Jan Materna, Ph.D. (Správa KRNAP, Krkonošské muzeum Vrchlabí), Mgr. František Šťáhlavský, Ph.D., doc. RNDr. Jitka Vilímová, CSc., Mgr. Jindra Mourková, Mgr. Dagmar Berneška Říhová (all four from Dept. of Zoology, Charles University, Faculty of Science), Mgr. Zdeněk Janovský, Prof. Romano Dallai (Department of Evolutionary Biology, University of Siena) and Jakub Šťastný (Prachatice, Czech Republic) helped to collect some material of Damaeidae or Gymnodamaeidae.

Dr. Gerhard Tarmann and Dr. Peter Huemer (both from Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria), Dr. Peter Jäger (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany), Mr. I. J. Smit (Naturalis National Museum of Natural History Leiden, Netherland), Dipl.-Biol. Stefan Friedrich (Zoologische Staatssammlung München, Germany) and Dr. Jason Dunlop (Museum für Naturkunde Berlin) kindly loaned specimens from the museum collections.

Kerstin Franke (Senckenberg Museum für Naturkunde Görlitz, Germany) and Dr. Sergey Ermilov (Nižnij Novgorod, Russia) kindly provided me with copies of important literature sources.

Dr. María Lourdes Moraza (Universidad de Navarra, Pamplona, Spain) kindly re-examined the nymphs of *Epidamaeus ibericus* and provided the information about their cornicle. Dr. Luís Subías (Universidad Complutense, Facultad de Biologia, Madrid, Spain) kindly provided some references to literature.

I am particularly grateful to my dear colleagues from the Dept. of biology and environmental studies (Charles University in Prague, Faculty of Education) and from the Dept. of teaching and didactics of biology (Charles University in Prague, Faculty of Education) for their kind support and tolerance during the finishing of my thesis. PhDr. Petr Novotný (Dept. of biology and environmental studies) helped me in solving some technical problems in final editing of this thesis.

Particular studies have been financially supported by the Grant Agency of the Charles University, Prague (grant *GAUK 217/2004/B-BIO/PrF*) and by the Grant Agency of the Academy of Science of the Czech Republic (grant *KJB601110718*). Deutscher Akademischer Austauschdienst (DAAD) funded my two-month study visit in the laboratory of Gerd Weigmann (Berlin) in 2003.

I would not be able to finish the thesis without the help, tolerance and encouragement of my dear wife Jindra during the twelve years of our common life. Our dear parents—Eva Fišerová, MUDr. Marta Mourková, ing. Oldřich Mourek and Jiří Fišer—have devoted us much of their time, energy and love in caring for our two sons. They were extremely helpful during the last months, when we both have been finishing our theses.

Finally, our small sons—Jiří Mourek and Jan Mourek jr.—have been surprisingly generous in sharing our time and interest with our subjects of study. I am especially grateful to them for not destroying any of my original drawings or reprints of literature, being interested in the long-legged creatures on the figures and keeping optimism in our home.

3 Introduction

In the presented thesis I integrate contributions on two independent aspects of acarology. The taxonomically oriented part aims to solve particular problems of taxomomy of European members of the oribatid families Damaeidae Berlese, 1896 and Gymnodamaeidae Grandjean, 1954 based on morphological study. The second part is ecologically oriented and presents a study of the feeding preferences of selected oribatid mites inhabiting pine litter and another study, which examines the influence of oribatid mites on soil saprotrophic ascomycetes. In total, the thesis includes seven primary scientific contributions. Four of them are already published—three in peer-reviewed journals and one in per-reviewed conference proceedings. The remaining three contributions are manuscripts submitted to peer-reviewed journals.

I elaborated this thesis in Department of Zoology, Charles University Prague, Faculty of Science under the supervision of Prof. RNDr. Jaroslav Smrž, CSc. and external co-supervision of Doc. RNDr. Ladislav Miko, Ph.D. (European Commission, DG Environment, Brussels, Belgium) in the period from October 2002 to May 2010. Further, Prof. Dr. Roy A. Norton (State University of New York, College of Environmental Science & Forestry, Syracuse, New York, USA) and Prof. Dr. Gerd Weigmann (Institut für Zoologie, Freie Universität Berlin, Germany) consulted particular as well as general topics of oribatid taxonomy related with my thesis.

I declare, that I substantially participated on all publications and manuscripts included in this Ph.D. thesis. The participation of me and of the other co-authors is described individually for each contribution in the synopsis and is confirmed by the co-authors in their agreements. Assistance and help of other people —either material, technical or moral—provided to me or to the co-authors is namely declared in general acknowledgements and in acknowledgements of particular contributions.

The conception of the thesis has gradually changed during the study period. Originally, the core of the thesis should have been the morphology of immature stages of the genus complex Damaeus *sensu lato*, supplemented with she study of feeding preferences of selected species. Later, after the review of preliminary results and consultation with Roy A. Norton, it became evident, that morphology of immature Damaeus *sensu lato* offers only a low number of characters, which are of rather limited value in the systematics on the genus level (see also Miko and Mourek, 2008, included as *contribution 1.2* in this thesis). Therefore, in co-operation with Ladislav Miko, we used immature morphology for partial resolving of some questions and turned our attention to study of adults and revisions of selected European species of the genera *Metabelba* and *Epidamaeus*. The contribution on two European species of Gymnodamaeus (Weigmann and Mourek, 2008, included as *contribution 1.1* in this thesis) is presented as a model study, demonstrating the value of the cerotegument micro- and ultrasculpture studied with the SEM in the systematic of Gymnodamaeidae.

The study of trophic interactions of oribatid mites with saprotrophic fungi begun in 2007, when I got the opportunity to participate on the research project of Ondřej Koukol. This theme is relatively independent from the taxonomical studies and the main link is through some of the used model organisms—the predominantly mycophagous members of Damaeidae.

In the following chapters I briefly review the current state of taxonomy of both considered oribatid families and of the knowledge on trophic interactions of oribatid mites with soil fungi. The subsequent synopsis contains a brief summary of each included contribution.

3.1 Damaeidae and Gymnodamaeidae in the context of current oribatid classification

The Damaeidae Berlese, 1896 and Gymnodamaeidae Grandjean, 1954 represent moderately diverse families of oribatid mites (Acari: Oribatida) with about 260 and 70 named species respectively (Subías, 2009). Both families belong to the cohort Brachypylina and its inner, probably monophyletic, clade Circumdehiscentiae Grandjean, 1954, which is characterised mainly by circumgastric ecdysial cleavage line (Norton and Kethley, 1994; Weigmann, 2006). Earlier authors (e.g. Kulczynski, 1902; Sellnick 1928; Bulanova-Zachvatkina, 1957a) included the members of both families in Damaeidae. Now it is evident, that they are not closely related and are included in different superfamilies. Damaeidae belong to monotypical Damaeiodea Berlese, 1896, whereas Gymnodamaeidae to Plateremaeoidea Trägardh, 1931 (see Weigmann, 2006; Norton and Behan-Pelletier, 2009) or to monotypical superfamily Gymnodamaeoidea Grandjean, 1954 (see Balogh and Balogh, 1992; Subías, 2004).

The relations between different superfamilies whithin Circumdehiscentiae are still poorly known. The monophyly of the five traditional groups (sections) distinguished by Grandjean (1953) was recently questioned by molecular phylogenetic study of oribatid mites by Maraun et al. (2004), but detailed studies integrating molecular and morphological data are still missing.

Grandjean (1953) included Damaeidae and Gymnodamaeidae in the group Euphérédermés, a large assemblage of different families, which is defined mainly by the nymphs and less often also adults carrying gastronotic exuviae of previous ontogenetic stages ("scalps") on the dorsal side of the gastronotic region (Fig. 1). Another remarkable morphological feature (but probably not independent from the previous one) characterizing the Euphérédermés, is the reduction of some gastronotic setae during the ontogeny. Setae *da*, *dm* and *dp* are absent from the nymphs and adults and seta *c3* is absent from adult.

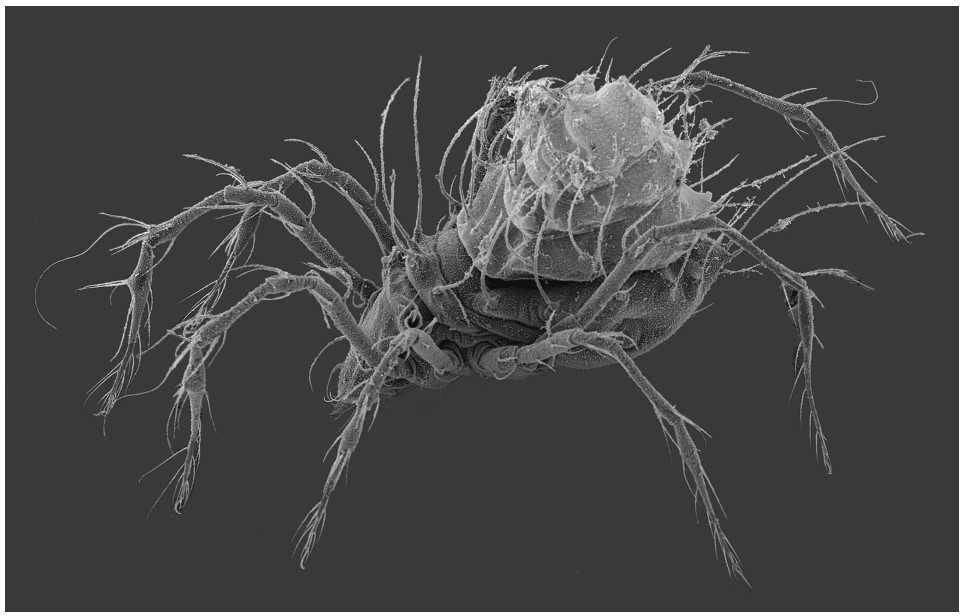


Fig. 1: Tritonymph of *Kunstidamaeus lengersdorfi* (Damaeidae) in dorsolateral view with gastronotic exuviae ("scalps"), typical for nymphs of the oribatid section Euphérédermes.

Monophyly of Euphérédermés was not supported by Maraun et al. (2004), but it might an effect insufficient taxon sampling. The group has not been used as a systematic unit in recent classifications of oribatid mites (Subías, 2004; Weigmann, 2006; Norton and Behan-Pelletier, 2009). Anyway, it has still not been examined in detail, whether the carrying of gastronotic exuviae in the nymphs is a real synapomorphy, symplesiomorphy or a convergent character, which developed independently several times, possibly as a camouflage or as a protection shield against desiccation and solar radiation.

Nymphs of the Damaeidae are unique within the euphéréderm families in having the "scalps" attached by a cornicle (*k*), an unpaired projection, present on dorsomedial part of the gastronotic region. The cornicle (Fig. 3) has been hitherto found also in adults of three damaeid species (Saloña, & Iturrondobeitia, 1989; Enami, 1994; Mourek et al., subm. - included as *contribution 1.4* in this thesis). Recently, Ermilov and Łochyńska (2009) revealed a minute cornicle also in the larvae of the damaeid mite *Porobelba spinosa*. No clearly homologous structures to the cornicle are known in other oribatid families. In the nymphs of Eremobelbidae Balogh, 1961, one of the families of Ameroidea according to Norton and Behan-Pelletier (2009), the gastronotic exuviae are attached with the so-called Z-point, which is probably not a cuticular process like the cornicle of Damaeidae, but a kind of secretion (Weigmann 2002).

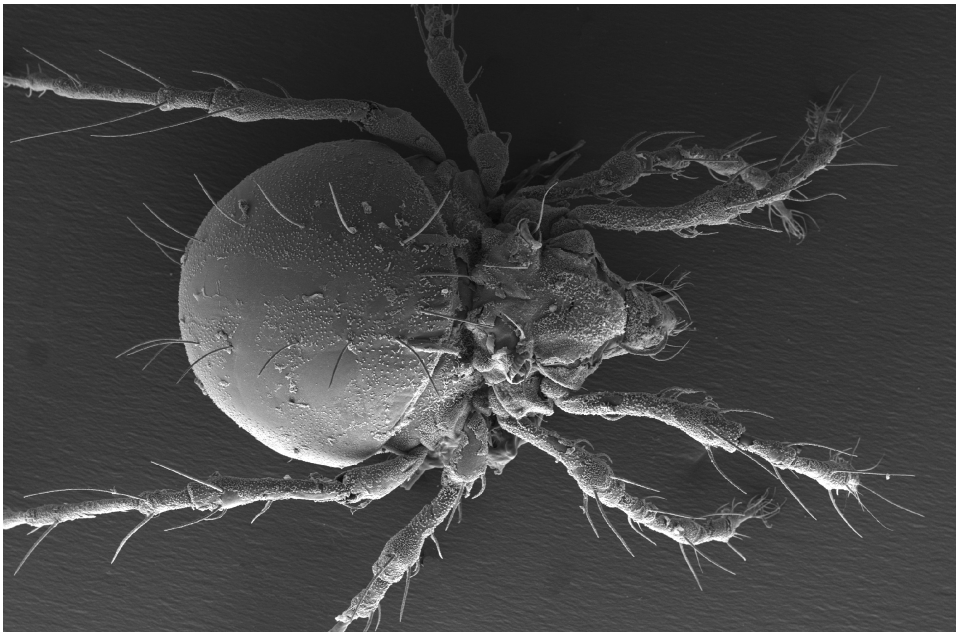


Fig. 2: Adult of *Damaeus (Adamaeus) onustus* (Damaeidae) in dorsal view.

3.2 Current state of taxonomy of Damaeidae

The family Damaeidae includes mostly middle sized to large oribatid mites inhabiting mostly litter and upper layers of forest soils. They seem to be predominantly mycophagous (Schuster, 1956; Luxton, 1972; Siepel and de Ruiter-Dijkman 1993), details in chapter 3.4. Their overall body form somewhat resembles the spiders; many species having very long legs. Their adults are characterized by roughly triangular prodorsum, which is distinctly separated from the usually hemispherical notogaster (Fig. 2). Nymphs are eupheredermous with the gastronotic exuviae being attached by a cornicle *k* (Fig. 3). The autapomorphies of the family include

notogastral setae of rows *c*, *l* and *h* being arranged in two more or less parallel longitudinal rows; rutella with a pair of distal globular hyaline expansions and cheliceral seta *chb* with fringe of barbs in distal third becoming shorter toward the tip. Expanded funnel-like bothridium is shared with the genus *Hungarobelba* Balogh 1943, which was originally included in Damaeidae, but was later transferred to a separate family Hungarobelbidae Miko et Travé 1996.

Adults of different damaeid genera and subgenera are distinguished mainly on the base of the leg chaetotaxy, presence/absence of spinae adnatae and presence/absence of propodolateral apophysis *P* (Kunst, 1971; Balogh and Balogh, 1992; Bulanova-Zachvatkina, 1975; Pérez-Iñigo, 1997; Miko, 2006). Species-specific characters include for example presence/absence of various tubercles on prodorsum and coxisternum, shape and relative length of sensillus and notogastral setae (e.g. Behan-Pelletier and Norton, 1983, 1985; Bayartogtokh, 2000a, 2000b, 2000c, 2001; Bayartogtokh and Norton, 2007).

Morphology of immature Damaeidae is more conservative than of the adults. Immature characters have been integrated in the diagnoses of some genera (Norton 1978a, 1979c), but the redescriptions of immature stages are available only in a small part of damaeid species (see Table 1 in Mourek and Miko, 2009 - included as *contribution 1.3* in this thesis). Diagnostic keys for immature stages of Damaeidae have not been developed yet and comparative morphological studies of immatures remain scarce (Norton, 1977a; Ermilov and Łochyńska, 2009).

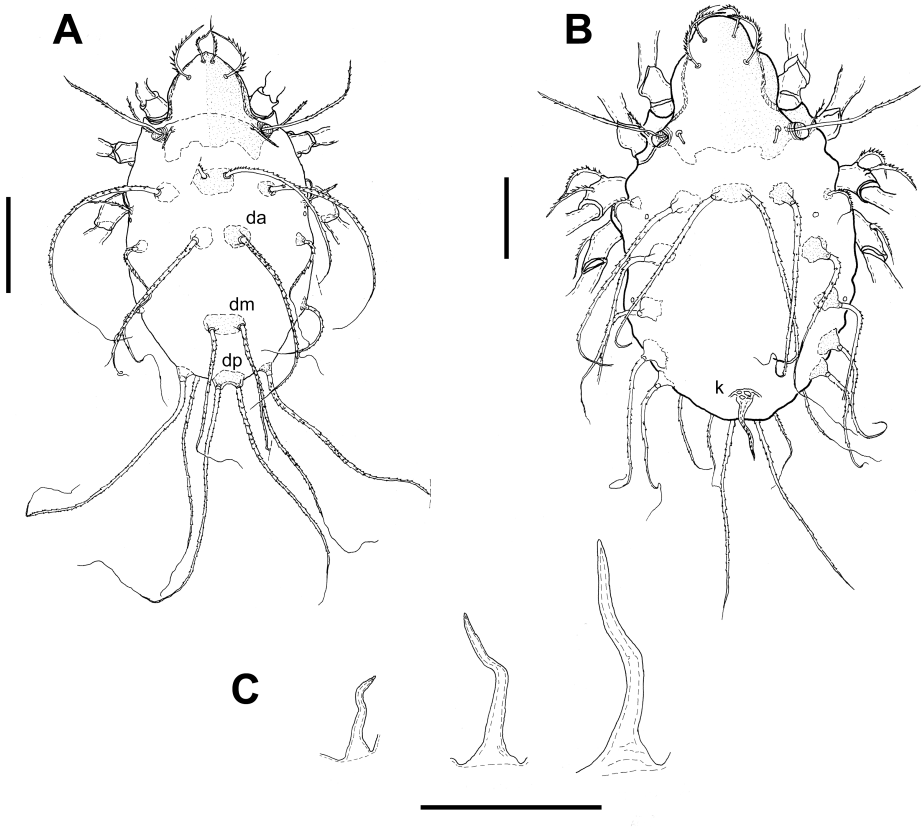


Fig. 3: *Spatiodamaeus verticillipes* (Damaeidae): A) larva in dorsal view; B) deutonymph in dorsal view; C) nymphal cornicles in lateral view, from left to right: protonymph, deutonymph, tritonymph. Scales: 100μm. Abbreviations: *da, dm, dp* - notogastral setae, present only in larva; *k* - cornicle.

Body, legs and part of setae of damaeid mites are coated with a distinct continuous cerotegument layer forming various excrescences Fig. 4), which may be e.g. granular, columnar, "vermicular" or reticular, depending on a species or a genus (Norton, 1979b; Alberti et al., 1981; Mourek et al. subm.). The type of excrescences often differs also between ontogenetic stages of a given species (Norton, 1977a; Miko and Mourek, 2008; Ermilov and Łochyńska, 2009). Although the type of cerotegument ornamentation offers valuable diagnostic characters, it has still been only scarcely incorporated in species diagnoses (Mourek et al. subm.)

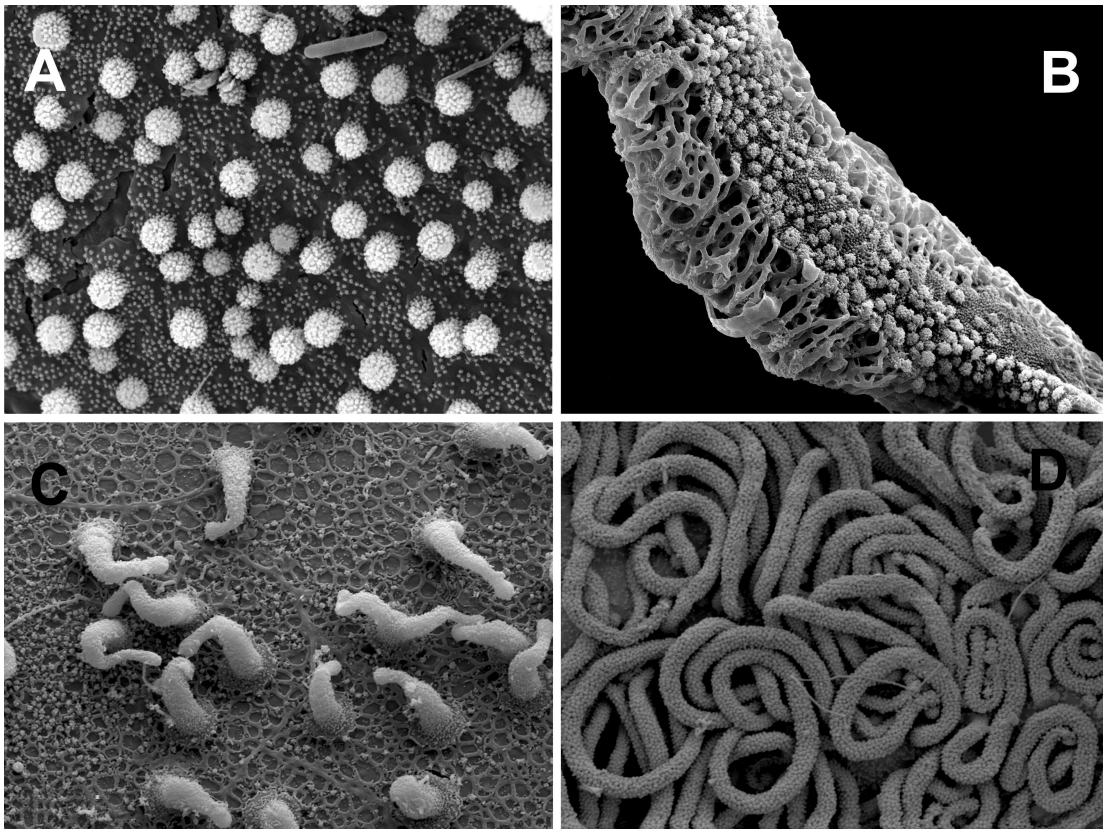


Fig. 4: Cerotegument details of selected adult Damaeidae. A) *Belba compta* - granular cerotegument on prodorsum; B) *Belba bartosi* - reticulate and granular cerotegument on femur I; C) *Damaeus onustus* - vermicular cerotegument with reticulate base layer on anterior part of notogaster; D) *Spatiodamaeus verticillipes* - filamentous cerotegument on femur I.

The Damaeidae are distributed mainly in the Northern Hemisphere and the majority of species are known from Palaearctic and Nearctic regions (Norton, 1979a; Bayartogtokh, 2000a, 2000b, 2000c; Subías, 2004). The most recent available inventory by Subías (2009) revealed 259 named species, but the synonymies of part of the species remain unclear. Number of recognized genera in recent classifications of different authors ranges from 12 to about 26 (e.g. Balogh and Balogh, 1992; Subías, 2004; Miko, 2006).

Areas of distribution of individual damaeid species are difficult to reconstruct in the present state of knowledge. Some of the species have a wide distribution over most of the Palaearctic or scarcely even Holarctic region; others are confined to certain subregions or to a range of longitudes crossing the Bering Strait (Behan-Pelletier and Norton, 1983, 1985; Bayartogtokh, 2000c; Subías, 2004). In contrast, some species have a narrow distribution, being probably endemic or relict, e.g. in high zones of the Alpes (Schatz and Schuster, 2009).

A detailed review of the historical development of the taxonomy of Damaeidae was published by Miko and Mourek (2008) and is included as *Contribution 1.2* in this thesis. Therefore, I repeat only the most important facts in this place.

The basis for the current generic classification of the family was created by Grandjean (1936). In his concept, based on the study of classical European species, he emphasized the leg chaetotaxy, namely the presence/absence of seta *d* on tibiae II-IV, coupled with the solenidia. Grandjean (1953) for the first time delimited the extent of the family (under the junior synonym Belbidae, Willmann, 1931) to a group, which seems to be monophyletic also in the current point of view (Norton, 1979b; Norton and Behan-Pelletier, 2009).

The generic concept based on the leg setation was further elaborated by Bulanova-Zachvatkina (1957a, 1957b, 1962, 1965, 1967), who proposed new damaeid genera and subgenera and described numerous new species from the territory of former Soviet Union. Her studies finally resulted in splitting the family into three independent families: Damaeidae, Belbidae and Belbodamaeidae (Bulanova-Zachvatkina, 1967), which were included in the identification key (Bulanova-Zachvatkina, 1975) and adopted by part of subsequent authors (e. g. Schatz, 1983; Olszanowski et al., 1996; Perez-Iñigo, 1997).

Norton (1979b) rejected the Bulanova-Zachvatkina's concept, clearly demonstrating that Belbidae and Belbodamaeidae are artificial taxa, based mainly on plesiomorphic characters. Even if many proposals by Bulanova-Zachvatkina are reasonable, some are rather problematic. Some of the new genera and subgenera proposed by Bulanova-Zachvatkina (1957a) were published only as names with diagnosis, without designating their type species and therefore remained *nomina nuda* until subsequent works (e.g. Bulanova-Zachvatkina, 1967). Moreover, some of the new species names were published without really describing the species, many other species, including the types of some genera, were described only briefly and were insufficiently illustrated. Therefore, detailed redescriptions of Bulanova-Zachvatkina's damaeid species are urgently needed. Unfortunately, their revision is complicated because of the bad accessibility of the type material, which is probably partly lost and partly deposited in the Siberian Zoological Museum in Novosibirsk, Russia. The museum does not loan the specimens and therefore personal study visit would be necessary (S. Ermilov, pers. comm., 2010).

Another remarkable contribution to systematics of Damaeidae on the generic level was the series by Norton (1977a, 1977b, 1978a, 1979b, 1979c), based on the study of Nearctic species. In contrast to previous authors, he integrated also the study of immature stages. He proposed several new genera and subgenera and substantiated that some of the classical damaeid genera, defined on the base of Palaearctic species, are probably polyphyletic or paraphyletic groups.

As noted above, the Damaeidae in the current sense, after the transfer of *Veloppia* and *Hungarobelba* to other oribatid superfamilies (see Norton, 1978b; Miko and Travé, 1996; Chen et al. 2004; Norton and Behan-Pelletier, 2009), seem to be a clearly defined monophyletic group with distinct autapomorphies on the family level. Still, the position of some poorly known taxa included in Damaeidae, remains uncertain. This is for example the case of the North American genus Dasybelba Woolley et Higgins, 1979, which might in fact belong to another oribatid family (see comments in Mourek et al., subm.).

The generic classification of Damaeidae still remains largely artificial and has not been subjected to a thorough revision with cladistic methodology. The revision of higher classification of Damaeidae is unfortunately hampered by the insufficient knowledge of many taxa, including some of the genotypes. Similar problems as with the species described by Bulanova-Zachvatkina have been with many European species described by some of the earlier authors (e.g. Koch, 1836a,b; 1841; Mihelčič, 1963, 1964).

Subías (2004) in the world catalogue of oribatid mites proposed extensive generic recombinations in many families including the Damaeidae. He introduced numerous new names for the homonyms arising from the recombinations. Unfortunately, he neither explained the reasons, nor published any modified diagnoses. Moreover, he did not give any references to previous works. He regularly updates his lists online (Subías 2007, 2008, 2009), but always only the last version is available from the web page. This rather unorthodox way of publishing taxonomical works is very much in conflict with International code of zoological nomenclature (1999). Although some of the recombinations proposed by Subías (2004, 2007, 2008, 2009) may be considered as reasonable, many of them are apparently based on very superficial analysis without comparing real specimens. This way of publishing nomenclatory acts may lead to further destabilisation of higher systematics of oribatid mites, rather than to identification of their real phylogenetic relationships.

Miko (2006), in the key of German oribatid mites (Weigmann, 2006), revised the majority of damaeid species known of the Central Europe. However, some problems remained unresolved and particular European taxa have been redescribed in subsequent series of papers (Miko and Mourek, 2008; Miko 2008; Miko, 2010; Mourek et al., subm.; Mourek and Miko, subm.); the parts in which I have participated are included in this thesis (see *Contributions 1.2, 1.4, 1.5*).

3.3 Current state of taxonomy of Gymnodamaeidae

Walter (2009) provided an excellent summary of nomenclatorical, methodical and conceptual problems of systematics of Gymnodamaeidae, reflecting the most recent state of knowledge. Therefore, I will review only the most important points with emphasis on European taxa.

Gymnodamaeidae have a very conspicuous body form (Fig 5). Their notogaster is distinctly flattened, usually slightly concave, dorsally with a slightly elevated margin and is distinctly separated from prodorsum by a well-defined dorsosejugal furrow. In many species the legs are slender and distinctly longer than body, which is carried over the substrate during walking. The entire body and leg surface, including most of setae, is coated with a distinct cerotegument layer with remarkable pustulate sculpture. The microsculpture and ultramicrosculpture of the cerotegument in Gymnodamaeidae studied with SEM offers valuable species-specific characters, but has been studied only scarcely yet (Wooley, 1972, 1973a; Weigmann and Mourek, 2008; Walter, 2009).

Characters common with other families of Plateremaeoidea include the distinctly developed terminal apophysis in tibia I bearing the solenidia and companion seta *d*, eupheredermous nymphs and reduced number of notogastral setae (ranging from 4 to 6 pairs) in adults (see Norton and Behan-Pelletier, 2009). Comprehensive amended diagnosis of the family was proposed by Walter (2009). The family can be distinguished from other Plateremaeoidea by the following combination of characters: pedotecta I-II present, pedotectum I auriculate; notogastral setae positioned posterior to lyrifissure *im*; two pairs of anal setae present; tarsus II with two solenidia; notogaster concave in lateral view; notogastral setae not twisted (Norton and Behan-Pelletier, 2009)

In my view, the polarity (plesiomorphy x apomorphy) of character states on the family level whithin Plateremaeoidea is not quite clear. The group has not yet subjected to cladistic methods and none members of Plateremaeoidea were included in the molecular-phylogenetic study of oribatid mites presented by Maraun et al. (2004).

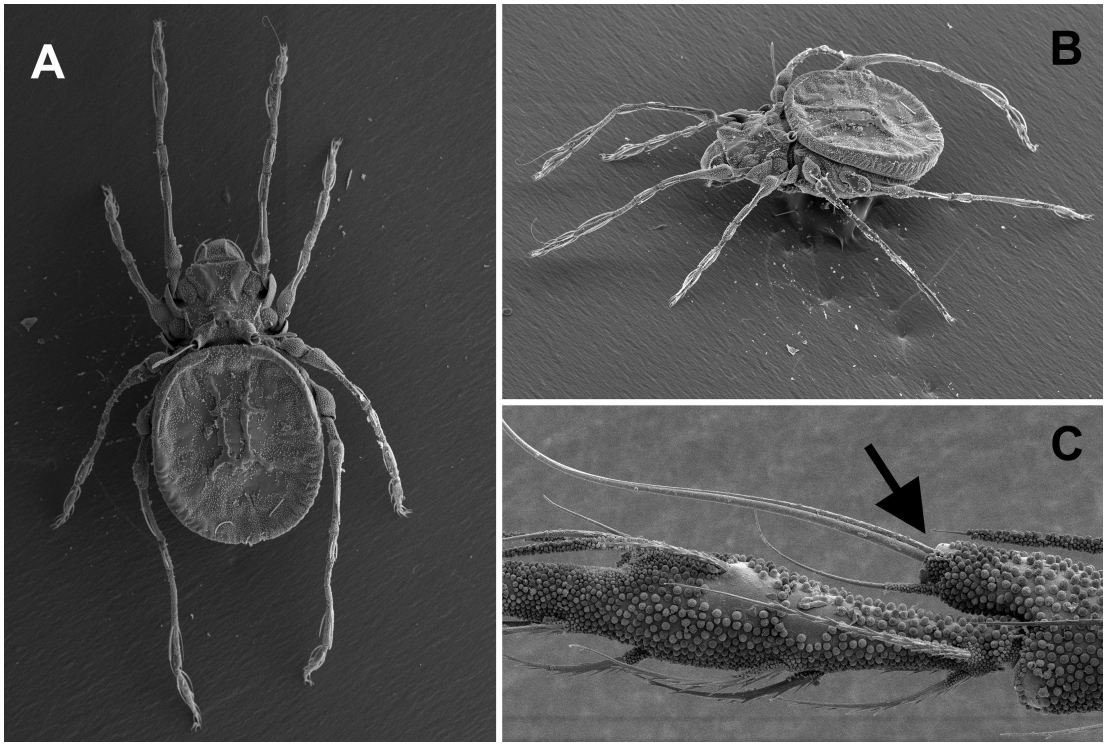


Fig. 5: Typical body form and characters of Gymnodamaeidae on the example of *Gymnodamaeus bicostatus*. A) adult in dorsal wiew; B) adult in dorsolateral view; C) proximal part of tarsus I and distal part of tibia I in lateral view with typical apophysis (arrow) bearing two solenidia and companion seta *d*.

Gymnodamaeidae seem to be early derivate forms, their fossils being known already from the Late Cretaceous amber (Labandeira, Philips and Norton, 1997). The family is nearly cosmopolitan (Subías, 2004; Norton and Behan- Pelletier, 2009). Subías (2009) reported in total 66 named species of Gymnodamaeidae worldwide, but the synonymy of some of them may be expected.

The representatives of Gymnodamaeidae are often found in dry open sites ranging from arid or semiarid zones, steppes and other grasslands, over light forests to alpine and tundra soils (Walter 2009). In Central Europe, the Gymnodamaeidae are mostly distributed in relatively warm regions (Weigmann and Miko, 2008). This may, however, relate more to dry conditions with fluctuating temperature and open vegetation cover, than to warm climate as such.

The systematics of the family on the genus level is still not stabilised. The number of genera accepted by different authors fluctuates between 11 distinguished by Paschoal and Johnston (1992) to only 5 genera recognized by Woas (1992). Also the genus diagnoses vary among different authors. Some of the Paschoal's genera seem to be artifficial and weakly defined. Some species display intermediate states of some characters used in the generic diagnoses, but Walter (2009) recommended to distinguish the genera, until the family is completely revised with cladistic methodology. Traditional characters used as the base for

generic diagnoses include mainly the presence/absence of basal retrotecta (reverse collars in the sense of Weigmann and Mourek, 2008), presence/absence of cuticular "bridge" separating the genital and anal openings, position of interlamellar setae, number of notogastral setae, presence/absence of reticulate cuticular sculpture on notogaster and form of apophyses bearing posterior notogastral setae (from Walter, 2009 and supplemented according to Subías et al., 1997 and Weigmann, 2006). Walter (2009) further proposed new differential characters generic based on the cerotegument microsculpture of notogaster.

The main problem of the taxonomy of Damaeidae is in my view a methodical one (see also Walter, 2009). Authors of species descriptions deal with two types of body ornamentation—the sculpture of the procuticle and that of the cerotegument. The procuticular and cerotegument strucures may be often confused. The procuticular sculpture seems to be is relatively stable, but its overall appearance in transmitted light depends on the degree of sclerotisation of a given specimen. For example, freshly hatched adults may look considerably different than the fully mature ones (Walter, 2009). It is also often not clear, whether the pattern consists of surface elevations and depressions or of inner thickenings. Most often, it is a combination of both types.

The cerotegument sculpture seems to be quite stable within a given species but it is easily detached from the body during the preparation and may be partly abraded during the mite's life as well (see Weigmann and Mourek, 2008). Unfortunately, some authors, even if otherwise being excellent illustrators, did not clearly distinguish between the procuticular and partly abraded cerotegument sculpture (e.g. Woas, 1992; Subías et al., 1997). The *ex post* interpretation of their figures is difficult. Some other authors illustrated their species without the cerotegument (e.g. Kunst 1958; Woolley and Higgins, 1973b). Bayartogtohk and Schatz (2009), in contrast, carefully distinguished both types of sculpture, but unfortunately did not study the details with SEM.

In Europe, the most confusion was caused by the poor knowledge of the gymnodamaeid species briefly described by Berlese (1910), who did not illustrate them at all. Mahunka and Mahunka-Papp (1995) reviewed the available material in the Berlese collection and provided schematic figures, but unfortunately did not make detailed redescriptions and some of the problems remained unresolved.

The satisfactory resolution of problems related with the systematics of Gymnodamaeidae would be the combination of SEM- and light microscopical observations, applied on the material from more local populations and combined with the study of type material, if available. A model study of this type, even if concerning only two Central European species of *Gymnodamaeus*, was done by Weigmann and Mourek (2008) and is included in this thesis as *contribution 1.1*. Walter (2009) applied similar approach in much larger extent on the Canadian genera of the family.

3.4 Trophic interactions between oribatid mites and soil fungi

Soil oribatid mites have been traditionally viewed as being predominantly saprophagous, feeding on decomposing plant tissues colonised with various microoorganisms, mostly different groups of fungi. The trophic differentiation of oribatid mites has been considered relatively low. Several attempts have been made to classify the oribatids to guilds or trophic groups (Schuster, 1956; Wallwork 1958, 1967; Luxton, 1972; Kaneko, 1988). In principle, the generalists (panphytophages) vs. the species more or less specialized on the higher plant material (macrophytophages) or on the microorganisms (microphytophages) have been distinguished, the details and terminology slightly differed between rhe above-mentioned authorsauthors.

Siepel and De Ruiter-Dijkmann (1993) further developed the previous concepts according to the presence/absence of different digestive enzymes (carbohydrases), enabling the oribatid mites to digest the principal storage or structural polysaccharides in the higher plant or fungal material.

The saprophagy/mycophagy still seem to be the most widespread feeding strategies of oribatid mites in soil (Schneider et al., 2004a), but some recent studies based on stable isotope ratios ($^{15}N/^{14}N$ and/or $^{13}C/^{12}C$) indicate, that the trophic differentiation of oribatid mites is much higher than previously expected (Schneider et al. 2004b; Erdmann et al., 2007; Fischer et al., 2010).

Especially in the litter of temperate forest, the saprotrophic fungi represent one of the major and widely utilized food source for oribatid mites (Luxton, 1972; Wallwork, 1983). Algal food is readily accepted or even preffered by most oribatid species in laboratory conditions (Hubert and Lukešová, 2001; Hubert et al., 2001; Smrž and Norton, 2004). Besides the saprotrophic fungal species the ectomycorrhizal fungi may be accepted by the oribatids as well (Schneider et al., 2005). The fungal communities are strongly influenced by the oribatid activity. On one hand, the fungal colonies are subjected to continuous grazing by numerous oribatid species (Mamilov et al., 2001); on the other hand the oribatids may disperse viable fungal propagules on their body surface and via their feaces (Jacot, 1930; Behan-Pelletier and Hill, 1978, 1983; Renker et al., 2005; Smrž, 2002). The oribatid mites facilitate the fungal colonisation of new substrates and may help to re-establish fungal communities after strong disturbance (Maraun et al., 1998b).

Most of oribatid mite species can feed on a variety of fungal species, but usually reveal distinct preference (Maraun et al. 1998a; Schneider and Maraun 2005; Schneider et al 2005). Even the species considered being predominantly macrophytophagous often ingest some amount of fungal material (Behan-Pelletier and Hill 1983; Smrž 1998). The spectra of fungi preferred by different oribatids partly overlap. It is still unknown to what extent the interspecific differences support the coexistence of high number of oribatid species (Maraun et al 1998; Schneider and Maraun 2005). Oribatids were supposed to prefer melanized ("dematiaceous") fungi to those with hyaline hyphae (Kaneko et al 1995; Maraun et al. 1998a). However, this hypothesis that fungal species belonging to an artificial taxonomic group "dematiaceae" may be preferred due to containing melanized hyphae has not been substantiated and different melanized fungi are preferred with different intensity (Schneider and Maraun 2005).

Koukol et al. (2009, included as *contribution 2.1* in this thesis) pointed the following three main gaps in knowledge of the oribatid-fungal trophic interactions, which have been hitherto studied mostly from the "zoocentric" point of view:

1. Most of the authors studying feeding preference of oribatid mites for particular fungi used fungal strains cultivated on artificial agar media, not on natural substrates. The substrate quality largely affects the fungal physiology; therefore the content of secondary metabolites and the production of volatile compounds may strongly differ from the natural conditions. This may strongly change the preferences of the studied animals, as was already documented for Collembola (Klironomos, 1992; Kaneko et al., 1995; Sadaka-Laulan et al., 1998).
2. In many feeding preference studies, only part of the fungi was identified to species level. This makes difficult the comparison of results between different studies. Moreover, the results may not be interpreted in the context of autecology of the fungal species included.
3. The hitherto published studies included mostly ubiquitous fungal species and almost completely ignored fungi restricted to particular types of substrates.

The results of our feeding preference tests indicate, that particular oribatid species may prefer not only ubiquitous fungi, but also the substrate-specific ones (Koukol et al., 2009). The feeding preference revealed to be context-dependent and the oribatids are able to "switch" to other fungal species, if the most preferred one is removed from the study system.

Members of the family Damaeidae represent suitable model oribatid species for laboratory studies aimed on mite-fungal interactions. It can be assumed, that they feed predominantly on saprotrophic fungi (Schuster 1956; Luxton 1972; Siepel and de Ruiter-Dijkman 1993). Most of them can be easily kept in laboratory cultures on green coccal algae. Accidentaly, they can consume other materials including higher plant tissues and dead arthropod bodies as well. Their anterior part of alimentary tract is swallen into a voluminous chamber called ingluvies, which may represent an adaptation for predigestion of fungal material (Schuster 1956; Hoebel-Mävers 1967; Smrž 1991). Some of the damaeid species revealed an intensive digestive chitinase activity and are thus expected to be able to digest the cell-wall of the fungal hyphae - “fungivorous grazers”, while some others without the chitinase are probably able to digest only the hyphal content -“fungivorous browsers” (Siepel & de Ruiter-Dijkman 1993).

Their thick cerotegument coat (see above chapter 3.2) often harbours large amount of fungal spores (Mourek, unpubl.), which may be distributed by these relatively mobile animals. The two species of Damaeidae included in our preference tests did not reveal stronger preferences for particular fungal species than the remaining tested oribatid species (Koukol et al., 2009). In our second study (Koukol et al., subm., included as *contribution 2.2* in this thesis) we demonstrated, that the grazing by two species of Damaeidae at low population density may increase the amount of viable propagules of anamorphic ascomycetes.

4 Synopsis of the contributions

4.1 Problems of taxonomy and morphology of European Damaeidae and Gymnodamaeidae

Contribution 1.1

Weigmann G., **Mourek J.** (2008) Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari: Oribatida: Gymnodamaeidae). ***Zoosystematics and Evolution*** 84, 255 - 264.

We provided a detailed redescription of *Gymnodamaeus barbarossa* Weigmann, 2006, which was originally only briefly described in the identification key to oribatid mites of Germany. We further provided detailed comparison of *G. barbarossa* with the second known Central European species of the genus—*G. bicostatus* (C. L. Koch, 1835) and summarized available data on distribution of both species. *Gymnodamaeus bicostatus* has a Holarctic distribution; *G. barbarossa* has been recorded in Eastern Germany at the Kyffhäuser Mountain (locus typicus), in Austria, Czech Republic and Slovakia, up to now. Each species has a characteristic cerotegument ornamentation, which is documented by SEM micrographs. Both species seem to prefer dry and warm habitats.

I substantially participated in data collection as well as in writing the manuscript of this publication, namely by conducting the SEM-study of both species, analysing their the leg setation, providing morphometrical data, drawing of some figures and writing some parts of the text.

Contribution 1.2

Miko L., **Mourek J.** (2008): Taxonomy of European Damaeidae (Acari: Oribatida) I. *Kunstidamaeus* Miko, 2006, with comments on *Damaeus* sensu lato. ***Zootaxa*** 1820, 1-26.

In this publication we reviewed the historical development of the taxonomy of the family Damaeidae and proposed a new concept of classification of the generic complex *Damaeus* sensu lato. *Epidamaeus* Bulanova-Zachvatkina, 1957, *Spatiodamaeus* Bulanova-Zachvatkina, 1967 and *Kunstidamaeus* Miko, 2006 were given generic status, whereas *Damaeus* (*Adamaeus)* Norton, 1977, *D. (Paradamaeus)* Bulanova-Zachvatkina, 1967 and the nominal subgenus *Damaeus* sensu stricto were considered to be subgenera of the genus *Damaeus* C. L. Koch, 1835. We further provided an amended diagnosis and description of the genus *Kunstidamaeus* Miko, 2006. The type species *K. lengersdorfi* (Willmann, 1932) and its immature stases were redescribed and the geographic distribution and ecology of this troglophilous species was discussed. The neotype of *K. lengersdorfi* was designated. Together with the type species, the genus *Kunstidamaeus* includes seven known European species: *K. tenuipes* (Michael, 1885), *K. tecticola* (Michael, 1888), *K. nivalis* (Kulczynski, 1902), *K. nidicola* (Willmann, 1936), *K. diversipilis* (Willmann, 1951), *K. granulatus* (Willmann, 1951), and *K. longisetosus* (Willmann, 1953).

I was substantially involved in all phases of preparation of this publication. I namely conducted the SEM-study of *K. lengersdorfi*, analysed the morphology of ontogenetic stages, analysed the ontogeny of leg chaetotaxis and compared it with representatives of other genera and subgenera of *Damaeus* sensu lato. I further wrote some parts of the text (part of the introduction, whole description of ontogeny of *K. lengersdorfi* and part of the remarks), drew some of the figures and graphically edited the final figure plates.

Contribution 1.3

Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. & Sabelis M. W. (eds.): ***Trends in Acarology*.** Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.

This contribution was originally presented as a poster on 12th International Congress of Acarology held in Amsterdam (August 2006) and published in final form in the reviewed conference proceedings. We concerned ontogeny of a specialised leg seta called famulus in the context of taxonomy of the family Damaeidae. The famulus is present on the dorsal side of the tarsus of the first pair of legs in acariform mites. It has various shapes, but a stable location within the whole group. In the Damaeidae, two states of famulus are known: emergent and sunken. The emergent famulus is a simple short seta with fully emergent insertion. It is present in the adult of all known Damaeidae and in immature stases of many damaeid genera. The sunken famulus is reduced in size and submerged in a fovea with an elevated rim, so that only its tip is visible. In this study, the ontogenetic development of the famulus in selected Central European damaeid species—namely *Damaeus (Adamaeus) onustus*, *D.* (*Paradamaeus*) *clavipes*, *Epidamaeus tatricus*, *Spatiodamaeus verticillipes*, *Kunstidamaeus lengersdorfi*, and *Belba compta*—was studied with light and scanning electron microscopy and compared with that of *Gymnodamaeus bicostatus* (Gymnodamaeidae). Literature data on the ontogeny of the famulus in Damaeidae are summarized and the significance of the famulus as a phylogenetic marker is discussed. In agreement with previous studies, adults of all studied members of Damaeidae had an emergent famulus. The immatures of all studied members of *Damaeus* sensu lato, except for *E. tatricus*, had a sunken famulus, whereas the immatures of *B. compta* had an emergent famulus. Immatures as well as adults of *G. bicostatus* had a sunken famulus. In contrast to Norton's phylogenetic hypotheses, all immature stases of *E. tatricus* possessed an emergent famulus, similar to *B. compta*. Therefore, either the monophyly of *Epidamaeus* is questionable, or, more likely, reversal to a plesiomorphic state occurred in *E. tatricus*.

I elaborated the main content of this paper. The second author contributed with some important ideas and helped with polishing the final manuscript.

Contribution 1.4

Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species.

In this manuscript, submitted to a peer-reviewed journal with impact factor, we review the current state of taxonomy of the oribatid mite genus *Metabelba* Grandjean, 1936 (Damaeidae) and present a new concept of the genus and a new generic diagnosis. We consider the subgenus *Metabelba* (*Parametabelba)* Mihelčič, 1964, to be a *nomen nudum* and propose a new subgenus name to replace it. The new subgenus includes the species of *Metabelba* without a propodolateral apophysis. Further, we propose a new species of *Metabelba* based on the material from Central Bohemia (Czech Republic), Upper Silesia (Poland) and South Tyrol (Italy). *Metabelba romandiolae* (Sellnick, 1943) and *M. sphagni* Strenzke, 1950 are redescribed and illustrated based on the study of their type series as well as of the type series of their junior synonyms and freshly collected material. Finally, we provide a diagnostic key to the species included in the new subgenus known from Palaearctic region and Canary Islands.

I prepared the major part of this paper. The remaining two authors contributed by studying part of the material, provided comments and ideas, writing parts of the text, drawing some of the figures and assisting in finalisation of the manuscript.

Contribution 1.5

Mourek, J., Miko, Skubała, P. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) V. Redescription of *Epidamaeus bituberculatus* (Kulczynski, 1902).

In this manuscript, submitted to a peer-reviewed journal with impact factor, we redescribed and illustrated *Epidamaeus bituberculatus* (Kulczynski, 1902)—type species of the genus *Epidamaeus* Bulanova-Zachvatkina 1957. The detailed knowledge of this species has been urgently missing and its absence made impossible the revision of the concept of the heterogeneous and weakly defined genus *Epidamaeus*. The redescription is based on adult specimens collected in dead wood and tree hollows in natural forest in Upper Silesia, Poland, by P. Skubała. The species is characterized mainly by single pair of postbothridial tubercles (*Ba*) on prodorsum; comparatively strong sensillus evenly thick throughout with slight subterminal expansion and blunt tip; fully developed propodoventral (*E2a*, *E2p*) and ventrosejugal (*Va*, *Vp*) enantiophyses. We designated the neotype, because the original type series is presumably lost. Further, we discussed the similarities and differences of *E. bituberculatus* in comparison with other known species of the genus. *Epidamaeus bituberculatus* seems to be comparatively rare. At least part of published records is probably based on confusion with other species of the genus.

I prepared the major part of this paper: examined the available specimens of *E bituberculatus*, drew the figures and wrote most of the text. L. Miko wrote part of the introduction and discussion, namely the comparison with other species of the genus, provided comments and ideas and helped with finalizing the manuscript. P. Skubała collected the material of *E. bituberculatus*, provided fauniscic and habitat data and examined the habitats of the original type locality. He also helped with final editing of the manuscript.

4.2 Feeding preferences of selected oribatid mites inhabiting pine litter and their interactions with saprotrophic ascomycetes

Contribution 2.1

Koukol O., **Mourek, J.**, Janovský Z., Černá K. (2009) Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? *Soil Biology and Biochemistry*. 1124-1131.

Previous studies of oribatid mite feeding preferences for different soil fungi were limited to ubiquitous fungal species, whereas saprophytes specialized to decompose particular substrates have been neglected. Moreover, most authors used fungal strains cultivated on artificial agar media, not on natural substrates. The results may thus be somewhat misleading.

In the present study we therefore examined the preference of seven oribatid mite species (*Adoristes ovatus, Eniochthonius minutissimus, Eueremaeus silvestris, Nothrus silvestris, Oppiella subpectinata, Porobelba spinosa* and *Spatiodamaeus verticillipes*) for nine autochthonous saprotrophic fungi from Scots pine litter (*Pinus sylvestris*). Among the fungal species offered to the oribatid mites were seven specific coniferous litter colonizers (*Allantophomopsis lycopodina, Ceuthospora pinastri, Hormonema dematioides, Scleroconidioma sphagnicola, Verticicladium trifidum, Marasmius androsaceus* and

Sympodiella acicola) and two ubiquitous species (*Cladosporium herbarum* and *Oidiodendron griseum*).

The fungi were inoculated on fragments of pine needles and offered simultaneously and separately to the mites. Our hypothesis, that oribatid mites (usually occurring in more than one type of ecosystems) would prefer the ubiquitous fungal species rather than those specific to pine litter, was supported only partly. The ubiquitous *C. herbarum* was highly preferred by all studied mites, but most of them preferred one or more of the specialized fungi with similar intensity. The basidiomycete *M. androsaceus* along with sterile needles were consistently avoided by all mites in all experiments.

Our results do not support the hypothesis, that the "true" fungivorous oribatid mites in traditional sense (*Oppiella subpectinata, Porobelba spinosa* and *Spatiodamaeus verticillipes*) are more selective fungal feeders than are the "unspecialized" panphytophagous ones (*Adoristes ovatus, Eniochthonius minutissimus, Eueremaeus silvestris, Nothrus silvestris*).

We observed no gradation in preference of fungi for oribatid mites as a group, but rather a discontinuous and dynamic mosaic with particular mites preferring particular fungal species. This heterogeneous mosaic shapes the feeding niches occupied by particular oribatid mite species and probably reduces competition for food source among numerous species coexisting in a given habitat and time.

I substantially participated in most phases of this study and was responsible for its acarological part. I selected the model species of oribatid mites, collected the mites for the experiments and together with the remaining three authors took part in suggesting the experimental designs, collection of data, interpretation of the results, writing the text and final editing of the manuscript.

Contribution 2.2

Koukol O., Janovský Z., Černá K., **Mourek J.** (*submitted*) The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes.

In this study we examined, if the grazing by oribatid mites influences the amount of dispersion propagules produced by soil anamorphic ascomycetes. We determined changes in the number of propagules (conidia and hyphal fragments) potentially used for the dispersal of two anamorphic ascomycetes after grazing by two mycophagous oribatid mites at two mite densities. We exposed fragments of pine litter needles precolonised by *Sympodiella acicola* and *Fusicladium cordae* to grazing by *Porobelba spinosa* and *Spatiodamaeus verticillipes*. The number of propagules was determined as the number of fungal colonies on agar plates originating from a suspension made by washing the surface of individual needle fragments.

Lower density grazing by *Spatiodamaeus verticillipes* surprisingly resulted in higher number of propagules of both fungal species and reversed the decrease in the number of propagules in the control treatment. In contrast, both oribatid mites at the higher density significantly decreased the number of colonies. Simultaneously, allochthonous fungi were introduced by the mites into the needle fragments.

Our results indicate that *Spatiodamaeus verticillipes* and *Porobelba spinosa* may represent an important force affecting the dispersal of particular fungal species and the composition and structure of fungal communities in pine litter, with the effects being mite-density dependent.

In this study I took part mainly in suggesting and optimalisation of the experimental design, collecting the mites for experiments, interpretation of the data and writing the manuscript. The experiments were carried out mostly by O. Koukol and K. Černá, whereas Z. Janovský performed the data analysis.

5 References

Alberti, G., Storch, V., Renner, H. (1981) Ultrastructure of the cuticle of Acari (Arachnida). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 105: 183-236.

Balogh, J. & Balogh, P. (1992) *The Oribatid Mites Genera of the World. Volume I.* Hungarian National Museum Press. 263 pp.

Bayartogtokh, B. (2000a) New oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Species Diversity* 5:183-200.

Bayartogtokh, B. (2000b) Two new species of oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Acarina* 8: 65-78.

Bayartogtokh, B. (2000c) Two species of damaeid mites (Acari: Oribatida: Damaeidae) from Mongolia, with notes on distribution of the genera *Epidamaeus* and *Dyobelba*. *Biogeography* 2: 67-79.

Bayartogtokh, B. (2001) Three new soil mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Zoosystema* 23: 29-49.

Bayartogtokh, B., Norton, R.A. (2007) The *Dyobelba tectopediosa* species-group (Acari: Oribatida: Damaeidae) from the Southeastern USA, with a key to world species of *Dyobelba* and notes on their distribution. *Zootaxa* 1591: 39–66.

Bayartogtokh, B., Schatz, H. (2009) Two new species of the genus Gymnodamaeus (Acari: Oribatida: Gymnodamaeidae) from Tyrol (Austria), with remarks on diversity and distribution of the known species. *Revue Suisse de Zoologie* 116: 31-51.

Behan, V.M., Hill, S.B. (1978) Feeding habits and spore dispersal of Oribatid mites in the North American Arctic. *Revue d'Écologie et de Biologie du Sol* 15: 497-516

Behan-Pelletier, V.M., Hill, S.B. (1983) Feeding habits of sixteen species of Oribatei (Acari) from an acid peat bog, Glenamoy, Ireland. *Revue d'Écologie et de Biologie du Sol* 20: 221-267.

Behan-Pelletier, V.M., & Norton, R.A. (1983) *Epidamaeus* (Acari: Damaeidae) of arctic western North America and extreme northeast, U.S.S.R. *Canadian Entomologist* 115: 1253-1289.

Behan-Pelletier, V.M., & Norton, R.A. (1985) *Epidamaeus* (Acari: Damaeidae) of subarctic western North America and extreme northeastern USSR. *Canadian Entomologist* 117: 277-319.

Berlese, A. (1910) Brevi diagnosi di generi e specie nuovi di Acari. *Redia* 6: 346-388.

Bulanova-Zachvatkina, E.M. (1957a) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Soobschchenije I. *Zoologicheskij Zhurnal* 36: 1167-1186.

Bulanova-Zachvatkina, E.M. (1957b) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Rod *Epidamaeus*, gen. n. (Acariformes, Oribatei). Soobschchenije II. *Zoologicheskij Zhurnal* 36: 1792-1801.

Bulanova-Zachvatkina, E.M. (1962) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berlese, 1896 (triba Belbini, triba n.). *Zoologicheskij Zhurnal*, 41: 203-216.

Bulanova-Zachvatkina, E.M. (1965) O diagnostike vidov roda *Metabelba* Grandjean, 1936 (Oribatei, Damaeidae). *Zoologicheskij Zhurnal* 36 (9), 1333 - 1343.

Bulanova-Zachvatkina, E.M. (1967) *Pancirnyje kleschchi – Oribatidy*. Vysshaja Shkola, Moskva. 254pp.

Bulanova-Zachvatkina, E.M. (1975): Nadsemejstvo Belboidea Dubinin, 1954 (=Damaeoidea Balogh, 1961). pp. 120-143. *In*: Gilijarov, M. S. & Krivolutskij, D. A. (Eds): *Opredelitel obitaiustschich v potschve kljeschtschei*. Nauka, Moskva. (in Russian).

Chen, J., Norton, R.A., Behan-Pelletier, V.M., & Wang, H-F. (2004) Analysis of the genus *Gymnodampia* (Acari: Oribatida), with redescription of G. setata and description of two new species from North America. *Canadian Entomologist* 136: 793–821.

Enami Y. (1994) A new species of the genus *Belba* (Acari: Damaeidae) from Japan. *Edaphologia* 51: 1-5.

Erdmann, G., Otte, V., Langel., R., Scheu, S., Maraun, M. (2007) The trophic structure of bark-living oribatid mite communities analysed with stable isotopes (^{15}N, ^{13}C) indicates strong niche differentiation. *Experimental and Applied Acarology* 41: 1-10.

Ermilov, S. G., Łochyńska, M. (2009) Morphology on juvenile stages of *Epidamaeus kamaensis* (Sellnick, 1925) and *Porobelba spinosa* (Sellnick, 1920) (Araci:Oribatida: Damaeidae). *Annales Zoologici* 54: 527-544.

Fischer, B.M., Schatz, H., Maraun, M. (2010) Community structure, trophic position and reproductive mode of soil and bark-living oribatid mites in an alpine grassland ecosystem. *Experimental and Applied Acarology* DOI 10.1007/s10493-010-9366-8.

Grandjean, F. (1936) Les Oribates de Jean Frederic Hermann et son pere, *Annales de la Société Entomologique de France* 105: 27-110.

Grandjean, F. (1953) Essai de classification des oribates (Acariens). *Bulletin de la Société Zoologique de France* 78: 421-446.

Grandjean, F. (1954) Observations sur les Oribates (28e série). - *Bulletin du Museum D'Histoire Naturelle* Paris 26: 204-211.

Hoebel-Mävers, M. (1967) *Funktionsanatomische Untersuchungen am Vrtdauungstrakt der Hornmilben (Oribatei).* Dissertation thesis, Braunschweig, 88 pp.

Hubert, J. and Lukešová, A. (2001) Feeding of the panphytophagous oribatid mite *Scheloribates laevigatus* (Acari: Oribatida) on cyanobacterial and algal diets in laboratory experiments. *Applied Soil Ecology* 16: 77-83.

Hubert, J., Žilová, M., Pekár, S. (2001) Feeding preferences and gut contents of three panphytophagous oribatid mites (Acari: Oribatida). *European Journal of Soil Biology* 37, 197-208.

International Commission on Zoological Nomenclature (1999): International code of zoological nomenclature. Available from: 4th edition, online version. http://www.nhm.ac.uk/hosted-sites/iczn/code/index.jsp [cited 24. 4. 2010]

Jacot, A.P. (1930) Moss mites as spore-bearers. *Mycologia*, 22: 94-96.

Kaneko, N. (1988) Feeding habits and cheliceral size of oribatid mites in cool temperate forest soil in Japan. *Revue d'Écologie et de Biologie du Sol* 25: 353-363.

Kaneko, N., McLean, M.A., Parkinson, D. (1995) Grazing preferences of *Onychiurus subtenuis* (Collembola) and *Oppiella nova* (Oribatei) for fungal species inoculated on pine needles. *Pedobiologia* 39: 538-546.

Klironomos, J.N. (1992) Feeding preferences of the collembolan *Folsomia candida* in relation to microfungal succession on decaying litter. *Soil Biology and Biochemistry* 24: 685-692.

Koch, C.L. (1836a) *Deutschlands Crustaceen, Myriapoden und Arachniden,* vol 2 (11).

Koch, C.L. (1836b) *Deutschlands Crustaceen, Myriapoden und Arachniden,* vol. 4-9.

Koch, C.L. (1841) *Deutschlands Crustaceen, Myriapoden und Arachniden,* vol. 38 (7).

Kunst, M. (1958) Bulgarische Oribatiden (Acarina) II. - Acta Universitatis Carolinae - Biologica 5: 13-31.

Koukol O, Mourek J, Janovský Z, Černá K (2009) Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? *Soil Biology & Biochemistry* 41: 1124-1131.

Koukol O., Janovský Z., Černá K., Mourek J. (*submitted*) The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes.
Kunst, M. (1971) Pancířníci – Oribatei. In: Daniel, M. & Černý, V. (eds.), *Klíč zvířeny ČSSR II.* Nakladatelství Československé Akademie Věd, Praha, (in Czech) 531-580.
Kulczynski, V. (1902) Species Oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. *Bulletin International de L'Académie des Sciences de Cracovie, Classe des sciences mathématiques et naturelles* 2: 89-96.
Labandeira C.C., Philips T.L., Norton, R.A. (1997) Oribatid mites and the decomposition of plant tissues in paleozoic coal swamp forests. *Palaios* 12: 319-353.
Luxton, M. (1972) Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional biology. *Pedobiologia* 12: 434-463.
Mahunka, S., Mahunka-Papp, L. (1995) *The oribatid species described by Berlese (Acari).* Hungarian National History Museum, Budapest. 325 pp.
Mamilov, A.S., Byzov, B.A., Zvyagintsev, D.G., Dilly, O.M. (2001) Predation on fungal and bacterial biomass in a soddy-podzolic soil amended with starch, wheat straw and alfalfa meal. *Applied Soil Ecology* 16: 131-139.
Maraun, M., Migge, S., Schaefer, M., Scheu, S. (1998a) Selection of microfungal food by six oribatid mite species (Oribatida, Acari) from different beech forests. *Pedobiologia* 42: 232-240.
Maraun M, Visser S, Scheu S (1998b) Oribatid mites enhance the recovery of the microbial community after a strong disturbance. *Applied Soil Ecology* 9: 175-181.
Maraun, M., Heethoff, M., Schneider, K., Scheu, S., Weigmann, G., Cianciolo, J., Thomas, R. H., Norton, R. A. (2004) Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. *Experimental and Applied Acarology* 33: 183-201.
Mihelčič, F (1963) Beitrag zur Kenntnis der Oribatidenfauna Kärntens (Oribatei, Acarina) *Zoologischer Anzeiger* 170: 230-240.
Mihelčič, F. (1964) Ein Beitrag zur Kenntnis der Familie Damaeidae Berl. *Zoologischer Anzeiger* 172: 360-385.
Miko, L. (2006) Damaeidae. In: Weigmann, G.: *Hornmilben (Oribatida)*, Die Tierwelt Deutschlands 76, Goecke&Evers Publ. 179-207.
Miko, L. (2008) Taxonomy of European Damaeidae (Acari: Oribatida) II. *Porobelba weigmanni* n. sp. (Oribatida, Damaeidae), from East Slovakia, with comments on other known species of the genus. Zootaxa 1844: 55–62
Miko, L. (2010) Taxonomy of European Damaeidae (Acari: Oribatida) III. Species of the *Kunstidamaeus tenuipes* (Michael, 1885) group, with a description of *Kunstidamaeus fraterculus* n. sp. from East Slovakia. Zootaxa 2327: 51–64
Miko, L., Mourek J. (2008) Taxonomy of European Damaeidae (Acari: Oribatida). I. *Kunstidamaeus* Miko, 2006 with comments on *Damaeus* sensu lato. *Zootaxa* 1820: 1–26.
Miko, L., & Travé, J. (1996) Hungarobelbidae n.fam., with a description of *Hungarobelba pyrenaica* n.sp. (Arachnida, Oribatida), *Acarologia* 37: 133-155.
Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. & Sabelis M. W. (eds.): *Trends in Acarology*. Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.
Mourek, J., Miko, Skubała, P. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) V. Redescription of *Epidamaeus bituberculatus* (Kulczynski, 1902).

Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species.
Norton, R. A. (1977a) A review of J.Grandjean's system of leg chaetotaxy in the Oribatei and its application to Damaeidae. In: Dindal, D. L. (Ed.), *Biology of oribatid mites*, 33, SUNY College of Environmental Science and Forestry, Syracuse, New York, 33-62.
Norton, R. A. (1977b) The genus *Damaeus* Koch (Acarina: Oribatei) in the United States. *Acarologia* 19: 331-353.
Norton, R. A. (1978a) Generic concepts in the Damaeidae (Acari: Oribatei) I. Three new taxa based on species of Nathan Banks. *Acarologia* 20: 603-621.
Norton, R. A. (1978b) *Veloppia kananaskis* n. sp., with notes on the familial affinities of *Veloppia* Hammer (Acari: Oribatei), *International Journal of Acarology* 4: 71-84.
Norton, R. A. (1979a) Aspects of the biogeography of Damaeidae sensu latu (Oribatei), with emphasis on North America. In: Rodriguez, J.G. (Ed.): *Recent Advances in Acarology,* vol. 2: 535-540.
Norton, R. A. (1979b) Familial concepts in the Damaeoidea as indicated by preliminary phylogenetic studies. In: Rodriguez, J.G. (Ed.): *Recent Advances in Acarology,* vol. 2: 529- 533.
Norton, R. A. (1979c) Generic concepts in the Damaeidae (Acari: Oribatei) Part 2. *Acarologia* 21: 496-513.
Norton, R.A., Behan-Pelletier, V. (2009) Chapter 15, Oribatida. In: Krantz, G.W. & Walter, D.E. (Eds) *A Manual of Acarology 3rd Edition*. Texas Tech University Press, Lubbock, pp. 421–564.
Norton R. A., Kethley, J. B. (1994) Ecdysal cleavage lines of Acariform mites (Arachnida, Acari). *Zoologica Scripta* 23: 175-191.
Olszanowski, Z., Rajski, A., Niedbala, W. (1996) *Roztocze Acari - Mechowce Oribatida. - Katalog Fauny Polski - Catalogus faunae Poloniae.* Muzeum i Institut Zoologii, Poznaň, 34: 243 pp.
Paschoal, A. D. & Johnston, D. E. (1982) Revised classification of the Gymnodamaeidae (Acari: Oribatei) with a key to the genera. *Revista brasileira de Biologia* 42: 461-466.
Perez-Iñigo C. (1997) Acari: Oribatei, Gymnonota. In: Ramos, M. A., (Ed.), *Fauna Iberica,* 9, Museo Nacional de Ciencias Naturales, Madrid, pp. 1-374.
Renker, C., Otto, P., Schneider, K., Zimdars, B., Maraun, M., Buscot, F. (2005) Oribatid Mites as Potential Vectors for Soil Microfungi: Study of Mite-Associated Fungal Species. *Microbial Ecology* 50: 518-528.
Sadaka-Laulan, N., Ponge, J.F., Roquebert, M.F., Bury, E., Boumezzough, A. (1998) Feeding preferences of the collembolan *Onychiurus sinensis* for fungi colonizing holm oak litter (*Quercus rotundifolia* Lam.). *European Journal of Soil Biology* 34: 179-188.
Saloña, M. & Iturrondobeitia, J.C. (1989) Especies interesantes, pertenecientes a la superfamilia Belboidea (Acari, Oribatei) recogidas en Vizcaya y una zona afín: *Epidamaeus plesiomorphicus* n.sp. - *Anales de Biología (Biologia Animal), Murcia* 4: 15-27.
Schatz, H. (1983) U.-Ordn. Oribatei, Hornmilben. *Catalogus faunae Austriae. Ein systematisches Verzeichnis aller auf osterreichischem Gebiet festgestellten Tierarten*, 9, Österreichische Akadademie der Wissenschaften, Wien, pp. 1-118.
Schatz H., Schuster R. (2009) Oribatida (Hornmilben) pp. 464-475. In: Rabitsch W. & Essl F. (eds): *Endemiten – Kostbarkeiten in Österreichs Pflanzen- und Tierwelt.* Naturwissenschaftlicher Verein für Kärnten & Umweltbundesamt, 924 pp.
Schneider, K., Renker, C., Scheu, S., Maraun, M. (2004a) Feeding biology of oribatid mites: a minireview. *Phytophaga* 14: 247-256.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., (2004b) Trophic niche differentiation in oribatid mites (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). *Soil Biology and Biochemistry 36*: 1769-1774.
Schneider, K., Renker, C., Scheu, S., Maraun, M. (2005) Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. *Mycorrhiza* 16: 67-72.
Schneider, K., Maraun M. (2005) Feeding preferences among dark pigmented fungal taxa (''Dematiacea'') indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). *Pedobiologia* 49: 61-67.
Schuster, R. (1956) Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. *Zeitschrift für Morphologie und Ökologie der Tiere* 45: 1-33.
Sellnick M. (1928) Formenkreis: Hornmilben, Oribatei. In: Brohmer P., Ehrmann P., Ulmer H. (Hrsg.) *Die Teirwelt Mitteleuropas* 3, 4. Lief. (Teil 9). Quelle & Meyer, Leipzig: 1-41.
Siepel, H. & de Ruiter-Dijkman, E. M. (1993) Feeding guilds of oribatid mites based on their carbohydrase activities. *Soil Biology and Biochemistry* 25: 1491-1497.
Smrž, J. (1991) Some aspects of the microanatomy of soil sarcoptiform mites (Acari: Oribatida and Acaridida). In: Dusbábek F. & Bukva V. (eds.): *Modern Acarology*, Academia, Prague and SPB Academic Publishing bv, The Hague, Vol. 2, 319-322.
Smrž, J. (1998) Interactions between oribatids and micro-organisms: A complex method of study. *Applied Soil Ecology* 9: 109-110.
Smrž, J. (2002) The excrement analysis - the useful tool for the biological and autecological studies in soil zoology. In: Tajovský K., Balík V. and Pižl V. (eds.) *Studies on Soil Fauna in Central Europe*. ISB AS CR, České Budějovice. pp. 185-189.
Smrž J., Norton R.A. (2004) Food selection and internal processing in *Archegozetes longisetosus* (Acari: Oribatida). *Pedobiologia* 48: 111-120.
Subías, L.S. (2004) Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1748-2002). *Graellsia* 60: 3–305.
Subías, L. (2007, 2008, 2009) *Listado sistematico, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (Excepto fósiles)*. 536. Available from: http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf/
Subías, L., Arillo, A., Subías J. (1997) The genus Arthrodamaeus Grandjean (Acariformes, Oribatida, Gymnodamaeidae). *Acarologia* 38: 297-307.
Walter, D. E. (2009) Genera of Gymnodamaeidae (Acari: Oribatida: Plateremaeoidea) of Canada, with notes on some nomenclatorial problems. *Zootaxa* 2206: 23–44
Wallwork, J.A. (1958) Notes on feeding behaviour of some forest soil Acarina. Oikos 9: 260-271.
Wallwork, J.A. (1967) Acari. In: Burges, A., Raw, F. (Eds,): *Soil biology.* Academic Press, London, pp. 362-395.
Wallwork, J.A., (1983) Oribatids in forest ecosystems. *Annual Review of Entomology* 28: 109-130.
Weigmann, G. (2002) Morphologie, Biogeographie und Ökologie einer in Zeintaleuropa neuen Hornmilbe: *Eremobelba geographica* Berlese, 1908 (Acari, Oribatida, Eremobelbidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 74: 31-36.
Weigmann, G. (2006) Hornmilben (Oribatida). In Dahl, F. (ed). *Die Tierwelt Deutschlands* 76: 1-520. Goecke & Evers, Keltern.
Weigmann G., Mourek J. (2008) Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari: Oribatida: Gymnodamaeidae). *Zoosystematics and Evolution* 84: 255 - 264.
Willmann, C. (1931) Moosmilben oder Oribatiden (Cryptostigmata). in: Dahl F. (Ed.), *Die Tierwelt Deutschlands* 22: 79-200.

Woas, S. (1992) Beitrag zur Revision der Gymnodamaeidae Grandjean, 1954 (Acari, Oribatei). *Andrias* 9: 121-161.
Woolley, T.A. (1972) A new species of *Gymnodamaeus* from Colorado (Acarina: Cryptostigmata, Gymnodamaeidae). *Great Basin Naturalist* 32: 97-103.
Woolley, T. A. (1973a) Scanning electron microscopy of oribatid mites. in: Daniel M. & Rosický B. (eds.) *Proceedings of the 3rd International Congress of Acarology.* Academia, Prague: pp 55-56.
Wooley, T.A. and Higgins, H.G. (1973b) A new *Gymnodamaeus* from Western Colorado (Acarina, Cryptostigmata, Gymnodamaeidae). *Proceedings of the Entomological Society of Washington* 75: 411-416.
Wooley, T.A. and Higgins, H.G. (1979) A new genus and two new species in Damaeidae. In: Rodriguez, J.G. (Ed.): *Recent Advances in Acarology*, vol. 2: 553-558.

6 Aggreements of the co-authors

Freie Universität Berlin

Fachbereich Biologie, Chemie, Pharmazie

Freie Universität Berlin
Zoologie, Königin-Luise-Str. 1-3. D-14195 Berlin

Dept of Zoology
Charles University, Faculty of Science
Viničná 7
CZ-128 44 **Prague** 2
Czech Republic

Prof. Dr. Gerd Weigmann
Institut für Biologie – Zoologie
Königin-Luise-Str. 1-3
D-14195 Berlin
Telefon (030)838-5 39 41 Weigmann
-5 39 15 Sekretariat
Fax (030)838-5 39 16
e-mail: weigmann@zedat.fu-berlin.de
Homepage: www.bodenzoologie.fu-berlin.de/

Berlin , 13.05.2010

On behalf of the Faculty Commission

Dissertation of Mag. Jan Mourek, Prag

Herewith I give my agreement that the original publication

Weigmann G., Mourek J. (2008): Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari,Oribatida, Gymnodamaeidae). – Zoosyst. Evol. 84: 255-264.

is part of the dissertation of Jan Mourek. The publication was concepted and co-authored by both of us. The parts of Jan Mourek (e.g. SEM-pictures, part of drawings, biometrical data, texts) may be valued as about 40 %.

Mit freundlichen Grüßen

Prof. Dr. Gerd Weigmann

CHARLES UNIVERSITY PRAGUE
Faculty of Science
Department of Botany
Benátská 2, CZ-128 01 PRAHA 2
CZECH REPUBLIC
Phone +420 2 2195 1646
Fax **+420 2 2195 1645**
E-mail botanika@natur.cuni.cz
http://www.natur.cuni.cz/~botanika

Mgr. Ondřej Koukol. Ph.D.

Praha, 19. 5. 2010

On behalf of the Faculty Comission

Ph.D. Thesis of Mgr. Jan Mourek, Praha

I hereby give my agreement in the name of other authors that the following publication and manuscript:

> Koukol O., Mourek J., Janovský Z. & Černá K. (2009): Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? Soil Biology & Biochemistry, 41: 1124-1131.
>
> Koukol O., Janovský Z., Černá K. & Mourek J.: The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes. Fungal Ecology, *subm.*

are part of the Ph.D. thesis of Jan Mourek. The publication and the manuscript were concepted and written with considerable proportion of Jan Mourek. Jan Mourek's work on the publication and the manuscript include participation in planning of the experiments, gathering data, writing parts of the text and final editing of the text.

Mgr. Ondřej Koukol, Ph.D.

Dept. of Zoology
Charles University, Faculty of Science
Viničná 7
CZ-128 44 Prague 2
Czech Republic

Concerns: **PhD thesis of Mgr. Jan Mourek**

Herewith I confirm my agreement to use following list of common original publications as part of PhD-thesis of Jan Mourek. The level of his participation/contribution is stated for each paper separately, as follows:

Miko L., **Mourek J.** (2008): Taxonomy of European Damaeidae (Acari: Oribatida) I. *Kunstidamaeus* Miko, 2006, with comments on *Damaeus* sensu lato. ***Zootaxa*** 1820, 1-26.

J. Mourek was substantially involved in all phases of preparation of this publication. He namely conducted the SEM-study of *K. lengersdorfi*, analysed the morphology of ontogenetic stages, analysed the ontogeny of leg chaetotaxis and compared it with representatives of other genera and subgenera of *Damaeus* sensu lato. He further wrote some parts of the text (part of the introduction, whole description of ontogeny of *K. lengersdorfi* and part of the remarks), drew some of the figures and graphically edited the final figure plates.

Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. & Sabelis M. W. (eds.): ***Trends in Acarology.*** Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.

J. Mourek was responsible for the main content of this paper. I contributed mainly with comments and ideas regarding the broader context and helped with polishing the final manuscript.

Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species.

J. Mourek prepared most of the content of this paper. The remaining two authors contributed by studying part of the material, provided comments and ideas, wrote parts of the text, drew some of the figures and helped with finalizing the manuscript.

Mourek, J., Miko, Skubała, P. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) V. Redescription of *Epidamaeus bituberculatus* (Kulczynski, 1902).

J. Mourek prepared the redescription of *E. bituberculatus*, drew the figures and wrote most of the text. I wrote part of the introduction and discussion, namely the comparison with other species of the genus, provided comments and ideas and helped with finalizing the manuscript. P. Skubała collected the material of *E. bituberculatus*, provided fauniscic and habitat data and examined the habitats of the original type locality. He also helped with finalizing the manuscript.

In Brussels, 25 May 2010

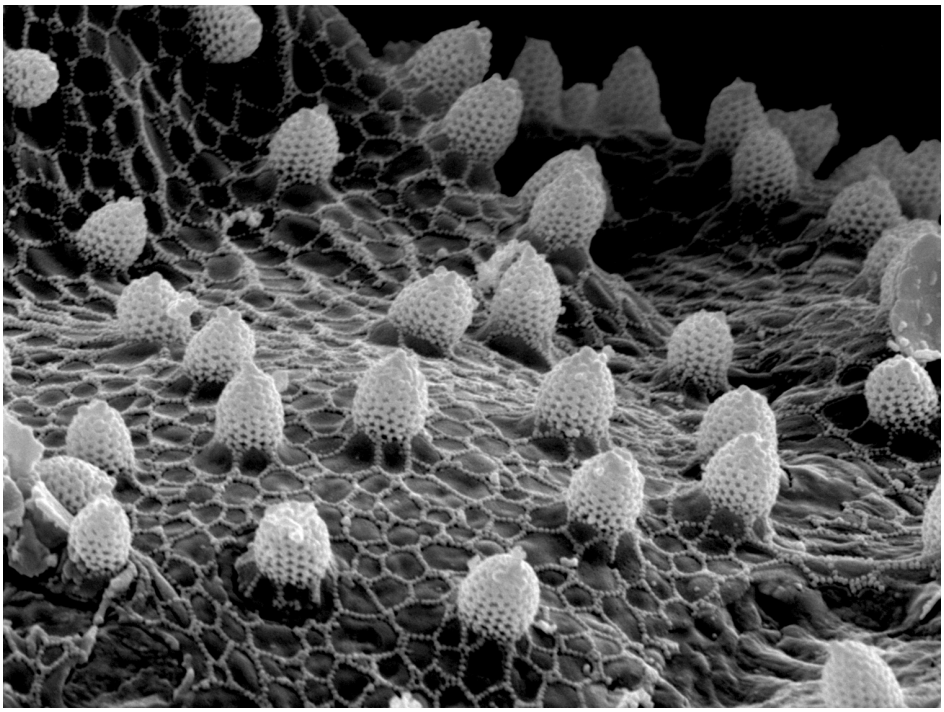
Ladislav Miko

doc. RNDr. Ladislav Miko, PhD.

7 Fulltext versions of contributions included in the thesis

Contribution 1.1

Weigmann G., **Mourek J.** (2008) Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari: Oribatida: Gymnodamaeidae). ***Zoosystematics and Evolution*** 84, 255 - 264.



Zoosyst. Evol. 84 (2) 2008, 255–264 / DOI 10.1002/zoos.200800010

WILEY-VCH

museum für naturkunde
der Humboldt-Universität zu Berlin

Contribution to the Central European *Gymnodamaeus* species *G. barbarossa* and *G. bicostatus* (Acari, Oribatida, Gymnodamaeidae)

Gerd Weigmann*, [1] and Jan Mourek [2, 3]

[1] Institut für Zoologie, Freie Universität Berlin, Königin Luise Str. 1–3, 14195 Berlin, Germany
[2] Charles University, Faculty of Science, Department of Zoology, Viničná 7, 128 44 Prague, Czech Republic
[3] Charles University, Faculty of Education, Department of Biology and Environmental Education, M. D. Rettigové 4, 116 39 Prague 1, Czech Republic

Received 16 January 2008
Accepted 8 April 2008
Published 24 September 2008

Key Words

taxonomy
distribution
Europe
leg setation
cerotegument
morphometrics

Abstract

A redescription of *Gymnodamaeus barbarossa* Weigmann, 2006, is presented and the species is compared with *Gymnodamaeus bicostatus* (C. L. Koch, 1835). Only these two species of the genus are known to occur in Central Europe. *Gymnodamaeus bicostatus* has a holarctic distribution, *G. barbarossa* has been recorded in Eastern Germany at the Kyffhäuser Mountain (locus typicus), in Austria, Czech Republic and Slovakia, up to now. Each species has a characteristic cerotegument ornamentation, which is documented by SEM micrographs. Both species seem to prefer dry and warm habitats.

Introduction

The Gymnodamaeidae were split into eleven genera by Paschoal & Johnston (1982) basing on numerical-taxonomical studies, resulting in five genera with European species: *Arthrodamaeus* Grandjean, 1954, *Gymnodamaeus* Kulczynski, 1902, *Jacotella* Banks, 1947, *Nortonella* Paschoal, 1982, and *Plesiodamaeus* Grandjean, 1954. This splitting was rejected by Woas (1992), who incorporated all named genera but *Arthrodamaeus* into *Gymnodamaeus*. Nevertheless, more recent taxonomical publications partly accept the subdivision (Marshall et al. 1987, Perez-Iñigo 1997, Subías 2004). This paper deals with the redescription of the adult *G. barbarossa* Weigmann, 2006, which was described briefly in Weigmann (2006), and the comparison with *G. bicostatus* (C. L. Koch, 1835) in regard of characteristical morphological details; both species belong to *Gymnodamaeus* s. str. and represent the only two species in Central Europe. A third species, described as *Gymnodamaeus helveticus* Woas, 1992, from Switzerland, belongs to *Nortonella*, following the splitted taxonomy (Subías 2004), and thus, differs in several characteristics.

Results

Redescription of *Gymnodamaeus barbarossa* Weigmann, 2006

Figures 1–4, 6a–c,e, 7a

Diagnosis. With typical characters of *Gymnodamaeus* s. str.: Articulation of all leg segments without collars ("crispins"); lamellar setae anterolaterally from large globular elevations and inserting on minute apophyses; interlamellar setae minute, on interlamellar costulae anterior to interbothridial region; notogaster flat; five pairs of notogastral setae at the posterior edge of notogaster; seven pairs of genital setae in one row each; two pairs of anal setae, two pairs of adanal setae. Specific characters: body length 460–540 μm; posterior submarginal notogastral setae h_1 and h_2 thin, covered with

* Corresponding author, e-mail: weigmann@zedat.fu-berlin.de

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

WILEY InterScience® DISCOVER SOMETHING GREAT

cerotegument, about 25–40 μm in length; posterior notogastral setae p_1–p_3 on the ventral border of notogaster, about 10–12 μm in length; notogaster at the posterior edge with characteristic double-indentation; sensilli moderately stalked, head flattened-claviform with spines; interlamellar setae very small and stout, not on projecting apophyses.

General characters. Body length 460–540 μm, width of notogaster 250–300 μm; colour yellow-brown to brown. Body, legs and most setae covered with a coarsely granulated cerotegument layer, as can be observed in light-microscope. Additionally, at the midline of the notogaster a more or less opaque cerotegument mass in fresh specimens, forming specific ornamentation (see section Notogaster and figures 1a, 2a, b). The opaque cerotegument ornamentation may be partly (fig. 6a) or totally abraded, especially in old preserved material. The normal cerotegument layer consisting of a thin base layer with a mesh net of about 1 μm mesh width; mesh net formed by rows of micro-granula, hardly visible in light microscope, but well visible in SEM micrographs (fig. 6b); cuticula with corresponding mesh net pattern below the micro-granula pattern visible at areas with abraded cerotegument. The large cerotegument granula of about 1–2 μm in diameter with roundish-pointed form like a *Morchella* mushroom and covered with a dense mesh-net pattern formed by micro-granula (granula on prodorsum: see figure 6b; on leg 1: see figure 7a).

Prodorsum. Rostrum roundish, with moderately long rostral setae (about 40 μm in length), covered with cerotegument granula; lamellar setae of the same shape inserted anterolaterally at base of two large lateral globular elevations; a smaller median elevation present anterior of the interbothridial region of the prodorsum (fig. 2a, b). Exobothridial setae of moderate length inserted anteriolaterally from the bothridia; interlamellar setae minute, inserted anterior of the interbothridial region at the end of indistinct interlamellar costulae (visible in light microscope view; figure 1a). Large auricular pedotecta I and II. Sensilli with short stalks, head flat, longish-claviform with spines, about 80–100 μm in length (figs 1a, 2c).

Notogaster. Flat with more or less sharp edges, centrodorsal part slightly elevated. With a specific cerotegument-mass ornamentation in shape of a slender Y; anterior near the notogaster border with another semicircular cerotegument-mass ornamentation. Cuticle in central part of the notogaster rugged transversally (visible only after the removal of cerotegument). Posterior border of notogaster with a characteristic double-indentation (figs 1a–b; 2d). Three pairs of lyrifissures, *ia, im, ip*. Five pairs of notogastral setae; h_1 and h_2 mostly covered with cerotegument granula, length about 25–40 μm, h_1 directed posteriad, h_2 laterad; p_1–p_3 at the posterior notogaster margin, visible only from ventral aspect (fig. 1b), length about 10–12 μm.

Ventral side. Without obvious specific characters (fig. 1b). Anal and genital plate near to each other; two pairs of small anal setae; two pairs of adanal setae; one pair of short aggenital setae, seven genital setae on each plate in one longitudinal row. Epimeral setation formula 3-1-3-3.

Legs. Typical for the family, tridactylous, anterior apophyses of tibia I very large, bearing two solenidia. Legs moderately long, shorter than body (see Table 1

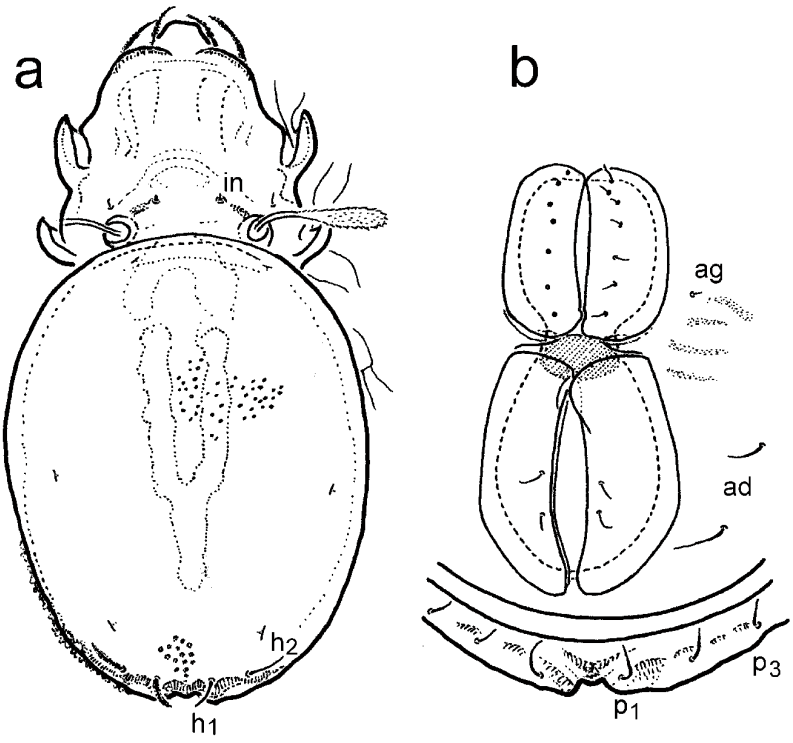


Figure 1. *Gymnodamaeus barbarossa*. **a**. Dorsal aspect without legs; **b.** Ventral aspect, ano-genital region.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

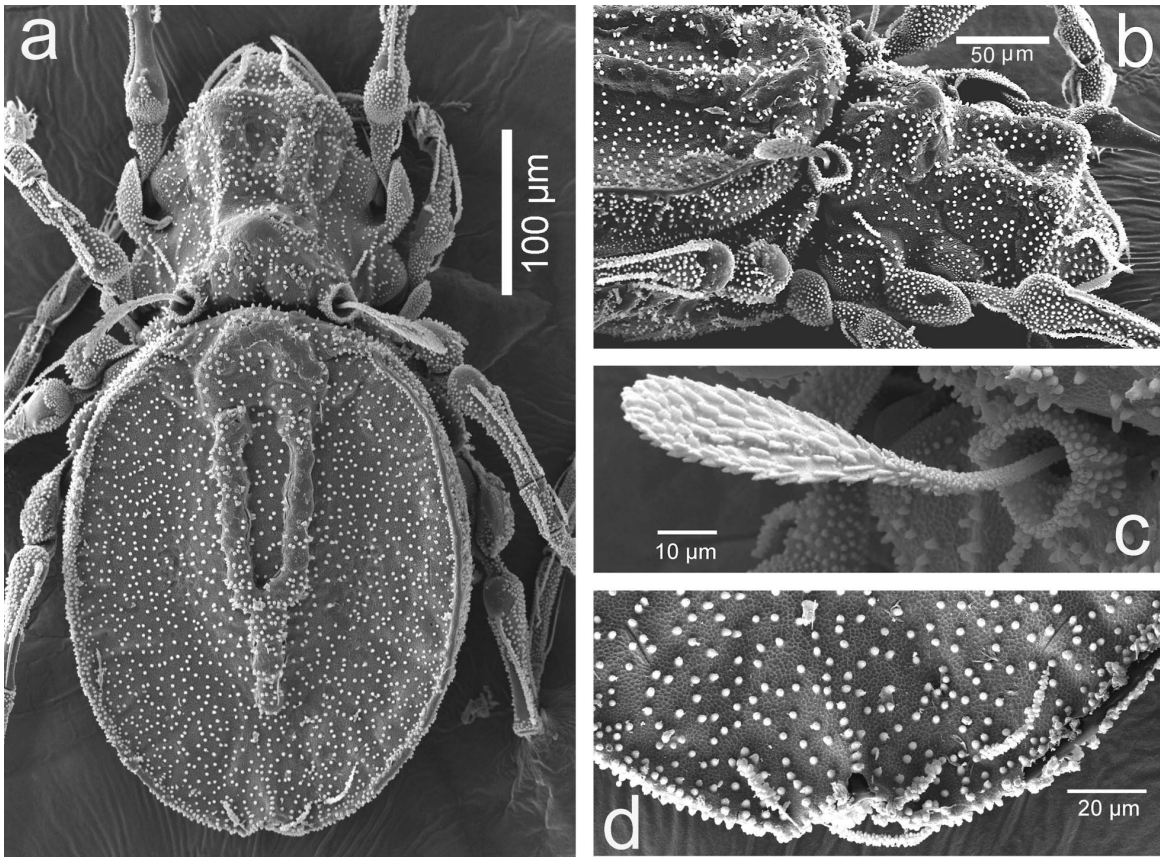


Figure 2. *Gymnodamaeus barbarossa*, SEM micrographs. **a.** Dorsal aspect; **b.** Lateral aspect of prodorsum; **c.** Sensillus; **d.** Posterior part of notogaster.

for details; figs 3, 4). Leg IV > leg I > leg III >leg II. In all legs femur > tarsus > tibia > genu. Femora with distinct widening ("bulb") in proximal part (maximal width in approximately 1/3 of their length). Setal formula of legs as follows (from trochanter to tarsus, famulus included, solenidia in parentheses, claws not included): I: 1-5-4(1)-5(2)-20(2); II: 1-4-4(1)-5(1)-16(2); III: 2-3-3(1)-4(1)-15; IV: 1-2-3-4(1)-12. Famulus ε on

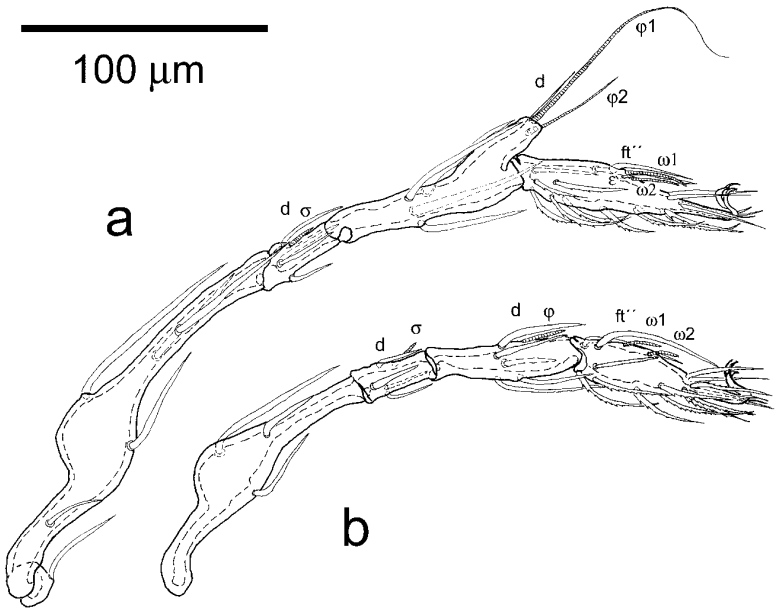


Figure 3. *Gymnodamaeus barbarossa*. **a.** Leg I; **b.** Leg II (without trochanter), (both right, antiaxial aspect). Cerotegument not drawn. – Abbreviations: **d** – dorsal seta of a given leg segment; **ft″** – posterior fastigial seta; ε – famulus; **ω1**, **ω2** – solenidia on tarsus; **φ1**, **φ2** – solenidia on tibia; **σ** – solenidion on genu.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

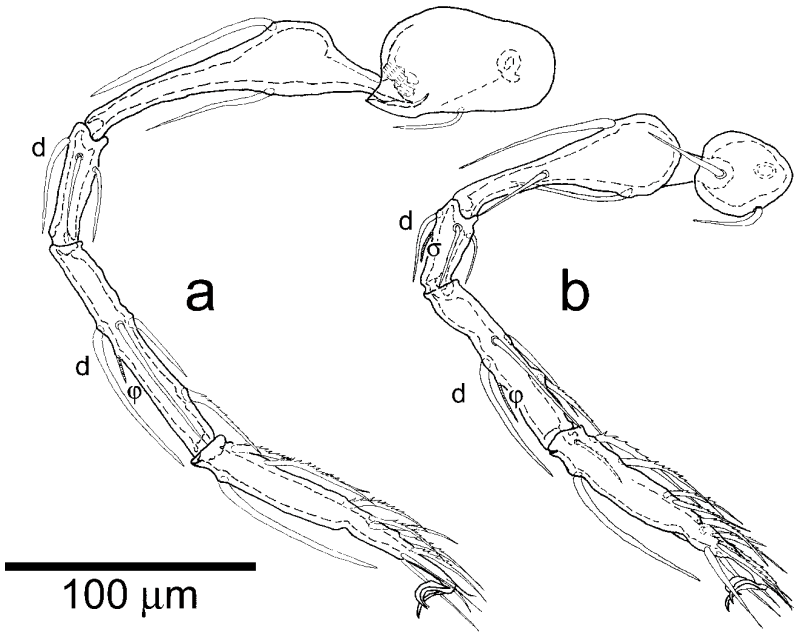


Figure 4. *Gymnodamaeus barbarossa*. **a.** Leg IV; **b.** Leg III, (both right, antiaxial aspect). Cerotegument not drawn. – Abbreviations: **d** – dorsal seta of a given leg segment; **φ** – solenidion on tibia; **σ** – solenidion on genu.

tarsus I minute, fully sunken in sclerotised cup (setal part invisible externally), hardly visible in light microscope. Leg setae comparatively long, thin, needle-like. Ventral seta on tibiae III and IV and most tarsal setae of all legs (except for prorals, iterals, tectals and fastigials) with short barbs on ventral side, the remaining leg setae smooth. Solenidion φ1 on tibia I long, flagellate, tactile, with a thin short companion seta *d* inserted in common alveolus (often tightly clamped to the dorsal side of the solenidion, therefore hardly visible in light microscope); φ2 much thinner than φ1, piliform, free, length about 0.4 of φ1. All remaining solenidia on tarsi, tibiae and genua short, baculiform to ceratiform (terminology of shapes of solenidia after Grandjean, 1935, 1940, as adopted by Norton 1977). Solenidia on tibiae II–IV and genua I–IV inserted in separate alveoli, not in a common alveolus with the respective seta *d*.

Material examined

Germany

(1) Type material deposited in the collection of M. Moritz in the Museum für Naturkunde in Berlin, labelled as "*Allodamaeus pusillus*" from the Kyffhäuser Mountain in Eastern Germany, near Bad Frankenhausen (51°21′ N, 11°06′ E); Collection Nr. 171/ B38 (the type specimen and 20 paratype specimens in alcohol), collected 29.9.1963; further specimens in 171/B41, B127, B159.

Czech Republic (listed chronologically)

(2) North Bohemia, České středohoří Mts., northwest from Lovosice, Lovoš Mt. (50°32′ N, 14°1′ E), altitude 400 m, rocky steppe on basalt, tussocks of *Festuca* sp. and *Sempervivum* sp., 30.04.1959, M. Kunst leg. (5 specimens in alcohol); collection of Miroslav Kunst (Dept. of Zoology, Faculty of Science, Charles University Prague), labelled as "*Gymnodamaeus sensillatus*".

(3) Vršíček (without any specification of region), 22.04.1971 (2 specimens in alcohol); coll. M. Kunst, labelled as "*Gymnodamaeus pusillus*".

(4) North Bohemia, České středohoří Mts., northwest from Lovosice, Lovoš Mt. (50°32′ N, 14°1′ E), altitude about 560 m, rocky steppe on basalt, south west slope, near the top of the mountain, tussocks of *Sempervivum* on rocks with a thin layer of soil, 18.03.2001, J. Mourek leg. (1 specimen); coll. J. Mourek (Dept. of Zoology, Faculty of Science, Charles University Prague).

(5) Southeast Moravia, northeast from the Pouzdřany village, Pouzdřanská step National Reserve (48°57′ N, 16°39′ E), altitude about 390 m, warm grassland with groups of *Staphylea pinnata*, *Prunus domestica*, *Acer campestre* and *Quercus pubescens* on loess soil, top of the hill and eastern slope, 17.11.2000 F. Št'áhlavský leg., (1 specimen in alcohol); 16.09.2006 J. Mourek leg., (14 specimens in alcohol); 14.05.2007 J. Mourek leg., (15 specimens in alcohol); all in coll. J. Mourek. Further voucher specimens from the same locality, 16.09.2006 J. Mourek leg., were deposited in coll. G. Weigmann, Berlin (10 specimens in alcohol) and in the Acarological Collections of Staatliches Museum für Naturkunde Görlitz, Germany (5 specimens in alcohol).

Slovakia

(6) South Slovakia, Štiavnické rudohoří, Žemberovce, (48°15′ N, 18°44′ E), altitude 450 m, Quercetum, dry litter and humus layer, 12.06.1962 M. Kunst leg. (5 specimens in alcohol); coll. M. Kunst, labelled as "*Gymnodamaeus sensillatus*". Kunst (1968) refers to both records as "*Gymnodamaeus pussillus*" (see in remarks).

(7) Southeast Slovakia, Slovak Karst National Park, Silická planina Mts., 4 km Southeast of Ardovo village (48°31′ N, 20°28′ E), forest steppe (extensive pasture) on karstic soil with bushes of *Cornus mas*, *Corylus avellana*, *Acer campestre*, *Juniperus communis* and *Carpinus betulus*, dry leaf litter, 13.07.2004 J. Mourek leg. (7 specimens in alcohol, 2 specimens mounted for SEM study).

Austria

(10) Carinthia, Steinkogel, near Völkermarkt, 46°41′ N 14°38′ E, knoll with arid meadow, haulm, grass litter moss. Numerous samples 17.06.2005 H. Perlinger and H. Schatz leg. (138 specimens); 08.10.2005 H. Perlinger leg. (38 specimens).

(11) Lower Austria, Hundsheimer Berge near Hundsheim, southern slope with oak forest (*Quercus pubescens*), 350 m a.s.l., in leaf litter, 04.06.2007 H. Schatz leg. (11 specimens).

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Some specimens from Steinkogel have been compared by one author (GW), the other material has been checked by H. Schatz. The material from Austria was deposited in coll. H. Schatz (Institut für Zoologie und Limnologie, Universität Innsbruck, Austria) except some specimens from Steinkogel (coll. G. Weigmann, Berlin).

Distribution. Central Europe: Germany, Austria, Czech Republic, Slovakia.

Ecology. The species seems to prefer warm and dry litter layer; habitat of the type series and other collections from south slope of Kyffhäuser Mountain in Germany which is wooded (*Quercus* and others), partly with grass; dry organic soil and litter.

Remarks. This species was found in the collection of M. Moritz in the Museum für Naturkunde in Berlin, labelled as "*Allodamaeus pusillus* (Berlese, 1910)", collected in Eastern Germany. Further specimens of *G. barbarossa*, labelled as "*Gymnodamaeus pusillus*" and "*Gymnodamaeus sensillatus*", collected in the Czech Republic and Slovakia (former Czechoslovakia), were found in the collection of M. Kunst (see Material examined). Kunst (1968) referred in his unpublished habilitation thesis to part of this material and wrote that he originally treated the form as a new species. Later he came to the conclusion, that it is most probably conspecific with *G. pusillus*, based on the comparison with the original description (Berlese, 1910).

Recently, Mahunka & Mahunka-Papp (1995) redescribed Berlese's species as *Arthrodamaeus pusillus* basing on specimens of the type series from Italy. Subías (2004) placed this species into the genus *Adrodamaeus* Paschoal, 1984, which seems to be questionable until a revision with fresh material. Without doubt, *G. barbarossa* is not conspecific. Main differences of *A. pusillus* are as characteristic for *Arthrodamaeus*, articulation of the leg segments with reverse collars ("crispins"), genital and anal plates near to each other with a common frame; specific main differences are minute interlamellar setae in posterior position between the bothridia, three pairs of moderately long notogastral setae of the *h*-row, two pairs of moderately long notogastral setae of the *p*-row. In consequence, all published records (referred in Mahunka & Mahunka-Papp 1995) need to be confirmed, whether they belong to *A. pusillus* or to *G. barbarossa*. The literature record of *Allodamaeus pusillus* (Berlese, 1910) from Slovakia (Starý, 2006) based on Kunst (1968) is *G. barbarossa* according to our study. Other records from Slovakia based on Miko (1992, 1995) are probably also conspecific with *G. barbarossa*, because the author used the diagnostic key of Kunst (1968) for identification (Miko, pers. comm.), but the material was not accessible to us.

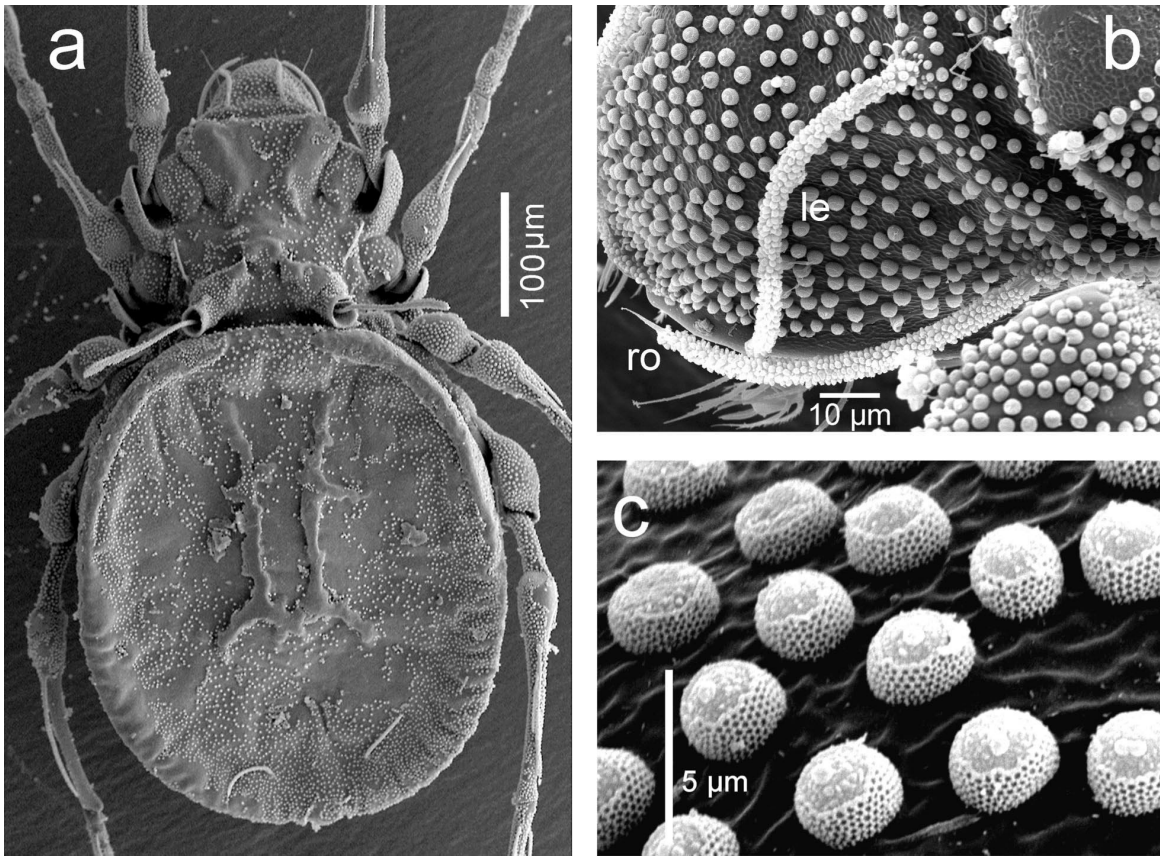


Figure 5. *Gymnodamaeus bicostatus*, SEM micrographs. **a.** Dorsal aspect; **b.** Dorso-lateral aspect of rostrum, rostral (**ro**) and lamellar setae (**le**) covered with cerotegument granula; **c.** Cerotegument microsculpture on prodorsum.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Two further European *Gymnodamaeus* species are known from Spain: *G. quadriseta* Ruiz, Kahwash and Subías, 1990, which is somewhat similar to *G. bicostatus* and thus is discussed below; *G. aprofundatus* Mihelcic, 1956, which is similar to *G. barbarossa* in the general outline and the sensillus, but this species is poorly described (Mihelcic 1956), it differs from *G. barbarossa* in body size (540–560 µm length) and in the notogastral setation (only two pairs of notogastral setae at the posterior margin, partly on apophyses). Even the genus seems to be uncertain, and in consequence the species is regarded as "species dubia" by Perez-Iñigo (1997).

Etymology. The species name refers to the Emperor Friedrich I in the middle ages, named *Barbarossa*, who remained sitting in the Kyffhäuser Mountain, after a popular myth.

Characteristics of *Gymnodamaeus bicostatus* (C. L. Koch, 1835)

Figures 5, 6d, 7b–c

Damaeus bicostatus C. L. Koch, 1835: CMA 2.12.

Gymnodamaeus bicostatus: Kulczynski 1902, Grandjean 1954, Ghilarov & Krivolutsky 1975, Paschoal 1982, Woas 1992, Perez-Iñigo 1997, Weigmann 2006.

Eremaeus asperulus Berlese, 1882: syn. after Mahunka & Mahunka-Papp 2004.

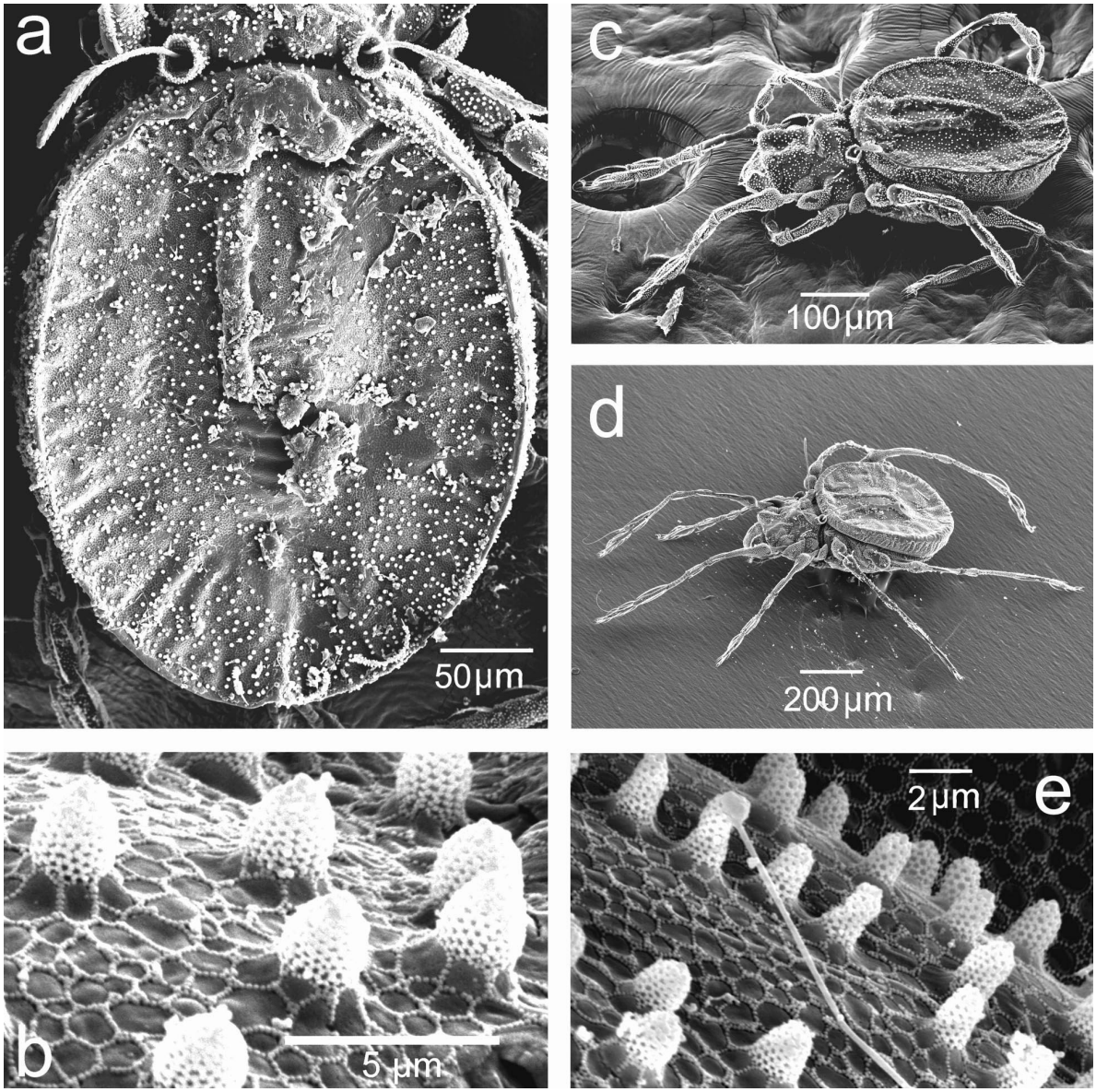


Figure 6. Cerotegument microsculpture (a, b, e) and total aspects (c, d) of *Gymnodamaeus* species, SEM micrographs. **a.** *Gymnodamaeus barbarossa* – dorsal aspect, notogaster with partly abraded cerotegument; **b.** *Gymnodamaeus barbarossa* – cerotegument microsculpture on prodorsum; **c.** *Gymnodamaeus barbarossa* – dorsolateral aspect; **d.** *Gymnodamaeus bicostatus* – dorsolateral aspect; **e.** *Gymnodamaeus barbarossa* – cerotegument microsculpture on anterior margin of notogaster.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

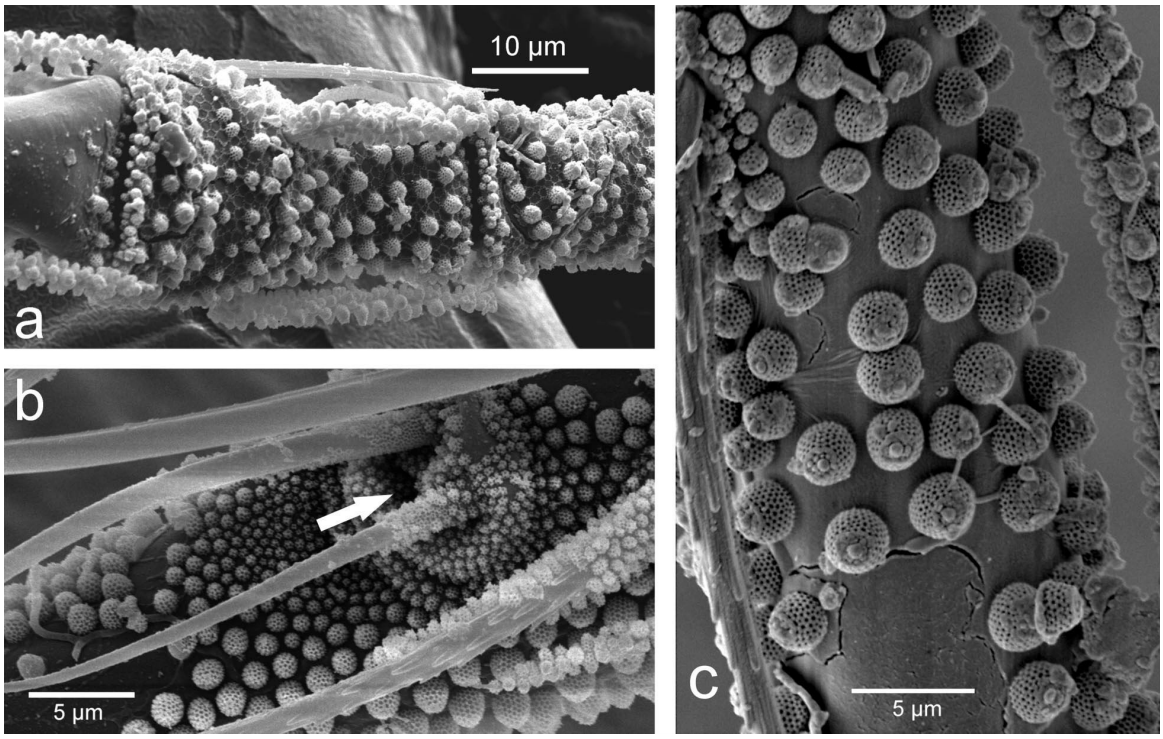


Figure 7. Cerotegument microsculpture on legs, SEM micrographs. **a.** Genu I of *G. barbarossa,* cerotegument abraded on femur (at left side); **b.** Tarsus I of *G. bicostatus*, insertion region of solenidia. Note the opening of the sclerotized "cup" with the externally invisible sunken famulus (arrow). **c.** Genu I of *G. bicostatus*.

Recently, *G. bicostatus* was redescribed by Perez-Iñigo (1997) and in detail by Woas (1992). In this paper we therefore restrict the comments to differences from *G. barbarossa* and to some new details of the cerotegument. We also studied complete leg setation, because Woas (1992) gave setal formulas for leg I and IV only.

Specific characters. Body length 636–756 µm (for details see Table 1); posterior submarginal notogastral setae h_1 and h_2 different, h_1 about 20 µm, h_2 about 50 µm in length; posterior notogastral setae p_1–p_3 situated on the ventral boarder of notogaster, about 8–12 mm in length; notogaster at the posterior edge without double-indentation; sensilli with long stalk, head slender, flattened-fusiform with fine spines, length up to 200 µm; interlamellar setae very small and stout, positioned on projecting apophyses at the medio-anterior edge of the interlamellar costulae. The ornamentation of the more or less opaque cerotegument mass at the centre of the notogaster forming namely two parallel length-ridges with a transversal connection at the posterior end (fig. 5a) and often with two pairs of short projections directed laterad. The normal cerotegument layer consisting of a thin cuticular cover with some irregular lines, but without a mesh net formed by microgranula; the large cerotegument granula on the body surface and on proximal segments of the legs of about 2,5 µm diameter with a semi-globular form and covered only at the lateral parts with a dense mesh-net pattern formed by micro-granula, tops of the granula smooth or covered with several irregular microgranula (granula on prodorsum: see figure 5c, granula on genu: see figure 7c). On tarsi of legs with different cerotegument granula, similar to those of *G. barbarossa* (see figure 7b). Legs relatively longer than in *G. barbarossa*, leg IV at least as long or longer than body (see Table 1); leg IV > leg I > leg III > leg II. Setal formulas of the legs as follows, identical with that of *G. barbarossa* (from trochanter to tarsus, famulus included, solenidia in parentheses, claws not included): I: 1-5-4(1)-5(2)-20(2); II: 1-4-4(1)-5(1)-16(2); III: 2-3-3(1)-4(1)-15; IV: 1-2-3-4(1)-12.

Material examined

Austria: Obergoldes south of Graz, leg. R. Schuster 2001; in thick litter layer, mixed forest with *Fagus*, *Castanea* and others (specimens for microscopical studies in Weigmann 2006). – Austria, Virgental, Central Alps, leg. H. Schatz 1993, dry meadow, partly in litter of *Juniperus* shrubs (Schatz 1995). – *Germany*: Berlin, leg. H. Woltemade 1978; litter of *Quercus* trees, at a roadside of a forest area. The material from Austria and Germany was deposited in coll. G. Weigmann (Berlin). – *Czech Republic*: Southeast Moravia, northeast from the Pouzdřany village, Pouzdřanská step National Reserve (48°57' N, 16°39' E, altitude about 390 m), warm grassland with groups of *Staphylea pinnata*, *Prunus domestica*, *Acer campestre* and *Quercus pubescens* on loess soil, top of the hill and eastern slope, 16.09.2006 J. Mourek leg., (11 specimens in alcohol, 6 specimens mounted for SEM study); 17.05.2007 J. Mourek leg., (7 specimens in alcohol), coll. J. Mourek – *Slovakia*: South Slovakia, Kováčovské kopce, about

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

3 km east of Kamenica nad Hronom (47°50′N, 18°38′47 E), forest steppe south-exposed slope near the top of the hill, 24.06.2004 F. Šťáhlavský leg. (18 specimens in alcohol, 2 specimens mounted for SEM study), the material from the Czech Republic and Slovakia deposited in coll. J. Mourek.

Distribution. Holarctic: in several countries of Europe and Asia; North Africa; North America (Marshall et al. 1987).

Ecology. Rajski (1967) discussed the controversial ecological preferences; in Southern Europe the species is more or less xerophilous and thermophilous (cf. Schatz 1983); for Eastern Austria Schuster (1960) indicated the preference for "moderately dry and moderately fresh habitats". In temperate and northern climatic conditions in the Palaearctic the species occurs predominantly in litter layer of mesohygric forest soils (cf. in Poland: Rajski 1967, Woas 1992; in Berlin, Germany: Woltemade 1982).

New findings in dry and warm forest areas in Germany (Horak et al. 1997; Russell et al. 1994; Kratzmann et al. 1993) support the thermophilous predominance of the species also for Central Europe. Remarkably, Strenzke (1952) found it in dry moss on a roof in Northern Germany. But there are northern Palaearctic and subalpine records, referred e.g. in Rajski (1967) and Schatz (1983), which indicate a broader temperature tolerance.

Comparative remarks

G. bicostatus (C. L. Koch, 1835) is the first species of Gymnodamaeidae, described in "Deutschlands Crustaceen, Myriapoden und Arachniden" vol. 2 (not published in 1836, as indicated by several authors) as *Damaeus bicostatus*, and it is the type species of *Gymnodamaeus* Kulczynski, 1902. There are about 20 species of the genus *Gymnodamaeus* s. str. (cf. Subías 2004), the taxonomical positions of some species are questionable, some with uncertain synonymy. The taxonomical conception is controversial, e.g. comparing that of Woas (1992) versus Parschoal (1982; Paschoal & Johnston 1982) but is not object of this paper. This contribution focuses on European species of *Gymnodamaeus* s. str. The Spanish species *G. quadriseta* Ruiz, Kahwash and

Table 1. Morphometrics of *G. barbarossa* and *G. bicostatus*. All measurements are given in µm. Body length and body width were measured in dorsal view, legs were measured without trochantera. Note that *G. bicostatus* has relatively longer legs than *G. barbarossa*.

	G. barbarossa (n = 8)			*G. bicostatus* (n = 8)		
	mean	min.	max.	mean	min.	max.
body length	493	456	540	701	636	756
body width	274	250	300	405	384	420
leg I	374	350	394	724	694	756
leg I : body length	**0.76**	0.72	0.80	**1.04**	0.93	1.14
femur I	154	139	161	292	267	311
genu I	40	39	44	85	83	89
tibia I	85	78	94	188	178	200
tarsus I	94	89	100	158	144	167
leg II	288	278	306	534	511	567
leg II : body length	**0.59**	0.51	0.62	**0.76**	0.70	0.87
femur II	117	111	128	215	200	233
genu II	32	28	33	55	50	56
tibia II	63	56	67	121	117	128
tarsus II	76	56	83	144	133	156
leg III	313	300	333	597	567	622
leg III : body length	**0.64**	0.57	0.66	**0.85**	0.79	0.92
femur III	105	100	111	199	189	211
genu III	35	33	39	56	56	61
tibia III	80	72	89	181	167	194
tarsus III	93	89	100	160	150	172
leg IV	390	361	411	788	767	811
leg IV : body length	**0.79**	0.74	0.83	**1.13**	1.03	1.25
femur IV	133	122	139	280	261	289
genu IV	41	33	44	78	72	83
tibia IV	99	89	106	246	222	261
tarsus IV	116	111	122	183	172	194

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Subías, 1990, is similar to *G. bicostatus* in regard of prodorsal characters (sensillus shape, insertion of interlamellar setae) but differs mainly in smaller body size (460–510 μm) and in reduced numbers of notogastral setae (only two pairs at the posterior margin).

Comparing the microstructure of the cerotegument granula in *G. bicostatus* and *G. barbarossa*, the granula of the body cerotegument are significantly different (Figs 5c, 6b,e), but not on distal segments of the legs (Figs 7a–c). Cerotegument granula similar to those of *G. barbarossa* can be found on the tarsi of legs of *G. bicostatus*, also. At the first sight, the cerotegument granula of *G. bicostatus* seem, that they are somehow abraded on their tops, but it was stable among the studied specimens from different localities. Already Woolley (1972, 1973) presented SEM micrographs of cerotegument granula in *G. chalazionus* Woolley, 1972; in principle, the granula are structured as those in the European species, in detail they are different on the notogaster and ventral plate of *G. chalazionus,* and both are not identical to those in *G. bicostatus* and *G. barbarossa*. The cerotegument granula are not studied in most *Gymnodamaeus* species, and therefore the taxonomy may use this character additionally, only.

Acknowledgements

The authors are very grateful to Heinrich Schatz and Ms. Heike Perlinger (Innsbruck, Austria) for providing their unpublished faunistic records of *G. barbarossa* in Austria, to František Št'áhlavský (Prague, Czech Republic) for collecting part of the material from the Czech Republic and Slovakia and to Ladislav Miko (Brussels, Belgium) for discussing probable localities of *G. barbarossa* in Slovakia. The SEM study was supported by the Grant Agency of the Charles University, Prague (grant *GAUK 217/2004/B-BIO/PrF*).

References

Berlese, A. 1910. Brevi diagnosi di generi e specie nuovi di Acari. – Redia 6: 346–388.

Ghilarov, M. S. & Krivolutsky, D. A. 1975. Sarcoptiformes. Opredelitel' obitajuschtschich w potschwe kleschtschej. Nauka, Moskau: 1–490.[russian]

Grandjean, F. 1935. Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Premiére partie. – Bulletin de la Société Zoologique de France 60: 6–39.

Grandjean, F. 1940. Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Deuxiéme partie. – Bulletin de la Société Zoologique de France 65: 32–44.

Grandjean, F. 1954. Observations sur les Oribates (28e série). – Bulletin du Muséum national d'Histoire naturelle. 2e série 26: 204–211.

Horak, F., Woas, St. & Eisenbeis, G. 1997. Untersuchungen der Oribatidenfauna eines xerothermen Waldgebietes bei Mainz (Rhein, Lennebergwald). – Abhandlungen und Berichte des Naturkundemuseums Görlitz 69 (2): 217–224.

Koch, C. L. 1835. Deutschlands Crustaceen, Myriapoden und Arachniden. Regensburg. Heft 2, No 12.

Kratzmann, M., Russell, D., Ludwig, M., Petersen, U., Wein, C., Storch, V. & Alberti, G. 1993. Untersuchungen zur Bodenarthropodenfauna zweier Buchenwaldstandorte im Einflußbereich geogener Schwermetalle. – Verhandlungen der Gesellschaft für Ökologie 22: 413–417.

Kulczynski, M. (1902): Species oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. – Bulletin international de l'Academie des Sciences de Cracovie, Classe des Sciences Mathematique et Naturales 2: 89–96.

Kunst, M. 1968. Roztoči nadřádu Oribatei Československa. Unpubl. habilitation thesis. Deposited in the Zoological library of the Faculty of Science, Charles University Prague. (in Czech) 1355 pp.

Mahunka, S. & Mahunka-Papp, L. 1995. The oribatid species described by Berlese (Acari). Hungarian National History Museum, Budapest.

Mahunka, S. & Mahunka-Papp, L. 2004. A catalogue of the hungarian oribatid mites (Acari: Oribatida). Pedozoologica Hungarica. vol. 2. Hungarian Natural History Museum, Budapest.

Marshall, V. G., Reeves, R. M. & Norton, R. A. 1987. Catalogue of the Oribatida (Acari) of continental United States and Canada. – Memoirs Entomological Society of Canada 139: 1–418.

Mihelcic, F. 1956. Oribatiden Südeuropas III. – Zoologischer Anzeiger 156: 9–29.

Miko, L., 1992. Pôdne článkonožce (Arthropoda) Dreveníka II. Pancierniky (Oribatida). Zborník Východoslovanského Múzea v Košiciach. Prírodné vedy 32–33: 113–130.

Miko, L., 1995. Taxocenózy pancířníků Acarina, Oribatida agroekosystémů Východoslovenské nížiny a Košické kotliny. Vol 1–2. Unpibl. candidate thesis. Deposited in the Zoological library of the Faculty of Science, Charles University Prague. [in Czech] 181 pp.

Norton, R. A., 1977. A review of J. Grandjean's system of leg chaetotaxy in the Oribatei and its application to Damaeidae. In Dindal, D. L. (ed.). Biology of oribatid mites. SUNY College of Environmental Science and Forestry, Syracuse, New York: pp. 33–62.

Paschoal, A. D. & Johnston, D. E. 1982. Revised classification of the Gymnodamaeidae (Acari: Oribatei) with a key to the genera. – Revista brasileira de Biologia 42: 461–466.

Paschoal, A. D. 1982. A revision of the genus *Gymnodamaeus* (Acari, Oribatei, Gymnodamaeidae), with descriptions of nine new species. – Revista brasileira de Entomologia 26: 113–132.

Perez-Iñigo, C. 1997. Acari, Oribatei, Gymnonota I. In Ramos, M. A. (ed). Fauna Iberica 9. Museo Nacional de Ciencias Naturales, Madrid: pp. 1–374.

Rajski, A. 1967. Autecological-zoogeographical analysis of moss mites (Acari, Oribatei) on the basis of fauna in the Poznan Environs. Part I. – Polish Journal of Entomology 37: 69–166.

Russell, D. J., Dastych, H., Zeller, U., Kratzmann, M. & Alberti, G. 1994. Zur Mesofauna des Bodens der Sandhausener Dünen. – Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg 80: 325–348.

Schatz, H. 1983. U.-Ordn. Oribatei, Hornmilben. Catalogus faunae austriae. Ein systematisches Verzeichnis aller auf österreichischem Gebiet festgestellten Tierarten. vol. 9i. Österreichische Akademie der Wissenschaften,Wien: pp. 1–118.

Schatz, H. 1995. Hornmilben in Trockenrasenböden des Virgentales (Osttirol, Österreich) 2. Teil: Faunistik (Acari, Oribatida). – Bericht des naturwissenschaftlich-medizinischen Vereins in Innsbruck 82: 121–144.

Schuster, R. 1960. Über die Ökologie und Verbreitung von Bodenmilben (Oribatei) am Alpen-Ostrand, insbesondere in der Steiermark. – Mitteilungen des naturwissenschaftlichen Vereins für die Steiermark 90: 132–148.

Starý J., 2006. List of oribatid mites (Acari: Oribatida) of the Slovak Republic. Sborník přírodovědného klubu v Uh. Hradišti 8: 21–38.

Strenzke, K. 1952. Untersuchungen über die Tiergemeinschaften des Bodens: Die Oribatiden und ihre Synusien in den Böden Norddeutschlands. – Zoologica 104: 1–173.

Subías, L. S. 2004. Lista sistematico, sinonimico y biogeografico de los Acaros Oribatidos (Acariformes, Oribatida) del mundo (1758–2002). – Graellsia 60 (num. extra.): 1–305.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Weigmann, G. 2006. Hornmilben (Oribatida). In Dahl, F. (ed). Die Tierwelt Deutschlands 76. Goecke & Evers, Keltern: pp. 1–520.

Woas, S. 1992. Beitrag zur Revision der Gymnodamaeidae Grandjean, 1954 (Acari, Oribatei). – Andrias 9: 121–161.

Woltemade, H. 1982. Zur Ökologie baumrindenbewohnender Hornmilben (Acari, Oribatei). – Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin (N.F.) 22: 118–139.

Woolley, T. A. 1972. A new species of *Gymnodamaeus* from Colorado (Acarina: Cryptostigmata, Gymnodamaeidae). – Great Basin Naturalist 32: 97–103.

Woolley, T. A. 1973. Scanning electron microscopy of oribatid mites. In Daniel, M. & Rosický, B. (eds.). Proceedings of the 3rd International Congress of Acarology. Academia, Prague: pp. 55–56.

© 2008 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Contribution 1.2

Miko L., **Mourek J.** (2008): Taxonomy of European Damaeidae (Acari: Oribatida) I. *Kunstidamaeus* Miko, 2006, with comments on *Damaeus* sensu lato. ***Zootaxa*** 1820, 1-26.

Zootaxa 1820: 1–26 (2008)
www.mapress.com/zootaxa/
Copyright © 2008 · Magnolia Press

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Taxonomy of European Damaeidae (Acari: Oribatida) I. *Kunstidamaeus* Miko, 2006, with comments on *Damaeus* sensu lato

LADISLAV MIKO[1,4] & JAN MOUREK[2,3]

[1]*European Commission, DG Environment, Avenue de Beaulieu 9, 1160 Auderghem, Brussels, Belgium.*
E-mail: ladislav.miko@ec.europa.eu
[2]*Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44 Prague, Czech Republic.*
E-mail: jan_mourek@yahoo.co.uk
[3]*Charles University, Faculty of Education, Department of Biology and Environmental Education, M. D. Rettigové 4, CZ-116 39 Prague 1, Czech Republic*
[4]*Coresponding author*

Abstract

The diagnosis of the genus *Kunstidamaeus* Miko, 2006 is given and a new generic concept within *Damaeus* sensu lato is proposed. *Epidamaeus*, *Kunstidamaeus* and *Spatiodamaeus* are given generic status, whereas *Adamaeus*, *Paradamaeus* and the nominal subgenus *Damaeus* s. stricto are considered to be subgenera of the genus *Damaeus*. The type species *K. lengersdorfi* (Willmann, 1932) including the immature stases is redescribed and its geographic distribution and ecology is discussed. The neotype of *K. lengersdorfi* is designated. Together with the type species, the genus *Kunstidamaeus* includes seven known European species: *K. tenuipes* (Michael, 1885), *K. tecticola* (Michael, 1888), *K. nivalis* (Kulczynski, 1902), *K. nidicola* (Willmann, 1936), *K. diversipilis* (Willmann, 1951), *K. granulatus* (Willmann, 1951), and *K. longisetosus* (Willmann, 1953).

Key words: type species, redescription, neotype, taxonomy, ontogeny, chaetotaxy, troglophilous species

Introduction

Oribatid mites of the family Damaeidae Berlese, 1896 occur mostly in the northern hemisphere, with the majority of known species living in forest soils of temperate, boreal and subarctic zones of palearctic and nearctic regions (Norton 1979a, 1979b).

The present paper represents the first part of a series which aims to revise the European Damaeidae based on the study of extensive material from Northern, Western and Central Europe, the types or topotypes of European authors when available, and recent discoveries on the family. This first part deals with the generic concept of *Damaeus* sensu lato, together with the detailed morphology of *Kunstidamaeus* Miko, 2006 including a redescription of its type species. Species of Central and Northern Europe belonging to other genera within *Damaeus* C. L. Koch, 1836 sensu lato (i.e. including *Damaeus* s. stricto, *Adamaeus* Norton, 1977b, *Epidamaeus* Bulanova-Zachvatkina, 1957, *Paradamaeus* Bulanova-Zachvatkina, 1957, *Spatiodamaeus* Bulanova-Zachvatkina, 1957 and *Kunstidamaeus* Miko, 2006) were revised (see Miko, 2006) and will be redescribed in detail in following articles of this series.

The family Damaeidae is reasonably diverse, being represented by more than 250 described species (Subías 2004). Grandjean (1954a) included the family in Euphérédermes, one of the five sections recognized within Brachypylina, which is characterised namely by the nymphs (less often also by the adults) carrying gastronotic exuviae of previous stages ("scalps") and by the reduction of the notogastral setae *f1, da, dm, dp* (the sete *da, dm, dp* are present only in the larvae). Monophyly of the Euphérédermes was questioned recently

Accepted by O. Seeman: 4 Apr. 2008; published: 9 Jul. 2008

(Maraun *et al.* 2004; Weigmann 2006) and the phylogenetic relations of Damaeidae to other families are not clear.

Damaeid mites are mostly long-legged, middle sized to large forms (rarely smaller than 500 µm, some species exceeding 1 500 µm) with roughly triangular prodorsum, which is separated from usually circular or ovoid notogaster by a deep dorsosejugal furrow. The nymphs and partly also adults, as in other euphéréderm families, carry gastronotic exuviae. Some species are remarkable by carrying a bulk of adherent dirt on the notogaster, serving probably as a kind of camouflage against predators (Luxton 1981).

From the studies of feeding habits of several model species (Schuster 1956; Luxton 1972; Siepel & de Ruiter-Dijkman 1993) it can be assumed that Damaeidae feed predominantly on saprotrophic fungi and readily accept or even prefer green algae. Occasionally, they can consume other materials including higher plant tissues and dead arthropod bodies as well. Their oesophagus is swollen into a voluminous chamber (ingluvies), which seems to be an adaptation for predigestion of fungal material (Schuster 1956; Hoebel-Mävers 1967; Smrž 1991). Based on the presence of chitinase activity, some damaeid species are expected to be able to digest the cell-wall of the fungal hyphae—"fungivorous grazers", while some others without the chitinase digest probably only the hyphal content—"fungivorous browsers" (Siepel & de Ruiter-Dijkman 1993).

As far as known, Damaeidae are mostly bisexual species with the sex ratio varying during the year, but several species are suspected to reproduce by facultative thelytokous parthenogeny, based on frequent absence of males from the populations (Luxton 1981). Fertilization is indirect, as usual in other oribatid mites, without any remarkable courtship behaviour (Pauly 1952; Norton 1994). Males deposit long-stalked spermatophores on the ground, which are collected by females with the genital atrium. The life history data are available for a few species. In members of *Damaeus* s. lato, a legless immovable prelarva (visible through a longitudinal split of the egg shell) was found and rests up to 2 weeks prior to the hatching of the larva, whereas in some other species (e.g. in *Belba corynopus*) the larva hatches directly from the egg (Grandjean 1954c; Luxton 1981). The duration of the life cycle may differ within a given species according to the temperature and other environmental conditions, as much as from 64 to 360 days in *Damaeus (Paradamaeus) clavipes* (Luxton 1981). In large forms, such as in *Damaeus (Adamaeus) onustus*, a surprising adult longevity of up to 634 days was observed (Pauly 1956).

Development of damaeid taxonomy

Given the large body size of many species, Damaeidae have been well known since the beginning of oribatid studies, and many classical species relate to this family (Koch 1836; 1841; Michael 1888; Nicolet 1855; Hermann 1804; Oudemans 1900). The first comprehensive study of the family was published at the beginning of the last century (Kulczynski 1902). Subsequently, a broad range of species was described by German (Willmann 1930, 1931, 1932, 1936, 1951, 1953, 1954; Sellnick 1926; Strenzke 1950; Märkel & Meyer 1960) and other European authors (Mihelčič 1954, 1955, 1957, 1963, 1964; Kunst 1957, 1961; Perez- Iñigo 1966; van der Hammen & Strenzke 1953). The first detailed morphological studies and a basis for the systematics of the group were published by Grandjean (1936, 1954a, 1954b, 1960). New taxonomical arrangements and descriptions of many new genera and species from the former Soviet Union were proposed by Bulanova-Zachvatkina (1957a, 1957b, 1962, 1965, 1967). Although some of these concepts were later questioned (Norton 1977b, 1978a, 1978b, 1979b, 1979c; Norton & Ryabinin 1994; Behan-Pelletier & Norton 1983, 1985; Wang & Norton 1989), they are still used as a basis for the recent taxonomy of the family (Balogh & Balogh 1992; Perez-Inigo 1997). Still, the taxonomy of the family is not stabilised, many relationships are unclear and the majority of authors have agreed on the need for a taxonomical revision.

The family concept of Damaeidae (under the junior synonym Belbidae) as a monophyletic group was proposed by Grandjean (1954a). It is well characterized by several autapomorphies (Norton 1979b), namely by the presence of horn-like cornicle (*k*) on the nymphal notogaster (by which the gastronotic exuviae are

attached); notogastral setae of rows *c*, *l* and *h* arranged in two more or less parallel longitudinal rows; rutella with a pair of distal globular hyaline expansions and cheliceral seta *chb* with fringe of barbs in distal third becoming shorter toward the tip. Expanded funnel-like bothridial rim is shared with Hungarobelbidae (Miko & Travé 1996)—originally placed within Damaeidae, now belonging to Ameroidea Grandjean, 1954 (see Chen *et al.* 2004). Based on Norton's (1979b) argumentation, we reject the splitting of Damaeidae into three families, as proposed by Bulanova-Zachvatkina (1967) and consider Belbidae and Belbodamaeidae in her sense to be artificial groups within Damaeidae.

Recently, Subías (2004, 2007) proposed extensive generic recombinations within the family, but unfortunately he neither explained the reasons, nor published any modified diagnoses. His work also lacks references to previous studies. In our view, this way of publishing taxonomic judgements may lead to confusion and destabilisation of the group systematics and should therefore be avoided (see also the opinion of Bayartogtokh and Norton 2007).

Generic concepts in Damaeidae are based mainly on the following characters: presence, arrangement and shape of setae on legs; development of different tubercles and apophyses on the prodorsum and coxisternum; presence of spines (*spinae adnatae*) on the anterior border of the notogaster; presence of the propodolateral apophysis; and development of cerotegument and cuticle. Other, more widely used characters include body size and colour; length and shape of prodorsal and notogastral setae, sensillus etc. In the present work we use the terminology and general approach of Grandjean (cit. see above) as modified by Norton (1977a), Behan-Pelletier and Norton (1983, 1985) and Miko and Travé (1996).

The morphological features of *Damaeus* sensu lato were discussed by several European and American authors (Grandjean 1960; Bulanova Zachvatkina date or cit. see above; Norton 1977b; Behan-Pelletier & Norton cit. see above; Bernini 1970, 1980; Bernini & Arcidiacono 1979; Cancela da Fonseca & Bahou 1970; Luxton 1989; Wang & Norton 1989), as well as by some of the authors describing new species from Asia (e.g. Bayartogtokh 2000a, 2000b, 2001; Fujikawa & Fujita 1985; Enami & Fujikawa 1989; Enami *et al.*1994).

Clear separation of genera within *Damaeus* sensu lato remains a problem, despite efforts to define natural species-groups with new morphological details (Norton 1978a, 1979a, 1979b; Norton & Ryabinin 1994; Wang & Norton 1989; Behan-Pelletier & Norton 1983, 1985), mostly because at the generic level (sensu Bulanova-Zachvatkina) and sometimes also at the species level, traits seem distributed in patterns that are closer to a mosaic rather than to hierarchical distributions.

Basically, two approaches have been used for *Damaeus*: recognizing *Damaeus* sensu lato (accepting a broadly defined genus with a broad range of subgenera) or splitting the genus into several smaller genera and subgenera. In the extreme form, the second approach may lead to the establishment of a new genus for every single combination of major characters states, resulting in many minor, closely related and probably artificial genera. On the other hand, some of these "narrow" genera include numerous species, and are broadly accepted. For example, *Epidamaeus*, originally proposed as a subgenus of *Damaeus* by Bulanova-Zachvatkina (1957), is currently usually accepted as the most species-rich genus of the family (see e.g. Behan-Pelletier & Norton 1983, 1985; Perez Inigo 1997; Balogh & Balogh 1992) with two clearly defined subgenera (*Epidamaeus* s. stricto and *Akrodamaeus* Norton, 1978a), but see Subías (2004). Also *Spatiodamaeus*, first established as a subgenus of *Damaeus*, is broadly accepted as a separate genus (see e.g. Schatz, 1983; Balogh & Balogh, 1992; Subías 2004, 2007), mostly because of quite uniform look of species with shared character states.

Proposed generic concept of *Damaeus* sensu lato

After a detailed study of European species of *Damaeus* sensu lato, and bearing in mind the above-mentioned trends, the following approach has been chosen (see also Miko, 2006). The genera *Damaeus* (with subgenera *Damaeus* sensu stricto, *Paradamaeus* Bulanova-Zachvatkina, 1957 and *Adamaeus* Norton, 1977), *Epidamaeus* Bulanova-Zachvatkina, 1957 and *Spatiodamaeus* Bulanova-Zachvatkina, 1957 are accepted and

characterised (Table 1). Most species as well as supraspecific taxa have been defined on the basis of adult characters, although it is clear that examination of immature morphology may bring some new and useful results as well.

The genus *Damaeus* is characterised by large body size, form and sculpture of prodorsum, with large and well-developed propodolateral apophyses, rugged surface with distinct ridges and a typical set of three pairs of prodorsal tubercles (*Da, Ba, Bp*). Subgenera within this genus differ in the degree of setal regressions on genu II and III (see Table 1).

The concept of *Spatiodamaeus* was narrowed (Miko, 2006) to species with interlamellar setae with form and size similar to that of the sensillus (which we consider to be the autapomorphy of this genus, based on its stability within the species group and the absence in other known Damaeidae), and arrangements of leg setae to form typical verticils. The genus *Spatiodamaeus* is probably closely related with *Damaeus* (they are likely sister groups), because they share e.g. the set of tubercles *Da, Ba, Bp* and presence of accessory seta *v2´* on tarsi I-IV (see also Norton 1977a). *Spatiodamaeus* lacks the rugged prodorsal surface present only in large species of *Damaeus* sensu Miko, 2006 (which may therefore be considered to be an autapomorphy of the genus), is generally smaller in size and has relatively shorter legs.

The genus *Epidamaeus* (European species of which are distinguished by the absence of the propodolateral apophysis) remains problematic in our view. There are at least three species groups, which differ quite significantly and may eventually be proposed as new supraspecific taxa. This idea is supported by recent findings (Mourek & Miko in press.) that some species of *Epidamaeus* lack a typical character that is—according to Norton (1979b)—shared by *Damaeus* sensu lato, *Dyobelba* Norton, 1978a and *Lanibelba* Norton, 1979c, i.e. a specialization of the famulus in immatures, being reduced, minute and sunken in a sclerotized "cup".

One particular set of European species cannot easily be included in any of the mentioned genera. Most of these are quite rare, poorly known and insufficiently described; in part, this is probably because they occur in somewhat specific habitats or microhabitats (caves, alpine zone of mountains, bird nests etc.). They include species currently in *Damaeus* sensu stricto (eg. *D. lengersdorfi*, *D. nidicola*—see Schatz 1983 and Olszanowski *et al*. 1996), *Epidamaeus* (eg. *E. tecticola*, *E. tenuipes*—see Luxton 1989), and *Spatiodamaeus* (eg. *S. diversipilis*, *S. tecticola*—see Schatz 1983). However, all these species share a set of character states. This was already mentioned in descriptions of some of these species by Willmann (1932, 1936), who recognised similarities in development of propodolateral apophysis.

Thorough study of particular species showed that the character set of this species group could be ranked at the same level as *Spatiodamaeus* or *Epidamaeus*, i.e. a new genus could be proposed to include them. Kunst (1971, see also 1968, unpublished)—apparently motivated by remarks of Willmann (1932, 1936)—had proposed the subgenus *Apodamaeus* for some members of this group. However, the name appeared only in determination keys, with no indication of a species that would be available for type designation. Thus, the taxon was a *nomen nudum* (see Norton 1977b). We believe that the proposal was correct in principle, but the real size of the taxon is greater than Kunst suspected, including among others all the misplaced species indicated above. Therefore, Miko (2006) proposed *Kunstidamaeus*, named after Miroslav Kunst, the outstanding Czech acarologist who first recognised the group, and developed a key to supraspecific taxa within *Damaeus* sensu lato. The present paper provides a more detailed description and diagnosis of the genus and its type species, *K. lengersdorfi*, including information about immature stages.

Kunstidamaeus Miko, 2006

Diagnosis. Propodolateral apophysis *P* developed as tubercle or tip perpendicular to body, rarely rounded. Typical set of 2 pairs of propodosomal tubercles (*Ba, La*) present, all other tubercles (*Da, Dp, Bp, Lp*) absent. Ventral tubercle *Va* present, usually strong. Interlamellar seta *in* much shorter than sensillus (usually less than

½). Spinae adnatae often strongly curved. Both tibial and genual setation 4-4-3-3 (solenidia not included), solenidia of genua I-III with companion seta *d*. Ventral accessory seta *v2´* absent from tarsi I-IV.

TABLE 1. Some characters of the European genera within *Damaeus* sensu lato. In the setal formulas, solenidia are not included.

Genus	Selected typical characters	Setation of genua	Subgenus	Setation of genua
Damaeus	large size, rugged prodorsum with distinct ridges, apophysis *P* strong, pedotectum-like, *in* much shorter than *ss*, tubercles *Da*, *Ba* and *Bp* present, spinae adnatae strong and straight	usually 4-4-3-3 subgenera with reductions	*Adamaeus*	3-3-2-3 (*d* lost on genua I-III)
			Paradamaeus	4-4-2-3 (*d* lost on genu III)
			Damaeus s.str.	4-4-3-3 (*d* present on all genua)
Spatiodamaeus	apophysis *P* present, usually tubercular or as a blunt tip, *in* as long as *ss* or almost so, tubercles *Da*, *Ba* and *Bp* present, spinae adnatae strong, straight or slightly curved, setae of legs in verticils	4-4-4-4 or 5-5-4-4 (*d* present on all genua)		
Epidamaeus	apophysis *P* absent, *in* distinctly shorter than *ss*, tubercle *Da* absent (rarely present), other prodorsal tubercles often absent, spinae adnatae straight (in the subgenus *Akrodamaeus* absent)	4-4-3-3 or rarely 4-4-4-4 (*d* present on all genua)		
Kunstidamaeus	apophysis *P* present as a perpendicular tip, or rarely almost absent, *in* shorter than *ss*, tubercle *Da* absent, tubercles *Ba* and *La* present, spinae adnatae often curved laterad and ventrad	4-4-3-3 (*d* present on all genua)		

Description. Body of medium to large size (majority of species within 580-820 μm, one alpine species up to 1100 μm), colour of different shades of brown or yellow. Cuticle (observed with light microscope) smooth, rarely microtuberculate or finely dotted. Body covered by granular, columnar and partly filamentous cerotegument. Lateral part of prodorsum broadly rounded. Propodolateral apophysis *P* anteriorly developed as transverse tubercle or tip, perpendicular to body; rarely with blunt or rounded tip or whole apophysis almost absent (in this case thicker and darker cuticle may be recognized in the same position). Typical set of 2 pairs of prodorsal tubercles (*Ba*, *La*) always present, *Da* and all posterior tubercles (*Bp*, *Lp*, *Dp*) absent. Propodosomal tubercles *E2a* and *E2p* usually small, reduced to sclerotised ridge or absent, *Va* present and usually strong, well developed, *Vp* usually absent. Prodorsum triangular, sometimes with short costulae, interbothridial ridges or cuticular thickenings. Sensillus setiform or short and slightly clavate, interlamellar seta *in* much shorter than sensillus (usually less than ½), setiform, thin. Spinae adnatae spiniform or triangular, often very strongly curved laterad and ventrad. Notogastral setae of different length, usually setiform, with blunt or sharp tip, often finely barbed. First pair (*c1*) always directed almost straight forward, usually longest of all notogastral setae; size of setae often diminishing from anterior to posterior part of notogaster; *h1-h3* sometimes shorter, finer and more lightly coloured, sometimes more curved than anterior setae. Adults often carrying exuvial scalps on notogaster, usually without or only with small amount of adherent dirt. Legs long, monodactylous,

leg IV usually significantly longer than body. Solenidia of tibiae I-IV free, without companion seta *d*; tibial setation (solenidia not included) 4-4-3-3. Solenidia of genua I-III with companion seta *d*; genual setation (solenidia not included) 4-4-3-3. Ventral accessory seta *v2´* absent from tarsi I-IV. Famulus in immature stages typical for *Damaeus* sensu lato: reduced, minute, sunken in a sclerotised cup. Typical setation of legs as follows (trochanter to femur; famulus included, solenidia not included): I: 1-7-4-4-20; II: 1-6-4-4-17; III: 2-4-3-3-17; IV: 1-4-3-3-14. Setation of ventral side as in other Damaeidae: *g*: 6, *ag*: 1, *an*: 2, *ad*: 3. Many species known from specific habitats (alpine, troglobiont, nidicole).

Type species. *Belba lengersdorfi* Willmann, 1932

Other included European species. *Belba diversipilis* Willmann, 1951; *Belba granulata* Willmann, 1951; *Belba longisetosa* Willmann, 1953; *Belba nidicola* Willmann, 1936; *Damaeus nivalis* Kulczynski, 1902; *Damaeus tecticola* Michael, 1888; *Damaeus tenuipes* Michael, 1885

Remarks. Species of the genus, while forming a quite uniform and well-defined taxon, can be separated into smaller groups based on the form of sensillus and development of notogastral setae. The type species and four other species have a long setiform sensillus, and form two subgroups. One includes *K. lengersdorfi, K. nidicola* (Willmann, 1936) and *K. diversipilis* (Willmann, 1951)–collectively the "lengersdorfi" group, with medium long or short notogastral setae that are often heterotrichous (*h1-h3* being smaller or finer than anterior setae). Two other species, *K. tecticola* and *K. longisetosus* (the "tecticola" group), are characterized by long to very long notogastral setae, with each seta clearly longer than distance to the insertion of following seta. Three species belonging to "tenuipes" group—*K. tenuipes* (Michael, 1885), *K. granulatus* (Willmann, 1951) and *K. nivalis* (Kulczynski, 1902)—share a shortened and slightly clavate sensillus, which may or may not be covered by dense spinuli; this character is unique within *Damaeus* sensu lato, and rare even within the whole family. Redescriptions of the species will follow in another paper of the series.

Redescription of the type species

Kunstidamaeus lengersdorfi (Willmann, 1932)

Synonymy. Belba lengersdorfi Willmann, 1932 Syn.: *Damaeus lengersdorfi* (see Sellnick 1960)

Diagnosis. Sensillus long, setiform. Propodolateral apophysis *P* variable: in dorsal view developed usually as strong, pointed spine, perpendicular to the body axis; may be reduced or rarely absent. Spinae adnatae strongly bent laterad and ventrad. Notogastral setae straight or only slightly bent, smooth or very weakly barbed. Setae *c1, c2, la, lm, lp* of approximately equal length; *c1* pointing anteriad, *c2, la-lp* erect, directed radially from the notogaster. Legs very long, gracile; leg IV at least 1.5 times body length.

Type material examined. Collection of C. Willmann (Zoologische Staatsammlung München, Germany): 1 mounted individual, labelled "*Belba lengersdorfi Willm., Harz, Hermanns-höhle VII.1933, Kosswig, det. C. Willmann*". The specimen is in relatively good condition, but the embedding medium is dark and does not allow the study of details other than those given in Fig. 3. The original description (Willmann 1932) was based on two specimens from Iburger Tropfsteinhöhle (Harz, Germany) without an explicit type designation. These specimens were not found in the collection, nor were any specimens of *Belba lengersdorfi* var. *moraviae* Willmann, 1954. Therefere, we designate the studied individual as the neotype of *Kunstidamaeus lengersdorfi*.

Other material examined. Collection of M. Moritz (Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany): Nr. 224, B-176, *Heimhelde S. – Harz*: 1 mounted adult, 16.4.1968. **Private collection of L. Miko (Brussels):** *Slovakia, Slovak Karst, Čertova diera pri Domici cave*, sample 218-97, 2 adults, 23.10.1997 P. Ľuptáčik lgt. *Slovakia, Slovak Karst, Domica cave* (Suchá chodba – „Dry corridor"): 5 adults

from alcohol trap exposed 29.4.-13.6.1997 P. Ľuptáčik lgt. *Slovakia, Slovak Karst, Ardovská* cave: 1 adult, 4.9.1997, P. Ľuptáčik lgt. *Belgium, Abime de Comblain, au-Pont (Liege B)*: 1 adult, 8.10.1998 Hubart and Dethier lgt. The specimen was kindly donated to us by P. Skubała. All material unmounted, preserved in 80% ethanol. **Collection of J. Mourek** (Dept. of Zoology, Faculty of Science, Charles University Prague, Czech Republic): *Slovakia, Slovak Karst, Ardovská cave*: 1 tritonymph on decaying wood in the middle part of the cave, 8 adults on decaying wood near the cave entrance, 14.7.2004 J. Mourek lgt.; 1 larva from a laboratory culture of J. Mourek, parental specimens collected in this cave, 14.7.2004 J. Mourek lgt. *Slovakia, Slovak Karst, Čertova diera pri Domici cave*: 1 protonymph, 2 deutonymphs and 2 tritonymphs, about 20 m from the entrance on decaying wood, 20.5.2005 P. Ľuptáčik lgt.; 8 adults collected in the same site as the previous sample, 1.10.2005, P. Ľuptáčik lgt.; 14 adults decaying wood at the entrance lattice, 3. 10. 2005 P. Ľuptáčik lgt.; 1 protonymph, 2 tritonymphs, 5 adults, about 20 m from the entrance on decaying wood, 17. 5. 2006 P. Ľuptáčik lgt.; 1 larva from a laboratory culture of J. Mourek, parental specimens collected in this cave, 6. 4. 2007 P. Ľuptáčik lgt. All material unmounted, preserved in 80% ethanol. **Acarological Collections of Staatliches Museum für Naturkunde Görlitz (Germany)**. Nr. 04/35622 *Slovakia, Slovak Karst, Ardovská cave:* 3 adults on decaying wood near the cave entrance 14.7.2004 J. Mourek lgt.; Nr. 05/35623 *Slovakia, Slovak Karst, Čertova diera pri Domici cave:* 5 adults about 20 m from the entrance on decaying wood, 1.10.2005, P. Ľuptáčik lgt. All material unmounted, preserved in 80% ethanol.

Description. Adult. *Measurements.* From Willmann (1932): body length 750 μm, notogaster width 450 μm. Specimen from Harz, Moritz collection: body length 740 μm, notogaster length 518 μm, notogaster width 463 μm. Material from Slovak caves: body length 730-850 μm, notogaster width 480-505 μm. For measurements of legs see Table 4.

Integument. Body colour yellowish to reddish brown. Surface of body and legs with fine granular and columnar cerotegument (Fig. 12 A,C), filamentous cerotegument present in sejugal area, on epimeres and around notogastral setae (Fig. 10 A, 11 A,B). Cuticle after the removal of cerotegument mostly smooth, apophyses and other emergent structures microtuberculate (Fig. 9). Adults often bearing exuvial scalps (gastronotic exuviae) on the notogaster but without or only with a small amount of adherent dirt.

Prodorsum (Fig. 2, 9). Short in dorsal view, length about half that of notogaster. Rostrum broadly rounded. Prodorsal setae indistinctly barbed with minute spinuli or almost smooth. Rostral (*ro*) and lamellar (*le*) seta almost equally long, but in dorsal view usually *le* seem longer than *ro*. Interlamellar seta (*in*) shorter, less than 1/3 of the sensillus length. Exobothridial seta fine, arched forwards. Bothridium funnel-like, with large, irregular and expanded hyaline rim. Sensillus long, setiform, straight, and slightly attenuate distally. Propodolateral apophysis in dorsal view developed as a strong, pointed spine, perpendicular to the body axis, tips only slightly or not overreaching the outline of prodorsum; in lateral view visible as a vertical ridge (Fig. 9 D). Tip of the apophysis may be reduced or rarely almost absent. Pair of short, perpendicular sclerotized elevations resembling costulae anterior to bothridia, directed mediad, not longer than diameter of bothridium. Two pairs of prodorsal tubercles well developed: *Ba* and *La* (Fig. 2, 9 B). Parastigmatic apophyses different in shape and size: *Sa* strong, long and spiniform, perpendicular; *Sp* shorter, triangular and oblique, directed more anteriad (Fig.2, 9B).

Notogaster. Broadly oval to obovate, with a pair of long, sharp and narrow spinae adnatae, bent strongly (about 90° in dorsal view) laterad and ventrad (see also in lateral view—Fig. 4 A, C); rarely with small setiform spine inserting on ventral side, unilaterally (Fig. 4 C, 9 C). Notogastral setae straight or very slightly bent, pointed, smooth or with very few minute barbs. Setae *c1*, *c2*, *la*, *lm*, *lp* of approximately equal length, but in dorsal view *c1* appear longer and *c2* shorter than others. Seta *c1* directed anteriorly, setae *c2*, *la*-*lp* erect, directed radially from notogaster. Setae *h1*-*h3* shorter than others, diminishing in size posteriad. Posterior notogastral setae *ps1*-*ps3* very thin, finer than *h1*-*h3* (Fig. 4 A, B).

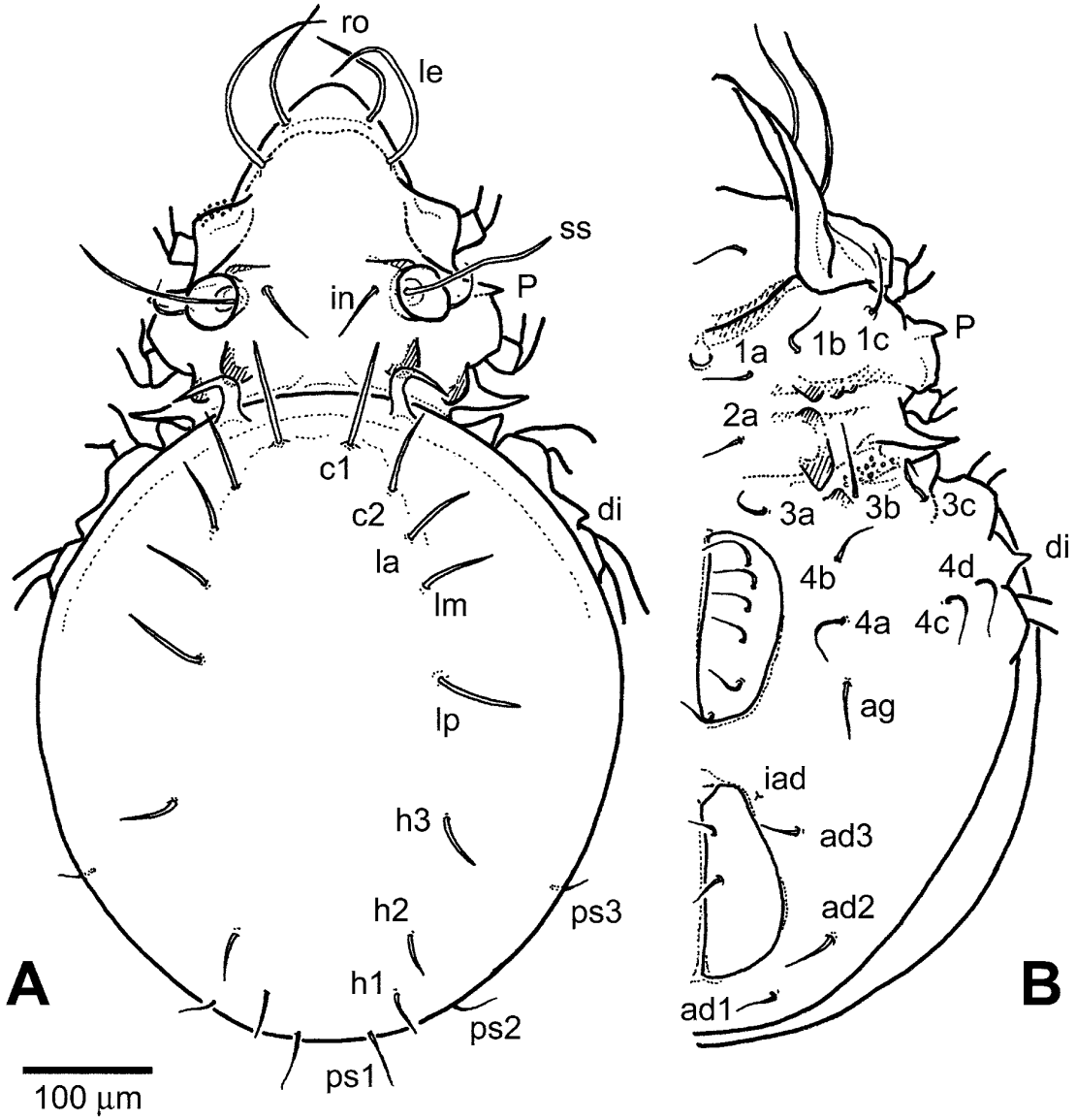


FIGURE 1. *Kunstidamaeus lengersdorfi*–adult specimen from Harz (Moritz Collection). A) dorsal view; B) partial ventral view. Legs, infracapitulum and cerotegument only partly drawn, lyrifissures and openings of opisthonotal glands not drawn.

Ventral region. Ventral setation as usual for Damaeidae (Grandjean 1960; Norton 1977b): epimeral setal formula (from epimere 1 to epimere 4): 3-1-3-4; genital *g*: 6; aggenital *ag*: 1; anal *an*: 2; adanal *ad*: 3. Ventral setae quite long, fine, setiform, at least partly with indistinct barbs, usually bent. Tectum of podocephalic fossa ending as a blunt tip, ventrally with three well developed lamellae (Fig. 2 C, 10 B). Medial pit *cp* on coxisternum I well developed, open anteriad. Propodoventral tubercles *E2a* and *E2p* weakly developed, usually as short, dentate or tuberculate sclerotised ridge. Ventrosejugal tubercle *Va* large, strong, dentiform, *Vp* weakly developed, in light microscope sometimes discernible only in lateral view (Fig. 2, 10 B). Tubercle *E2p* and *Va* laterally connected by a longitudinal ridge. Discidium of variable shape, usually developed as small, sharp tubercle pointing laterad, slightly anteriad or slightly posteriad (Fig. 2D).

Legs (Fig. 5, 6). Legs monodactylous, gracile and long, both first and fourth pairs longer than body: leg I: 815 µm, length of leg IV: 1 100 µm in measured individual (Harz, Germany, Moritz collection); leg IV

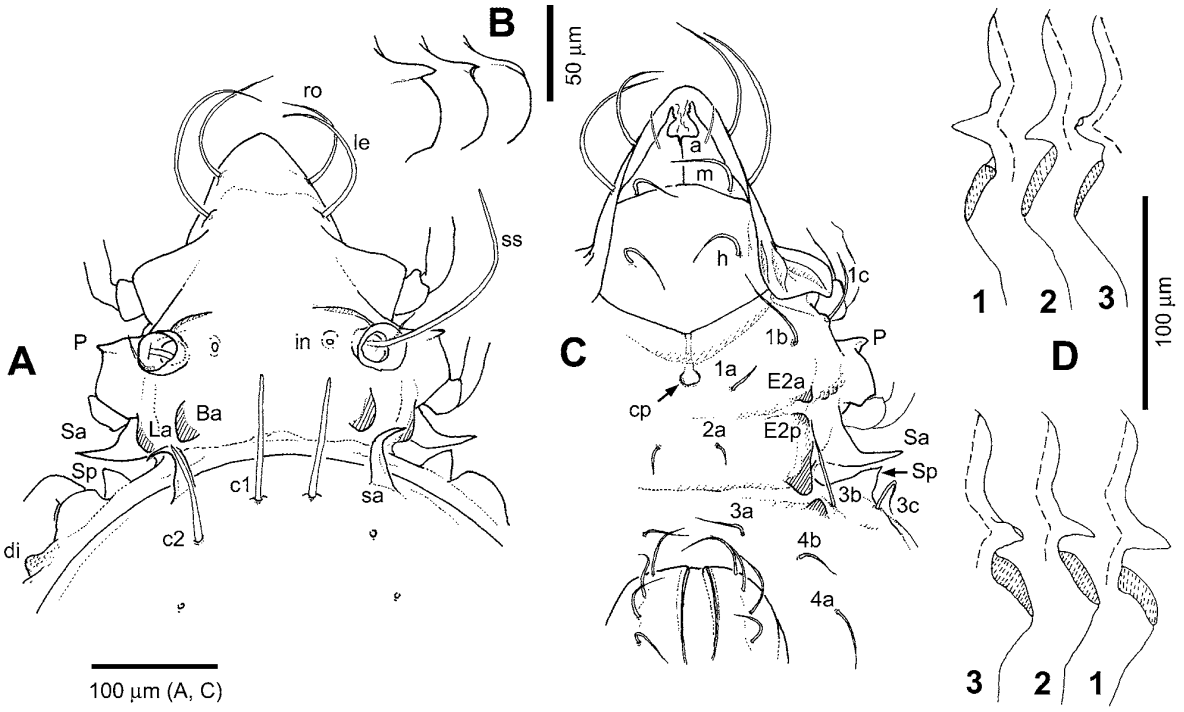


FIGURE 2. *Kunstidamaeus lengersdorfi*–prodorsum of adult specimen from caves of the Slovak Karst. A) dorsal view; B) variation in development of propodolateral apophysis *P*; C) partial ventral view; D) variation in shape of discidium (ventral view, numbers refer to discidia on both body sides of the same specimen, orifice of acetabulum IV shaded). Legs only partly drawn, cerotegument not drawn.

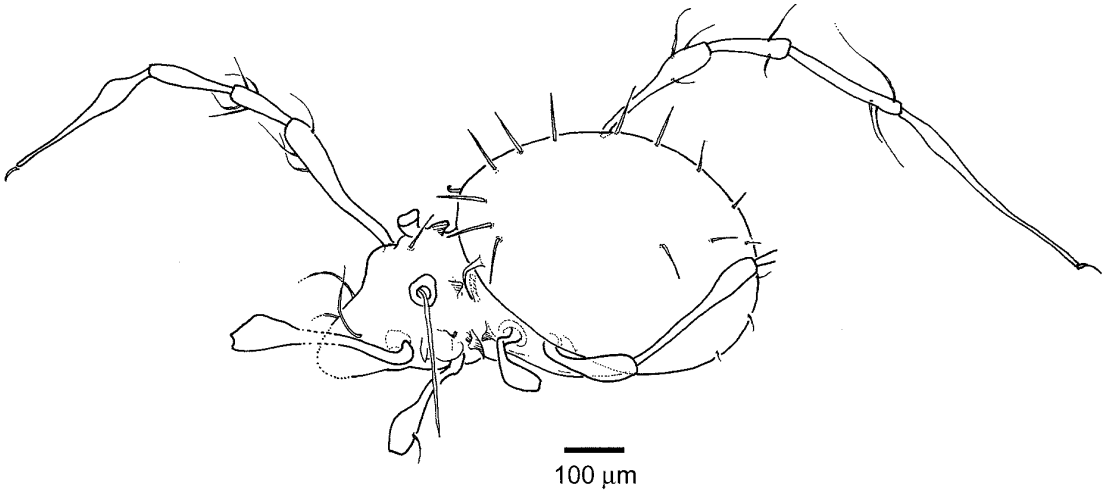


FIGURE 3. *Kunstidamaeus lengersdorfi*–adult specimen from Harz (Willmann Collection). Legs and leg setation setation only partly drawn, cerotegument not drawn.

at least 1.5 times body length. Willmann (1932) gives lengths of legs I: 810 µm, II 650 µm, III 750 µm and IV 1010 µm. In our material from the caves of Slovak Karst maximal lengths were as follows: leg I 855 µm, II 700 µm, III 955 µm and IV 1270 µm. Legs I and II were measured without trochanter, whereas legs III and IV were measured with trochanter. For detailed measurements see Tab 4. Setal formulas of legs as follows (from trochanter to tarsus, famulus included, solenidia not included): I: 1-7-4-4-20; II: 1-6-4-4-17; III: 2-4-3-

3-17; IV: 1-4-3-3-14. Solenidia of tibia and tarsus I and tibia IV very long, tactile. Solenidia of genua I-III with companion seta *d*, all genual solenidia shorter than their companion setae. Leg chaetotaxy of all developmental stases as presented in Table 2 and 3. Famulus normal, emergent in adults.

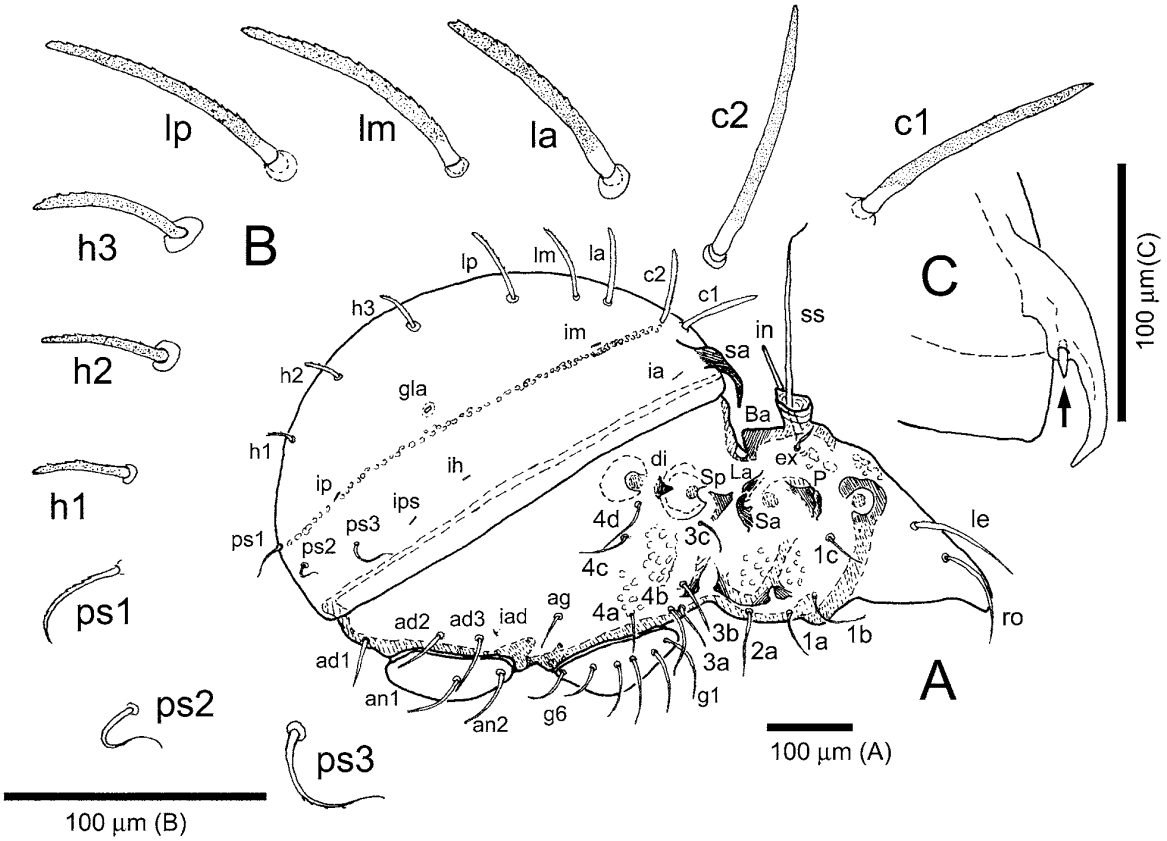


FIGURE 4. *Kunstidamaeus lengersdorfi*–adult specimen from the caves of the Slovak Karst. A) lateral view; B) details of notogastral setae; C) detail of spina adnata in lateral view with setiform spine (arrow). Legs and cerotegument not drawn.

Remarks. In some populations from Slovak caves the forms with very small or completely reduced tips of propodolateral apophysis *P* were found together with typical specimens (Fig. 2 B). This rather unusual variability shows that development of the propodolateral apophysis may not have as important role at the generic level as usually believed.

The peculiar setiform spine, asymetrically present on one spina adnata in two examined specimens, may represent atavistic reappearance of notogastral seta *c3* (Norton pers. comm.), which is normally absent from adults of Damaeidae. Similar setiform spines on spinae adnatae were noted in *Epidamaeus tenuissimus* Hammer, 1967 and *E. tritylos* Behan-Pelletier and Norton, 1983 (see Behan-Pelletier & Norton 1985).

Ontogeny. Drawings and SEM micrographs of tritonymph are in Fig. 7, 8, 10, 11 and 12. The following description applies to all immature stages unless otherwise specified.

Measurements. See Table 4.

Integument. Body cuticle colourless to pale yellowish. Legs, epimeres and prodorsum slightly more sclerotised. Entire body including legs and most of the setae covered by cerotegument with granular sculpture, uniform throughout, no filamentous elements present; slightly more distinct in tritonymph. Two sizes of granular elements distinguishable: *macrogranules* (1-2 µm in diameter, visible in light microscope) of spherical or

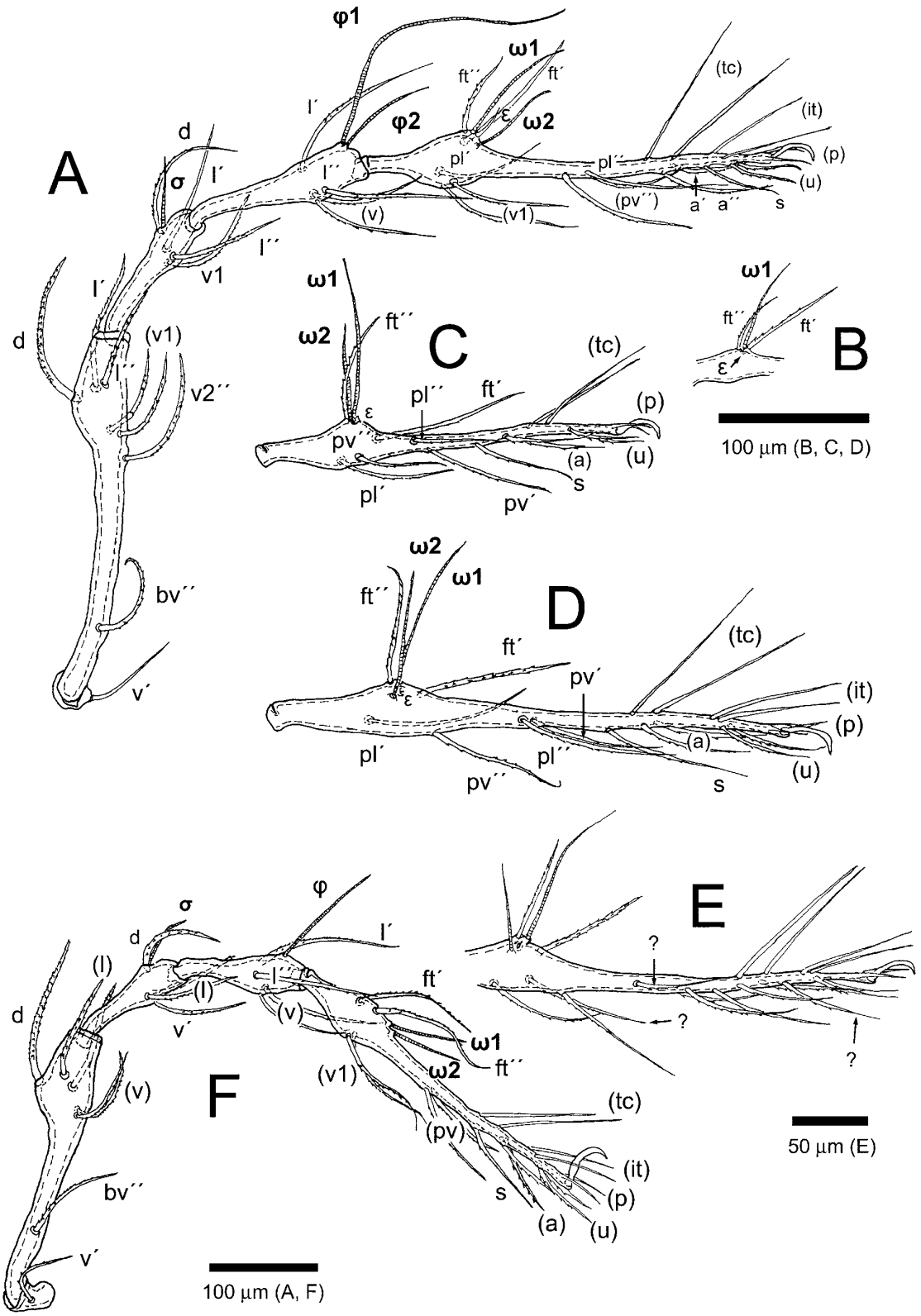


FIGURE 5. *Kunstidamaeus lengersdorfi*–legs (right, antiaxial aspect), specimens from the caves of the Slovak Karst. A) adult—leg I; B) larva—proximal part of tarsus I; C) deutonymph—tarsus I; D) tritonymph—tarsus I with normal chaetotaxy; E) tritonymph—tarsus I with an abnormal chaetotaxy (arrows with question-marks point to additional setae of unknown homology); F) adult—leg II. Cerotegument not drawn.

nearly spherical shape with granulated surface, irregularly distributed and separated by more than their diameter; *microgranules* (0.2 μm or less in diameter, invisible in light microscope) of irregular shape, spaced much more densely than macrogranules. Loose growth of fungal hyphae or of other filamentous microorganisms often present on body surface.

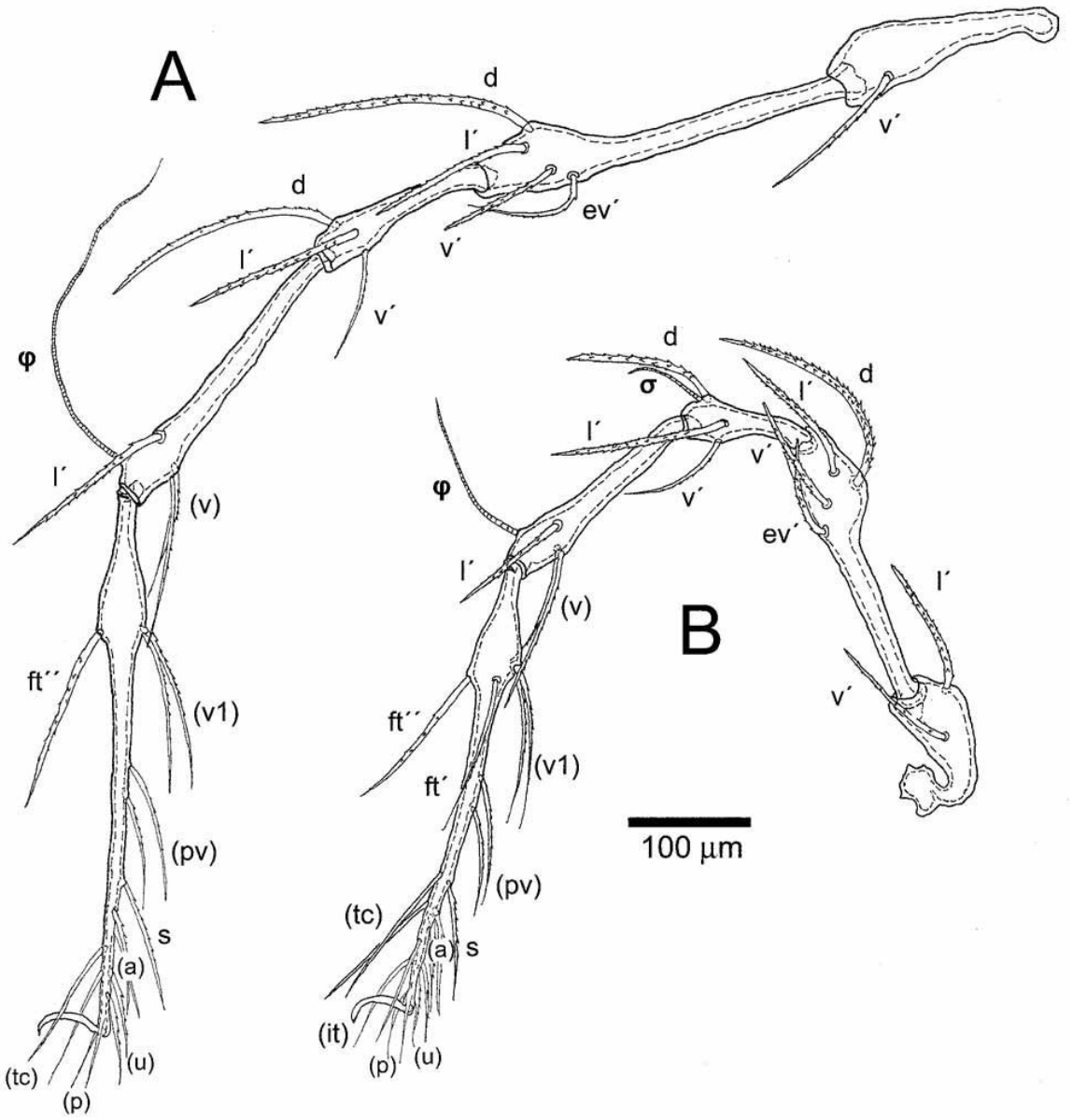


FIGURE 6. *Kunstidamaeus lengersdorfi*—adult—legs III and IV(right, antiaxial aspect), specimen from the caves of the Slovak Karst. A) leg IV; B) leg III. Cerotegument not drawn.

Prodorsum. Relatively short, about half-length of gastronotic region in lateral view. Rostrum broadly rounded. Pair of distinct horizontal ridges (similar to tutoria of adults in some poronotic families) present laterally, above acetabula I (Fig. 7, 8). All prodorsal setae (except for nymphal *in*) with short barbs. Setae *ro* and *le* comparatively long, but *ro* distinctly shorter and slightly thinner than *le*; both arched mediad and ventrad. Larval seta *in* comparatively long, barbed, erect, directed posteriad, inserted on minute apophyses. Nymphal *in* (Fig. 7 C) short, strong, smooth with blunt and slightly swollen tip, erect, directed posteriorly, inserted on

minute apophyses. Sensillus long, attenuate with fine tip, barbed in distal 2/3. Seta *ex* very short, directed anteriad (Fig. 7 C).

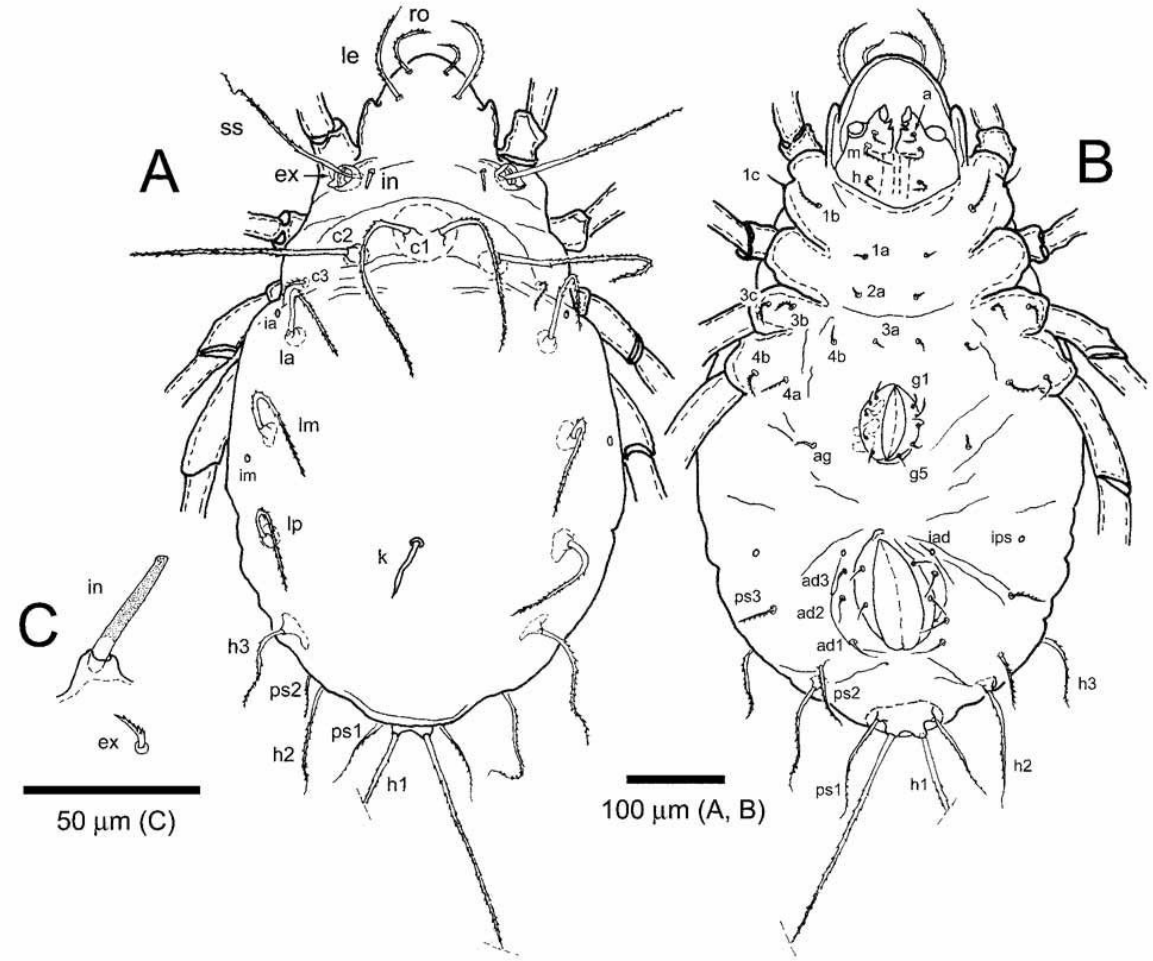


FIGURE 7. *Kunstidamaeus lengersdorfi*—tritonymph from the caves of the Slovak Karst. A) dorsal view; B) ventral view, C) detail of interlamelar and exobothridial seta (lateral view). Legs only partly drawn, cerotegument not drawn.

Gastronotic region. Larva more or less truncate posteriorly, nymphs rounded or slightly tapered with apophyses bearing setae *h1*. Anterior margin, bearing setae *c1, c2, c3,* distinctly elevated, cuticle behind this setal row folded (Fig. 8, 10 C). Ontogeny and distribution of gastronotic setae similar to that of other Damaeidae (cf. Grandjean 1954a; Norton 1977b, 1978a, 1979c; Norton & Ryabinin 1994): Seta *h3* vestigial in larva. Setae *ps1*, *ps2*, and *ps3* appear first in protonymph. All nymphs and adults lack setae *da*, *dm*, *dp*. Seta *c3* is absent from adult. Gastronotic setae pigmented light brown with hyaline base, finely barbed with small spinuli; inserted on small sclerites (only weakly defined in larva and protonymph) with more or less developed apophyses. Sclerites of nymphal *ps2* and *ps3* minute and hardly visible. Setal pair *c1* inserted very close together on unpaired anterior sclerite. Setal pairs *h1* and *ps1* inserted on common unpaired posterior sclerite (Fig. 7, 8). Nymphal setae *c1*, *c2*, *la*, *lm*, *lp*, *h1*, *h2*, *h3* long, comparatively strong and erect, with long, flagellate tips (often broken); seta *c3* short and thinner. Seta *ps1* very thin, comparatively long; *ps1* > *ps2* > *ps3*.

Cornicle *k* narrow, long, erect, slightly S-shaped, with pointed tip directed anteriad (Fig. 7 A, 8, 10 D). Gastronotic exuviae loosely attached to notogaster, arranged in pyramidal shape with highest point approximately in middle of gastronotic region (Fig. 10C). Cuticle of gastronotic exuviae distinctly reticulated, almost clean or with a small amount of debris or fungal hyphae.

TABLE 2. *Kunstidamaeus lengersdorfi*–ontogeny of leg setation (solenidia in parentheses, famulus included).

	trochanter	femur	genu	tibia	tarsus
leg I					
larva	0	2	3(1)	4(1)	16(1)
protonymph	0	2	3(1)	4(1)	16(2)
deutonymph	1	4	4(1)	5(2)	16(2)
tritonymph	1	5	4(1)	5(2)	18(2)[1]
adult	1	7	4(1)	4(2)	20(2)
leg II					
larva	0	2	3(1)	3(1)	13(1)
protonymph	0	2	3(1)	3(1)	13(1)
deutonymph	1	4	4(1)	4(1)	13(2)
tritonymph	1	4	4(1)	5(1)	15(2)
adult	1	6	4(1)	4(1)	17(2)
leg III					
larva	0	2	2(1)	3(1)	13
protonymph	1	2	2(1)	3(1)	13
deutonymph	2	3	3(1)	4(1)	13
tritonymph	2	3	3(1)	4(1)	15[2]
adult	2	4	3(1)	3(1)	17
leg IV					
protonymph	0	0	0	0	7
deutonymph	0	2	3	3(1)	12
tritonymph	1	3	3	4(1)	12
adult	1	4	3	3(1)	14

[1] in one tritonymph 21 (2) setae were observed on right tarsus I (setal homology discussed in the text)

[2] in one tritonymph 16 setae were observed on right tarsus III (setal homology discussed in the text)

Ventral region. Setae of infracapitulum indistinctly barbed on one side, or smooth. Epimeral setal formulas as follows: larva: 2-1-2; protonymph: 3-1-2-1; deutonymph: 3-1-2-2; tritonymph: 3-1-3-3; adult: 3-1-3-4. Larval seta *1c* (not included in the epimeral larval formula) similar to other Oribatida—scale-like, covering the Claparède's organ. Epimeral setae finely barbed on one side, some with very few minute spinuli or smooth. Cuticle of anogenital region weakly folded. Ontogeny of setal formulas in anogenital region typical of the family (see Norton 1977b): from larva to adult as follows: aggenital *ag*: 0-0-1-1-1; genital *g*: 0-1-3-5-6; pseudanal *ps*: 0-3-3-3-3; adanal *ad*: 0-0-3-3-3; anal *a*: 0-0-0-2-2.

Legs. Legs of all stases long, gracile (see Fig. 10A). For detailed measurements see Table 4. Leg IV is longest and leg II shortest, with difference most pronounced in adult. Leg IV exhibits positive allometric growth: 1.14–1.20 times body length in tritonymph, but over 1.5 times body length in adult.

Leg setae comparatively long, thin, most are distinctly barbed. Ontogeny of setation e given in Table 2, detailed ontogeny with homologies of setae given in Table 3. Variations in leg setation are described in Remarks. Famulus ε minute, sunken in a sclerotised cup in all immature stases, as typical for most members of *Damaeus* sensu lato (Norton 1977a, 1977b; 1979b). Ontogeny of solenidiotaxy normal for family (Norton 1977a).

Remarks on the ontogeny. The knowledge of ontogeny in Damaeidae is still fragmentary. Leg chaetotaxy seems to offer the most relevant characters. Individual asymmetrical setal variation on tarsus I (see Fig.

5E) and III in tritonymphs and on tarsus IV in adults was observed. In one tritonymph three additional setae were found on the right tarsus I (see Fig 5E). One of them can be homologised with *v1´* (normally appearing in adult), but homology of the remaining two setae is unknown. In another tritonymph one additional seta on tarsus I was found, probably also homologous with *v1´*.

TABLE 3. *Kunstidamaeus lengersdorfi.* detailed ontogeny of leg setation with homologisation of the setae. Roman letters refer to normal setae, Greek letters refer to solenidia, ε—famulus. One apostrophe (´) marks setae on anterior and double apostrophe (´´) setae on posterior side of the given leg segment. Parentheses refer to a pair of setae. Only the setae appearing first in the given stase are listed.

	trochanter	femur	genu	tibia	tarsus
leg I					
larva	-	bv´´, d	(l), d, σ	(l), v´, d, φ1	(ft), (pl), (pv), s, (a), (u), (tc), (p), ω1, ε sunken
protonymph	-	-	-	-	ù2
deutonymph	v´	(l)	v´	v´´, φ2	-
tritonymph	-	v1´´	-	-	(it)
adult	-	v1´, v2´´	-	d lost	(v1), ε emergent
leg II					
larva	-	bv´´, d	(l), d, ó	l´, v´, d, φ	(ft), (pv), s, (a), (u), (tc) (p), ω_1
protonymph	-	-	-	-	-
deutonymph	v´	(l)	v´	l´´	ù2
tritonymph	-	-	-	v´´	(it)
adult	-	(v)	-	d lost	(v1)
leg III					
larva	-	ev´, d	l´, d, σ	l´, v´, d, φ	(ft), (pv), s, (a), (u), (tc), (p)
protonymph	v´	-	-	-	-
deutonymph	l´	l´	v´	v´´	-
tritonymph	-	-	-	-	(it)
adult	-	v´	-	d lost	(v1)
leg IV					
protonymph	-	-	-	-	ft´´, (pv), (u), (p)
deutonymph	-	ev´, d	l´, d, v´	l´, d, v´, φ	s, (a), (tc)
tritonymph	v´	l´	-	v´´	-
adult	-	v´	-	d lost	(v1)

We were not able to define any immature characters distinguishing *Kunstidamaeus* from *Epidamaeus*, except for differences in famulus development in *E. tatricus* (Mourek & Miko in press). From the nomenclatural point of view, a major problem is the inaccessibility of the type species *Epidamaeus bituberculatus* (Kulczynsky, 1902) and therefore the lack of any information on its immature morphology. Moreover, until present, ontogenetic data are available only for *K. lengersdorfi* and a few species of *Epidamaeus*. Ontogeny of the leg chaetotaxy in *K. lengersdorfi* is identical with the Nearctic species *Epidamaeus (Akrodamaeus) longiseta* (Banks, 1906), redescribed by Norton (1978a). Therefore, we consider the removal of *Akrodamaeus* from *Epidamaeus* to *Metabelbella* Bulanova-Zachvatkina, 1957, proposed by Subías (2004) as unjustified. Even the scarce knowledge of ontogeny in *Epidamaeus* indicates interspecific variation within the genus. For example, *Epidamaeus (Epidamaeus) tatricus* (Kulczynski, 1902) differs from both former species in several details: *v´* on femur III is tritonymphal (adult in *K. lengersdorfi*); *v´*on genu IV is tritonymphal (deutonymphal

in *K. lengersdorfi*); *v´´* is added on femur IV and on genu III + IV in adult (Mourek unpubl.); and the famulus is emergent in all stases (Mourek & Miko in press). Norton (1977a) analysed the setation of three undescribed species of *Epidamaeus*, in two of them *v´* on genu IV was tritonymphal (as in *E. tatricus*). On the other hand, *Kunstidamaeus lengersdorfi* and all mentioned *Epidamaeus* species share several differences in ontogeny of the leg setation from *Damaeus* (including *Adamaeus* and *Paradamaeus*) and *Spatiodamaeus* (see Norton 1977a, 1977b):

1. Seta *v´* on trochanter IV is tritonymphal instead of deutonymphal. The former character state can be found also in some other Damaeidae, e.g. in *Belba corynopus*.

2. Seta *l´*on femora I and II is deutonymphal (as in most other studied genera of Damaeidae) instead of protonymphal.

TABLE 4. *Kunstidamaeus lengersdorfi*–measurements of developmental stases; all specimens from Slovak Karst. Note, that only one specimen per immature stase and three adults were measured. All measurements are given in μm.

	larva	protonymph	deutonymph	tritonymph	adult, mean (min-max)
	n=1	n=1	n=1	n=1	n=3
body length	-	411	600	792	808 (804-816)
notogaster width	-	194	288	420	488 (480-504)
leg I	367	533	678	822	961 (950-967)
leg I:body length	-	1.30	1.13	1.04	1.19 (1.18-1.20)
trochanter I	22	28	28	33	-
femur I	111	167	211	239	315 (306-322)
genu I	33	50	67	83	120 (117-122)
tibia I	50	83	122	150	156 (150-161)
tarsus I	150	206	250	317	370 (367-372)
leg II	306	378	517	639	759 (744-772)
leg II:body length	?	0.92	0.86	0.81	0.94 (0.91-0.96)
trochanter II	28	28	28	28	-
femur II	72	83	144	194	231 (222-239)
genu II	33	44	56	67	104 (100-106)
tibia II	39	67	89	111	117 (111-122)
tarsus II	133	156	200	239	307 (306-311)
leg III	350	467	622	756	935 (911-956)
leg III:body length	-	1.14	1.04	0.95	1.16 (1.13-1.17)
trochanter III	39	56	67	83	111 (100-117)
femur III	72	106	139	167	211 (206-217)
genu III	39	39	61	72	100 (100-100)
tibia III	56	89	128	167	169 (161-172)
tarsus III	144	178	228	267	344 (339-350)
leg IV		467	722	911	1256 (1250-1261)
leg IV:body length		1.14	1.20	1.15	1.55 (1.53-1.57)
trochanter IV		67	100	117	167 (161-172)
femur IV		100	156	233	281 (267-289)
genu IV		39	78	106	143 (139-144)
tibia IV		67	139	189	241 (233-244)
tarsus IV		194	250	267	424 (417-439)

3. Seta *v´* on genu III is deutonymphal instead of protonymphal.

4. Ventral accessory seta *v1´* on tarsi I-IV appears in the adult instead of the tritonymph.

5. Ventral accessory seta *v1´´* is absent from all tarsi (as in other genera of Damaeidae except *Damaeus* and *Spatiodamaeus*), instead of being present in the adult.

These differences support the separation of *Kunstidamaeus* from *Damaeus* and *Spatiodamaeus*, but knowledge of ontogeny in more species of the former genus is needed. The shared character states in setation of *Kunstidamaeus* and *Epidamaeus* are probably plesiomorphic within Damaeidae (cf. Norton 1977) and do not imply the monophyly of the *Kunstidamaeus—Epidamaeus* clade. Therefore they are not in conflict with the proposal of *Kunstidamaeus* as a separate genus, which is based on adult morphology.

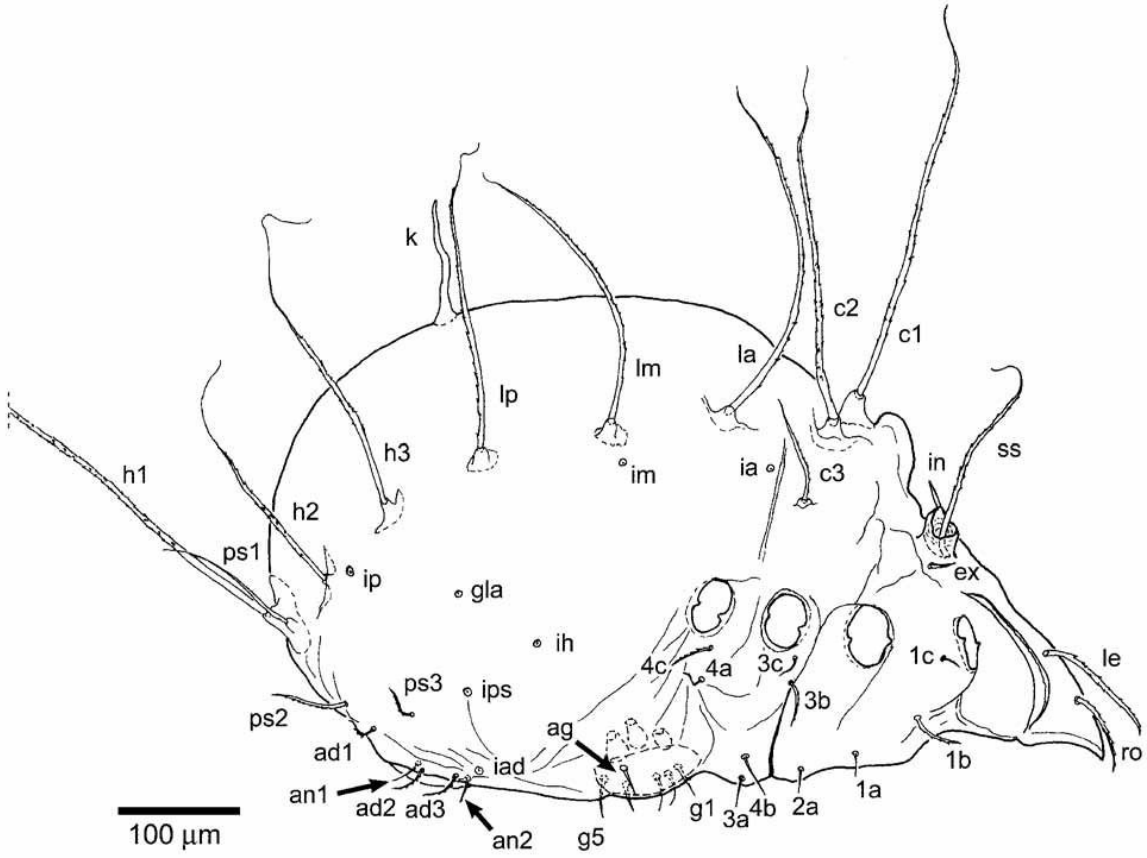


FIGURE 8. *Kunstidamaeus lengersdorfi*—tritonymph from the caves of the Slovak Karst, lateral view. Legs and cerotegument not drawn.

Ecology, geographical distribution. The species has been found only in caves or in cave entrances, usually on organic debris such as bat guano, rotten wood or even old candle paraffine (Ľuptáčik & Miko 2003; Ľuptáčik unpubl.). Probably, the species is a true troglobiont (Lebrun 1967) or at least troglophile (Ľuptáčik & Miko 2003). The nominate form was described from the cave "Iburger Tropfsteinhöhle" in Harz, Germany (Willmann 1932). *Kunstidamaeus lengersdorfi* is also known from caves in Slovak Karst, Slovakia (Ľuptáčik & Miko 2003). It was also recorded in caves in Belgium (Willmann 1935; Hubart and Dethier unpubl.), French Jura, France (Willmann 1938) and Germany (Griepenburg 1939). *Kunstidamaeus l.* var. *moraviae* as well as the nominate form were reported from caves of Moravian Karst in southeast of the Czech Republic (Willmann 1954; see Remarks). The occurence of *K. lengersdorfi* in further European karstic cave systems can be also expected. It is probable that the species occurs in Hungarian caves of Aggtelek that are interconnected with the cave system of Slovak Karst.

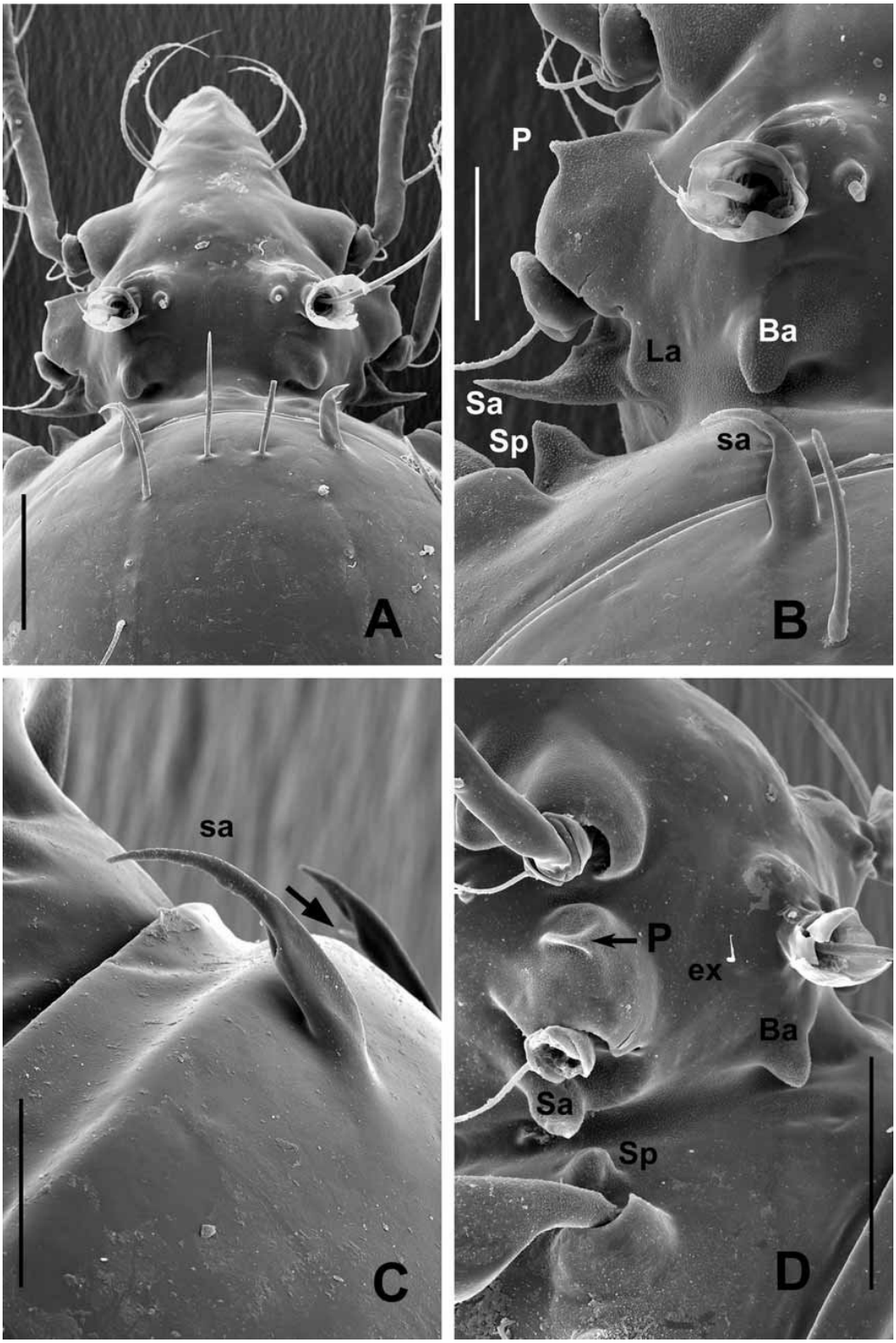


FIGURE 9. *Kunstidamaeus lengersdorfi*—SEM micrographs of adult from the caves of the Slovak Karst, macerated in lactic acid, cerotegument removed, some of the setae are broken. A—prodorsum and anterior part of notogaster in dorsal view; B—detail of apophyses in the sejugal area in dorsal view; C—detail of spina adnata in lateral view (note the setiform spine—arrow); D—detail of apophyses in the dorsosejugal and sejugal area in lateral view. Scale bars: A—100 μm; B—50 μm; C—50 μm; D—100 μm.

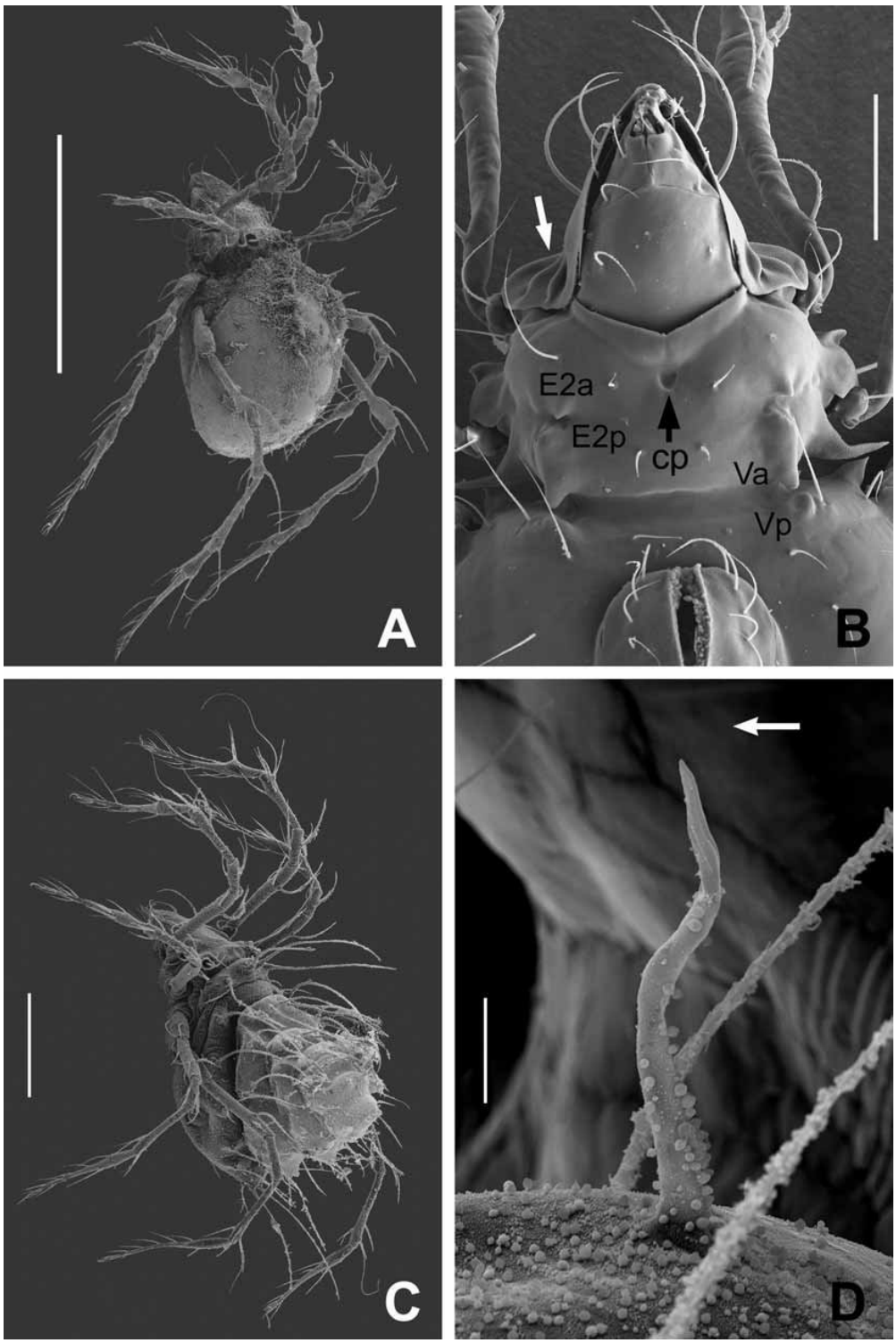


FIGURE 10. *Kunstidamaeus lengersdorfi*—SEM micrographs of adult and tritonymph from the caves of the Slovak Karst. A—adult in dorsolateral view; B—adult in ventral view—detail of gnathosoma and coxisternal region, specimen macerated in lactic acid, cerotegument removed. Black arrow points to medial pit on coxisternum I (*cp*), white arrow points to ridges on ventral side of tectum of the podocephalic fossa; C—tritonymph with gastronotic exuviae—dorsolateral view; D—tritonymph (gastronotic exuviae removed)—detail of cornicle *k* in lateral view (arrow points anteriad). Scale bars: A—500 μm; B—100 μm; C—250 μm; D—25 μm.

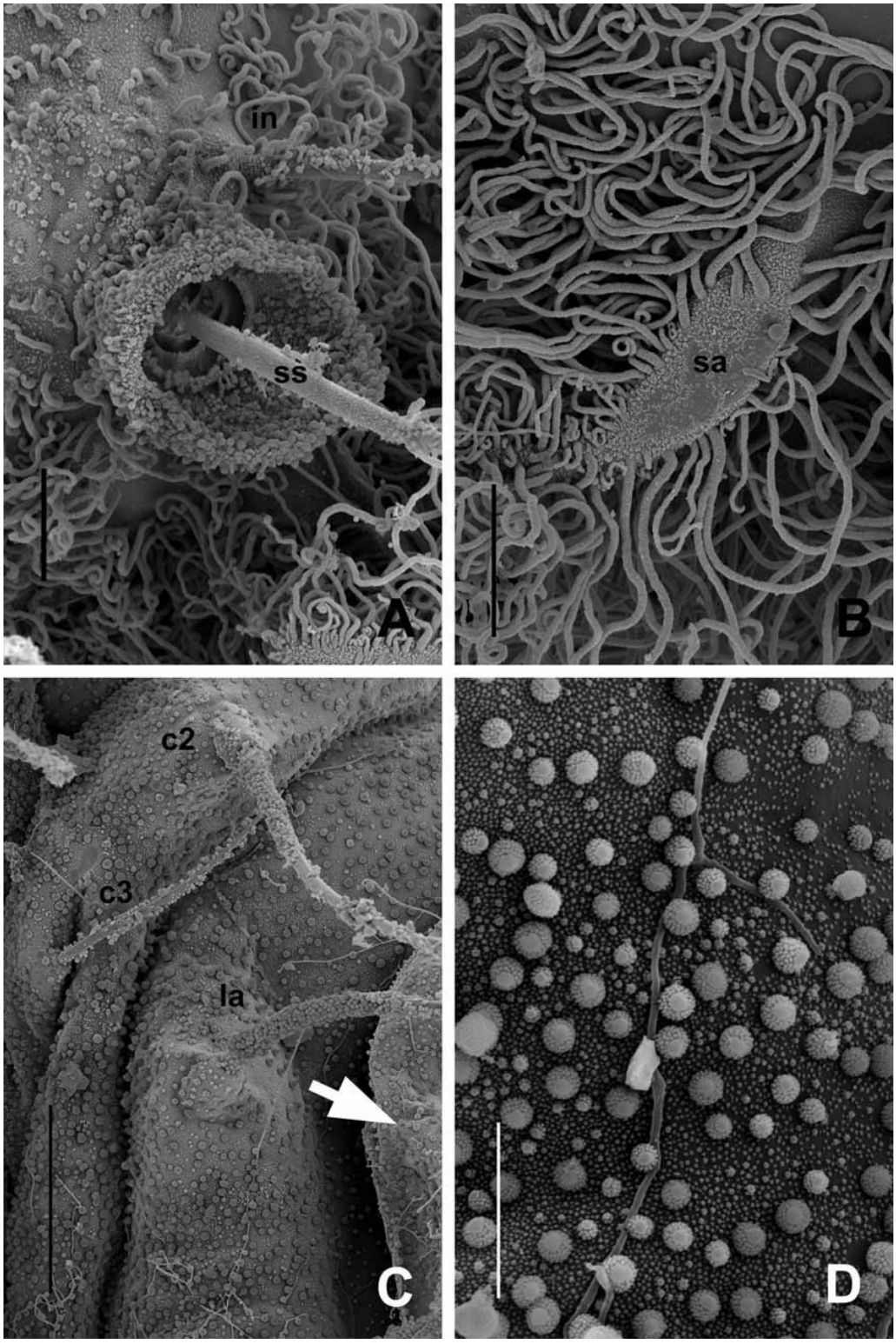


FIGURE 11. *Kunstidamaeus lengersdorfi*—SEM micrographs of adult and tritonymph from the caves of the Slovak Karst. A—adult, detail of bothridium in dorsofrontal view, note granular cerotegument on botridial rim and filamentous cerotegument in dorsosejugal region; B—adult, detail of spina adnata in lateral view partly covered with filamentous cerotegument; C—tritonymph, cuticular folds of the gastronotic region with granular cerotegument and gastronotic exuvia (arrow). Scale bars: A—20 μm; B—20 μm; C—50 μm; D—10 μm.

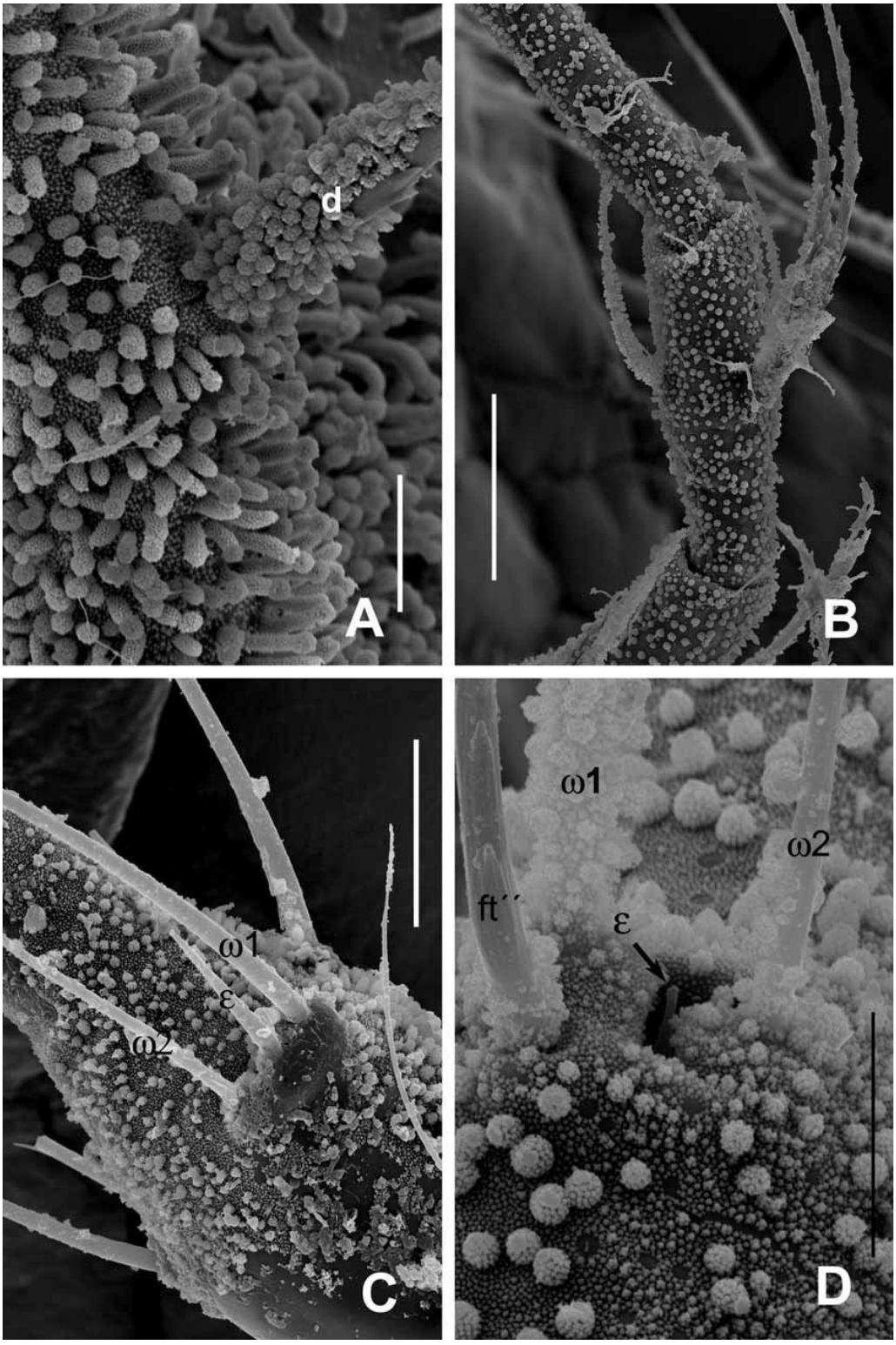


FIGURE 12. *Kunstidamaeus lengersdorfi*—SEM micrographs of adult and tritonymph from the caves of the Slovak Karst. A—adult, detail of columnar cerotegument on femur I, lateral view; B—tritonymph, granular cerotegument on genu I, lateral view; C—adult, tarsus I, detail of the emergent famulus and solenidia, dorsolateral view; D—tritonymph, tarsus I, detail of the sunken famulus (arrow) and solenidia, dorsal view. Scale bars: A—10 μm; B—40 μm; C—20 μm; D—10 μm.

Remarks: Willmann (1954) described "*Belba lengersdorfi* var. *moraviae"*, slightly different from the nominal form, based on specimens from a cave in Moravian Karst (now in the Czech Republic). Kunst (1968) regarded this form as a valid subspecies, taking into account specific habitat (caves) and geographical separation of populations from Harz and Moravia. However, Willmann (1954) reported the nominal form from other caves in Moravian Karst as well. Morphological differences are very slight—"*Belba lengersdorfi* var. *moraviae"* has according to Willmann (1954) finer and more curved notogastral hairs, the anterior four pairs (*c1–lm*) being distinctly longer than the rest. Most of our Slovak specimens are closer to the "Moravian variety" or have intermediate form, but specimens very similar to the nominate form were also found. Notogastral setae have different lengths also in the specimen from Harz (Moritz Collection; see Fig. 1). Since the Moravian form was described from only two individuals, and variability of the species was not sufficiently studied, the status of the Moravian form is equivocal. For now, we treat all individuals as belonging to one taxon—*Kunstidamaeus lengersdorfi*.

Acknowledgements

The study was supported by the Grant Agency of the Charles University, Prague (grant *GAUK 217/2004/B-BIO/PrF*). The authors are very grateful to Peter Ľuptáčik, Ľubomír Kováč and Andrej Mock (Institute of Biology and Ecology, Faculty of Science, University of P. J. Šafárik, Košice, Slovakia) for specimens of *Kunstidamaeus lengersdorfi* from Slovak caves and to Piotr Skubała (University of Upper Sillesia, Katowice, Poland) for specimens of *K. lengersdorfi* from Belgian caves. The administrations of Zoologische Staatsammlung München and of Museum für Naturkunde der Humboldt-Universität zu Berlin kindly allowed the first author to study material from the collections of C. Willmann and M. Moritz. We are very grateful to Gerd Weigmann (Institut für Zoologie, Freie Universität Berlin, Germany) for making it possible to work in his laboratory during this study. The authors are also very grateful to Roy A. Norton (SUNY College of Environmental Science and Forestry, Syracuse, New York, USA), to the self-identified reviewers Heinrich Schatz (Institut für Zoologie und Limnologie, Universität Innsbruck, Austria) and Valerie Behan-Pelletier (Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada) and to the editor Owen Seeman (Queensland Museum, South Brisbane, Australia) for reading the manuscript, providing valuable comments and linguistic and stylistic improvements.

References

Balogh, J. & Balogh, P. (1992) *The Oribatid Mites Genera of the World. Volume I.* Hungarian National Museum Press, 263 pp.

Bayartogtokh, B. (2000a) New oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Species Diversity*, 5, 183–200.

Bayartogtokh, B. (2000b) Two new species of oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Acarina*, 8, 65–78.

Bayartogtokh, B. (2001) Three new soil mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. *Zoosystema*, 23, 29–49.

Bayartogtokh, B. & Norton, R.A. (2007) The *Dyobelba tectopediosa* species-group (Acari: Oribatida: Damaeidae) from the Southeastern USA, with a key to world species of *Dyobelba* and notes on their distribution. *Zootaxa*, 1591, 39–66.

Behan-Pelletier, V.M. & Norton, R.A. (1983) *Epidamaeus* (Acari: Damaeidae) of arctic western North America and extreme northeast, U.S.S.R. *Canadian Entomologist*, 115, 1253–1289.

Behan-Pelletier, V.M. & Norton, R.A. (1985) *Epidamaeus* (Acari: Damaeidae) of subarctic western North America and extreme northeastern USSR. *Canadian Entomologist*, 117, 277–319.

Berlese, A. (1896) *Acari, Myriapoda et Scorpiones hucusque in Italia reperta. Ordo Cryptostigmata II (Oribatidae).* Portici, Padova, 96 pp.

Bernini, F. (1970) Notulae Oribatologicae II. Gli Oriatei (Acarida) delle Alpi Apuane (1a serie). *Lavori Della Societa Italliana di Biogeografia*, Nuova Seria, 1, 390–429.
Bernini, F. (1980) Notulae Oribatologicae XXIV. Gli Acari Oribatei di alcune piccole grotte del Senese. *Redia*, 63, 359–405.
Bernini, F. & Arcidiacono, R. (1979) Notulae Oribatologicae XXII. The redescription of *Damaeus (Damaeus) flagellifer* Michael, 1890 (Acarida, Oribatida). *Animalia*, 6 (1/3), 181–196.
Bulanova-Zachvatkina, E.M. (1957a) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Soobschchenije I. *Zoologicheskij Zhurnal*, 36 (8), 1167–1186.
Bulanova-Zachvatkina, E.M. (1957b) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Rod *Epidamaeus*, gen. n. (Acariformes, Oribatei). Soobschchenije II. *Zoologicheskij Zhurnal*, 36 (12), 1792–1801.
Bulanova-Zachvatkina, E.M. (1962) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berlese, 1896 (triba Belbini, triba n.). *Zoologicheskij Zhurnal*, 41 (2), 203–216.
Bulanova-Zachvatkina, E.M. (1965) O diagnostike vidov roda *Metabelba* Grandjean, 1936 (Oribatei, Damaeidae). *Zoologicheskij Zhurnal*, 36 (9), 1333–1343.
Bulanova-Zachvatkina, E.M. (1967) *Pancirnyje kleschchi—Oribatidy.* Vysshaja Shkola, Moskva, 254 pp.
Cancela da Fonseca, J.P. & Bahou, F. (1970) Questions de synonymie: Les especes *Damaeus verticillipes* Nicolet, 1855 et *Damaeus quadrihastatus* Markel & Meyer, 1960. *Acarologia*, 12, 605–611.
Chen, J., Norton, R.A., Behan-Pelletier, V.M., & Wang, H-F. (2004) Analysis of the genus *Gymnodampia* (Acari: Oribatida), with redescription of *G. setata* and description of two new species from North America. *Canadian Entomologist*, 136, 793–821.
Enami, Y., Aoki, J.-I., & Hu, S.-H. (1994) Oribatid mites from tropical forest of Yunnan province in China. IV. Family Damaeidae. *Proceedings of the Japanese Society of Systematic Zoology*, 52, 43–46.
Enami, Y., Fujikawa, T. (1989) Two new species of the genus *Epidamaeus* (Acari: Damaeidae) from Japan. *Edaphologia*, 40, 13–20.
Fujikawa, T. & Fujita, M. (1985) Five new species belonging to the genus *Epidamaeus* from Nayoro of Hokkaido, North Japan (Oribatida). *Edaphologia*, 32, 19–28.
Grandjean, F. (1936) Les Oribates de Jean Frederic Hermann et son pere, *Annales de la Société Entomologique de France*, 105, 27–110.
Grandjean, F. (1954a) Essai de classification des oribates (Acariens). *Bulletin de la Société Zoologique de France*, 78 (5–6), 421–446.
Grandjean, F. (1954b) Observations sur les Oribates (30e série). *Bulletin du Museum D'Histoire Naturelle*, Paris, 26 (2), 482–490.
Grandjean, F. (1954c) Observations sur les Oribates (31e série). *Bulletin du Museum D'Histoire Naturelle*, Paris, 26 (5), 582–589.
Grandjean, F. (1960) *Damaeus arvernensis* n. sp. (Oribate). *Acarologia*, 2, 250–275.
Griepenburg W. (1939) Die Tierwelt der Höhlen bei Kallenhardt. *Mitteilungen über Höhlen-und Karstforschung*, 1, 17–26.
Hammen, L. van der & Strenzke, K. (1953) A partial revision of the genus *Metabelba* Grandjean (Oribatei, Acari). *Zoologische Mededelingen*, 32(14), 141–154.
Hammer, M. (1967) Some Oribatids from Kodiak Island near Alaska. *Acta Arctica*, 14, 1–25.
Hermann, J.F. (1804) *Mémoire Aptèrologique.* Strassbourg, 144 pp.
Hoebel-Mävers, M. (1967) *Funktionsanatomische Untersuchungen am Vrtdauungstrakt der Hornmilben (Oribatei).* Dissertation thesis, Braunschweig, 88 pp.
Koch, C.L. (1836) *Deutschlands Crustaceen, Myriapoden und Arachniden*, vol. 2 (11).
Koch, C.L. (1836) *Deutschlands Crustaceen, Myriapoden und Arachniden*, vol. 4–9.
Koch, C.L. (1841) *Deutschlands Crustaceen, Myriapoden und Arachniden*, vol. 38 (7).
Kunst, M. (1957) Bulgarische Oribatiden (Acarina) I. *Universitas Carolina, Biologica*, 3, 133–165.
Kunst, M. (1961) Bulgarische Oribatiden IV. (Acari:Oribatei). *Acta Universitatis Carolinae,Biologica*, 8, 151–183.
Kunst M. (1968) *Roztoči nadřádu Oribatei Československa*. Unpubl. habilitation thesis. Deposited in the Zoological library of the Faculty of Science, Charles University Prague. (in Czech) 1355 pp.
Kunst, M. (1971) Pancířníci – Oribatei. In: Daniel, M. & Černý, V. (eds.), *Klíč zvířeny ČSSR II*. Nakladatelství Československé Akademie Věd, Praha, (in Czech) 531–580.
Kulczynski, V. (1902) Species Oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. *Bulletin International de L'Académie des Sciences de Cracovie, Classe des sciences mathématiques et naturelles*, 2, 89–96.
Lebrun P. (1967) Note sur quelques oribates (Acarina: Oribatei) de la faune cavernicole de Belgique. *Bulletin et Annales de la Société Royale d' Entomologie de Belgique*, 103, 183–188.
Ľuptáčik P. & Miko L. (2003) Oribatid mites (Acarina, Oribatida) of Slovak caves. *Subterranean Biology*, 1, 25–29.
Luxton, M. (1972) Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional biology. *Pedobiologia*, 12, 434–463.

Luxton, M. (1981) Studies on the oribatid mites of a Danish beech wood soil. IV. Developmental biology. *Pedobiologia*, 21, 312–340.
Luxton, M. (1989) Michael's British Damaeids (Acari: Cryptostigmata). *Journal of Natural History*, 23, 1367–1372.
Maraun, M., Heethoff, M., Schneider, K., Scheu, S., Weigmann, G., Cianciolo, J., Thomas, R. H., Norton, R. A. (2004) Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. *Experimental and Applied Acarology*, 33, 183–201.
Märkel, K. & Meyer, I. (1960) *Belba pseudocorynopus* n.sp. und *Damaeus quadrihastatus* n.sp. (Acari, Oribatei). *Zoologischer Anzeiger*, 165, 13–22.
Michael, A.D. (1885) New British Oribatidae. *Journal of the Royal Microbiological Society, ser. 2*, London, 5, 385–397.
Michael, A.D. (1888) *British Oribatidae. vol. II*. Ray Society, London, pp. 337–657.
Mihelčič, F. (1954) Einige neue Oribatiden (Acarina). *Zoologischer Anzeiger*, 154(1/2) 26–30.
Mihelčič, F. (1955) Oribatiden Südeuropas I. *Zoologischer Anzeiger*, 155 (9/10), 244–248.
Mihelčič, F. (1957) Oribatiden Südeuropas VII. *Zoologischer Anzeiger*, 159 (3/4), 44–68.
Mihelčič, F (1963) Beitrag zur Kenntnis der Oribatidenfauna Kärntens (Oribatei, Acarina) *Zoologischer Anzeiger*, 170, 230–240.
Mihelčič, F. (1964) Ein Beitrag zur Kenntnis der Familie Damaeidae Berl. *Zoologischer Anzeiger*, 172, 360–385.
Miko, L. (2006) Damaeidae. In: Weigmann, G.: *Hornmilben (Oribatida)*, Die Tierwelt Deutschlands Begründet 1925 von Friedrich Dahl, Teil 76., Goecke & Evers, Keltern, pp. 179–207.
Miko, L., & Travé, J. (1996) Hungarobelbidae n.fam., with a description of *Hungarobelba pyrenaica* n.sp. (Arachnida, Oribatida). *Acarologia*, 37, 133–155.
Mourek, J., & Miko, L. (in press) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. Proceedings of the 12th International Congress of Acarology. 21–26 August 2006, Amsterdam, The Netherlands.
Nicolet, H. (1855) Histoire naturelle des Acariens qui se trouvent aux environs de Paris. *Archives du muséum d'histoire naturelle, publiées par les professeurs administrateurs de cet établishment*, 7, 381–482.
Norton, R. A. (1977a) A review of F.Grandjean's system of leg chaetotaxy in the Oribatei and its application to Damaeidae. In: Dindal, D. L. (Ed.), *Biology of Oribatid Mites*. SUNY College of Environmental Science and Forestry, Syracuse, New York, pp. 33–62.
Norton, R. A. (1977b) The genus *Damaeus* Koch (Acarina: Oribatei) in the United States. *Acarologia*, 19, 331–353.
Norton, R. A. (1978a) Generic concepts in the Damaeidae (Acari: Oribatei) I. Three new taxa based on species of Nathan Banks. *Acarologia*, 20(4), 603–621.
Norton, R. A. (1978b) *Veloppia kananaskis* n. sp., with notes on the familial affinities of *Veloppia* Hammer (Acari: Oribatei). *International Journal of Acarology*, 4, 71–84.
Norton, R. A. (1979a) Aspects of the biogeography of Damaeidae sensu latu (Oribatei), with emphasis on North America. In: Rodriguez, J.G. (Ed.), *Recent Advances in Acarology, Volume 2*. Acadamic Press, New York. pp. 535–540.
Norton, R. A. (1979b) Familial concepts in the Damaeoidea as indicated by preliminary phylogenetic studies. In: Rodriguez, J.G. (Ed.), *Recent Advances in Acarology, Volume 2*. Acadamic Press, New York, pp. 529–533.
Norton, R. A. (1979c) Generic concepts in the Damaeidae (Acari: Oribatei) Part 2. *Acarologia*, 21, 496–513.
Norton, R. A. (1994) Evolutionary aspects of oribatid mite life histories and consequences for the origin of the Astigmata. In: Houck, M. (Ed.): *Mites. Ecological and Evolutionary Analyses of Life-History Patterns.* Chapman & Hall, New York, pp. 99–135.
Norton, R. A., Ryabinin, N. A. (1994) New alpine damaeid mite (Acari: Oribatida) from New Hampshire, USA. *Acarologia*, 35, 373–380.
Olszanowski, Z., Rajski, A., Niedbala, W. (1996) *Roztocze Acari—Mechowce Oribatida. Katalog Fauny Polski Catalogus faunae Poloniae.* Muzeum i Institut Zoologii, Poznaň, 34 (9), 243 pp.
Oudemans, A. C. (1900) New List of Dutch Acari, Ist part. *Tijdschrift voor Entomologie*, 43, 129–139.
Pauly, F. (1952) Die "Copula" der Oribatiden (Moosmilben). Naturwissenschaften, 39 (24), 572–573.
Pauly, F. (1956) Zur Biologie einiger Belbiden und zur Funktion ihrer Pseudostigmatischen Organe. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere*, 84, 275–328.
Perez-Iñigo C. (1966) *Damaeus selgae* n.sp., nouvelle espèce d'oribate (Acari) d'Espagne centrale. *Acarologia*, 8 (2), 365–373.
Perez-Iñigo C. (1997) Acari: Oribatei, Gymnonota. In: Ramos, M. A., (Ed.), *Fauna Iberica*, 9, Museo Nacional de Ciencias Naturales, Madrid, pp. 1–374.
Schatz, H. (1983) U.-Ordn. Oribatei, Hornmilben. *Catalogus faunae Austriae. Ein systematisches Verzeichnis aller auf osterreichischem Gebiet festgestellten Tierarten*, 9, Österreichische Akadademie der Wissenschaften, Wien, pp. 1–118.
Schuster, R. (1956) Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. *Zeitschrift für Morphologie und Ökologie der Tiere*, 45, 1–33.
Sellnick, M. (1926) Novyje russkie Oribatidae. *Izvestija Biologicheskich Nauk, Issledovanija Instituta Permskogo Gosu-*

darstvennogo Universiteta, Perm, 4, 339–342.
Sellnick M. (1960): Formenkreis: Hornmilben, Oribatei. Nachtrag. In: Brohmer, P. Ehrmann P. & Ulmer G. (Eds.), *Die Tierwelt Mitteleuropas*, Leipzig, 3(4), Erg., pp. 45–134.
Siepel, H. & de Ruiter-Dijkman, E. M., 1993: Feeding guilds of oribatid mites based on their carbohydrase activities. *Soil Biology and Biochemistry*, 25, 1491–1497.
Smrž, J. (1991) Some aspects of the microanatomy of soil sarcoptiform mites (Acari: Oribatida and Acaridida). In: Dusbábek F. & Bukva V. (Eds.), *Modern Acarology*, Academia, Prague and SPB Academic Publishing bv, The Hague, Vol. 2, pp. 319–322.
Strenzke, K. (1950) Die Belbiden Holsteins (Acarina: Oribatei). *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein*, 24 (2), 63–65.
Subías, L.S. (2004) Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1748–2002). *Graellsia*, 60, 3–305.
Subías, L. (2007) *Listado sistematico, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (Excepto fósiles)*. 536. Available from: http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf/ 14. 10. 2007.
Wang Hui-Fu, Norton, R. A. (1989) Two new species of *Damaeus* (Acari: Oribatida) from Mt. Wuyi, Fujian Province, China. *Acarologia*, 30, 163–170.
Weigmann, G. 2006. *Hornmilben (Oribatida)*. Die Tierwelt Deutschlands Begründet 1925 von Friedrich Dahl, Teil 76., Goecke & Evers, Keltern, pp. 1–520.
Willmann, C. (1930) Neue und bemerkenswerte Oribatiden aus der Sammlung Oudemans. *Abhandlungen Naturwissenschaftlicher Verein Brehmen*, 26, 1–12.
Willmann, C. (1931) Moosmilben oder Oribatiden (Cryptostigmata). in: Dahl F. (Ed.), *Die Tierwelt Deutschlands*, 22, 79–200.
Willmann, C. (1932) Milben aus Harzer Hohlen. *Mitteilungen über Höhlen- und Karstforschung*, 107–111.
Willmann, C. (1935) Exploration biologique des cavernes de la Belgique et du Limbourg hollandais. XXV^{e} contribution: Acari. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 11 (29), 1–41.
Willmann, C. (1936) Die Vogelwelt des Glatzer Schneeberges. *Belba nidicola*, eine neue Oribatide aus Vogelnestern in Wolfelsgrund. *Beiträge zur Biologie des Glatzer Schneeberges*, 2, 117–120.
Willmann, C. (1938) Die Acarofauna der Höhlen des Frankischen Jura und einiger anderer Höhlen. *Mitteilungen über Höhlen- und Karstforschung* 1/2, 15–29.
Willmann, C. (1951) Die Hochalpine Milbenfauna der mittleren Hohen Tauern, insbesondere des Gorssglockner-Gebietes (Acari). Bonner Zoologische Beiträge, 2, 141–176.
Willmann, C. (1953) Neue Milben aus den Ostlichen Alpen. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Klasse, Abteilung 1*, 162, 449–515.
Willmann, C. (1954) Mährische Acari hauptsachlich aus dem Gebiete des Mährischen Karstes. *Československá parasitologie*, 1, 213–272.

Abbreviations

Setae
on prodorsum
ex—exobothridial seta
in—interlamellar seta
le—lamellar seta
ro—rostral seta
ss—sensillus
on notogaster
c1, c2, c3, la, lm, lp, h1, h2, h3, ps1, ps2, ps3
on ventral side
a, m, h—setae on the subcapitulum of gnathosoma
1a, 1b, 1c—setae of epimere 1
2a—seta of epimere 2
3a, 3b, 3c—setae of epimere 3
4a, 4b, 4c, 4d—setae of epimere 4
g1-g6—genital setae
ad1-ad3—adanal setae
ag—aggenital seta
an1-an2—anal setae

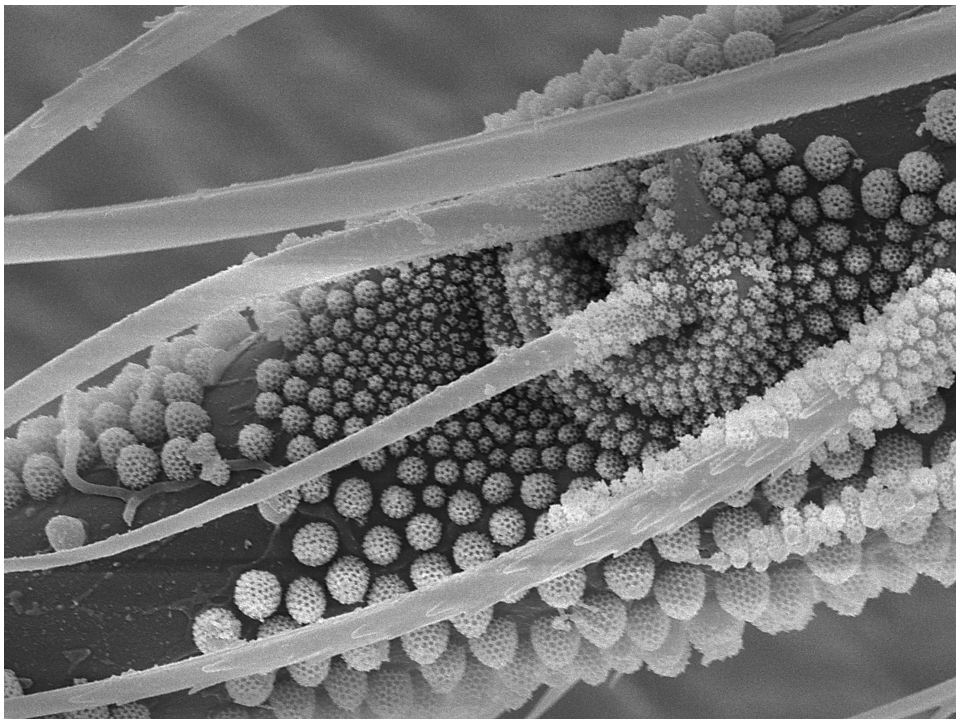
Notation of the leg setae is according to Norton (1977a), the abbreviations are not explained here. Letters in parentheses refer to a pair. Greek letters refer to solenidia (ω, φ, σ) and famulus (ε), Roman letters refer to normal setae.

Apophyses and other elevated or depressed cuticular structures
di—discidium
sa—spina adnata
Ba—anterior postbothridial apophysis
Da—anterior centrodorsal apophysis
La—anterior lateral apophysis
P—propodolateral apophysis
Sa—anterior sejugal apophysis
Sp—posterior sejugal apophysis
E2a, E2p—anterior and posterior propodoventral apophyses
Va, Vp—anterior and posterior ventrosejugal apophyses
k—cornicle (in nymphs)
cp—medial pit on coxisternum I

Glands and lyrifissures
gla—opening of the opisthonotal gland
ia, im, ip, ips, ih—notogastral lyrifissures
iad—adanal lyrifissure

Contribution 1.3

Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. & Sabelis M. W. (eds.): ***Trends in Acarology*.** Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.



Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker

Jan Mourek[1,2] & Ladislav Miko[3]

[1]Department of Zoology, Charles University Prague, Faculty of Science, Viničná 7, CZ 128 44 Prague 2, Czech Republic. E-mail: jan_mourek@yahoo.co.uk; [2]Department of Biology and Environmental Education, Charles University, Faculty of Education, MD Rettigové 4, CZ-116 39 Prague 1, Czech Republic; and [3]Directorate ENV/B: Protecting natural resources, Avenue de Beaulieu 9, BE-1160 Brussels, Belgium

The famulus is a specialised seta on the dorsal side of the tarsus of the first pair of legs in acariform mites. It has various shapes, but a stable location within the whole group. In the oribatid family Damaeidae, two states of famulus are known: emergent and sunken. The emergent famulus is a simple short seta with fully emergent insertion. It is present in the adult of all known Damaeidae and in immature stases of many damaeid genera. The sunken famulus is reduced in size and submerged in a fovea with an elevated rim, so that only its tip is visible. In this study, the ontogenetic development of the famulus in selected Central European damaeid species, namely *Damaeus* (*Adamaeus*) *onustus*, *D.* (*Paradamaeus*) *clavipes*, *Epidamaeus tatricus*, *Spatiodamaeus verticillipes*, *Kunstidamaeus lengersdorfi*, and *Belba compta*, was studied with light and scanning electron microscopy and compared with that of *Gymnodamaeus bicostatus* (Gymnodamaeidae). Literature data on the ontogeny of the famulus in Damaeidae are summarized and the significance of the famulus as a phylogenetic marker is discussed. In agreement with previous studies, adults of all studied members of Damaeidae had an emergent famulus. The immatures of all studied members of *Damaeus* sensu lato, except for *E. tatricus*, had a sunken famulus, whereas the immatures of *B. compta* had an emergent famulus. Immatures as well as adults of *G. bicostatus* had a sunken famulus. In contrast to Norton's phylogenetic hypotheses, all immature stases of *E. tatricus* possessed an emergent famulus, similar to *B. compta*. Therefore, either the monophyly of *Epidamaeus* is questionable, or, more likely, reversal to a plesiomorphic state occurred in *E. tatricus*.

Key words: Famulus, ontogeny, morphology, Oribatida, Damaeidae, *Epidamaeus tatricus*, SEM

The current generic classification of the oribatid family Damaeidae is largely artificial (Bulanova-Zachvatkina, 1967; Balogh & Balogh, 1992; Perez Iñigo, 1997). Except for the preliminary phylogenetic study and partial revisions published by Norton (1977, 1978, 1979a,b) it has not been subjected to a cladistic analysis. Diagnoses of most damaeid genera are based mainly on leg chaetotaxy. According to Norton (1977a), identical setal formulas of a given leg segment may, at least in some cases, be the result of convergence due to reduction of particular setae or due to neotrichy, and thus are of limited value in phylogenetic classification. Therefore, careful homologisation of particular setae (including tracing their fate during ontogeny) and inclusion of qualitative characters are necessary.

Norton (1979a) attributed high value in phylogenetic classification of Damaeidae to the state of the famulus (sensu Grandjean, 1935) in immature stases. This minute setiform organ is present in proximal parts of the dorsal or dorsolateral side of tarsi I in Acariformes, usually close to the tarsal solenidia (Grandjean 1940, 1941, 1954a,b). Due to its stable location, the famulus can be homologised within the Acariformes. In several families of Prostigmata and rarely in species of Palaeosomata, a famulus is present also on tarsus II (Grandjean, 1957; Norton, 1977a). The famulus has various shapes, but in most Brachypylina it has the form of a simple short pointed seta (Grandjean, 1935, 1940, 1941, 1946, 1951). Unlike the isotropic solenidia, the famulus is birefringent under polarised light (Grandjean, 1940). Alberti & Coons (1999) classified the famulus as a seta-like sensillum with a cytoplasmic core. The biological function of the famulus has not been explained completely. Based on its ultrastructure, it is probably a thermo-hygroreceptor (Leonovich, 1994; Alberti & Coons, 1999).

Among damaeid genera, two character states of the famulus are known (Grandjean, 1954b; Norton, 1979a): emergent and sunken (we consistently use the neutral descriptive terms 'emergent' and 'sunken' famulus, instead of 'normal' and 'reduced', to avoid phylogenetic assumptions about the character polarity).

Emergent famulus (Figs. 1a-d, 3a) – a simple short seta with fully emergent insertion. This is the form in adults of all known damaeid genera and also in immature stases of the majority of damaeid genera, e.g., *Belba*, *Caenobelba*, *Metabelba*, *Quatrobelba*, and *Porobelba*. According to Norton (1979a) the emergent famulus (referred as 'normal') in immatures represents the plesiomorphic state within the family.

Sunken famulus (Figs. 2a-c) – the seta is reduced in size and submerged in a fovea with an elevated rim ('sclerotised cup'), so that only its tip is visible. It is known from all immature stases of *Damaeus* (including all subgenera), *Epidamaeus*, *Spatiodamaeus*, *Dyobelba*, and *Lanibelba* (Grandjean, 1954b; Norton, 1979a). Norton (1979a) proposed that the sunken famulus (referred to as 'reduced' or 'vestigial') in immatures is apomorphic within the Damaeidae, and suggested that the group of genera sharing this character is monophyletic.

The ontogeny of the famulus is known only for a limited number of damaeid species (Table 1) and detailed studies of more species might change the distribution pattern within the family. For example, Norton & Ryabinin (1994) described *Dyobelba reevesi* Norton et Ryabinin as having an emergent famulus in the immatures. In out-group comparisons, the polarity of the character is not so clear, because the sunken famulus is also known in the immatures, as well as in the adults, of several other families of the group Eupheredermes sensu Grandjean (1953), such as Zetorchestidae and Gymnodamaeidae (Grandjean, 1951, 1954a).

In the present study, the ontogeny of the famulus in five European members of *Damaeus* sensu lato, representing dif-

ferent genera/subgenera, was studied with light and scanning electron microscopy (SEM) and compared with members of *Belba* (Damaeidae) and *Gymnodamaeus* (Gymnodamaeidae).

Notes on the nomenclature

The studied species were identified according to Miko (2006) and we follow the same generic concepts. *Epidamaeus* Bulanova-Zachvatkina, *Spatiodamaeus* Bulanova-Zachvatkina, and *Kunstidamaeus* Miko are considered separate genera, whereas *Damaeus* (*Paradamaeus*) Bulanova-Zachvatkina and *Damaeus* (*Adamaeus*) Norton are classified as subgenera within *Damaeus* CL Koch. We use the term '*Damaeus* sensu lato' for members of all these taxa including *Epidamaeus*. We accept the single family concept of Damaeidae as proposed by Norton (1979a) and reject the splitting into three separate families (Damaeidae, Belbidae, Belbodamaeidae), as proposed by Bulanova-Zachvatkina (1967). On the other hand, we accept the transfer of *Hungarobelba* Balogh from Damaeidae to Hungarobelbidae Miko et Travé.

MATERIAL AND METHODS

Species studied and collection of specimens

Adult specimens of the species studied were obtained in the following 11 localities of the Czech Republic (CR) and Slovak Republic (SR).

Belba compta (Kulczynski): CR, north-eastern Bohemia, Krkonoše Mountains, Údolí Bílého Labe, 50°44'46"N, 15°37'47"E, about 1,000 m above sea level (asl), dead spruce forest (*Picea abies*) with young spruce trees in the undergrowth, wet mosses (*Polytrichum commune*, *Sphagnum* sp.) on granite blocks, 11-06-2003, J Mourek & J Materna leg.

Damaeus (*Paradamaeus*) *clavipes* (Hermann): CR, central Bohemia, west from Karlštejn village, western slope of the Prostřední vrch hill, 49°56'13"N, 14°10'1"E, about 280 m asl, decidous forest of hornbeam (*Carpinus betulus*) and oak (*Quercus* sp.), mixed litter and upper soil layers, 26-05-2003, J Mourek leg.

Damaeus (*Adamaeus*) *onustus* CL Koch: CR, central Bohemia, east from Davle town, valley of the last left tributary of the Záhoranský brook near the confluence, 49°53'50"N, 14°25'25"E, about 260 m asl, deciduous forest of hornbeam, oak, and lime, mixed litter and upper soil layers, 28-05-2003, J Mourek leg.; CR, eastern Bohemia, Nekoř village, 50°3'57"N, 16°32'41"E, about 480 m asl, shrubs of hazel (*Corylus avellana*) and European elder (*Sambucus nigra*), mixed litter and upper soil layers, 18-06-2006, J Mourek leg.

Epidamaeus tatricus (Kulczynski): CR, north-eastern Bohemia, Krkonoše Mountains, beech forest (*Fagus sylvatica*) Buková stráň, eastern slope, 50°44'31"N, 15°32'14"E, about 1100 m asl, south from Malá Kotelní jáma, beech litter and upper soil layers, 11-06-2003, J Mourek & J Materna leg.; SR, Malá Fatra Mountains, mixed growth of dwarf pine (*Pinus mugho*), rowan tree (*Sorbus* sp.), willow (*Salix* sp.), 49°13'5"N, 19°5'40"E, about 1,350 m asl, mixed litter and upper soil layers, 09-08-2004, J Mourek leg.

Spatiodamaeus verticillipes (Nicolet): CR, southern Bohemia, Třeboňsko Biosphere Reservation, peat bog 'Červené Blato' and adjacent scots pine forest (*Pinus sylvestris*), 48°51'20"N, 14°47'46"E, about 470 m asl, mixed litter of scotch pine and birch (*Betula* sp.) and upper soil layers, 17-05-2003, J Mourek leg.; CR, southern Bohemia, Trebonsko Biosphere Reservation, avenue of old oaks on dam between ponds Nový Vdovec and Ženich, 49°1'24"N, 14°50'30"E, 430 m asl, oak litter and upper soil layers, 17-05-2003, F Štáhlavský leg.; CR, central Bohemia, east from Družec village, 50°5'49"N, 14°3'2"E, about 390 m asl, mixed forest of scots pine, beech, lime, and hornbeam, mixed litter and upper soil layers, 25-05-2003, J Mourek leg.

Kunstidamaeus lengersdorfi (Willmann): SR, Slovak karst, 'Čertova diera pri Domici' cave, 49°28'0"N, 20°27'30"E, about 350 m asl, rotten wood, 20-05-2005, P Ľuptáčik leg.

Gymnodamaeus bicostatus (CL Koch): CR, southeastern Moravia, northeast from Pouzdřany village, Pouzdřanská step national reserve, eastern slope, shrubs of bladdernut (*Staphylea pinnata*), plum tree (*Prunus domestica*), and field maple (*Acer campestre*), 48°56'35"N, 16°38'37"E, about 390 m asl, mixed litter, 16-09-2006, J Mourek leg.

The mites were extracted in modified Berlese-Tullgren extractors. Part of the samples was extracted into 80% ethanol and adults were sorted and used for light microscopic and SEM observation. The rest of the samples were extracted into plastic vials with a layer of moistened plaster of Paris on the bottom; live adult specimens were sorted and used as stock for laboratory cultures. The specimens of *K. lengersdorfi* were hand-collected directly in the field, using a fine brush.

Laboratory cultures

Immature stases were obtained from laboratory cultures kept in polyethylene test-tubes (3 cm in diameter, 3.5 cm high). The bottom of the tube was removed and replaced with a 5-8 mm layer of plaster of Paris mixed with charcoal (20:1). A central hole (3 mm in diameter) in the polyethylene lid covered with fine mesh (0.1 × 0.1 mm) ensured aeration. The bottoms of the rearing tubes were embedded in regularly moistened sand in plastic containers, to avoid dessication. Five to 20 adults were introduced in a tube. The mites were fed green bark algae (*Desmococcus* spp.) and kept at 16 °C. Culturing of *K. lengersdorfi* failed, therefore field-collected immatures were studied.

Sample preparation and SEM-observation

Adults and immatures were fixed in 80% ethanol, then dehydrated in an ascending series of ethanol (80, 96, and 100%), next in a series of mixtures of 100% ethanol and acetone (2:1, 1:1, and 1:2) ending with 100% acetone, and finally dried with the critical point method. Specimens were mounted on aluminium stubs with double-sided carbon adhesive tape and coated with gold. Adults of *E. tatricus* were macerated in hot pure lactic acid and the thick layer of filamentous cerotegument was removed with fine needles prior to preparation for SEM. This procedure allowed the observation of details of the setae. Mites were observed and photographed with a Jeol 6100 SEM in the Lab. of Electron Microscopy (Inst Parasitology, Acad Sciences, Ceské Budejovice, CR) and with a Jeol 6380 LV SEM in the Lab. of Electron Microscopy (Dept Parasitology, Fac Science, Charles Univ, Prague, CR). Three-five specimens per particular stase of each species were examined.

RESULTS

The famulus did not vary noticeably within any particular developmental stase of any species studied. The famulus in

all stases of all species, except for the immatures of *E. tatricus*, was inserted on a line connecting the insertions of solenidia ω1 and ω2 (or lateral to solenidion ω1 in the larva, since ω2 appears first in the protonymph). By contrast, the famulus in immatures of *E. tatricus* was inserted slightly distally from the line connecting both solenidia. Adults of all studied damaeids had a normally developed emergent famulus (Figs. 1d, 2d), in the form of a simple short pointed seta, either straight or slightly curved.

In all immature stases of *D.* (*A.*) *onustus*, *D.* (*P.*) *clavipes*, *K. Lengersdorfi*, and *S. verticillipes*, the famulus was sunken (Figs. 2a-c). Its base was submerged in a narrow fovea beneath the general tarsal surface and cuticle surrounding the fovea formed a slightly elevated rim. The foveal opening was either oval or guttiform. At high magnification (≥4,000×) the minute pointed famulus, with slightly emergent tip, was recognizable inside the fovea.

In contrast to other species of *Damaeus* sensu lato, all immature stases of *E. tatricus* had a fully emergent famulus (Figs. 1a-c) of the same appearance as that of adults. It did not differ noticeably among particular stases, except that it was relatively shorter in the larva than in later stases. In some specimens, the famulus was sparsely covered with a fine granular cerotegument. In immatures of *B. compta* (Fig. 3a) the famulus was emergent as in *E. tatricus*. In *G. bicostatus*, the famulus was sunken in all developmental stases, including the adult (Fig. 3b). The tip of the seta was not visible even at high magnification (≥4,000×). The famulus was inserted slightly distally from the line connecting the tarsal solenidia.

DISCUSSION

All published data on the ontogeny of the famulus in Damaeidae are summarized in Table 1. Morphology of immature Damaeidae is known in a few species and most of the genera are insufficiently represented. Moreover, several authors did not include small morphological details such as the ontogeny of the famulus (Sitnikova, 1959; Moraza et al., 1990; Enami, 1992).

Our observations of the emergent famulus in all stases of *B. compta* are consistent with findings of Grandjean (1954b), Norton (1977a, 1978), and Norton & Pallacios-Vargas (1982) on several other species in this genus. Also our finding of a sunken famulus in immatures of *D.* (*A.*) *onustus*, *D.* (*P.*) *clavipes*, and *S. verticillipes* agrees with observations of Grandjean (1935, 1954b) and Norton (1977a) for the same species. The same character state was previously documented in seven species of the nominal subgenus *Damaeus* (*D.*), which was not included in our study (Grandjean, 1954a, 1960; Norton, 1977b). The hypothesis of Norton (1979a) on the synapomorphy of the sunken famulus in immatures of

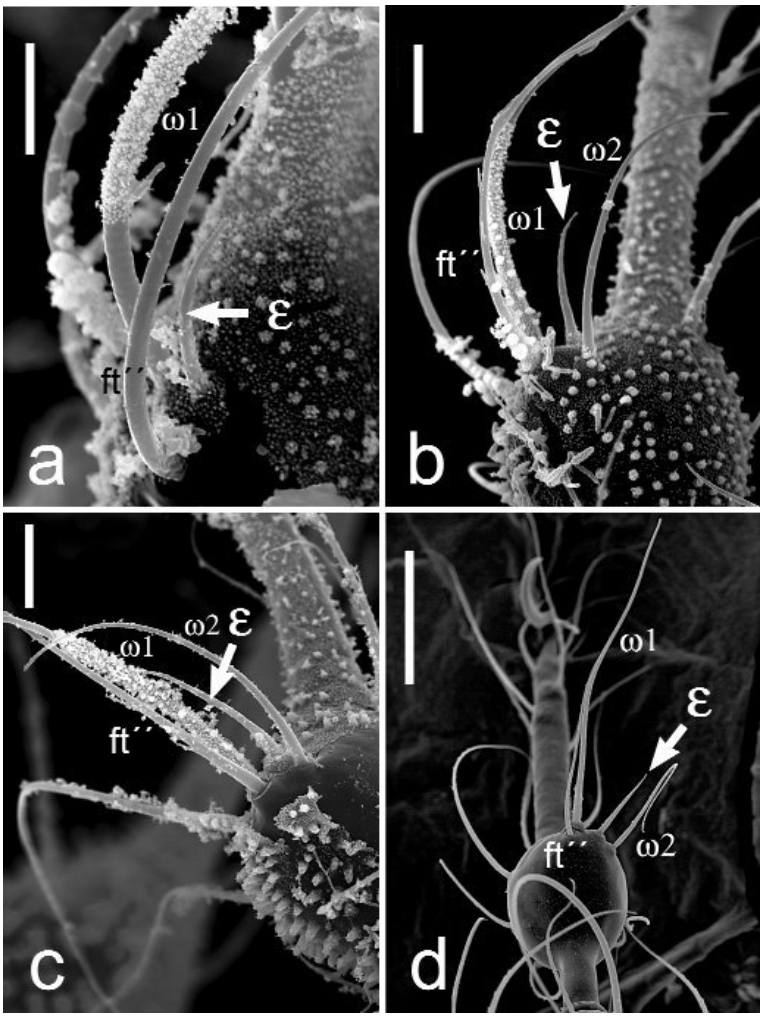


Figure 1 SEM micrographs showing ontogeny of the famulus (arrows) and solenidia on tarsus I (on the right leg) in *Epidamaeus tatricus*. The famulus is emergent in all stases of this species. (a) larva, dorsolateral aspect; (b) protonymph, dorsolateral aspect; (c) deutonymph, dorsolateral aspect; (d) adult, dorsal aspect (specimen macerated in hot lactic acid, cerotegument removed). Scales: (a) 5 μm; (b,c) 10 μm; (d) 50 μm. Abbreviations used: ft", antiaxial fastigial seta; ε, famulus; ω1,ω2, tarsal solenidia.

Damaeus sensu lato, *Lanibelba*, and *Dyobelba* is further supported by our findings on *K. lengersdorfi*.

The unexpected presence of an emergent famulus in immatures of *E. tatricus* is the second known case within the clade including *Damaeus* sensu lato, *Lanibelba*, and *Dyobelba*. Norton & Ryabinin (1994) found emergent famuli in all nymphal stages of *Dy. reevesi* (the larva was not available), although they were uncertain about the generic placement of this species. These two exceptions do not necessarily disprove synapomorphy of the sunken famulus in this clade, but they show that it should be given less 'weight' or at least be interpreted with caution. Pending a more detailed

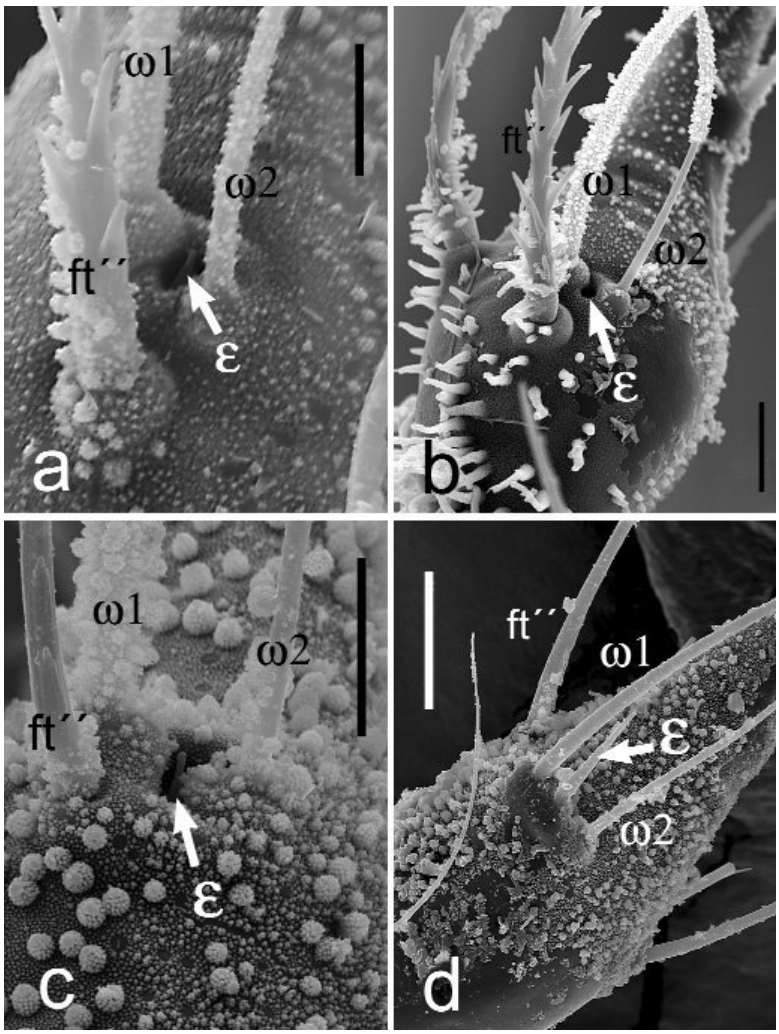


Figure 2 SEM micrographs showing ontogeny of the famulus (arrows) and solenidia on tarsus I (on the right leg) in *Spatiodamaeus verticillipes* and *Kunstidamaeus lengersdorfi*. The famulus is sunken in immature stases of these species and emergent in adults. (a) *S. verticillipes*, deutonymph; (b) *S. verticillipes*, tritonymph; (c) *K. lengersdorfi*, tritonymph; (d) *K. lengersdorfi*, adult. All figures are in dorsolateral aspect. Scales: (a) 5 µm; (b,d) 20 µm; (c) 10 µm. Abbreviations used: ft", posterior fastigial seta; ε, famulus; ω1,ω2, tarsal solenidia.

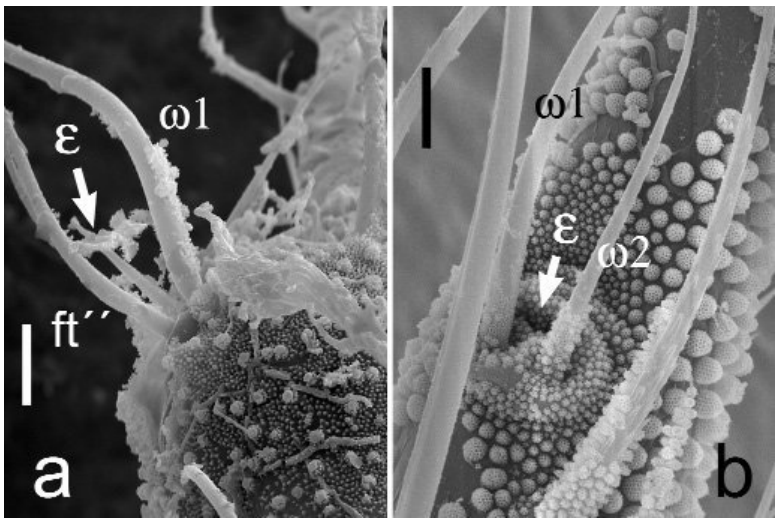


Figure 3 SEM micrographs showing ontogeny of the famulus (arrows) and solenidia on tarsus I in *Belba compta* and *Gymnodamaeus bicostatus*. The famulus is emergent in all stases of *B. compta* and sunken (externally invisible) in all stases of *G. bicostatus*. (a) *B. compta*, protonymph, dorsomedian aspect; (b) *G. bicostatus*, adult, dorsolateral aspect. Scales: (a,b) 5 µm. Abbreviations used: ft", antiaxial fastigial seta; ε, famulus; ω1,ω2, tarsal solenidia.

Table 1 Current knowledge of famulus ontogeny in members of the family Damaeidae. All species with described morphology of immatures are included. Famulus in immatures is emergent (E), sunken (S), or the description does not include information on the state of the famulus (?).

Species	Famulus	Source
Belba (B.) compta (Kulczynski)	E	present study
Belba (B.) corynopus (Hermann)	E	Grandjean, 1954b
Belba (*B.*) *clavasensilla* Norton et Pallacios-Vargas	E	Norton & Pallacios-Vargas, 1982
Belba sp. A[1]	E	Norton, 1977a
Belba sp. B[1]	E	Norton, 1977a
Belba (Protobelba) californica (Banks)	E	Norton, 1978
Caenobelba alleganiensis Norton	E	Norton, 1979b
Metabelba pulverosa Strenzke	E	Norton, 1977b
Metabelba papillipes (Nicolet)	E	Grandjean, 1954a
Porobelba spinosa (Sellnick)	E	Grandjean, 1954a
Quatrobelba montana Norton	E	Norton, 1979b
Damaeus (*Adamaeus*) *onustus* CL Koch	S	Grandjean, 1935, 1954b; Norton, 1977a; present study
Damaeus (*D.*) *angustipes* (Banks)	S	Norton, 1977a,b
Damaeus (D.) arvernensis Grandjean	S	Grandjean, 1960
Damaeus (*D.*) *grossmanni* (Wilson)	S	Norton, 1977b
Damaeus (*D.*) *opilioides* Norton	S	Norton, 1977b
Damaeus (*D.*) *atlanticus* Norton	S	Norton, 1977b
Damaeus (*D.*) *riparius* (Nicolet)	S	Grandjean, 1954b
Damaeus (D.) crispatus (Kulczynski)	S	Grandjean, 1954b
Damaeus (*Paradamaeus*) *clavipes* (Hermann)	S	Grandjean, 1954b; Norton, 1977a; present study
Epidamaeus (Akrodamaeus) longiseta (Banks)	S	Norton, 1978
Epidamaeus (E.) tatricus (Kulczynski)	E	present study
Epidamaeus (E.) verrucatus Enami et Fujikawa	?	Enami & Fujikawa, 1989; Enami, 1992
Epidamaeus sp. A[1]	S	Norton, 1977b
Epidamaeus sp. B[1]	S	Norton, 1977a
Epidamaeus sp. C[1]	S	Norton, 1977a
Kunstidamaeus lengersdorfi (Willmann)	S	present study
Spatiodamaeus boreus Bulanova - Zachvatkina	?	Sitnikova, 1959
Spatiodamaeus verticillipes (Nicolet)	S	Grandjean, 1954b; present study
Dyobelba carolinensis (Banks)	S	Norton, 1978
Dyobelba reevesi Norton et Ryabinin	E[2]	Norton & Ryabinin, 1994
Dyobelba dindali Bayartogtokh et Norton	S	Bayartogtokh & Norton, 2007
Lanibelba pini Norton	S	Norton, 1979b

[1] subgenus is unknown; [2] larva is unknown.

cladistic analysis that includes more species and other independent characters, it is unclear whether these two cases represent ancestral or derived states within the clade, or whether they are misplaced in *Epidamaeus* and *Dyobelba*.

In *Epidamaeus*, ontogeny of the famulus is known in few of the >70 described species (Bayartogtokh, 2000c). Norton (1977a, 1979a) did not explicitly list the species of *Epidamaeus* he studied and some of them are still undescribed (Norton, pers. comm.). *Epidamaeus longiseta* (Banks), a member of the subgenus *Epidamaeus* (*Akrodamaeus*), is the only species of the genus for which the sunken state of famulus in immatures was explicitly documented (Norton, 1978). *Epidamaeus tatricus* belongs to the nominate subgenus *Epidamaeus* (*E.*). Furthermore, even the nominate subgenus *Epidamaeus* in the current sense represents a morphologically heterogeneous group and might be polyphyletic or paraphyletic (e.g., Behan-Pelletier & Norton, 1983, 1985; Luxton, 1989; Enami & Fujikawa, 1989; Enami, 1992; Enami et al, 1994; Bayartoktokh, 2000a,b,c, 2001). The genus diagnosis of *Epidamaeus* is weakly defined and should be further revised.

In our view, *E. tatricus* is not a typical member of *Epidamaeus* (*E.*). This species, together with, e.g., *E. setiger*, differs from most other known species of the genus by the presence of four setae (instead of three) on genua III and IV. They might represent a sister taxon to the rest of the genus. However, complete reduction of prodorsal tubercles in *E. tatricus* (seen also in several other members of *Epidamaeus*) does not indicate a basal position within the group. There is no doubt that *E. tatricus* is a member of *Damaeus* sensu lato and we believe that independent reversal of the famulus in its immatures from the sunken to the emergent state is the most likely explanation, and perhaps the same is true of *D. reevesi*, if indeed the later is congeneric with other species of *Dyobelba* (see also Bayartogtokh & Norton, 2007). Because the emergent famulus is retained in adults, its reappearance in immatures would probably require only a minor change in the genetic control of development. Even such a conserved character as the famulus is subject to variation; Grandjean (1960) described a case of accidental loss of the famulus in some adult specimens of *Damaeus arvernensis* (Grandjean).

The polarity of famulus character states in immatures of Damaeidae proposed by Norton (1979a) also needs careful revision (see Norton & Ryabinin, 1994). It is uncertain whether the sunken famulus in all stases (including adults) of Gymnodamaeioidea (Grandjean, 1954a; confirmed in our study) and Zetorchestidae (Grandjean, 1951) developed independently from that in immatures of Damaeidae. The phylogenetic relations of Damaeidae and other families within *Eupheredermes* are still unresolved (Maraun et al., 2004).

Functional aspects of the sunken famulus have not yet been studied. We believe that this state represents a specialized and functional sensory organ, rather than a vestigial or nonfunctional state. It is possible that the fovea provides

some protection of the setal part of the famulus or that it somehow increases the efficiency of the reception.

Acknowledgements

The study was supported by the Grant Agency of Charles University (grant No: 217/2004/B-BIO/PrF). We are grateful to Drs. Jan Materna, Peter Luptácik, and František Štáhlavský for help with the collection of material; to Dr. Miroslav Hyliš and the staff of the Laboratories of Electron Microscopy in Prague and Ceské Budejovice, repectively, for technical service. The authorities of the Krkonošský National Park kindly allowed the collection of soil samples. We are also grateful to Prof. Roy A. Norton for reading the manuscript and providing valuable comments and linguistic and stylistic improvements.

REFERENCES

Alberti G & Coons B (1999) Acari: Mites. Microscopic Anatomy of Invertebrates, Vol. 8C: Chelicerate Arthropoda (ed. by FW Harrison & RF Foelix RF), pp 515-1215. Wiley & Sons, Chichester, UK.

Balogh J & Balogh P (1992) The Oribatid Mites Genera of the World. Vol I. Hungarian National Museum Press, Budapest, Hungary.

Bayartogtokh B (2000a) New oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. Species Diversity 5: 183-200.

Bayartogtokh B (2000b) Two new species of oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. Acarina 8: 65-78.

Bayartogtokh B (2000c) Two species of damaeid mites (Acari: Oribatida: Damaeidae) from Mongolia, with notes on distribution of the genera *Epidamaeus* and *Dyobelba*. Biogeography 2: 67-79.

Bayartogtokh B (2001) Three new soil mites of the genus *Epidamaeus* (Acari, Oribatida, Damaeidae) from Mongolia. Zoosystema 23: 29-49.

Bayartogtokh B & Norton RA (2007) The *Dyobelba tectopediosa* species-group (Acari: Oribatida: Damaeidae) from the Southeastern USA, with a key to world species of *Dyobelba* and notes on their distribution. Zootaxa 1591: 39-66.

Behan-Pelletier VM & Norton RA (1983) *Epidamaeus* (Acari: Damaeidae) of arctic western North America and extreme northeast USSR. Canadian Entomologist 115: 1253-1289.

Behan-Pelletier VM & Norton RA (1985) *Epidamaeus* (Acari: Damaeidae) of subarctic western North America and extreme northeastern USSR. Canadian Entomologist 117: 277-319.

Bulanova-Zakhvatkina EM (1967) Pancirnyje kleschci – Oribatidy. Vysshaja Shkola, Moskva, Russia (in Russian).

Enami Y (1992) Life history of *Epidamaeus verrucatus* Enami et Fujikawa (Acari: Damaeidae), with morphological description of its immature stage. Edaphologia 48: 23-29.

Enami Y, Aoki J & Hu S (1994) Oribatid mites from tropical forests of Yunnan province in China. Proceedings of the Japanese Society of Systematic Zoology 52: 43-46.

Enami Y & Fujikawa T (1989) Two new species of the genus *Epidamaeus* (Acari: Damaeidae) from Japan. Edaphologia 40: 13-20.

Grandjean F (1935) Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Premiére partie. Bulletin de la Société Zoolique de France 60: 6-39.

Grandjean F (1940) Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Deuxiéme partie. Bulletin de la Société Zoologique de France 65: 32-44.

Grandjean F (1941) Observations sur les Acariens (6e série). Bulletin du Muséum national de l' Histoire naturelle 13: 532-539.

Grandjean F (1946) Observations sur les Oribates (30e série). Bulletin du Muséum national de l' Histoire naturelle 2e série 26: 482-490.

Grandjean F (1951) Etude sur les Zetorchestidae (Acariens, Oribates). Memoires du Muséum national d'Histoire naturelle. Série A. Zoologie 4: 1-50.

Grandjean F (1953) Essai de classification des Oribates (Acariens). Bulletin de la Société Zoologique de France 78: 421-446.

Grandjean F (1954a) Observations sur les Oribates (28e série). Bulletin du Muséum national d'Histoire naturelle. 2e série 26: 204-211.

Grandjean F (1954b) Observations sur les Oribates (30e série). Bulletin du Muséum nationale d' Histoire naturelle 2e série 26: 482-490.

Grandjean F (1957) Observations sur les Palaeacaroides (4e série). Bulletin du Muséum, 2e série 29: 213-220.

Grandjean F (1960) *Damaeus arvenensis* n. sp. (Oribate). Acarologia 2: 250-275.

Leonovich SA (1994) Morfologia specializirovannych set pridatkov tela u krasnotelkovych kleschcej semeistva Trombiculidae. Parasitologia 28: 445-451 (in Russian).

Luxton M (1989) Michael's British damaeids (Acari: Cryptostigmata). Journal of Natural History 23: 1367-1372.

Maraun M, Heethoff M, Schneider K et al. (2004) Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. Experimental and Applied Acarology 33: 183-201.

Miko L (2006) Damaeidae Berlese, 1896. Tierwelt Deutschlands 76. Teil. Hornmilben (Oribatida) (G Weigmann), pp. 179-207. Goecke and Evers, Keltern, Germany.

Miko L & Travé J (1996) Hungarobelbidae n. fam. with a desctiption of *Hungarobelba pyrenaica* n.sp. (Acarina, Oribatida). Acarologia 37: 133-155.

Moraza ML, Moreno AI & Saloña M (1990) *Epidamaeus ibericus* sp. n. de bosques del norte de la Peninsula Iberica (Acari, Oribatei, Damaeidae). Eos 66: 201-207.

Norton RA (1977a) A review of F. Grandjean's system of leg chaetotaxy in the Oribatei and its application to the Damaeidae. Biology of Oribatid Mites (ed. by DL Dindal), pp. 33-63. SUNY College of Environmental Science and Forestry, Syracuse, NY, USA.

Norton RA (1977b) The genus *Damaeus* Koch (Acarina: Oribatei) in the United States. Acarologia 19: 331-353.

Norton RA (1978) Generic concepts in the Damaeidae (Acari: Oribatei). I. Three new taxa based on species of Nathan Banks. Acarologia 20: 603-621.

Norton RA (1979a) Familial concepts in the Damaeoidea as indicated by preliminary phylogenetic studies. Recent Advances in Acarology 2: 529-533.

Norton RA (1979b) Generic concepts in the Damaeidae (Acari, Oribatei). Part II. Acarologia 21: 496-513.

Norton RA & Palacios-Vargas JG (1982) Nueva *Belba* (Oribatei: Damaeidae) de musgo epifitos de Mexico. Folia Entomológica Mexicana 52: 61-73.

Norton RA & Ryabinin NA (1994) New alpine damaeid mite (Acari: Oribatida) from New Hampshire, USA. Acarologia 35: 373-380.

Perez Iñigo C (1997) Acari. Oribatei. Gymnonota I. Fauna Iberica 9 (ed. by A Ramos et al.), pp. 373. Museo de Ciencias Naturales, Madrid, Spain.

Sitnikova LG (1959) Ziznennye cikly nekotorych pancyrnych kleschcej i metody ich kultivirovanija. Zoologicheskii Zhurnal 38: 1663-1673 (in Russian).

Contribution 1.4

Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species.

Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescriptions of two known species

Jan Mourek[1,2] Ladislav Miko[3]and Fabio Bernini[4]

[1] *Charles University, Faculty of Science, Department of Zoology and Dept. of Teaching and Didactics of Biology, Viničná 7, CZ-128 44 Prague, Czech Republic; E-mail: jan_mourek@yahoo.co.uk (coresponding author)*

[2] *Charles University, Faculty of Education, Department of Biology and Environmental Studies, M. D. Rettigové 4, CZ-116 39 Prague 1, Czech Republic*

[3]*European Commission, DG Environment, Avenue de Beaulieu 9, 1160 Auderghem, Brussels, Belgium; E-mail: ladislav.miko@ec.europa.eu*

[4] *Department of Evolutionary Biology, University of Siena, via Aldo Moro, 2 - 53100 Siena, Italy; E-mail: bernini@unisi.it*

Abstract

We review the current state of taxonomy of the oribatid mite genus *Metabelba* Grandjean, 1936 (Damaeidae) and present an amended generic diagnosis. In contrast to Subías (2004) we consider *Allobelba* Kunst, 1961 and *Neobelba* Bulanova-Zachvatkina, 1967 as separate genera, not subgenera of *Metabelba*. We consider the subgenus *Metabelba* (*Parametabelba)* Mihelčič, 1964, to be a nomen nudum and propose a new subgenus—*Metabelba* (**n. subg.1**), with type species *Metabelba sphagni* Strenzke (1950)—to replace it. *Metabelba* (**n. subg.1**) includes the species of *Metabelba* without the propodolateral apophysis. Together with the type species, the following named species (new combinations) belong to this subgenus: *Metabelba italica* (Sellnick, 1931); *M. romandiolae* (Sellnick, 1943); *M. platynotus* Grendjean, 1954; *M. ericius* Kunst, 1957; *M. rhodopeia* Kunst, 1961; *M. filippovi* Bulanova-Zachvatkina, 1965; *M. flagelliseta* Bulanova-Zachvatkina, 1965; *M. monilipeda* Bulanova-Zachvatkina, 1965; *M. pseudoitalica* Bulanova-Zachvatkina, 1965; *M. paraitalica* Kulijev, 1967 and *M. machadoi* Pérez-Iñigo 1986. A new species *Metabelba* **n. sp**. 1 is described and illustrated; it is characterized mainly by the presence of a notogastral cornicle in the adult. It was found in Central Bohemia (Czech Republic), Upper Silesia (Poland) and South Tyrol (Italy). *Metabelba romandiolae* (Sellnick, 1943) and *M. sphagni* Strenzke, 1950 are redescribed and illustrated. *Metabelba gladiator* Mihelčič, 1963 is considered to be junior synonym of *M. romandiolae*. *Metabelba lanceolata* Hammen, 1952 is considered to be a junior synonym of *M. sphagni*. We also provide a tentative diagnostic key and a table of characters of the known species of *Metabelba (***n. subg**.**1**), based on review of literature data.

Key words: oribatid mite, new species, new subgenus, new combination, description, nomen nudum, leg setation, cerotegument, paedomorphy, SEM, Czech Republic, Central Europe, identification key

Note: To aviod confusion, the name of one newly described species and one newly described subgenus was omited from this manuscript (see declaration on the beginning of the present thesis).

1. Introduction

This work is the fourth part of a series dealing with the taxonomic revision of European Damaeidae (Acari: Oribatida), following the works of Miko & Mourek (2008), Miko (2008) and Miko (2010). In the present part we review the development and current state of taxonomy of *Metabelba* Grandjean, 1936, which long has been in need of complete critical revision. Such revision is currently impossible, due to incomplete descriptions for many species and the lack of relevant material for some of them. However, our aim is to start the process by reviewing the available literature data and using it to provide a tentative diagnostic key to species.

Further, we describe a new species of *Metabelba* found in Central Bohemia (Czech Republic), Upper Silesia (Poland) and South Tyrol (Italy) and redescribe *Metabelba romandiolae* (Sellnick, 1943) and *M. sphagni* Strenzke 1950. The redescription of *M. romandiolae* will be presented on the basis of the ***neotypus*** and the more recently collected specimens of, and the type material of its junior synonym *M. gladiator* Mihelčič, 1963. The redescription of *M. sphagni* will be based on the study of its type series and on recently collected material from South Bohemia (Czech Republic). We further examined holotype of *M. lanceolata* Hammen, 1952 and substantiate, that it is a junior synonym of *M. sphagni*.

The new species along with *M. romandiolae* and *M. sphagni* belong to the group of *Metabelba* species that lack propodolateral apophysis (*P*), which have been grouped by recent authors (Subías 2004, 2008; Miko 2006) as the subgenus *Metabelba* (*Parametabelba*) Mihelčič, 1964. As we discuss below, *Parametabelba* cannot be considered a valid name, so we propose a new replacement name. Redescriptions of further European species of *Metabelba* will follow in subsequent parts of the series.

2. Material and methods

We follow mostly the conventions of morphological terminology and abbreviations developed by Grandjean (1960) and modified by subsequent authors (see Miko & Mourek 2008 for complete references and a list of abbreviations). For the leg chaetotaxy we used Grandjean´s notation, reviewed by Norton (1977). Setal formulas of appendages are given as numbers per segment (from trochanter to tarsus), famulus included, solenidia in parentheses. Epimeral setal formulas are given as numbers per podosomal segment (I-IV).

For each species, the number of specimens, locality and habitat description is given in the "material examined" section. Fresh specimens of given mite species were extracted by heat with modified Berlese-Tullgren funnels and fixed in 80% ethanol. They were cleared in pure lactic acid and mounted in temporary microscopic slides with a central excavation for light microscopic observation. Additionaly, permanent slides and unmounted specimens of different origin deposited in museum collections were studied.

The first author prepared the figures, othervise noted in respective figure captions (Fig. 11). Observations, measurements and drawings of both species were made with a compound microscope equipped with a camera lucida.

All measurements are given in μm as a range, usually followed with a mean in parentheses and number of measured specimens (n). Instead of the total body length we used the ventral length, measured in lateral view from the tip of the rostrum to the posterior edge of the ventral plate, to avoid discrepancies due to different degrees of notogastral distension (see also Bayartogtokh & Norton, 2007). This could not be applied in specimens mounted in permanent slides, for which only approximate values of total body length measured in ventral or dorsal view are given.

The maximal notogastral width was measured in dorsal view. Legs I and II were measured without trochantera, legs III and IV were measured including the trochantera. The length of individual leg segments was measured including the proximal part immersed in the previous segment and the total length of a given leg is given as a sum of all measured segments (including the immersed proximal parts). Length of trochanter III, which is curved in its proximal part, was measured as indicated in Fig 5 B.

The light micrographs were made using a compound microscope equipped with Nomarski DIC and a digital camera. The final micrographs were combined from various numbers of optical layers using Helicon Focus®.

For the SEM-study, adults of *Metabelba* **n. sp. 1** were fixed in 80% ethanol, then dehydrated in an ascending series of ethanol (80, 96, and 100%), next in an ascending series of mixtures of 100% ethanol and acetone (2:1, 1:1, and 1:2) ending with 100% acetone, and finally dried with the critical point method. Specimens were mounted on aluminium stubs with double-sided carbon adhesive tape and coated with gold. Mites were observed and photographed with a Jeol 6380 LV SEM in the Laboratory of Electron Microscopy (Dept Parasitology, Fac Science, Charles Univ, Prague, CR) at 8 - 15 kV. The scanned drawings and digital micrographs were edited and assembled to plates using Adobe Photoshop CS2®.

3. Review of *Metabelba* Grandjean, 1936

3.1 Development of the genus concept

The genus *Metabelba*—with the type species *Damaeus papillipes* Nicolet, 1855—was originally proposed by Grandjean (1936) to encompass species having solenidia on tibiae II and III coupled with a companion seta (*d*), whereas the solenidion on tibia IV is free. The generic diagnosis was further developed by van der Hammen and Strenzke (1953), Sellnick (1960), Bulanova-Zachvatkina (1965, 1975), Kunst (1971), Norton (1977), Pérez-Iñigo (1997) and Miko (2006). Bulanova-Zachvatkina (1965) restricted the genus to those species with a higher than usual number of setae on trochantera III and IV, i.e., with the trochanteral setal formula 1-1-4-3. She also noticed the high number of setae (10) on femur I in such species.

Diagnostic keys for the species of *Metabelba* of different parts of Europe and/or the former Soviet Union were provided by van der Hammen and Strenzke (1953), Sellnick (1960), Kunst (1961, 1968 unpubl.), Bulanova-Zachvatkina (1965, 1967, 1975), Perez-Iñigo (1997) and Miko (2006). Characters often used for species diagnoses within *Metabelba* include the presence/absence of propodolateral apophysis (*P*); presence/absence of centrodorsal apophyses (*Da*, *Dp*) and postbothridial apophysis (*Ba*); shape of parastigmatic apophyses (*Sa*, *Sp*); shape, relative length, direction and position of notogastral setae and the lenght ratio of trochanter and femur IV.

The presence of apophysis *P*, in combination with other mentioned characters, is often used within Damaeidae as a diagnostic character at the generic or subgeneric level, e.g. its absence distinguishes *Epidamaeus* from other genera within the complex of *Damaeus* s. lato (Bulanova-Zachvatkina, 1957, 1975; Miko 2006; Miko & Mourek 2008). Mihelčič (1964), following this approach, proposed a division of *Metabelba* into two subgenera: *Metabelba* s. str. with apophysis *P* present and well developed, and the subgenus *Parametabelba* Mihelčič, 1964 with *P* absent (fully reduced). While he listed the species assigned to each subgenus—including *Metabelba gladiator* Mihelčič, 1963 together with seven other species in *Parametabelba*—he failed to designate the type species of *Parametabelba.*

Mihelčič's (1964) concept of *Metabelba* with two subgenera was adopted by some authors (Kunst 1968 unpubl.; Subías 2004, 2008; Miko 2006); some even listed *Parametabelba* as a separate genus (e.g. Schatz 1983; Starý 2000a, 2000b). Other authors, in contrast, did not accept the division at all (e.g. Bulanova-Zachvatkina 1965, 1967, 1975; Balogh & Balogh 1992; Pérez-Iñigo 1986). Recently, Subías (2004) listed *Metabelba* (*Parametabelba*) Mihelčič as a valid subgenus with the type *Metabelba gladiator* Mihelčič, 1963. Miko (2006) assumed that in this case article 13.4 of the ICZN can be applied and that *Parametabelba* is a valid taxon. After further consideration (International Commission on Zoological Nomenclature, 1999), and consultation (R. A. Norton, pers.comm.) we concluded, however, that article 13.4 of the ICZN cannot be applied in this case because the description of *M. gladiator* Mihelčič, 1963 was published in another work, one year earlier than the subgenus was proposed. We also consider, that Subías (2004) did not make *Parametabelba* an available name because the type was neither fixed in an original publication, nor expressly proposed as a new replacement name, as required by article 13.3 of ICZN. Moreover, Subías (2004) did not explicitly indicate the name as intentionally new, as required by article 16.1 of the ICZN for names published after 1999. It is therefore apparent, that *Parametabelba* remains a nomen nudum, and cannot be used as a valid name. The name "*Parabelba* Mihelčič, 1964" used in the identification key of Kunst (1971) was probably a misprinting of *Parametabelba*; similarly, it is not available because Kunst neither designated the type species, nor indicated in any way that the name was intentionally new.

Conceptually, we accept the grouping of *Metabelba* species into two subgenera distinguished by the presence/absence of propodolateral apophysis, as proposed by Mihelčič (1964). Therefore, we propose the new name *Metabelba* (**n. subg.1**) with the type species *Metabelba sphagni* Strenzke, 1950 as a replacement for *Metabelba* (*Parametabelba*),

Subías (2004) further included *Allobelba* Kunst, 1961 and *Neobelba* Bulanova-Zachvatkina, 1967 as subgenera of *Metabelba* and thereby changed the classical concept of the genus. Unfortunately, he neither gave reasons, nor referred to any previous works and did not publish a modified diagnosis. We therefore reject his proposal for the following reasons.

The hitherto monotypical genus *Allobelba*—type species *A. aculeata* Kunst, 1961—seems to be more closely related to *Metabelbella* Bulanova-Zachvatkina, 1967 (the name was used first by Bulanova-Zachvatkina, 1957, but in our view it became an available name as late as in 1967, when Bulanova-Zachvatkina designated a type species), particularly due to the absence of companion setae *d* on tibiae of all legs. While Kunst (1961) reported the presence of *d* on tibia I in the diagnosis of *Allobelba*, his fig. 7 clearly shows that he confused *d* with solenidion φ2; the latter is invariably present on tibia I of adult Damaeidae, while *d* is invariably absent on tibia I. *Allobelba* thus differs from *Metabelbella* only in having 3 setae on trochanter III (instead of 4 in the later genus). This character might have only the specific value and after a thorough revision *Allobelba* might be synonymised with *Metabelbella* (see also Miko 2006). For the present we consider *Allobelba* as a separate genus.

According to Bulanova-Zachvatkina (1967, 1975) the hitherto monotypical genus *Neobelba*—type species *Neobelba pseudopapillipes* Bulanova-Zachvatkina, 1967—has respective trochanteral and genual setations of 1-1-4-3 and 4(1)-4(1)-4(1)-4, which are identical to those of *Metabelba*, but it differs from the later by the presence of coupled seta *d* also on tibia IV. *Neobelba* was poorly described, without figures, so important characters that might indicate close relation with *Metabelba* (e.g. the setation

of femora), remain unknown. We therefore consider *Neobelba* as a separate genus, until *N. pseudopapillipes* is revised in detail.

Based on the presented analysis, we propose the concept of *Metabelba* with two subgenera, *Metabelba* s. stricto and *Metabelba* (**n. subg.1**), and provide new diagnoses.

3.2 Proposed classification of *Metabelba* Grandjean, 1936 and list of named species

Genus *Metabelba* Grandjean, 1936

Type species. *Damaeus papillipes* Nicolet, 1855

Diagnosis. Small to middle-sized Damaeidae (body length usually 375-560 μm, rarely over 700 μm), coloured various shades of brown. Propodolateral apophysis (*P*) present or absent. Spinae adnatae absent. Setal formula of trochantera 1-1-4-3 or 1-1-3-3, femora I and II with 10 (rarely 9) setae, femora III and IV with 9 (rarely 8) setae. Setal formula of genua 4(1)-4(1)-4(1)-4. Solenidia on tibiae II and III coupled with a companion seta (*d*), solenidion on tibia IV long, free, tactile. Ventral accessory seta v_2' absent from tarsi I-IV, setal formula of tarsi (famulus included, solenidia in parentheses) 20(2)-17(2)-17(0)-14(0). Famulus in all developmental stages "normal", setiform, emergent.

Subgenus *Metabelba (Metabelba)* Grandjean, 1936

Type species: *Damaeus papillipes* Nicolet, 1855

Diagnosis. *Metabelba* with propodolateral apophysis (*P*) present, well developed.

Other included species: *Metabelba propexa* (Kulczynski, 1902); *Metabelba obtusa* Hammer, 1966 (probably junior synonym of *M. papillipes* according to Norton 1979a); *Metabelba pulverosa* Strenzke, 1953; *Metabelba parapulverosa* Moritz, 1966; *Metabelba singularis*, Mihelčič 1964; *Metabelba rara* Bulanova-Zachvatkina, 1965; *Metabelba rohdendorfi* Bulanova-Zachvatkina, 1965

***Metabelba* (n. subg. 1)**

Diagnosis. *Metabelba* with propodolateral apophysis (*P*) absent, fully reduced.

Type species. *Metabelba sphagni* Strenzke, 1950**.**

Other included species: *Metabelba italica* (Sellnick, 1931); *Metabelba romandiolae* (Sellnick, 1943); *Metabelba lanceolata* van der Hammen, 1952 (= junior synonym of *M. sphagni*); *Metabelba platynotus* Grandjean, 1954; *Metabelba ericius* Kunst, 1957; *Metabelba rhodopeia* Kunst, 1961; *Metabelba gladiator* Mihelčič, 1963 (= junior synonym of *M. romandiolae*); *Metabelba filippovi* Bulanova-Zachvatkina, 1965; *Metabelba flagelliseta* Bulanova-Zachvatkina, 1965; *Metabelba monilipeda* Bulanova-Zachvatkina, 1965; *Metabelba pseudoitalica* Bulanova-Zachvatkina, 1965; *Metabelba paraitalica* Kulijev, 1967, *Metabelba machadoi* Pérez-Iñigo 1986 and *Metabelba* **n. sp**. 1

Species incertae sedis: *Damaeus propinquus* Sellnick, 1943; *Metabelba benoiti* Balogh, 1958, *Metabelba angolensis* Balogh, 1958; *Metabelba heteropoda* Balogh, 1958; *Metabelba horrida* Balogh, 1958; *Metabelba tanganyikensis* Balogh, 1958

Remarks

The above species lists are based partly on Subías (2004, 2008, 2009), who listed 30 named species of *Metabelba*, including six species marked as "*species inquirenda"*. However, some of the synonymies that he proposed (without explanation) need to be substantiated. Also, the concept of the genus differs according to author (see chapter 2.1), so several previously included species are not members of *Metabelba* in its current sense. This is the case of *Oribata montanus* Kulczynski, 1902, which was considered by several authors (van der Hammen & Strenzke 1953; Sellnick 1960; Kunst 1961; Mihelčič 1964) to be a member of *Metabelba* due to the presence of companion setae *d* on tibiae II and III. However, it has a different setation of trochantera (1-1-2-1) and femora (7-6-4-4) and Miko (2006) recently included this species in *Caenobelba* Norton, 1979d.

Metabelba craigheadi Jacot, 1939 apparently does not belong to the genus as it was recombined to *Epidamaeus* by Marshall et al. (1987). The transfer was based on the study of the type specimen and numerous freshly collected specimens (R. A. Norton, pers. comm. 2010). Moreover, already Jacot (1939) stated in the original description of *M. craigheadi* the presence of spinae adnatae and figured only one seta on trochanter IV and four setae on femur IV, which is not consistent with the diagnosis of *Metabelba*.

The taxonomic position of several other species remained uncertain untill now. Sellnick (1943) described two species of Damaeidae from Central Italy (Romagna): *Damaeus propinquus* and *D.* romandiolae. The original descriptions are unfortunately brief, lack figures, and do not include details on the leg setation, which are important diagnostic characters on the genus level. Hammen and Strenzke (1953) suggested that both species probably belong to *Metabelba*. Bernini (1982) also considered *romandiolae* to be a member of *Metabelba*, but did not offer a redescription. These opinions seem to have been accepted by Subías (2004, 2008), who included *propinquus* in *Metabelba* s. stricto and *romandiolae* in *Metabelba* (*Parametabelba*), whereas Subías (2009) listed the former species as *Metabelba (Metabelba) propinqua "species inquirenda"*. We confirm that *romandiolae* has indeed characters of *Metabelba* transfer to *Metabelba* **(n subg. 1)**, which is substantiated with the detailed redescription presented below. *Damaeus propinquus* has small body size, spinae adnatae are absent, and apophysis *P* is present, which is consistent with membership in *Metabelba* s. stricto. Unfortunately, the original description contains no information on the leg setation; therefore we consider *D. propinquus* being a *species incertae sedis*, until it is thoroughly revised.

Balogh (1958) described five species of *Metabelba* from tropical Africa, but the descriptions are insufficient and lack figures. In one of these, *Metabelba benoiti* Balogh, 1958, the propodosoma is angular between legs I and II, so it might belong to *Metabelba* s. stricto. In the remaining four species—*Metabelba angolensis* Balogh, 1958; *Metabelba heteropoda* Balogh, 1958; *Metabelba horrida* Balogh, 1958 and *Metabelba tanganyikensis* Balogh, 1958—the propodosoma is rounded between legs I and II, so might belong to *Metabelba* (**n subg**.**1**). Unfortunately, Balogh (1958) provided no information on the leg setation. Therefore, it is not possible to confirm if the species really belong to *Metabelba* in its modern sense, so we consider them to be *species incertae sedis* (see also Subías 2004, 2008, who classified them as "*species inquirenda*").

Metabelba pulverosa Strenzke 1953 has been considered by some authors (Bulanova-Zachvatkina 1965, 1975; Subías 2004, 2008, 2009) as a junior synonym of "*Metabelba pulverulenta"* (C. L. Koch, 1839), which was originally described as *Nothrus pulverulentus*. However, Hammen and Strenzke (1953) documented, referring to Oudemans (1937) who reproduced Koch's description and figures, that the identity of *M. pulverosa* and "*M. pulverulenta*" can be rejected, since the form described by Koch lacks propodolateral apophysis and notogastral setae are inserted more laterad than in *M. pulverosa*. They supported the hypothesis of Grandjean (1936) that *Nothrus pulverulentus* C. L. Koch, 1839 is in fact a member of *Porobelba* Grandjean, 1936, possibly a senior synonym of *P. spinosa* (Sellnick, 1920). We therefore consider *M. pulverosa* Strenzke 1953 as a valid species. For further details on this synonymy see Hammen and Strenzke (1953) and Miko (2006).

Subías (2009) transferred *Belba limasetosa* Bulanova-Zachvatkina, 1962 to *Metabelba* s. stricto. In our view, this recombination is unjustified, because Bulanova-Zachvatkina (1962, 1975) figured tibia IV of this species with seta *d* present, whereas in *Metabelba* seta *d* is absent from tibia IV. *Metabelba filippovi* Bulanova-Zachvatkina, 1965; *M. flagelliseta* Bulanova-Zachvatkina, 1965; *M. monilipeda* Bulanova-Zachvatkina, 1965; *M. pseudoitalica* Bulanova-Zachvatkina, 1965 and *M. paraitalica* Kulijev, 1967 all lack apophysis *P*., so were misplaced in *Metabelba* s. stricto by Subías (2004; 2008) but were recombined to *Metabelba* (*Parametabelba*) by Subías (2009). In contrast, *M. rohdendorfi* Bulanova-Zachvatkina, 1965 and *M. rara* Bulanova-Zachvatkina, 1965 have apophysis *P* well developed and thus belong to *Metabelba* s. stricto.

Subías (2009) synonymised *M. paraitalica* with *M. pseudoitalica*, the latter name having priority, but gave no reasons. According to original descriptions, the species are similar, but *M. paraitalica* differs in having flagellate notogastral seta *ps1*, apophysis *Sa* being shorter than *Sp* and the propodosoma being comparatively long and narrow (cf. Bulanova-Zachvatkina 1965 and Kulijev 1967). Therefore, we consider *M. paraitalica* as a separate species, until the type material is studied in detail.

Metabelba orientalis Balogh et Mahunka, 1967, described from Vietnam and *M. glabriseta* Mahunka, 1982, described from Ethiopia, also lack apophysis *P*, but the authors provideed no information on the leg setation. Therefore their generic position is unclear and we consider them to be **species incertae sedis**, until the type material is revised. *Metabelba flagellata* Balogh et Mahunka, 1969, described from Bolivia, was redescribed and recombined to *Epidamaeus (Akrodamaeus) flagellatus* by Norton (1979c).

Dasybelba aphelesa Woolley et Higgins, 1979, described from Colorado (USA), was considered as member of *Metabelba* s. stricto by Subías (2004, 2008). According to the characters presented in the text and figures of the original description, the species definitely does not belong to *Metabelba*. *Dasybelba* Woolley et Higgins, 1979 is probably not monophyletic, and its relations with other damaeid genera are uncertain and need further study (R. A. Norton, pers comm. 2009).

In chapter 5 we present a tentative determination key for the species of *Metabelba* (**n. subg. 1)** known from Palaearctic region and Canary Islands, which is based on literature survey and detailed study of available species. Species incertae sedis are not included in the key.

4. Description of species

4.1 *Metabelba* n. sp. 1

Synonymy. unknown.

Diagnosis (adult). Propodolateral apophysis (*P*) on prodorsum absent. Posterior centrodorsal tubercle (*Dp*) and lateral tubercle (*La*) on prodorsum absent, but cuticle slightly thickened and elevated at normal location of anterior centrodorsal tubercle (*Da*). Anterior postbothridial tubercle (*Ba*) strong, conical, oblique, directed posterolaterad, posterior postbothridial tubercle (*Bp*) weakly developed as low rounded protuberance, directed anterolaterad. Parastigmatic apophyses (*Sa*, *Sp*) developed as blunt conical tubercles, not visible in dorsal view. Sensillus (*ss*) very long, thin, smooth flagellate. Bothridial funnel of irregular shape with lateral slit. Interlamellar seta (*in*) comparatively short (slightly longer than half of mutual distance *in-in*), strong, erect, directed posterodorsad. Notogaster eccentrically conical in lateral view with the highest point shifted posteriad, often bearing remains of gastronotic exuviae with mass of adherent dirt. Notogastral setae *c1 - h1* thin, shorter than half of their mutual distances, not reaching insertions of the next setal pair, irregularly curved, with short barbs ("serrate") on outer curvatures. Notogaster of adult with long cornicle (*k*), slightly bent posteriad. Epimere III with an additional seta 3d inserted lateral from apophysis *Sp*, epimeral setal formula 3-1-4-4. Cerotegument sculpture formed from irregular excrescences (auricular, rugged, or stellate), covered with microgranula, filamentous excrescences absent.

Type material examined
Holotype (female) and 30 paratypes: **Czech Republic**, central Bohemia, the Medník National reserve, northwestern slope of the Medník hill, 49°52' 26"N; 14°26' 44" E, about 280 m a. s. l., old beech (*Fagus sylvatica*) forest with young hornbeam (*Carpinus betulus*) in the understory, mixed leaf litter, 21 specimens, 25. 11. 2004, leg. Jan Mourek; the same locality and habitat, 10 specimens 25. 3. 2007 leg. Zdeněk Janovský; all specimens unmounted, preserved in 80% ethanol or pure glycerine.

The type series will be deposited in the followint collections: The holotype and 5 paratypes in the Acarological Collections of Senckenberg Museum für Naturkunde Görlitz (Germany), 5 paratypes in the collections of National Museum of Natural History Naturalis, Leiden (Netherlands); 5 paratypes in Arachnological Collections in zoological department of the National Museum in Prague (Czech Republic). 8 paratypes in the collection of J. Mourek, Dept. of Zoology, Faculty of Science, Charles University Prague (Czech Republic); 5 paratypes in private collection of L. Miko; 2 paratypes in collection of F. Bernini, Department of Evolutionary Biology, University of Siena (Italy).

Further material examined (not included in the type series)
Czech Republic, central Bohemia, east from the Davle town, valley of the last left tributary of the Záhořanský brook near the confluence, 49°53'50"N, 14°25'25"E, about 260 m a. s. l., western slope deciduous forest on scree with predominant hornbeam (*Carpinus betulus*) and interspersed oak (*Quercus* sp.) and lime *(Tilia* sp.) , mixed litter and upper soil layers, 1 specimen, 25. 11. 2004 leg. J. Mourek. Deposited in collection of J. Mourek, Dept. of Zoology, Faculty of Science, Charles University Prague (Czech Republic).

Poland, Upper Silesia, Beskid Zywiecki Mountains, "Pod Rysianka" Reserve, 49°31'N, 19°11'E: 1 specimen *Luzulo nemorosa-Fagetum* (beech forest): 1000 m a. s. l., 27.09 1986, leg. Piotr Skubała. Deposited in private collection of L. Miko.

Collection of Franz Mihelčič, Tiroler Landesmuseum Ferdinandeum, Innsbruck: Slide **MIH 1-70**, labelled "Belba" (originally labelled as "Metabelba montana Kulcz.", but the words were stricken) and "*M. pulverosa* Strenzke", Bozen 10, Südtirol, Italy, September 1958. The slide contains 2 badly preserved specimens of *Metabelba* **n.sp. 1** and 1 specimen of another species of *Metabelba* s. stricto, which could not be identified due to its very bad condition. Slide **MIH 4-38**, labelled "*Oppia concolor*, *Porobelba spinosa*, *Belba* sp.", Bozen 10, Südtirol, Italy, September 1958. The slide contains 3 badly preserved specimens of. *Metabelba* **n.sp.1**, 2 specimens of other damaeid mites, which could not be identified due to their very bad condition, and 1 specimen of an oppiid mite. The locality is difficult to read on both slides, but it can be obtained from the catalogue of the collection (Totschnik, 2001).

Description (adult) Figs. 1-8.

Dimensions. Ventral length 517-533 (527) μm; maximal notogastral width 317-328 (323) μm; n = 5. See Table 1 for detailed measurements of legs and other details.

Integument. Colour yellowish brown to medium brown. Most of body covered by thick cerotegument having unusual microsculpture without filamentous excrescences, details visible with SEM only (Fig. 6D, 7CD, 8ACD); microsculpture often partly abraded or covered with adherent dirt (Fig. 8B). Cerotegument excrescenses usually more distinct on prominant parts (apophyses, ridges etc.). On prodorsum, parastigmatic apophyses, around leg acetabula and on legs. cerotegument roughened, with excrescences having shape of irregular ridges (auricular, rugged, or stellate) and densely microgranulate (Figs. 6CD, 8ACD). On notogaster, cerotegument very thin (or even partly absent), microgranulate with loosely scattered globular or lenticular excrescences (Fig. 7CD). Underlying cuticle microtuberculate on prodorsum and apophyses (Fig. 6D) and more or less smooth on venter, notogaster (Fig. 7) and legs. Notogaster often bearing large mass of amorphous foreign material fixed to remains of gastronotic exuviae (Fig 6B).

Prodorsum. Prodorsum of roughly triangular shape, relatively narrow. Rostrum with weakly developed nose-like protuberance visible in dorsal view (Fig 1A, 6A) and with one or two weakly defined transverse eleveated lines connecting insertions of rostral (*ro*) setae. Apophysis *P* absent. Posterior centrodorsal tubercle (*Dp*) and lateral tubercle (*La*) on prodorsum absent, but cuticle slightly thickened and elevated at normal location of anterior centrodorsal tubercle (*Da*). Anterior postbothridial tubercle (*Ba*) strong, conical, oblique, directed posterolaterad, posterior postbothridial tubercle (*Bp*) weakly developed as low rounded protuberance, directed anterolaterad (Fig. 1A, 3B). Parastigmatic apophyses (*Sa*, *Sp*) developed as blunt conical tubercles of almost equal size, not visible in dorsal view; *Sa* directed posterolaterad, *Sp* directed anterolaterad.

Lateral part of prodorsum, above acetabula I, with distinct elevated ridge (Fig. 1A, 3B, 6CD) terminating in minute anterolateral apophysis (*ALa*) directed posteriad; latter opposed by minute apophysis (*ALp*) positioned on anterior base of bothridium. Apophysis *ALp* confluent with another weakly defined, short longitudinal elevations at anterior margin of bothridium, directed anteromediad and gradually effacing (Fig. 1, 3B).

Rostral (*ro*) and lamelar (*le*) setae strong, barbed with minute spinuli on outer curvature, both curved inwards in dorsal view; *ro* distinctly longer than *le*, overreaching tip of rostrum. Interlamellar seta (*in*) arising on minute apophysis, comparatively short,

slightly longer than half of mutual distance *in-in*, strong, straight and erect, roughed with indistinct spinuli in distal part. Exobothridial seta (*ex*) thin and smooth (but covered with amorphous cerotegument), directed anteriad (Fig. 3B, 6D), hidden under bothridium in dorsal view. Sensillus (*ss*) smooth, thin, long, flagellate, often covered with fine microgranulate cerotegument in proximal half (Fig. 6D). Bothridial funnel of unusual irregular shape (Fig. 1B, 6 CD), posterior wall less arched than anterior one, distinct transverse fold formed in dorsomedial part and transverse slit formed in lateral part.

Pair of distinct fields of concentrated sigillae (muscle insertions) present between acetabula I; unpaired medial field of sigillae located slightly behind line connecting bothridia; pair of small sigillar fields located posteromediad from insertions of *in* (slightly anteriad from paired cuticular thickening resembling *Da*).

Notogaster. Notogaster slightly ovate or "pyriform" in dorsal view; distinctly eccentrically conical, slightly “pyramidal”, in lateral view, with maximum height posterior to center. Cornicle (*k*) present medially at level of setae *lm-lp*; shape slightly variable (Fig. 3C), about 50 μm long and bent posterodorsad to variable degree (Fig. 1A, 3AC, 7ACD), sometimes with doubled tip (7C). Notogastral setae *c1* to *h1* thin, short (none reaching insertion of next seta), twisted, unilaterally serrate with minute spinuli. Setae *c1* and *c2* directed anteriad, direction of setae from *la* to *h1* varies. Setae *ps1-3* very short and spiniform, almost straight, directed posteriad.

Circumgastric row of muscle sigillae (insertions of dorsoventral muscles) distinct, interrupted anteriorly between setae *c1* and behind setae *c2*. Pair of minute light spots present slightly medial to insertions of setae *la* (Fig. 1A).

Gnathosoma. Subcapitulum (Fig. 2A) in type and form typical of family, with three pairs of setae, all with few minute barbs and with two pairs of setiform processes (*or1,2*). Seta *h* distinctly shorter than *a* and *m*. Setal formula of pedipalp (from trochanter to tarsus, solenidion in parenthesis): 0-2-1-3-8(1), (Fig. 2B). Chelicera in shape and relative size typical of family, cheliceral seta *cha* with row of short barbs on outer (dorsal) curvature, seta *chb* in distal third with short barbs diminishing towards tip (Fig. 2C).

Epimeral region. Fig. 2A, D. Propodoventral(*E2a*, *E2p*) and ventrosejugal (*Va*, *Vp*) tubercles absent (Fig. 2A). Apodemes I dark in transmitted light, short, not touching medially. Apodeme 2 weakly developed, ventrosejugal furrow well developed only laterally. Epimere III with 4 setae, *3d* inserted lateral from apophysis *Sp* (Fig. 2D). Epimeral setal formula (from I to IV): 3-1-4-4. Epimeral setae inserted mostly on minute tubercles; setae *1a*, *1b* and *2a* short, straight, remainder distinctly longer, some of them with minute barbs.

Anogenital region. Fig. 2A. Discidium (*di)* weakly developed as rounded protuberance. Setal formulae of anogenital region normal for Damaeidae (Grandjean 1960; Norton 1977b); genital *g*: 6; aggenital *ag*: 1; anal *an*: 2; adanal *ad*: 3. Seta *g1* about twice longer than remaining genital setae, with slightly broadened base (Fig. 2E). Lyrifissure *iad* oblique, divergent posteriad.

Legs. Fig. 4, 5. Legs monodactylous, moderately long, segments with distinctly swollen distal parts (moniliform); leg IV slightly longer than body, legs I and III as long as body, leg II shorter than body (details in Table 1). Leg setae shorter than their respective leg segments, thick, most roughened with minute spines on outer curvature. Leg setal formulas typical of genus, identical with that of *Metabelba pulverosa* Strenzke, 1953 (see Norton 1977), as follows (from trochanter to tarsus, famulus included, solenidia in parentheses): leg I: 1-10-4(1)-4(2)-20(2), leg II: 1-10-4(1)-5(1)-17(2), leg III: 4-9-4(1)-5(1)-17(0), leg IV: 3-9-4(0)-4(1)-14(0). Solenidia on tibiae I and

IV free, those on tibiae II and III and on genua I, II and III coupled with companion seta *d*. Solenidion ω1 on tarsus I, φ1 tibia I, ω1,2 on tarsus II and φ on tibia IV long, tactile; φ1 on tibia I more than 4.5x longer than φ2; φ on tibia IV shorter than tibia itself. Solenidia of tibiae II and III and genua I, II and III short, of about equal in length to respective seta *d*.

Ontogeny. Unknown.

Geographical distribution and ecology

Metabelba **n. sp. 1** is hitherto known from two localities in Central Bohemia (Czech Republic), one locality in Upper Silesia (Poland) and one locality in South Tyrol (Italy), but might be widely distributed in forests of Central Europe. The habitats of the specimens in the collection of Mihelčič are unknown (Totschnig 2001). The findings from Central Bohemia are from broad-leaved deciduous forests on slopes in the altitude 260 and 280 m a. s. l. Skubała (unpubl.) collected this species in mountaine beech forests (*Luzulo nemorosa-Fagetum*), mixed spruce-fir forests (*Abieti-Piceetum montanum*) and spruce forests (*Plagiothecio-Piceetum tatricum*) in the altutude 1000 - 1170 m a. s. l. It therefore seems that the species inhabits a wide range of forest types in different altitudes.

Remarks

Metabelba **n. sp. 1** is unusual in several respects, when compared to other known species of the genus. These include the presence of cornicle *k* in the adult, very short and irregularly curved notogastral setae, the irregularily shaped funnel of bothridium, notogaster with conical shape, gastronotic exuviae covered with a compact mass of fine soil particles and organic debris, the presence of four setae on epimere III, anterolateral tubercles on the prodorsum (*ALa, ALp*) and a cerotegument that lacks filamentous excrescences. Postbothridial tubercles (*Ba, Bp*) are to our knowledge absent from other species of *Metabelba* (**n. subg.1**), but are present in some species of *Metabelba* sensu stricto. Below, we comment on each of these characters individually.

1. To our knowledge, *M.* **n. sp.** 1 is the first known species of *Metabelba* with cornicle *k* retained in the adult; this represents only the third published case within Damaeidae. This character was first observed in *Nortonbelba plesiomorphica* (Saloña et Iturrondobeitia, 1989) from Spain, originally described as a member of *Epidamaeus*. In adults of this species, the cornicle is very long, pointed and only slightly curved. The second known damaeid with cornicle *k* in adults is the Japanese species *Belba unicornis* Enami, 1994, which is closely related to *B. corynopus* Hermann, 1804 and *B. bartosi* Winkler, 1955. The cornicle in adults of *B. unicornis* has a shape and relative size similar to that of *Metabelba* **n.sp. 1** The taxonomically and geographically scattered and isolated occurrence of cornicle *k* in damaeid adults indicates that it appeared independently at least three times within Damaeidae. In all three cases the character seems to be stable within each species. This retention may be interpreted as a paedomorphic feature, in which a character that is ancestrally present only in immatures evolves to persist in adults (Norton pers. comm.). Cornicle *k* is normally present on the gastronotic region in all nymphal stages of all Damaeidae and serves for attachment of gastronotic exuviae ("scalps") from previous instars (see Grandjean 1960). The deutonymph of *Epidamaeus ibericus* Moraza, Moreno et Saloña, 1990 was described and illustrated without a cornicle, (see Fig. 8 in Moraza et al. 1990), but the presence of this cornicle was confirmed by M. L. Moraza (2009 pers comm.), who kindly re-examined the original specimens. While this cornicle is always present in nymphal

stages of Damaeidae, it is present in the larvae of only one, *Porobelba spinosa* (Sellnick, 1920) (Ermilov and Łochyńska 2009).

Another case of paedomorphosis in Damaeidae may be the accidental presence of a setiform process on the spina adnata in some adults of *Epidamaeus tenuissimus* Hammer (1967), *E. tritylos* Behan-Pelletier and Norton (1985) and *Kunstidamaeus lengersdorfi* (Willmann, 1932), which might be an atavistic reappearance of notogastral seta *c3* (see Behan-Pelletier & Norton 1985; Miko &Mourek 2008), otherwise absent from damaeid adults.

2. Most species of *Metabelba* (**n. subg. 1**) have more or less straight notogastral setae, arranged in a radial pattern, which are usually longer than the distance of insertions between two succeeding setae. By contrast, *M. platynotus* has very short notogastral setae, that are erect and spiniform; *M. flagelliseta* has irregularly curved (S-shaped) setae, but they are much longer than those of *Metabelba* **n. sp. 1** and their insertions are distributed in a different pattern.

3. To our knowledge, *Metabelba platynotus* Grandjean 1954 is the only further species of the genus having conical shape of notogaster with flattened anterior part. This form of notogaster is otherwise typical for several species of *Belba* sensu stricto (*corynopus* species group sensu Norton 1979b), namely *B. corynopus* (Hermann, 1804), *B. bartosi* Winkler, 1955 and *B. unicornis* Enami, 1994. Similar shape of notogaster is found in *Belba aegrota* (Kulczynski, 1902), which has an uncertain generic position, as we discuss below.

4. To our knowledge *Metabelba* **n. sp. 1** is the only named *Metabelba* species bearing a compact mass of dirt on notogaster. This character is otherwise present in particular species of several damaeid genera (Norton 1979d, Mourek unpubl.), e.g. *Belba corynopus*, *B. bartosi*, *B. rossica* Bulanova - Zachvatkina, 1962, *Belba (Protobelba) californica* (Banks, 1904), *Caenobelba alleganiensis* Norton, 1979d and *Damaeus crispatus* (Kulczynski, 1902). In *Damaeus (Adamaeus) onustus*, usually the nymphs carry the mass of debris, but sometimes it is present also in adults (J. Mourek, unpublished). It seems to be a case of convergence, which is probably supported by the general tendency of damaeid immatures to attach foreign particles to the gastronotic exuviae as a kind of camouflage against predators (Luxton 1981).

5. *Metabelba* **n. sp. 1** is unusual within the genus in having four pairs of setae on epimere III. The additional seta, *3d*, is inserted on the lateral margin of the coxisternum, lateral to apophysis *Sp*. Epimeral setal formulas have been published only for part of the named species of *Metabelba*. Most of them have the formula 3-1-3-4 (see also Hammen & Strenzke 1953; Mihelčič 1963, Kunst 1957, 1961; Moritz 1966; Kulijev 1967; Pérez-Iñigo 1986), which is normal for Damaeidae. We observed intraspecific variation of epimeral setal formula in *M. romandiolae*, one of the studied specimens had four pairs of setae on epimere III as *Metabelba* **n. sp. 1** (see below, chapter 4.2 and Fig. 9B), but the remaining had the usual three pairs. The epimeral formula in *M. platynotus* is not quite clear. From Fig 1B in Grandjean (1954) it seems that the normal formula in this species is 3-1-2-4. The author did not give the formula in text, but it seems that he incorrectly treated seta 4b as if it belonged to epimere III (the formula would then be 3-1-3-3). He also noted interspecific variation; some specimens having one additional seta on epimere III and in some others one seta on epimere IV is missing. Epimeres I and II are neotrichous in several other damaeid genera, including *Nortonbelba* Bernini, 1980, which has the formula 5-4-3-4 (see also Perez-Iñigo, 1997), and some species of *Belba* (see Travé, 1978), e.g. *Belba unicornis* Enami, 1994 with the formula 4-4-3-4. *Hungarobelba* Balogh, 1943, which has been transfered from Damaeidae to

Hungarobelbidae (Miko and Travé 1996), also has epimeral neotrichy with the formula 4-3(or 2)-3-4.

6. *Metabelba* **n. sp. 1** has two pairs of minute tubercles positioned on the dorsolateral region of the propodosoma, between acetabulum I and the bothridium. We designate them the anterolateral enantiophysis, with tubercles *ALa* and *ALp*. Bayartogtokh and Norton (2007) described a structure similar and probably homologous to *ALa* in several species of the *Dyobelba tectopediosa* species-group and designated it "*lt*" (lateral tooth), but the posterior pair of apophysis was absent. They considered "*lt*" (our *ALa*) to be a part of acetabular tectum I.

7. Detailed information on the microsculpture of the cerotegument is available for only some species of *Metabelba*, but that of *Mwtabelba* **n. sp. 1** seems to be unique within the genus. Most of the species have filamentous cerotegument excrescences. In *M. platynotus* the excrescences are short, columnar (Grandjean, 1954). In *M. propexa* (Kulczynski, 1902), a member of *Metabelba* s. stricto, the excrescences are granular on most of the body and leg surface and short, columnar in the sejugal area (Mourek, unpubl.).

9. *Metabelba* **n. sp. 1** has a general habitus similar to that of *Belba aegrota* (Kulczynski, 1902), originally described as *Oribata aegrotus*, which was described from the vicinity of Cracow, Poland. This poorly known species was redescribed by Willmann (1954) as *Belba aegrota* from a cave in Moravian karst (Moravia, Czech Republic). Most of later authors accepted the recombination of this species to *Belba* (see Miko, 2006 for complete references), although Willmann (1954) did not distinguish damaeid genera in the modern sense and used the name *Belba* for all Damaeidae. Kulczynski (1902) did not figure the legs of the species, but Willmann (1954) depicted leg IV with a free solenidion, not coupled with seta *d*. This indicated, that the species might not belong to to *Belba* in the modern sense (i.e., the sense of Grandjean 1936). Unfortunately, he apparently depicted the setation of leg I and IV incompletely, so that the generic placement of his *B. aegrota* remains uncertain until the original material is studied in detail. This, however, will be complicated by the very bad condition of the mounted specimens (see below). Sellnick (1960) transfered the species in *Damaeus*, a genus with setae *d* absent from all tibiae (with tibial solenidia free). For the present we consider *Belba aegrota* to be a *species incertae sedis*.

The similarities of *B. aegrota* and *Metabelba* **n. sp. 1** include the following: the prodorsum lacks distinct tubercles; apophysis *Sa* is strongly developed, directed posterodorsad; *Sp* is weakly developed and rounded; the notogaster is slightly ovoid in dorsal view and slightly conical in lateral view, with the highest point shifted posteriad; notogastral setae are short and weak, irregularly curved. In the figure of Kulczynski (1902) all notogastral setae are directed posteriad or posterolaterad, whereas in that of Willmann (1954) *c1* and *c2* are directed anteriad as in *Metabelba* **n. sp**. 1 Also the relative length and shapes of leg segments are similar in both species and solenidion on tibia IV is comparatively short (see fig. 16 in Willmann 1954). In contrast, *Metabelba* **n. sp**. **1** differs from *B. aegrota* mainly by the presence of cornicle *k* in the adult and by the unique shape of bothridium. A detailed study of *B. aegrota* is unfortunately not possible for the moment, since the type collection of Kulczynski is presumably lost (D. Krivoluckij, pers. comm.) and the material of *B. aegrota* in the collection of C. Willmann was not found (S. Friedrich, pers. comm. 2010).

4.2 *Metabelba romandiolae* (Sellnick, 1943)

Synonymy. *Damaeus romandiolae* Sellnick, 1943. *Metabelba gladiator* Mihelčič, 1963. *Metabelba romandiolae*: Bernini (1982); Bernini et al. (1987); Bernini et al. (1996)

Diagnosis. Propodolateral apophysis *P* absent. Single pair of anterior centrodorsal tubercles (*Da*) present on prodorsum posteromedial from insertions of interlamellar setae; posterior centrodorsal (*Dp*) postbothridial (*Ba*, *Bp*) and lateral (*La*) tubercles absent. Parastigmatic apophyses (*Sa*, *Sp*) slender, spiniform, with convergent tips. Sensillus (*ss*) very long, thin, flagellate, with minute barbs in middle part, basal part and flagellate tip smooth. Interlamellar seta (*in*) longer than ½ sensillus length, thin, attenuate, covered with minute barbs. Notogastral setae *c1-h3* longer than mutual distances between insertions of both respective setae in pairs; strong, erect, directed in radial pattern; darkly pigmented with hyaline bases and faintly serrate tips. Leg setae, except on distal parts of tarsi, of unique shape: broadly flattened basally with long attenuate tip, sparsely covered with minute spines. Leg setal formulas normal for *Metabelba*. Discidium spiniform, curved posterolaterad, well developed. Cerotegument with long filamentous excrescences.

Type material examined

Collection of Pietro Zangheri, Museo Civico di Storia Naturale, Verona: slide n. 17897 (box 42) containing two specimens, labelled as "*Oribata Romandiolae* Selln. n. sp.". The localization is "Poggio Orticai terr.[*iccio di*] faggete, 5.V.1929, racc. Zangheri, det. Sellnick". The dorsally placed specimen, even if crushed (Fig. 11A), is complete and, according to Bernini (1982) has been stated as the ***neotypus***, while the second ventrally placed, but completely embedded in cerotegument and in a dirty medium, was utilized only for measurements. The two specimens are prepared by Zangheri and embedded "in Faure Andrè , Nov. 1946" as registered in a separate label on the slide. Presumably, the other two specimens of the type series mentioned by Sellnick (1943) in original description, were destroyed by the fire of the Sellnick's house in Königsberg (now Kaliningrad, Russia) during the World War II (Bernini, 1982; H. Dastych, 2009 - pers. comm.). The Sellnick's collection in the *Zoologisches Institut und Zoologisches Museum Universität Hamburg* contains only the material collected after 1950.

Collection of Franz Mihelčič, Tiroler Landesmuseum Ferdinandeum, Innsbruck: Slide MIH 1-42 with the type specimen, labelled as " *Metabalba gladiator* n. sp. Mih. Type". The locality is hardly legible; according to Totschnig (2001) it is "St. Veit, Jauntal, Kärnten, A, Boden, Moos, trocken Juli 1962." The specimen is crushed (see Fig. 9), but complete. It is embedded probably in a medium based on gum arabic and mounted between two cover slides, which are attached to a piece of pasteboard with central hole. The remaining three specimens mentioned in the original description were not found in the collection.

Further material examined

Collection of Fabio Bernini, Department of Evolutionary Biology, Siena: six specimens (two of which given to the Collection of J. Mourek, Dept. of Zoology, Faculty of Science, Charles University Prague, Czech Republic) labelled as *Metabelba romandiolae* and collected by the colleague Prof. R. Dallai in the forest of *Picea abies* near the village of S. Benedetto in Alpe, about 900 m a.s.l., 10 km from the *locus typicus*, Poggio Orticai, Tosco-Emiliano Apennine.

Collection of Carl Wilmann, Zoologische Staatssammlung München: slide labelled as "*Belba setiger* Kulcz./Abs. Det C. Willmann", 1 specimen (sex unknown), locality and date of collection not given.

Redescription (adult). Figs. 9-16.

Dimensions. The crushed ***neotype*** from Zangheri's collection (Fig 11AB) could not be measured accurately, then we have measured the second specimen present in the same slide placed ventrally: total length about 640 μm and notogastral width 420 μm. Similarily the ***type*** specimen of *Metabelba gladiator* from Mihelčič's collection (Figs. 10B, 12 - 16) is crushed, ventral length approximately 585 μm. Specimen from Willmann's collection labelled as "*Belba setiger*" (Fig. 11CDE): ventral length measured in dorsal view 584 μm, maximum notogastral width 408 μm. In the original description of *M. gladiator* by Mihelčič (1963) the body length ranged from 680 to 720 μm (mean calculated by us 708 μm) and the maximum notogastral width 410 - 430 μm (mean calculated by us 421 μm); n = 4. Ventral length of specimens of *M. romandiolae* from S. Benedetto in Alpe was 568-576 (572) μm, maximum notogastral width 408-440 (424) μm; n = 2. Detailed measurements of legs in Table 1.

Integument. Body colour medium brown. Cerotegument with long "wool-like" filamentous excrescences (Fig. 11E, 16AB); excrescences shorter on legs, longer in sejugal area, on epimeres and around notogastral setae. Underlying cuticle mostly smooth, but faintly granular on apophyses. Gastronotic exuviae (scalps) not present in the studied specimens and not noted in original descriptions (Sellnick, 1943; Mihelčič, 1963).

Prodorsum. Figs. 9A, 12A. Prodorsum of roughly triangular shape. Apophysis *P* absent. Anterior centrodorsal tubercle (*Da*) present, posterior centrodorsal tubercle (*Dp*) absent, but cuticle slightly thickened in normal position of *Dp*; postbothridial (*Ba*, *Bp*) and lateral (*La*) apophyses absent. Parastigmatic apophyses (*Sa*, *Sp*) slender, spiniform, with convergent tips. Rostral (*ro*) and lamellar (*le*) setae thin long, of approximately equal length, strognly curved inwards. Seta *ro* thin, almost hyaline, with few minute barbs on outer curvature. Seta *le* thicker and darker than *ro*, with dense short barbs on outer curvature. Interlamellar seta (*in*) arising on minute apophysis, comparatively long, slightly longer than half of the sensilus length, dark, densely covered with short barbs, flagellate. Exobothridial seta (*ex*) comparatively long, thin, covered with short barbs on outer curvature (Fig. 10A, 12B). Sensillus (*ss*) long, thin, flagellate; covered with short barbs in middle 1/3, basal part and flagellate tip smooth. Bothridial funnel of regular shape, normal for family.

Notogaster. Figs. 9A, 10AB. Notogaster of roughly circular outline in dorsal view. Notogastral setae of series *c1-c2*, *la-lp* and *h1-h3* longer than mutual distances whithin respective setal pairs, strong, erect, directed in radial pattern. Setae darkly pigmented with hyaline bases and faintly serrate tips, the "teeth" directed backwards (Fig. 10B). Seta *c1* shorter than *c2-h3*. Setae *ps1-ps3* comparatively long, thin, with row of short barbs on outer curvature, *ps1* > *ps2* > *ps3*, seta ps1 very long with attenuate fragile tip (Fig. 10AB), projecting distinctly more posteriad than seta *h1*.

Gnathosoma. Fig 9B, 13A. Subcapitulum normal for family: diarthric, with three pairs of thin and comparatively long setae (*m* > *h* > *a*) and two pairs of setiform processes (*or1,2*). Setation of chelicera not discernable, setal formula of pedipalp (from trochanter to tarsus, solenidion in parenthesis): 0-2-1-3-8(1).

Epimeral region. Fig. 9B, 13A. Propodoventral (*E2a, E2p*) and ventrosejugal (*Va, Vp*) enantiophyses absent. Apodeme I well developed in lateral parts and weakly defined in medial part, apodemes 2 confluent, ventrosejugal furrow complete. Epimeral setal formula (I to IV): 3-1-3-4, normal for *Metabelba*, rarely 3-1-4-4 (Fig. 9B). Epimeral setae comparatively long, smooth or with several minute indistinct barbs. All epimeral setae at least slightly flattened and broadened with long attenuate tips), similar to leg setae; broadening especially well developed in setae *3a,b,c* and *4b,c,d* (Fig. 13B).

Anogenital region. Fig. 9B, 13A. Discidium (*di*) spiniform, well developed, curved posterolaterad. Setal formulas of anogenital region normal for the Damaeidae (Grandjean 1960; Norton 1977b); genital *g*: 6; aggenital *ag*: 1; anal *an*: 2; adanal *ad*: 3; all setae slightly flattened and broadened. Lyrifissure *iad* oblique, divergent posteriad.

Legs. Figs. 14, 15. Legs monodactylous, moderately long, segments distinctly swollen in distal part (moniliform). Leg IV distinctly longer than body, leg I and III approximately as long as body, leg II slightly shorter than body (detailed measurements of leg segments in Table 1). Leg setae, except those on distal parts of tarsi, of unique conspicuous shape: broadly flattened in basal part, with long attenuate tip, sparsely covered with minute spines on outer surface. Leg setal formulas identical with those of *Metabelba pulverosa* Strenzke, 1953 (see Norton 1977), as follows (from trochanter to tarsus, famulus included, solenidia in parentheses): leg I: 1-10-4(1)-4(2)-20(2), leg II: 1-10-4(1)-5(1)-17(2), leg III: 4-9-4(1)-5(1)-17(0), leg IV: 3-9-4(0)-4(1)-14(0). Solenidia on tibiae I and IV free, those on tibiae II and III and on genua I, II and III coupled with companion seta *d*. Solenidia ω1,2 on tarsus I, φ1 on tibia I, ω1,2 on tarsus II and φ on tibia IV long, tactile; φ1 on tibia I about 3x longer than φ2; φ on tibia IV more than 2x longer than tibia itself. Solenidia of tibiae II and III and genua I, II and III of approximately same length as their respective setae *d*.

The two specimens from Zangheri' collection present variations in the leg setation: in ***neotypus*** femur I with 9 setae on the right and 10 on the left; genua II with 4 on the right and 5 on the left; tibia III with 5 setae in the ***neotypus*** and 4 in the other specimen.

Geographical distribution and ecology

M. romandiolae was collected originally by Pietro Zangheri (Zangheri 1966, as *Damaeus r.*), a well-known naturalist from Romagna (Ruffo 1987), on Poggio Orticai (about 1000 m, Tosco-Emiliano Apennine, at present in the territory of the Italian National Park of Foreste Casentinesi) in the humus of *Fagus sylvatica*, and later determined and described by Max Sellnick (Sellnick 1943).

Twenty years later, Mihelčič (1963) collected and described this species as *M. gladiator*. We found no published record of *Metabelba gladiator* besides the type locality, Sankt Veit im Jauntal in South Austria (Mihelčič 1963), a village located at approximately 540-560 m a. s. l. Mihelčič (1963) found the specimens in open landscape and forest margins, all dry stands.

The specimen from Willmann's collection may relate to the record of one individual of "*Belba setiger* (Kulcz.)" from Moravian Karst (Moravia, Czech Republic), published by Willmann (1954). It was collected by Prof. Karel Absolon in 1900 from moss in the cave of Michalova jeskyně (about 440 - 450 m a. s. l.).

M. romandiolae was collected in further Italian localities: Farma valley (2-300 m a.s.l.), near Siena (southern Tuscany) and Altopiano del Cansiglio (Mt. Pizzoc, 1200 m a.s.l., Treviso, Venetian Pre-Alps) (Bernini, 1982), Pollino Massif (Southern Italy, Calabria) (Bernini et al., 1987) and Nebrodi Mountains (north-eastern Sicily) (Bernini et al., 1996).

This species occurs mainly in the Italian peninsula reaching to the south the Sicily Island, but large populations are found very rarely. Despite these southern localizations, *M. romandiolae* is considered as a mesophilous species generally inhabiting montane sites all characterized by humus of *Fagus sylvatica*, and by elevations over the thousand meters. The unique exception is constituted by Farma valley, a site located at 2-300 m a.s.l., but retained a “mesic oasis”, almost an “island”, colonized during the past glaciations by montane elements (Bernini et al. 1995). The putative record of this species from a cave in Moravian Karst presented above (Willmann 1954), might represent another relict of distribution in past glaciations.

Remarks

M. romandiolae can be easily recognized by the unique shape of its leg setae. Moreover, tips of the notogastral setae are finely serrated with minute backward teeth.

The original description of *M. romandiolae* (Sellnick, 1943) is insufficient and not illustrated; Bernini (1982) designated the *neotypus* of this species on the specimens returned by Sellnick to Pietro Zangheri and belonging to the type series of Sellnick (1943), but did not make a redescription.

The original description of *M. gladiator* by Mihelčič (1963) is comparatively detailed and sufficiently illustrated, but some important characters were described incorrectly, as we revealed with the detailed study of the type specimen. Namely, he described and illustrated the species with two pairs of centrodorsal tubercles (*Da*, *Dp*), but in fact only *Da* is present. He presented the following incorrect leg setal formulas (solenidia and famulus were not distinguished from normal setae): leg I (from femur to tarsus) 7-3-6-18; leg II (from femur to tarsus) 7-3-5-16; leg III (trochanter to tarsus) 3-6-4-5-11; leg IV (trochanter to tarsus) 3-6-3-5-11. The generally lower numbers on particular segments might raise doubts about the generic placement of *M. gladiator*, but in fact the leg setation of the type specimen is normal for *Metabelba* (see above). Parastigmatic apophyses (*Sa*, *Sp*) are neither illustrated nor described in text. Mihelčič also did not describe the filamentous cerotegument and only stated that the body surface is smooth or covered by dirt ("Schmutz" in German original).

Subías (2004, 2008, 2009) was the first author who listed *M. gladiator* as a junior synonym of *Metabelba romandiolae* (Sellnick 1943). He provided no reasons or reference to previous works, but kindly informed us (L. Subías pers. comm., 2010) that his assumption was based on Bernini et al. (1987), who hypothetised that the species might be identical.

In the present paper we considered and analyzed the type material of both names and provided a modern redescription. Our study seems therefore conclusive to establish the synonymy of *M. gladiator* (Mihelčič, 1963) respect to *M. romandiolae* (Sellnick, 1943).

4.3 *Metabelba sphagni* Strenzke, 1950

Synonymy: *Metabelba sphagni*: Strenzke, 1950; Miko (2006). *Metabelba lanceolata* Hammen, 1952 (holotype documented in Fig. 23).

Diagnosis. Propodolateral apophysis *P* absent. Two pairs of centrodorsal tubercles (*Da, Dp*) present, well developed, *Dp* hidden under anterior margin of notogaster in dorsal view; postbothridial (*Ba, Bp*) and lateral (*La*) tubercles absent. Parastigmatic apophyses (*Sa, Sp*) of equal length, conical, pointed with convergent tips. Sensillus (*ss*) long with flagellate tip; covered with minute barbs in distal 1/2, flagellate tip virtually smooth. Interlamellar seta (*in*) almost as long as sensillus, thin with flagellate tip, covered with minute barbs in distal part. Notogastral setae inserted on minute protuberances, *c1-c2*, *la-lp* and *h1-h3* strong, erect, spiniform, directed in radial pattern, smooth, darkly pigmented with hyaline base; *c2-h2* shorter than mutual distances in respective setal pairs; Leg setal formulas and shape of leg setae normal for *Metabelba*. Discidium well developed, spiniform, straight, directed laterad. Cerotegument with long filamentous excrescences. Adults often carrying gastronotic exuviae (scalps).

Type material examined

Collection of Karl Strenzke, Senckenberg Naturmuseum, Frankfurt am Main, Germany: holotype (SMF 14439) and 2 paratypes (14441), individually mounted in 3 permanent mounts labelled as "*Metabelba sphagni*, Holstein 1949, Nr 902". All three individuals are females mounted with dorsal side upwards with stretched legs, cleared, undamaged, allowing detailed study. One of the paratypes has gastronotic exuviae on notogaster. Ventral side could not be studied in detail because of the relatively thick slide.

Collection of Leendert van der Hammen, Naturalis National Museum of Natural History Leiden, the Netherlands: permanent slide with 1 specimen labelled as "*Metabella lanceolata* v.d. Hammen Holotype. l ad. Faure., Lattrop Bergvennen 22-IV-1949 *Sphagnum* monster A09." Habitat data from Hammen (1952): A19. *Sphagnum cuspidatum* Ehr. and *Sphagnum magellanicum* Brid. from the border of the pool.The specimen (male?) is crushed, strongly damaged and cleared, tarsi and tibiae of all legs and large part of notogastral setae missing.

Further material examined

Collection of Leendert van der Hammen, National Museum of Natural History Leiden, the Netherlands: permanent slide with 1 crushed specimen (female) with remains of gastronotic exiviae on notogaster, labelled as "*Metabella* cf. *sphagni* Strenzke l Ad. Faure., Markelo (Twente) 29-X-1948 Vochtige heide leg. L. v.d. Hammen monster A16".

Collection of Miroslav Kunst, Dept. of Zoology, Charles University Prague, Faculty of Science, Czech Republic: 1 specimen (female) mounted in permanent slide, 5 specimens unmounted, preserved in alcohol, labelled as "*M. lanceolata*, M. Tisý, 27. 8. 58". Details of the locality and habitat from Kunst (1959): moist Sphagnum meadow. Kunst (1959) originally identified specimens from this locality as *M. sphagni*. Kunst (1968) reindentified them as *M. lanceolata*. We confirmed the identity with *M. sphagni* through comparison with the type series.

Private collection of Gerd Weigmann, Berlin, Germany: 1 female and 1 male, Hochmoor "Hechtdiebel" 2.5 km north of Glambeck, near Eberswalde, Brandenburg, Germany, 53° 1.846' N, 13°48.740' E, floating Sphahnum, May 1991, leg. Christine Kehl.

Freshly collected material: Czech Republic, south Bohemia, Třeboňsko Protected Landscape Area, peat bog Ruda, in the vicinity of the field station of Dept. of Zoology, Charles University Prague, about 3 km south of Veselí nad Lužnicí 49°9' 4" N, 14°41'34" E, about 420 m a. s. l., weat meadow with *Sphagnum*: 40 specimens, 12. 4. 2009, 1 specimen 12. 7. 2009; 13 specimens, 9/2009; 35 specimens, 27. 3. 2010, all leg. Jitka Vilímová. All specimens unmounted, preserved in 80% ethanol or pure glycerine. From this material vaucher specimens will be deposited the following museum collections: 5 specimens in Acarological Collections of Senckenberg Museum für Naturkunde Görlitz (Germany), 5 specimens in National Museum of Natural History Naturalis, Leiden (the Netherlands), 5 specimens in Arachnological Collections in zoological department of National Museum in Prague (Czech Republic), 14 specimens in the collection of J. Mourek, Dept. of Zoology, Faculty of Science, Charles University Prague (Czech Republic); 5 specimens in private collection of L. Miko; 5 specimens in collection of F. Bernini, Department of Evolutionary Biology, University of Siena (Italy); 5 specimens in private collection of Gerd Weigmann, Berlin (Germany).

Redescription (adult). Figs. 17-22.
Dimensions. Holotype (female): ventral length 448 μm, maximum notogastral width 296 μm; paratype (female): ventral length 448 μm, total notogastral width 300 μm. The mounted type specimens measured in dorsal view. Specimens from South Bohemia: ventral length 416-448 (434) μm, maximum notogastral width 280-304 (293) μm; n= 5. Detailed measurements of legs in Table 1.

Integument. Body colour of fresh specimens usually medium brown, mounted holotype and paratypes pale yellowish (probably cleared for study by Strenzke or vanished in the medium). Cerotegument with "wool-like" filamentous excrescences; excrescences dense and comparatively short on legs (Fig 22B), anogenital area and anterior part of coxisternum, long and loose on prodorsum, sejugal area and around notogastral setae. Underlying cuticle mostly smooth, but faintly granular on apophyses. Gastronotic exuviae (scalps) often present on notogaster of adult. Muscle insertions (sigillae) distinct in holotype and freshly collected fully sclerotized specimens, but hardly visible in paratypes.

Prodorsum. Fig. 17, 18A. Prodorsum of roughly triangular shape, maximum width behind bothridia, about 0.7 of maximum notogastral width. Rostrum blunt with weakly defined nose-like protuberance on dorsal side, separated from rest of prodorsum by a paired shallow lateral indentation. Prodorsum broadened in dorsal aspect by a pair of distinct swellings at level of acetabula I. Apophysis *P* absent. Two pairs of centrodorsal tubercles (*Da, Dp*) present, well developed, *Dp* hidden under anterior margin of notogaster in dorsal view; postbothridial (*Ba, Bp*) and lateral (*La*) tubercles absent. Parastigmatic apophyses (*Sa, Sp*) of equal length, conical, pointed with convergent tips only partly visible in dorsal view. Rostral (*ro*) and lamellar (*le*) setae comparatively long and strong, of approximately equal length. Seta *ro* slightly thinner than *le*, virtually smooth; inserted distinctly ventrolaterad from insertion of *le*, insertion of *ro* not visible in dorsal view. Seta *le* with a few minute barbs on outer curvature. Interlamellar seta (*in*) arising on minute apophysis, almost as long as sensillus, thin with flagellate tip,

covered with minute barbs in distal half, flagellate tip virtually smooth. Exobothridial seta (*ex*) comparatively long, thin, curved anteromediad, covered with a few indistinct minute barbs on outer curvature. Sensillus (*ss*) long with short flagellate tip, sparsely covered with minute barbs in distal part. Bothridial funnel slightly irregular rim, more developed on posterolateral side, normal for family.
Pair of distinct elongated fields of concentrated sigillae (muscle insertions) present between acetabula I and reaching anteiror margin of bothridia; unpaired medial field of sigillae located between bothridia; pair of small sigillar fields located at anterior base of *Da*.

Notogaster. Figs. 17, 18B. Notogaster of broadly ovoid outline in dorsal view, hemispherical in lateral view. Broadest part of notogaster positioned slightly behind half of notogaster, anterior margin of notogaster covering dorsosejugal area in dorsal view. Notogastral setae of series *c1-c2*, *la-lp* and *h1-h3* strong, erect, spiniform, directed in radial pattern; smooth, darkly pigmented with hyaline base; setae *c2-h2* shorter than mutual distances in respective setal pairs. Mutual distance between insertions of *c1* smaller than half mutual distance of insetrions of *c2*. Setae *ps1-ps3* comparatively long, thin, virtually smooth with attenuate tips, directed dorsolaterad, *ps1* ≅ *ps2* > *ps3*. Circumgastric row of muscle sigillae (insertions of dorsoventral muscles) distinct, present laterally from setae *c2- h3*; groups of distinct sigillae present between insertions of setae *c2* and posteromedialy from seta *h1*. Pair of minute light spots present slightly posteromedial to insertions of setae *la*; smaller and less dinsinct pair of spots present medial from insertions of *h3*. Normal set of five lyrifissures (*ia*, *im*, *ih*, *ip*, *ips*) and opening of opisthonotal gland (*gla*) present on lateral part of notogaster. Notogaster often with gastronotic exuviae (scalps) arranged in pyramidal shape, but never with a compact mass of dirt. Cornicles *k* of nymphal gastronotic exuviae comparatively long, more or less straight (Fig. 22D).

Gnathosoma. Fig.19. Subcapitulum normal for family: diarthric, with three pairs of thin and comparatively long setae (*m* > *h* > *a*), covered with a few minute barbs on outer curvatures and two pairs of setiform processes (*or1,2*). Chelicera in shape and relative size typical of family, cheliceral seta *cha* with row of short barbs on outer (dorsal) curvature, seta *chb* with short barbs in distal third. Setation of chelicera not discernable, setal formula of pedipalp (from trochanter to tarsus, solenidion in parenthesis): 0-2-1-3-9(1).

Epimeral region. Fig. 19. Medial pit *cp* on coxisternum I not developed. Anterior tectum of podocephalic fossa extending laterally slightly under trochanter I, suture of podocephalic fossa almost perpendicular to body axis, without a tooth-like projection. Propodoventral (*E2a*, *E2p*) and ventrosejugal (*Va*, *Vp*) enantiophyses absent. Ventrosejugal furrow complete, body distinctly narrowed between acetabula II and III. Epimeral setal formula (I to IV): 3-1-3-4, normal for *Metabelba*. Muscle sigillae on epimeres discinct in most of studied specimens. Epimeral setae comparatively long, smooth, thin, with attenuate tips.

Anogenital region. Fig. 19. Discidium (*di*) well developed, spiniform, pointed, straight, directed laterad. Setal formulas of anogenital region normal for the Damaeidae (Grandjean 1960; Norton 1977b); genital *g*: 6; aggenital *ag*: 1; anal *an*: 2; adanal *ad*: 3; all setae comparatively long, thin with pointed attenuate tips. Lyrifissure *iad* oblique, divergent posteriad.

Legs. Figs. 20, 21AB. Legs monodactylous, moderately long, segments distinctly swollen in distal part. Leg IV slightly longer than body, leg I and III as long or slightly shorter than body, leg II distinctly shorter than body (detailed measurements in Table 1). Leg setae normal for family, comparatively long and thin, pointed; most covered with minute barbs on outer curvatures. Dorsal seta (*d*) on femora strong, roughened with distinct barbs on outer curvatures. Leg setal formulas identical with those of *Metabelba pulverosa* Strenzke, 1953 (Norton 1977), as follows (from trochanter to tarsus, famulus included, solenidia in parentheses): leg I: 1-10-4(1)-4(2)-20(2), leg II: 1-10-4(1)-5(1)-17(2), leg III: 4-9-4(1)-5(1)-17(0), leg IV: 3-9-4(0)-4(1)-14(0). Dorsal seta (*d*) on tibiae I and IV absent (respective solenidia free); seta *d* those on tibiae II and III and on genua I, II and III present, coupled with respective solenidia. Solenidia *ω1,2* on tarsus I moderately long, tactile; *φ1* on tibia I and *φ* on tibia IV very long, tactile; *ω1,2* on tarsus II moderately long, setiform; *φ1* on tibia I about 3.5x longer than *φ2*; *φ* on tibia IV slightly less than 2x longer than tibia itself. Solenidion *φ* slightly shorter than respective setae *d* on tibia II and slightly longer than respective setae *d* on tibia III. Solenidion *σ* as long as respective setae *d* on genu I and II and slightly shorter than respective seta *d* on genu III.

Geographical distribution and ecology

Metabelba sphagni is hitherto known from north of Germany: Schleswig-Holstein (Strenzke 1950, Strenzke 1952) and Brandenburg (Kehl, 1997); the Netherlands (Siepel et al. 2009; unpublished record by Hammen—see our Material examined); Czech Republic: Central Bohemia (Kunst 1959, 1962; Starý 2000a); Austria: Tyrol (Jahn 1967; Schatz 1983); Switzerland: Swiss Jura mts. (Borcard, 1992); Sweden (Tarras-Wahlberg 1961; Lundquist 1987) and Russia: Kola Peninsula (Krivoluckij et al., 1995).

The species sems to be comparatively rare and has been reported almost exclusively from *Sphagnetum*—peat bogs or moist meadows with predominating *Sphagnum* mosses—in relatively low altitudes above see level (Strenzke 1950; Kunst 1959, 1962; Tarras-Wahlberg 1961; Lundquist 1987; Kehl 1997). The recent findings from Ruda in South Bohemia and other examined specimens from museum collections (see Material examined) are from the same type of habitat. Similarily, *M. lanceolata*, junior synonym of *M. sphagni* was collected in weat Sphagnum on a border of a pool in the Netherlands (Hammen 1952). In contrast, Jahn (1967) reported *M. sphagni* from a larch forest (*Larix decidua*) in the altitude about 1100 m a.s.l. and Borcard (1992) reported it from a peat-bog in the altitude 1090 m a. s. l.

Most authors found only a few individuals of *M. sphagni* and the abundant population found in the peat bog Ruda in South Bohemia (see our Material examined) seems to be an exception. It is possible that the rarity of records of *M. sphagni* is caused by the fact that this type of habitat has been poorly studied.

Remarks

Metabelba sphagni is easily distinguished from other species of the subgenus by the presence of two pairs of well-developed centrodorsal tubercles (*Da*, *Dp*) and strong, almost straight and smooth spiniform notogastral setae, shorter than their mutual distance, which are inserted on distinct protuberances.

The possibility that *Metabelba lanceolata*, van der Hammen, 1952, may be a junior synonym of *M. sphagni* was suggested by Miko (2006). Subías (2008, 2009) stated the synonymy of both species as a fact, without providing a reference, probably

influenced by Miko (2006). In this study we compared type specimens of both species and substantiated the synonymy, based on the following analysis:

1. The original description of *M. lanceolata* is brief and incomplete, based on a single crushed and strongly damaged individual (Hammen, 1952; see also our Material examined and Fig. 23): tarsi and tibiae of all legs were missing, so that the presence of setae *d* on tibiae II and III could not be studied, therefore he noted that the generic position of the species was uncertain. Moreover, many of notogastral setae were missing. Hammen (1952) illustrated the specimen with strongly obovate notogaster strongly narrowing posteriad, which is very unusual in Damaeidae. We conclude that this was an incorrect and misleading reconstruction of the shape of the crushed specimen in permanent slide.

2. The main difference of *M. lanceolata* from *M. sphagni* should be the broadened - "lanceolate"- shape of notogastral setae (Hammen, 1952) and this character was adopted in diagnostic keys by subsequent authors (Hammen and Strenzke, 1953; Kunst 1961; Bulanova-Zachvatkina 1975). However, from the careful examination of the holotype of *M. lanceolata* we conclude, that the "lanceolate"- shape of notogastral setae is only an artefact, caused probably by intensive maceration of the specimen and subsequent strong compressin of the setae by the cover glass in permanent slide. From our Fig 23B is evident, that in the seemingly "lanceolate" setae *lm*, *lp*, *h3* and *h2* the surface layer is detached from the core of the seta and flattened by the compression. In contrast, seta *h1* has normal appearance as in *M. sphagni*.

The thickness of notogastral setae in *M. sphagni* is slightly variable, some specimens from South Bohemia having somewhat thicker setae than the type series (Fig. 21 CD). However, the "impression of thickness" of the setae depends also on the position of a given specimen during the observation—the setae appear to be thicker in dorsolateral view than in exactly dorsal position—as we demonstrate on Fig. 21 CD.

3. Kunst (1968) found also the length ratio between trochanter and femur IV to be a distinguishing character between *M. sphagni* and *M. lanceolata*, the former species having trochanter IV shorter than femur IV and contrary in the later species. His assumption was not based on the study of type or topotypical material of either species, but on comparison of specimens from South Bohemia identified as *M. lanceolata* with original description by Strenzke (1950). However, we did not confirm the difference; in fact all available specimens from the type series of *M. sphagni* had trochanter IV slightly longer than femur IV, in holotype of *M. lanceolata* both segments were equally long and the ratio slightly varied among the material of *M. sphagni* from South Bohemia (see Table 1). The two species therefore cannot be distinguished according to the lenght ratio of trochanter IV and femur IV. It that Strenzke (1950) measured the given leg segments in different way. The possibile synonymy is supported by the fact that both species have been found in wet habitats, particularily peat bogs in lowland (Strenzke 1950, Hammen 1952, Kunst 1968).

5. Tentative key to adults of species of *Metabelba* (n. subgen. 1) known from the Palaearctic and Canary Islands.

1. Legs extremely long, leg IV at least twice as long as body. Centrodorsal tubercles (*Da*, *Dp*) on prodorsum absent. Notogastral setae very long and smooth; notogastral seta *lm* displaced distinctly laterad from remaining notogastral setae; interlamellar seta short, serrate, not flagellate. Parastigmatic apophyses (*Sa*, *Sp*) short, tuberculate, with convergent tips. Body length 660 μm. .... ***M. filippovi*** Bulanova-Zachvatkina, 1965

- Legs not extremely long, leg IV not longer than 1.5 of the body length. 2

2. Notogastral setae shorter than the distance to next more posterior seta. Notogaster conical in lateral view, with highest point shifted posteriad; anterior part of notogaster distinctly flattened..... 3

- Notogastral setae in dorsal view at least as long as distance to next more posterior seta. Notogaster of normal shape, in lateral view evenly rounded, more or less hemispherical, with highest point approximately in the middle. 4

3. (2) Notogaster of adults with strong cornicle (*k*) positioned medially. Notogastral setae weak, iregularly curved, with minute barbs on outer curvature. Centrodorsal tubercles (*Da, Dp*) on prodorsum absent, tubercle *Da* sometimes weakly indicated as cuticular thickening. Distinct two pairs of postbothridial tubercles (*Ba, Bp*) present posterolateral from bothridia. Discidium reduced to low rounded protuberance; notogaster often with gastronotic exuviae (scalps) covered with compact mass of debris. Body length (measured as ventral length) 515-540 μm. ..... ***M.* n. sp. 1**

- Notogaster of adults without cornicle (*k*). Notogastral setae short, strong, smooth erect spines. Two pairs of centrodorsal tubercles (*Da, Dp*) oppose each other in dorsosejugal area, dorsomedial to interlamellar setae. Discidium normal, spiniform; notogaster often with gastronotic exuviae (scalps), but without compact mass of debris Body length 368-415 μm. ..... ***M. platynotus*** Grandjean, 1954

4. (3) Notogastral setae strongly and irregularly curved (S-shaped), very thin, flagellate. Their insertions arranged in irregular pattern, not forming two parallel rows. Seta *lm* displaced distinctly more laterad than remaining notogastral setae. One pair of centrodorsal tubercles (*Da*) present posterior to interlamellar setae. Body length about 420 μm ..... ***M. flagelliseta*** Bulanova-Zachvatkina, 1965

- Notogastral setae straight or only slightly curved, not flagellate. Insertions of setae *c2 - h1* forming two more or less parallel rows, seta *lm* not displaced distinctly more laterally than the remaining notogastral setae. 5

5. (4) Most leg setae with broad flat base and long attenuate tip, often curved (see Figs. 11, 12, 14). Notogastral setae comparatively long and thin. Seta *ps1* very long, projecting distinctly more posteriad than *h1*. One pair of distinct centrodorsal tubercles (*Da*) present posteromedial to interlamellar setae. Body length 680-720 μm. ..... ***M. romandiolae*** (Sellnick, 1943)

- Leg setae normal, without broad base and attenuate tip. 6

6. (5) Two pairs of centrodorsal tubercles (*Da, Dp*) oppose each other in dorsosejugal area, dorsomedial to interlamellar setae. Notogastral setae strong, spiniform, smooth, comparatively short, riected in radiate pattern; setae *c1 - h1* in dorsal view shorter than half mutual distance between insertions of recpective setae. Body length 450-500 μm. ....***M. sphagni*** Strenzke, 1950

- One pair of centrodorsal tubercles (*Da*) present basally on prodorsum, dorsal or dorsomedial from interlamellar setae..... 7

7. (6) Notogastral setae arranged more or less parallel with body axis - setae *c1* and *c2* directed anteriad, the remaining setae posteriad; setae comparatively short, as long as or only slightly longer than the distance between insertions of two successive setae. Body length 420-440 μm. ..... ***M. rhodopeia*** Kunst, 1961

- Notogastral setae erect, directed in radial pattern - *c1* directed anteriad, the remaining setae anterolaterad, laterad or posterolaterad; setae comparatively long, in dorsal view distinctly longer than the distance between insertions of two successive setae. 8

8. (7) Notogastral seta *ps1* very long, flagellate (sometimes with broken tips). 9

- Notogastral seta *ps 1* normal, comparatively short, not flagellate. 12

9. (8) Body length over 600 μm (630-700 μm according to original description). Setae *h1-h3* in lateral view longer than *c1-lp*. Parastigmatic apophyses (*Sa, Sp*) short, conical with blunt convergent tips. Probably endemic to Canary Islands (Gran Canaria). ..... ***M. machadoi*** Pérez-Iñigo 1986

- Body size less than 500 μm. Setae *h1-h3* in lateral view not longer than *c1-lp*. 11

10. (9) Parastigmatic apophyses (*Sa, Sp*) long, slender, spiniform, *Sp* distinctly longer than *Sa*. Body length about 460 μm. ..... ***M. paraitalica*** Kulijev, 1967

- Parastigmatic apophyses (*Sa, Sp*) short blunt tubercles, *Sp* larger than *Sa*, but not long and spiniform. Body length 460-480 μm. .... ***M monilipeda*** Bulanova-Zachvatkina, 1965

11 (9) Discidium slender, long, spiniform, curved posterolaterad. Parastigmatic apophyses (*Sa, Sp*) of equal length, very long, slender and pointed, directed in parallel. Body length 500-560 μm. .... ***M. pseudoitalica*** Bulanova-Zachvatkina, 1965

- Discidium in form of blunt tubercle..... 12

12 (11) Trochanter IV distinctly shorter than femur. Body length unknown. Ionian Islands (Korfu and Levkas). ..... ***M. italica*** Sellnick, 1931

- Trochanter IV distinctly longer than femur. Body length 560-570 μm. .... ***M. ericius*** Kunst, 1957

Remarks

The above identification key is based mainly on a survey of original descriptions and illustrations of the species. We had opportunity to study only the type material of *Metabelba* **n. sp.1** , *M. romandiolae* (including the holotype of its junior synomym *M. gladiator*) and *M. sphagni* (including the holotype of its junior synomym *M. lanceolata*). The key must be therefore used with caution, since some of the species were described incompletely and detailed redescriptions have not yet been made.

The hitherto most comprehensive keys to species of *Metabelba*, covering the territory of former USSR, were published in Russian by Bulanova-Zachvatkina (1965, 1967 and 1975), who did not distinguish subgenera. None of these keys contains *M. romandiolae*, *M. paraitalica* or, of course, *M. machadoi* or *M.* **n. sp. 1,** which were described later. The keys of Bulanova-Zachvatkina (1965, 1967, 1975) contain some mistakes, which may lead to confusion, but the illustrations may be used to supplement our key.

We restricted the scope of our key to the Palaearctic region plus the Canary Islands, because the systematic position of species described from other regions (Balogh 1958, Mahunka 1982) is rather uncertain.

The differentiation of *M. italica* and *M. ericius* by the length ratio of trochanter and femur IV (see Kunst, 1957) must be done with caution and the material should be compared with original illustrations. It is uncertain, if both authors measured trochanter

IV of their species in the same way. Unfortunately, Sellnick (1931) provided only schematic drawings of the notogaster in dorsal view and leg IV of *M. italica*, while Kunst (1957) depicted *M. ericius* in detail.

Acknowledgements
The study was partially financially supported by the Grant Agency of the Charles University, Prague (grant *GAUK 217/2004/B-BIO/PrF*).
Prof. Roy A. Norton (State University of New York, College of Environmental Science & Forestry, Syracuse, NY, USA) helped us in solving nomenclature problems and contributed many ideas. Assoc. Prof. Konrad Thaler († 11. 7. 2005), Dr. Heinrich Schatz and Dr. Irene Schatz (Institut für Zoologie und Limnologie, Universität Innsbruck, Austria) and Mechthild Schatz (Innsbruck, Austria) kindly supported J. Mourek during his stay in Innsbruck in November 2004, when studying Damaeidae in the collection of Dr. Franz Mihelčič. Dr. Piotr Skubała (University of Upper Silesia, Katowice, Poland) donated us a specimen of *Metabelba* **n. sp.1** from Poland. Jindra Mourková, Zdeněk Janovský, Dagmar Berneška Říhová (Charles University, Faculty of Science, Prague, Czech Republic) and Jakub Šťastný (Prachatice, Czech Republic) helped to collect the material of *Metabelba* **n. sp.1,** Assoc. Prof. Jitka Vilímová (Charles University, Faculty of Science, Prague, Czech Republic) collected the material of *M. sphagni* in South Bohemia. Prof. Romano Dallai kindly donated the specimens of *M. romandiolae* to F. Bernini. Prof. Gerd Weigmann (Freie Universitaet Berlin, Germany) kincly loaned specimens of *M. sphagni* collected by Cristine Kehl. Dr. Gerhard Tarmann and Dr. Peter Huemer (Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria) borrowed the material from the Mihelčič collection for study. Dr. Peter Jäger (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany) kindly loaned the type series of *M. sphagni* from the collection of K. Strenzke. Dipl.-Biol. Stefan Friedrich (Zoologische Staatssammlung München, Germany) kindly loaned the specimen of *M. romandiolae* labelled as "*Belba setiger*" from the collection of C. Willmann. Mr. I. J. Smit (Naturalis National Museum of Natural History Leiden, Netherland) kindly loaned a slide of *M. sphagni* and the holotype of *M. lanceolata* from the collection of. L. van der Hammen. Mr. Dr. Miroslav Hyliš (Charles University, Faculty of Science, Prague, Czech Republic) assisted with the preparation of specimens for SEM-study. Kerstin Franke (Senckenberg Museum für Naturkunde Görlitz, Germany) provided copies of important literature. Dr. María Lourdes Moraza (Universidad de Navarra, Pamplona, Spain) kindly re-examined the nymphs of *Epidamaeus ibericus* and provided information about the cornicle. Dr. Luís Subías (Universidad Complutense, Facultad de Biologia, Madrid, Spain) kindly provided some references to literature. We are grateful to all.

References

Balogh, J. (1958) Oribatides nouvelles de l'Afrique tropicale. - *Revue de Zoologie et de Botanique Africaines*, 58(1-2): 1-34.

Balogh, J. & Mahunka, S. (1967) New Oribatids (Acari) from Vietnam. *Acta Zoologica Academiae Scentiarum Hungaricae* 13(1-2): 39-74.

Balogh, J. & Mahunka, S. (1969) The scientific results of the Hungarian Soil Zoological expedition to South America. 11. Acari: Oribatids from the material of the second expedition. II. *Opuscula Zoologica*, Budapest, 9(1): 31-69.

Balogh, J. & Balogh, P. (1992) *The Oribatid Mites Genera of the World. Volume I.* Hungarian National Museum Press, 263 pp.

Banks N. (1904) Some Arachnida from California. *Proceedings of the California Academy of Sciences* 3: 331-374. Ex: Norton, R. A. (1979d) Generic concepts in the Damaeidae (Acari, Oribatei). I. Three taxa based on species of Nathan banks. *Acarologia*, 20: 603-621.

Bayartogtokh, B. & Norton, R.A. (2007) The *Dyobelba tectopediosa* species-group (Acari: Oribatida: Damaeidae) from the Southeastern USA, with a key to world species of *Dyobelba* and notes on their distribution. *Zootaxa*, 1591: 39–66.

Behan-Pelletier, V.M., & Norton, R.A. (1985) *Epidamaeus* (Acari: Damaeidae) of subarctic western North America and extreme northeastern USSR. *Canadian Entomologist*, 117: 277-319.

Bernini, F. (1980) –Notulae Oribatologicae XXIV. Gli Acari Oribatei di alcune piccole grotte del Senese. *Redia*, 63: 359-405.

Bernini, F. (1982) Notulae Oribatologicae XXVII. Contributo alla conoscenza degli Oribatei della Val di Farma (Toscana meridionale). *Redia*, 65: 377-405.

Bernini F., Avanzati A. M, Bernini S. (1987) Notulae Oribatologicae XXXVII. Gli Acari Oribatei del Massiccio del Pollino (Italia Meridionale): aspetti faunistici e biogeografici. *Biogeographia. Lavori della società italiana di biogeografia*. Nuova serie, 10: 379-488.

Bernini F., Avanzati A. M., Baratti M., Migliorini M. (1995) Oribatid mites (Acari Oribatida) of the Farma Valley (Southern Tuscany). Notulae Oribatologicae LXV. *Redia*, 78: 45-129.

Bernini F., Arcidiacono R., Migliorini M. (1996) Notulae Oribatologicae LXII. Contributo alla conoscenza degli Acari Oribatei dei Monti Nebrodi e dei Peloritani (Sicilia Nordorientale). *Animalia*, 21: 131-172.

Borcard, D.: (1992): Les Oribates des tourbières du Jura Suisse (Acari, Oribatei). Faunistique III. Nanhermannoidea, Hermannoidea, Belboidea, Cepheoidea, Liacaroidea. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 65: 81-93.

Bulanova-Zachvatkina, E.M. (1957b) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Rod *Epidamaeus*, gen. n. (Acariformes, Oribatei). Soobschchenije II. *Zoologicheskij Zhurnal*, 36 (12), 1792–1801. (in Russian).

Bulanova-Zachvatkina, E.M. (1962) Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. 1896 (trib. Belbini tr. nov.). *Zoologicheskij Zhurnal*, 41: 203-216. (in Russian).

Bulanova-Zachvatkina, E.M. (1965) O diagnostike vidov roda *Metabelba* Grandjean, 1936 (Oribatei, Damaeidae). *Zoologicheskij Zhurnal,*36 (9), 1333 - 1343. (in Russian).

Bulanova-Zachvatkina, E.M. (1967): *Pancirnje kleschtschi - Oribatiyi*. Vysshaya Shkola, Moscow: 1-254. (in Russian).

Bulanova-Zachvatkina, E.M. (1975): Nadsemejstvo Belboidea Dubinin, 1954 (=Damaeoidea Balogh, 1961). *In*: Gilijarov, M. S. & Krivolutskij, D. A. (Eds): *Opredelitel obitaiustschich v potschve kljeschtschei*. Nauka, Moskva. pp. 120-143. (in Russian).

Enami Y. (1994) A new species of the genus *Belba* (Acari: Damaeidae) from Japan. *Edaphologia*, 51: 1-5.

Ermilov S. G., Łochyńska M. (2009): Morphology on juvenile stages of *Epidamaeus kamaensis* (Sellnick, 1925) and *Porobelba spinosa* (Sellnick, 1920) (Araci:Oribatida: Damaeidae). *Annales Zoologici (Warszawa)*, 54: 527-544.

Grandjean, F. (1936) Les Oribates de Jean Frederic Hermann et de son pere, *Annales de la Société Entomologique de France*, 105: 27–110.

Grandjean, F. (1954) Observations sur les Oribates (29° série). *Bulletin du Museum National d'Histoire Naturelle, Paris, 2 séries*, 26: 334-341.

Grandjean, F. (1960) *Damaeus arvernensis* n. sp. (Oribate). *Acarologia*, 2, 250-275.

Hammen, L. van der (1952): The Oribatei (Acari) of the Netherlands (Acari). - *Zoologische Verhandelingen, Leiden*, 17: 1-139.

Hammen, L. van der & Strenzke, K. (1953) A partial revision of the genus *Metabelba* Grandjean (Oribatei, Acari). *Zoologische Mededelingen*, 32(14), 141-154.

Hermann F. (1804) *Memoire apterologique*. Strassbourg. 1-144. Ex: Grandjean, F. (1936) Les Oribates de Jean Frederic Hermann et de son pere, *Annales de la Société Entomologique de France*, 105: 27–110.

International Commission on Zoological Nomenclature (1999): International code of zoological nomenclature. Available from: 4th edition, online version. http://www.nhm.ac.uk/hosted-sites/iczn/code/index.jsp [cited 24. 4. 2010]

Jacot, A.P. (1939): New mites from the White mountains. - *Occasional Papers of the Boston Society of Natutal History*, 8: 321-332.

Jahn, E. (1967) Ergebnisse bodenfaunistischer Untersuchungen an ver'schiedenen Lärchenstandorten Tirols. *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck*, 55: 59-79. (in German)

Kehl, C. (1997) Die Hornmilbenzönosen (Acari, Oribatida) unterschiedlich stark degradierter Moorstandorte in Berlin und Brandenburg. Inaugural-Dissertation zur Erlangung der Doktorwürde des Fachbereichs Biologie der Freien Universität Berlin: 1-264 pp. (in German)

Kofler A. (1978): Biographie und Bibliographie des Acarinologen und Tardigradologen Pfarrer Dr. Franz Mihelcic (1898-1977). *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck*, 65: 213-224.

Krivolutsky D.A., Lebrun P., Kunst M. et al. (1995): <Oribatid mites. Morphology, development, phylogeny, ecology, methods of study and characteristics of the model species *Nothrus palustris* >. Nauka Publishers, Moscow: 224 pp. (in Russian)

Kulczynski, V. (1902) Species Oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. *Bulletin International de L'Académie des Sciences de Cracovie, Classe des sciences mathématiques et naturelles*, 2, 89-96.

Kulijev, K. A. (1967) Novye vidy semeistva Damaeidae Berl. *Doklady Akademii Nauk Azerbaidzhanskoi* SSR 23(11): 63-70. (in Russian).

Kunst, M. (1957) Bulgarische Oribatiden (Acarina) I. *Universitas Carolinae Biologica*, 3, 133-165.

Kunst, M. (1959) Roztoči skupiny Oribatei z reservace 'Velký a Malý Tisý' - *Ochrana přirody*, 14(2), pp. 33-42 (in Czech).

Kunst, M. (1961) Bulgarische Oribatiden IV. (Acari:Oribatei). *Acta Universitatis Carolinae Biologica*, 8, 151-183.

Kunst, M. (1962) *Anoribatella* n. g., a new genus of Oribatid Mites from Central Europe - *Acta Univ. Carolinae Biologica*, 1962: 89-98.

Kunst M. (1968) *Roztoči nadřádu Oribatei Československa*. Unpubl. habilitation thesis. Deposited in the Zoological library of the Faculty of Science, Charles University Prague. 1355 pp. (in Czech).

Kunst, M. (1971) Pancířníci – Oribatei. In: Daniel, M. & Černý, V. (eds.), *Klíč zvířeny ČSSR II*. Nakladatelství Československé Akademie Věd, Praha, 531–580. (in Czech).

Luxton, M. (1981) Studies on the oribatid mites of a Danish beech wood soil. IV. Developmental biology. *Pedobiologia* 21, 312-340.

Lundqvist, L.: (1987) Checklist of Swedish Oribatids (Acari: Oribatei), 1941-1985. *Ent. Tidskr.*, 108: 3-12.

Mahunka, S. (1982): Oribatids from eastern part of the Ethiopian region (Acari). I. *Acta Zoologica Academiae Scentiarum Hungaricae*, 28(3-4): 293-336.

Marshall, V. G., Reeves, R. M. & Norton, R. A. (1987): Catalogue of the Oribatida (Acari) of Continental United States and Canada**.** *Memoirs of the Entomological Society of Canada*, 139: 418 pp.

Mihelčič, F (1963) Beitrag zur Kenntnis der Oribatidenfauna Kärntens (Oribatei, Acarina) *Zoologischer Anzeiger*, 170, 230-240.

Mihelčič, F. (1964) Ein Beitrag zur Kenntnis der Familie Damaeidae Berl. *Zoologischer Anzeiger*, 172, 360-385.

Miko, L. (2006) Damaeidae. In: Weigmann, G.: *Hornmilben (Oribatida)*, Die Tierwelt Deutschlands 76, Goecke&Evers Publ., 179-207.

Miko, L. (2008) Taxonomy of European Damaeidae (Acari: Oribatida) II. *Porobelba weigmanni* n. sp. (Oribatida, Damaeidae), from East Slovakia, with comments on other known species of the genus. *Zootaxa* 1844: 55–62

Miko, L. (2010) Taxonomy of European Damaeidae (Acari: Oribatida) III. Species of the *Kunstidamaeus tenuipes* (Michael, 1885) group, with a description of *Kunstidamaeus fraterculus* n. sp. from East Slovakia. *Zootaxa* 2327: 51–64

Miko, L. and Mourek J. (2008) Taxonomy of European Damaeidae (Acari: Oribatida). I. *Kunstidamaeus* Miko, 2006 with comments on *Damaeus* sensu lato. *Zootaxa* 1820: 1–26.

Miko, L. and Travé, J. (1996) Hungarobelbidae n. fam. with a description of *Hungarobelba pyrenaica* n. sp. (Acarina, Oribatida). *Acarologia*, 37: 133-155.

Moraza M. L., Moreno A. I., Saloña M. (1990) *Epidamaeus ibericus* sp. n. de bosques del norte de la Peninsula Iberica (Acari, Oribatei, Damaeidae). *Eos* 66: 201-207.

Moritz, M. (1966) *Metabelba papapulverosa* n. sp., eine neue oribatide (Acarina) aus Bulgarien. *Bulletin de l'Institut de Zoologie et Musée, (Sofia)*, 21: 5-10.

Norton, R. A. (1977a) A review of J.Grandjean's system of leg chaetotaxy in the Oribatei and its application to Damaeidae. In: Dindal, D. L. (Ed.), *Biology of oribatid mites*, 33, SUNY College of Environmental Science and Forestry, Syracuse, New York, 33-62.

Norton, R. A. (1977b) The genus *Damaeus* Koch (Acarina: Oribatei) in the United States. *Acarologia* 19: 331-353.

Norton, R. A. (1979a) Aspects of the biogeography of Damaeidae sensu latu (Oribatei), with emphasis on North America. In: Rodriguez, J.G. (Ed.): *Recent Advances in Acarology*, vol. 2: 535-540.

Norton, R. A. (1979b) Familial concepts in the Damaeoidea as indicated by preliminary phylogenetic studies. In: Rodriguez, J.G. (Ed.): *Recent Advances in Acarology*, vol. 2: 529- 533.

Norton, R. A. (1979c) Damaeidae (Acari: Oribatei) collected by the Hungarian Soil Zoological Expedition to South America. *Folia Entomologica Hungarica*, 32: 55-64.

Norton, R. A. (1979d) Generic concepts in the Damaeidae (Acari, Oribatei). I. Three taxa based on species of Nathan banks. *Acarologia*, 20: 603-621.

Norton, R. A. (1979e) Generic concepts in the Damaeidae (Acari, Oribatei). Part II. *Acarologia*, 21: 496-513.

Oudemans, A.C. (1937): *Kritisch Historisch Overzicht der Acarologie*. - Leiden, 3 F: I-XV: 2521-2735. Ex: Hammen, L. van der & Strenzke, K. (1953) A partial revision of the genus *Metabelba* Grandjean (Oribatei, Acari). *Zoologische Mededelingen*, 32(14), 141-154.

Pérez-Iñigo, C. (1986): Contribución al conocimiento de los Oribátidos (Acari, Oribatei) de La Gomera (Islas Canarias). - *Eos*, 62: 187-208.

Perez-Iñigo C. (1997) Acari: Oribatei, Gymnonota. In: Ramos, M. A., (Ed.), *Fauna Iberica*, 9, Museo Nacional de Ciencias Naturales, Madrid, pp. 1–374.

Ruffo S. (1987) Ricordo di Pietro Zangheri (1889-1983). *Biogeographia. Lavori della società italiana di biogeografia.* Nuova serie, 10: 823-826.

Saloña, M. & Iturrondobeitia, J.C. (1989): Especies interesantes, pertenecientes a la superfamilia Belboidea (Acari, Oribatei) recogidas en Vizcaya y una zona afín: *Epidamaeus plesiomorphicus* n.sp. - *Anales de Biología (Biologia Animal), Murcia*, 4: 15-27.

Schatz, H. (1983) U.-Ordn. Oribatei, Hornmilben. *Catalogus faunae Austriae. Ein systematisches Verzeichnis aller auf osterreichischem Gebiet festgestellten Tierarten*, 9, Österreichische Akadademie der Wissenschaften, Wien, 118 pp.

Sellnick, M. (1920) Neue und seltene Oribatiden aus Deutschland. *Schriften der Physik-okonomischen Gesellschaft zu Konigsberg,* 61: 35-42.

Sellnick, M. (1931) Acari. In: M. Beier, Zoologische Forschungsreise nach den Ionischen Inseln und dem Peloponnes, XVI. *Sitzungsberichte der Akademie der Wissenschaften. Wien*, 140: 693-776.

Sellnick, M. (1943): Einige neue Milben aus der Romagna. *Bollettino della Societa Entomologica Italiana* 75(3): 22-26.

Sellnick M. (1960): Formenkreis: Hornmilben, Oribatei. Nachtrag. In: Brohmer, P. Ehrmann P. & Ulmer G. (eds.): *Die Tierwelt Mitteleuropas*, Leipzig, 3(4), Erg.: 45-134.

Siepel, H., Zaitsev, A. & Berg, M. (2009): Checklist of the oribatid mites of the Netherlands (Acari: Oribatida). *Nederlandse faunistische mededelingen*, 30: 83-111.

Starý, J. (2000a): List of oribatid mites (Acari: Oribatida) of the Bohemia, Czech Republic. - *Sborník Přirodovědného klubu v Uherském Hradišti*, 5: 129-154. [in Czech]

Starý, J. (2000b): List of oribatid mites (Acari: Oribatida) of the Moravia, Czech Republic. - *Sborník Přirodovědného klubu v Uherském Hradišti*, 5: 155-173. [in Czech]

Strenzke, K. (1950) Die Belbiden Holsteins (Acarina: Oribatei) - *Schriften und Naturwissenschaflichen Vereins für Schleswig-Holstein (Kiel)*, 24(2): 63-65.

Strenzke, K. (1952). Untersuchungen über die Tiergemeinschaften des Bodens: Die Oribatiden und ihre Synusien in den Böden Norddeutschlands. - *Zoologica, Stuttgart*, 104: 1-173.

Subías, L.S. (2004) Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1748-2002). *Graellsia*, 60, 3–305.

Subías, L. (2008) *Listado sistematico, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (Excepto fósiles)*. 540 pp. Available from: http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf [last changes in May 2008; cited 15. 2. 2009]

Subías, L. (2009) *Listado sistematico, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (Excepto fósiles)*. 547 pp. Available from: http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf [last changes in April 2009; cited 24. 4. 2010]

Tarras-Wahlberg, N. (1961) The Oribatei of a central Swedish bog and their Environment. *Oikos*, Suppl., 4: 1-56.

Totschnig U. (2001) Die Hornmilbensammlung (Acari, Oribatida) Franz Mihelcic im Tiroler Landesmuseum Ferdinandeum, Innsbruck. *Veröffentlichungen des Tiroler Landesmuseum Ferdinandeum*, 81: 205-240.

Travé J. (1978) La néotrichie chez les oribates (Acarines). *Acarologia* 20: 590-602.

Weigmann, G. 2006. Hornmilben (Oribatida). In Dahl, F. (ed). *Die Tierwelt Deutschlands* 76: 1-520. Goecke & Evers, Keltern.

Willmann, C. (1954) Mährische Acari, hauptsächlich aus dem Gebiete des mährischen Karstes, gesammelt von Prof. Dr. K. Absolon, Brünn. *Československá parasitologie* 1: 213-272.

Winkler, J. (1955) Nový druh pancířníků, *Belba bartoši* n. sp., z Pradědu (Acari, Oribatoidea). Ochrana přírody 10: 306.

Woolley, T. A. and Higgins, H. G. (1979) A new genus and two new species in Damaeidae. *Recent Advances in Acarology*, 2: 553-558:

Zangheri P. (1966) Ord. Acari. Sottord. Oribatei. pp. 611-634. In: "Repertorio sistematico e topografico della Flora e Fauna vivente e fossile della Romagna.". *Museo Civico di Storia naturale di Verona*, *Memorie fuori serie* n. 1, 1966-1970, vol. 1-5, pp. 2174.

TABLE 1: Own measurements of *Metabelba* **n.sp.1**, *M. romandiolae* (Sellnick, 1943), *M. sphagni* Strenzke, 1950 including the available type material of their junior synonyms. All measurements are given in μm. Legs I and II were measured without trochantera, whereas legs III and IV were measured with trochantera; * approximate value measured on crushed type specimen, "-" measurement is not available because the measured specimen was incomplete, crushed or skewly mounted in permanent slide.

Species	***Metabelba.* n.sp. 1**			***M. romandiolae* (Sellnick, 1943)**					***M. sphagni* Strenzke, 1950**						
Origin	Czech Republic, Central Bohemia, Medník			Italy, S. Benedetto in Alpe			"*Belba setiger*" coll. Willmann	type *M. gladiator* Mihelčič, 1963	holotype	paratype	paratype	holotype *M. lanceolata* Hammen 1952	South Bohemia: Malý Tisý, Ruda		
Nr. of measured spec.	5			2			1	1	1	1	1	1	5		
	mean	min.	max.	mean	min	max							mean	min	max
ventral length	**527**	**517**	**533**	**572**	**568**	**576**	**584**	***585**	**448**	**448**	**-**	**-**	**434**	**416**	**448**
notogastral width	**323**	**317**	**328**	**424**	**408**	**440**	**408**		**296**	**300**	**-**	**-**	**293**	**280**	**304**
leg I	**526**	**522**	**533**	**640**	**632**	**648**	**-**	**586**	**-**	**-**	**428**	**-**	**416**	**408**	**422**
leg I:veltral length	**1.00**	**0.98**	**1.02**	**1.12**	**1.10**	**1.14**	**-**	**1.00**	**-**	**-**	**-**	**-**	**0.96**	**0.94**	**0.98**
femur I	188	183	189	206	196	216	208	189	148	146	150	-	141	136	148
genu I	61	58	61	82	80	84	80	76	56	54	56	-	54	50	58
tibia I	91	89	94	112	112	112	-	106	68	66	74	-	72	70	74
tarsus I	187	183	189	240	236	244	-	215	-	-	148	-	148	146	152
leg II	**426**	**411**	**436**	**556**	**556**	**556**	**-**	**485**	**350**	**-**	**372**	**-**	**370**	**358**	**376**
leg II:veltral length	**0.81**	**0.77**	**0.84**	**0.97**	**0.97**	**0.98**	**-**	**0.83**	**0.78**	**-**	**-**	**-**	**0.85**	**0.83**	**0.87**
femur II	151	144	156	184	184	184	176	161	104	122	126	120	120	118	124
genu II	53	50	56	74	72	76	76	60	46	48	50	50	49	48	50
tibia II	77	72	78	94	92	96	92	87	66	60	66	0	66	64	70
tarsus II	145	144	147	204	204	204	-	177	134	-	130	0	135	126	140
leg III	**521**	**517**	**528**	**688**	**676**	**700**	**-**	**594**	**446**	**-**	**438**	**-**	**436**	**420**	**446**
leg III:veltral length	**0.99**	**0.98**	**1.00**	**1.20**	**1.19**	**1.22**	**-**	**1.02**	**1.00**	**-**	**-**	**-**	**1.01**	**0.99**	**1.03**
trochanter III	94	89	100	110	108	112	88	115	84	82	88	80	77	74	80
femur III	129	122	139	160	152	168	132	134	104	106	104	102	104	102	108
genu III	54	50	56	74	72	76	72	58	46	46	44	44	46	44	46
tibia III	88	83	92	110	108	112	104	93	72	68	66	-	71	68	74
tarsus III	156	150	167	234	232	236	-	193	140	-	136	-	138	128	146
leg IV	**546**	**539**	**550**	**822**	**804**	**840**	**772**	**732**	**556**	**-**	**538**	**-**	**526**	**516**	**534**
leg IV:veltral length	**1.04**	**1.02**	**1.06**	**1.44**	**1.42**	**1.46**	**1.32**	**1.25**	**1.24**	**-**	**-**	**-**	**1.21**	**1.19**	**1.24**
trochanter IV	134	128	139	156	152	160	156	145	118	118	122	110	112	106	118
femur IV	148	144	150	168	168	168	164	160	114	112	112	112	109	106	110
genu IV	73	72	78	92	88	96	84	74	54	52	44	-	56	54	60
tibia IV	118	117	122	130	124	136	132	119	96	88	90	-	88	86	88
tarsus IV	207	200	211	276	272	280	236	234	174	-	170	-	162	154	168

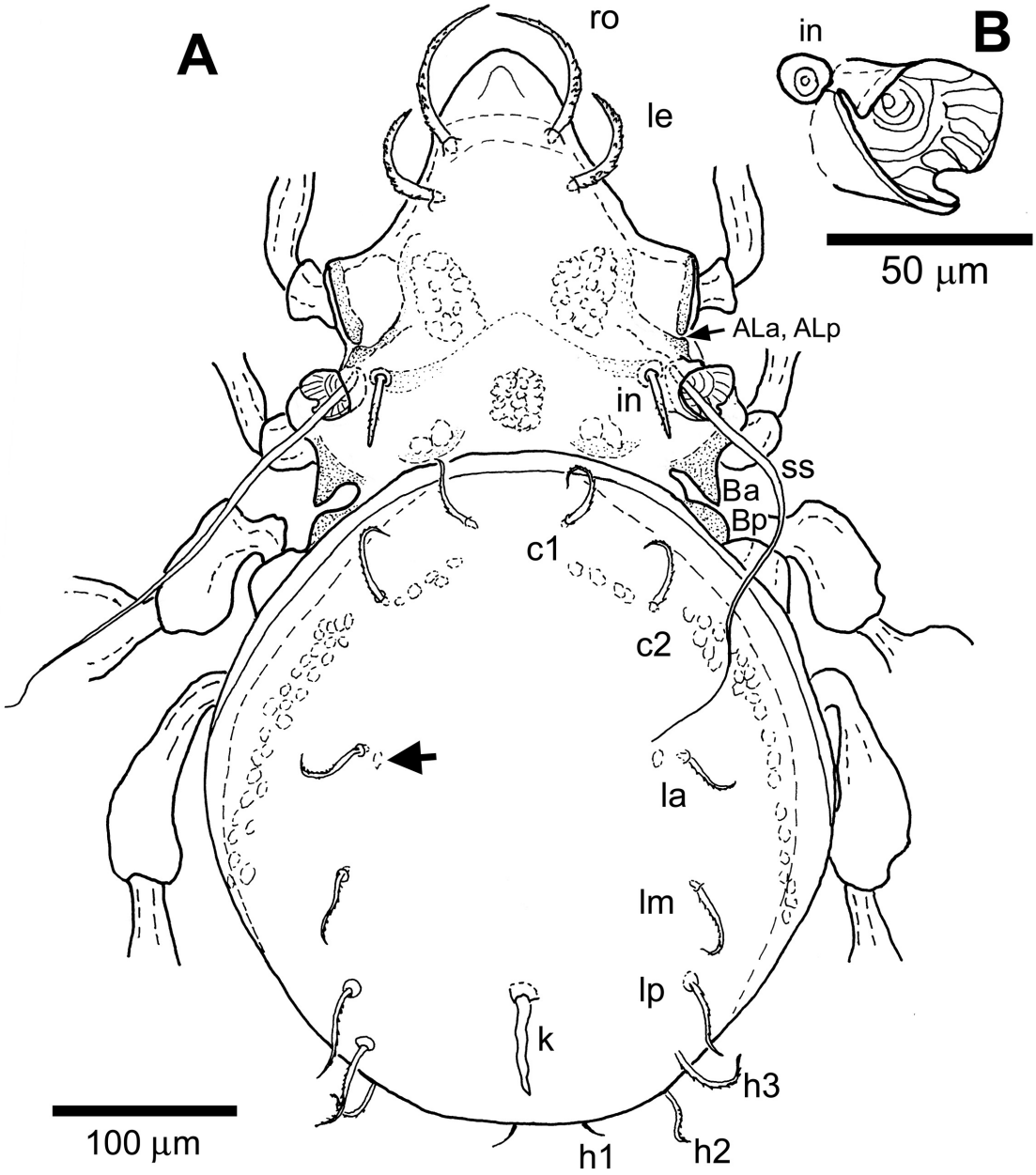


FIGURE 1. *Metabelba* **n. sp. 1** A) dorsal view. larger arrow points to light spot adjacent to seta *la*; B) left bothridium with insertion of interlamellar seta (*in*) – dorsolateral view (sensillus not drawn). Gastronotic exuviae and adherent debris removed, legs only partly drawn, leg setae and cerotegument not drawn.

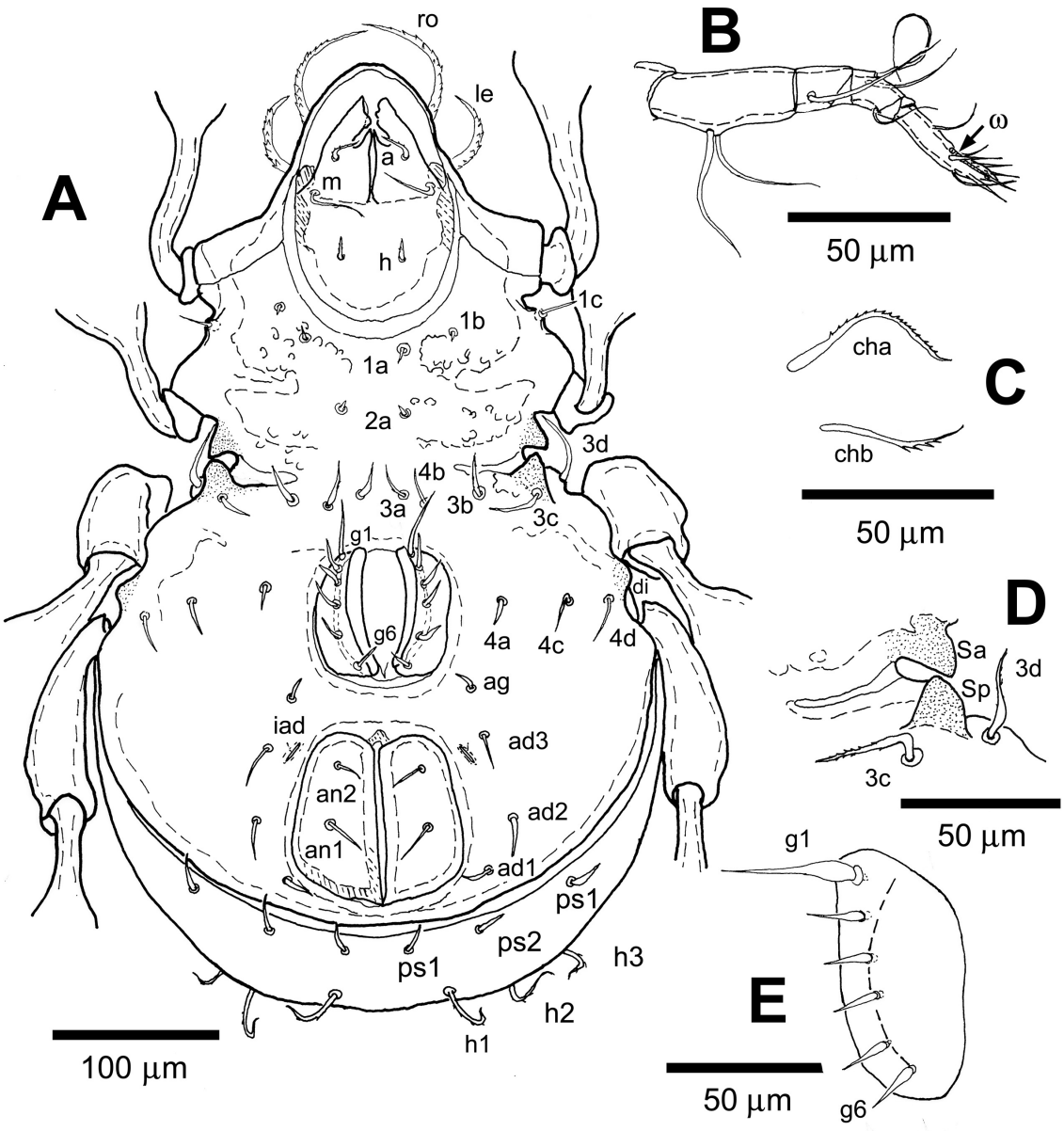


FIGURE 2. *Metabelba* **n. sp. 1** A) ventral view; B) detail of pedipalp – antiaxial view; C) detail of cheliceral setae (*cha*, *chb*) - lateral view; D) detail of ventrosejugal apophyses (*Va, Vp*) with adjacent epimeral setae (*3c*, *3d*); E) detail of genital plate - drawn in open state in lateral view. Legs only partly drawn, leg setae and cerotegument not drawn.

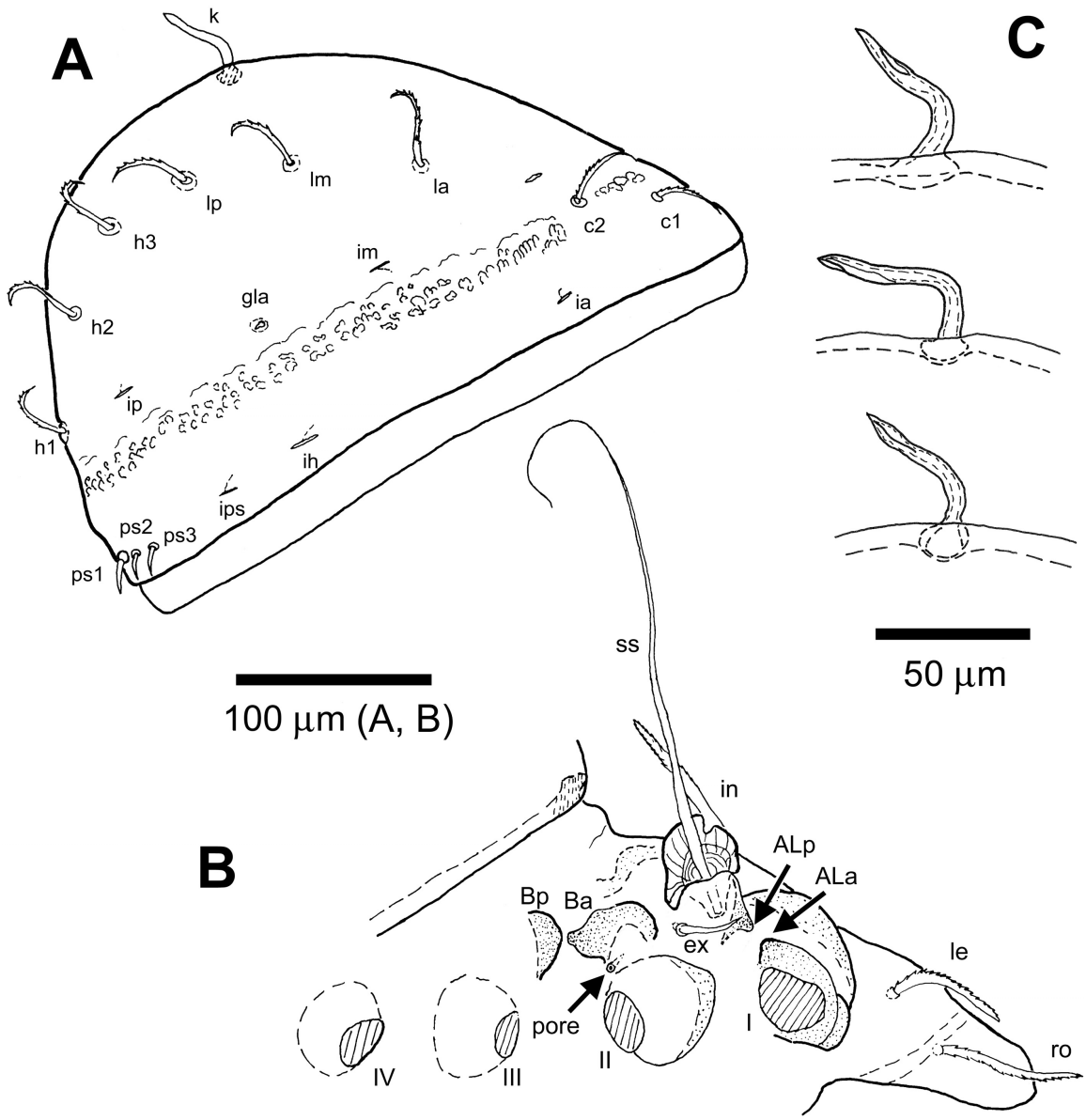


FIGURE 3. *Metabelba denscanis* **n. sp. 1** A) notogaster - lateral view; B) prodorsum and dorsosejugal area – partial lateral view. Roman numerals mark leg acetabula; C) variation in shape of the cornicle *k*- lateral view. Gastronotic exuviae and adherent dirt removed, cerotegument not drawn.

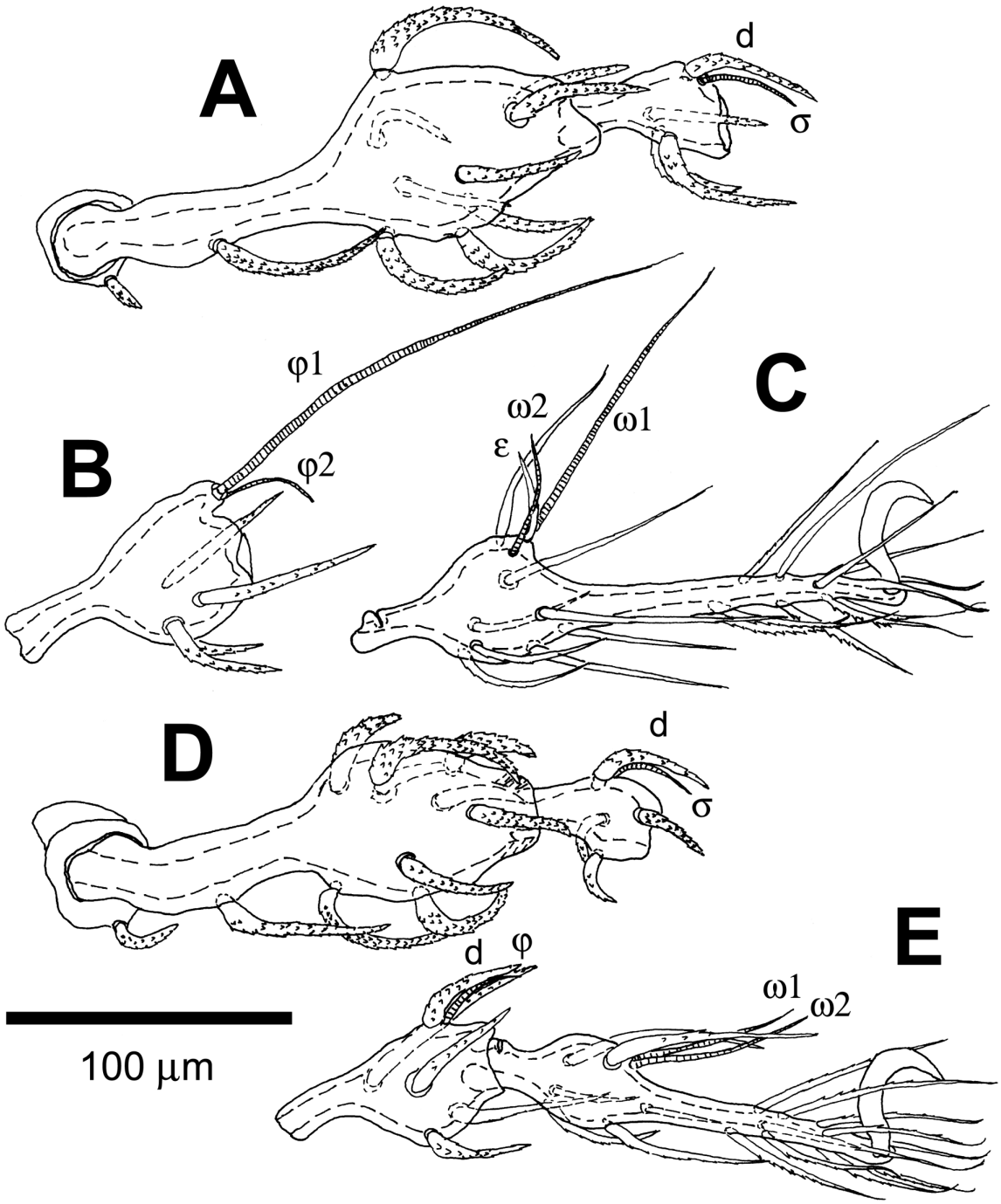


FIGURE 4. *Metabelba* **n. sp. 1** - leg I and II, antiaxial view. A) trochanter, femur and genu I; B) tibia I; C) tarsus I; D) trochanter, femur and genu II; E) tibia and tarsus II. Cerotegument not drawn.

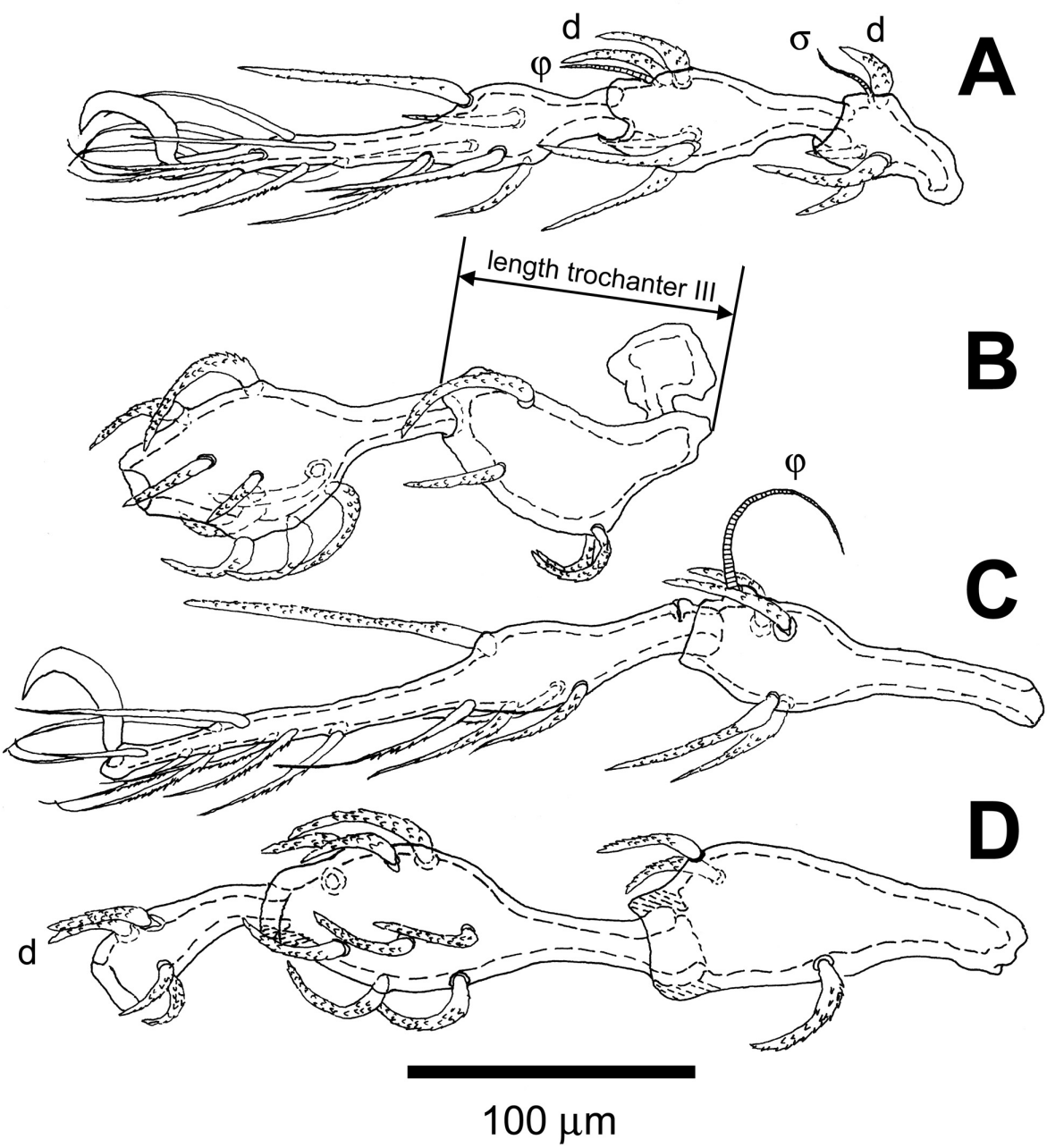


FIGURE 5. *Metabelba* **n. sp. 1**, leg III and IV, antiaxial view. A) tarsus, tibia and genu III; B) femur and trochanter III; C) tarsus and tibia IV; D) genu, femur and trochanter IV. Cerotegument not drawn.

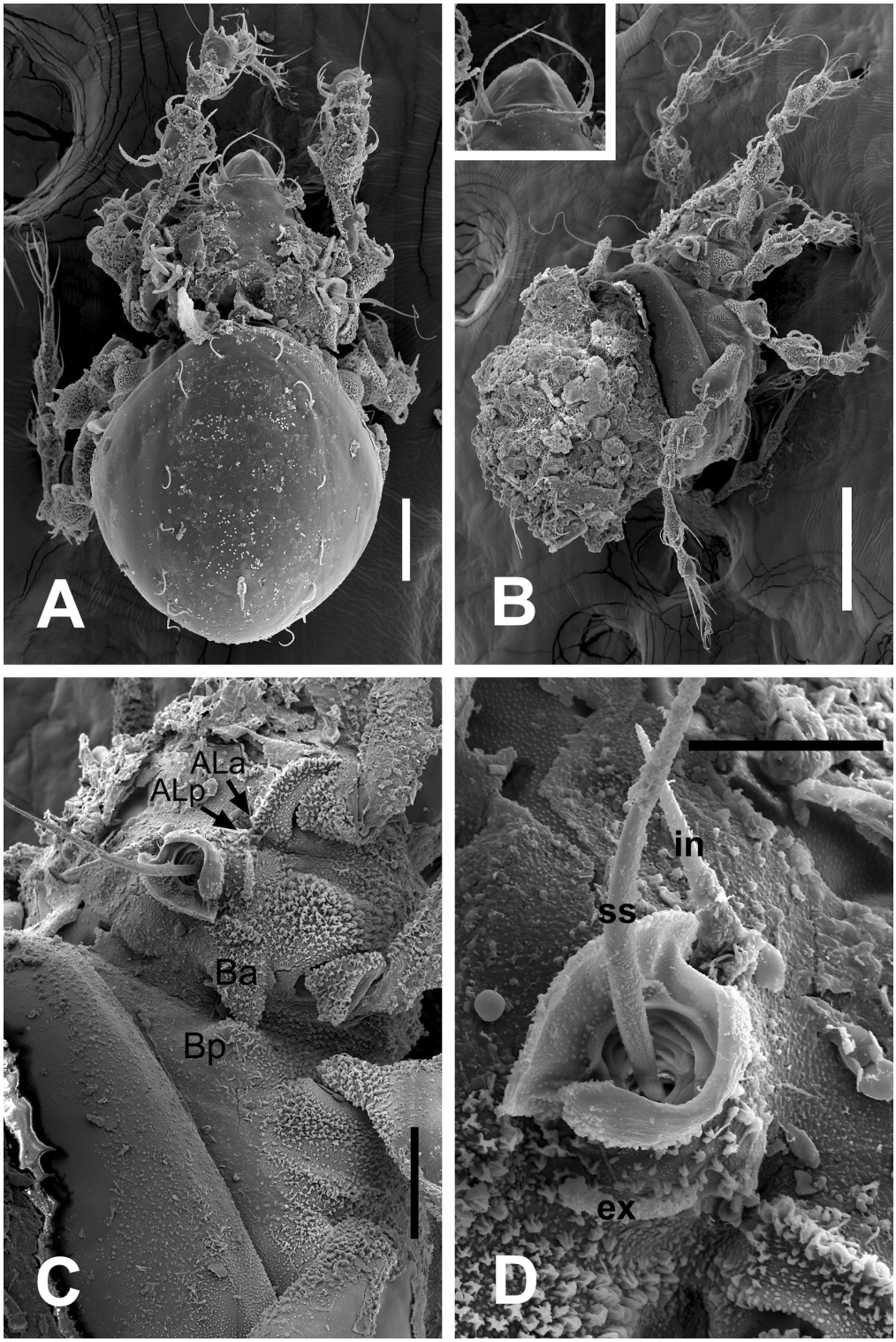


FIGURE 6. *Metabelba* **n. sp. 1** - SEM micrographs. A) dorsal view, gastronotic exuviae and adherent dirt removed from the notogaster; B) lateral view. Note presence of gastronotic exuviae covered with mass of adherent dirt. Inserted small image - detail of rostrum in dorsal view; C) detail of bothridial region of prodorsum and sejugal area with parastigmatic apophyses (*Sa, Sp*) and propodolateral apophyses (*ALa, ALp*)- lateral view; D) detail of bothridium - lateral view. Cerotegument partly damaged during the preparation of specimens. Scale bars: A – 100 μm; B – 200 μm; C – 50 μm; D – 25 μm.

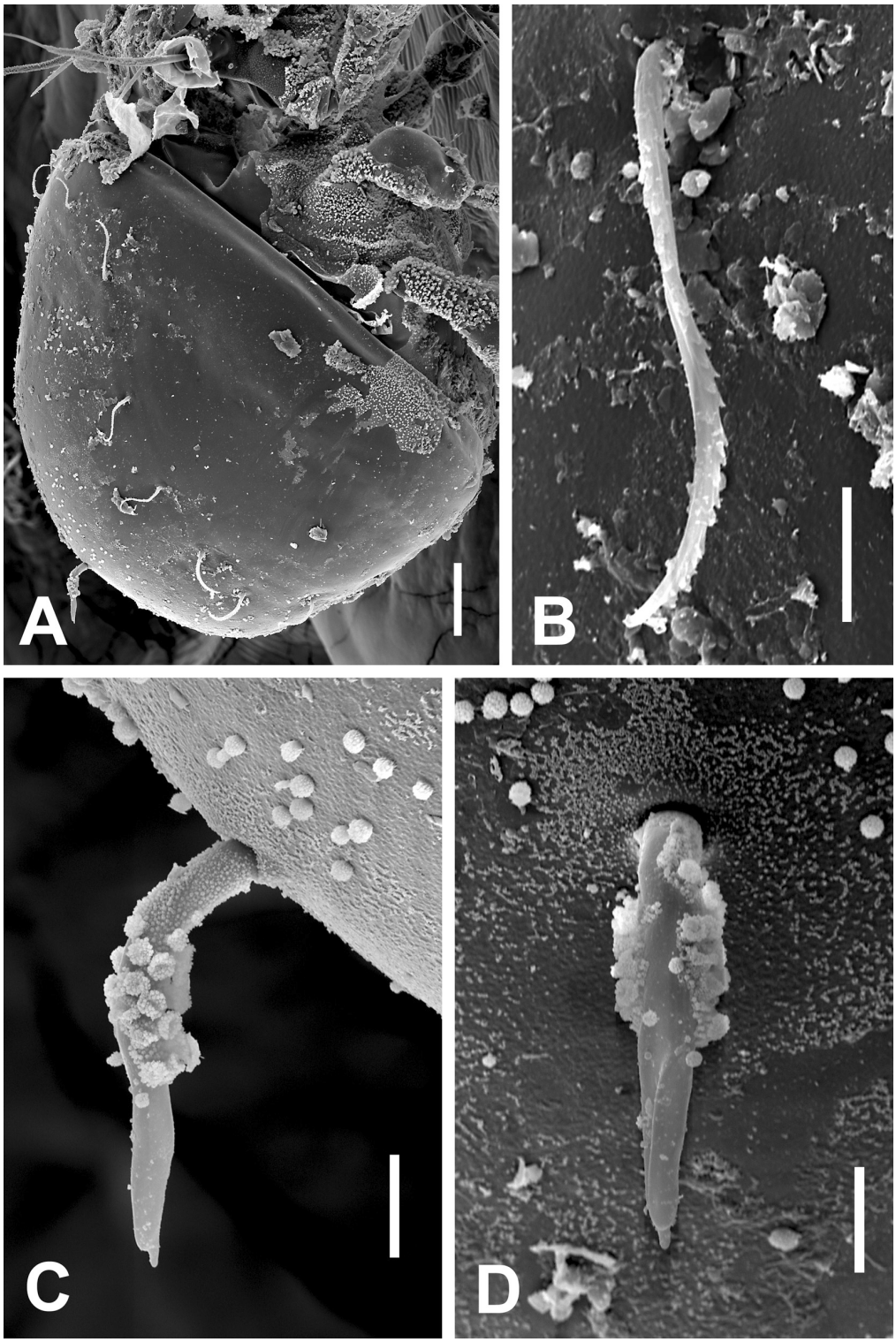


FIGURE 7. *Metabelba* **n. sp. 1**. - SEM micrographs. A) notogaster - lateral view; B) detail of notogastral seta *c2* - lateral view; C) detail of cornicle *k* - lateral view; D) detail of cornicle *k* - dorsal view. Gastronotic exuviae and adherent dirt removed from the notogaster, cerotegument partly damaged during the preparation. Scale bars: A – 50 μm; B – 10 μm; C -10 μm; D – 10 μm.

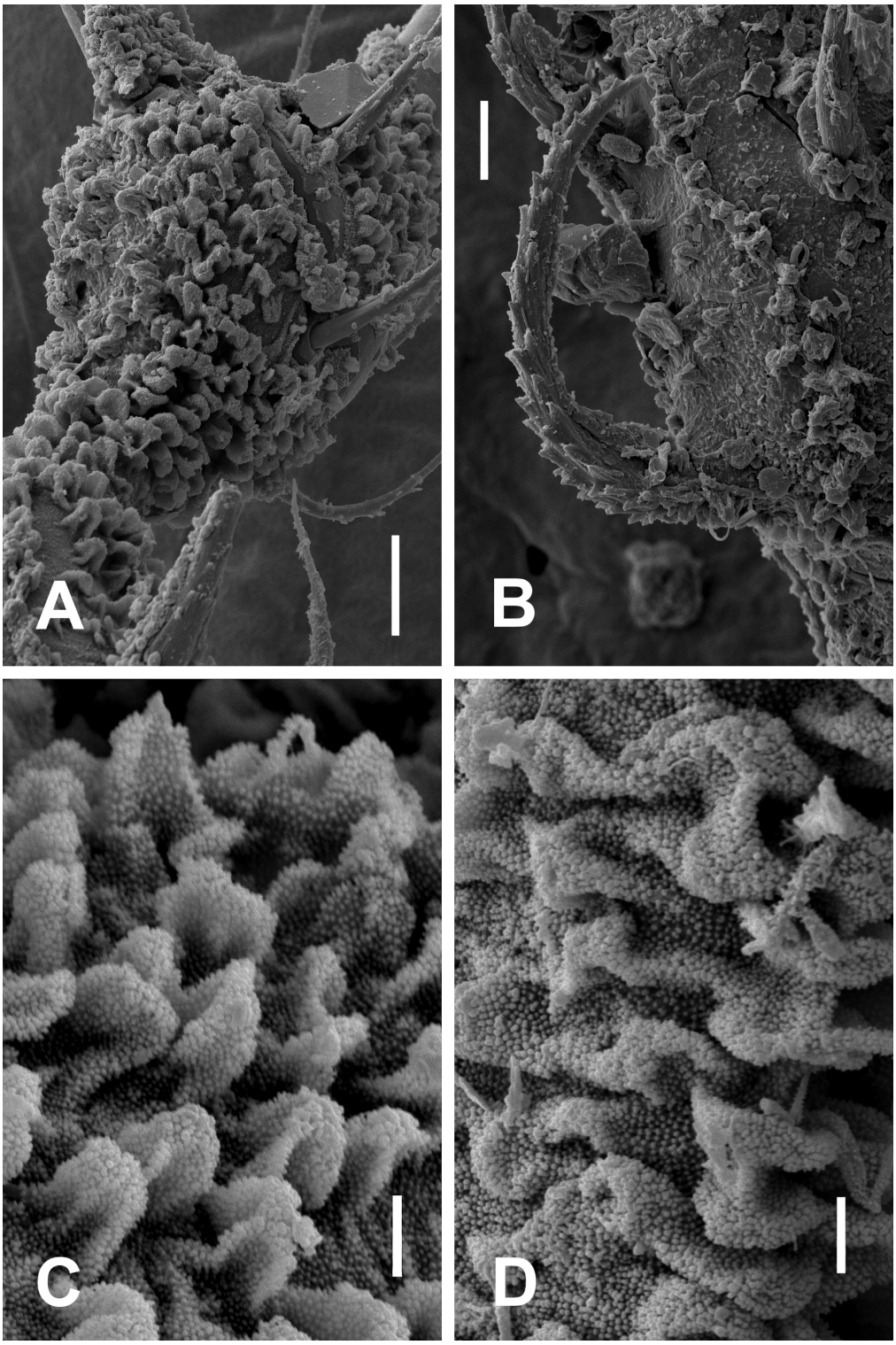


FIGURE 8. *Metabelba* **n. sp. 1** - SEM micrographs. A) cerotegument on distal part of tibia I and proximal part of tarsus I; B) detail of seta *d* on femur I (cerotegument microsculpture abraded); C) detail of cerotegument on epimere II; D) detail of cerotegument on proximal femur I. Scale bars: A – 10 μm; B – 10 μm; C -2 μm; D – 2 μm.

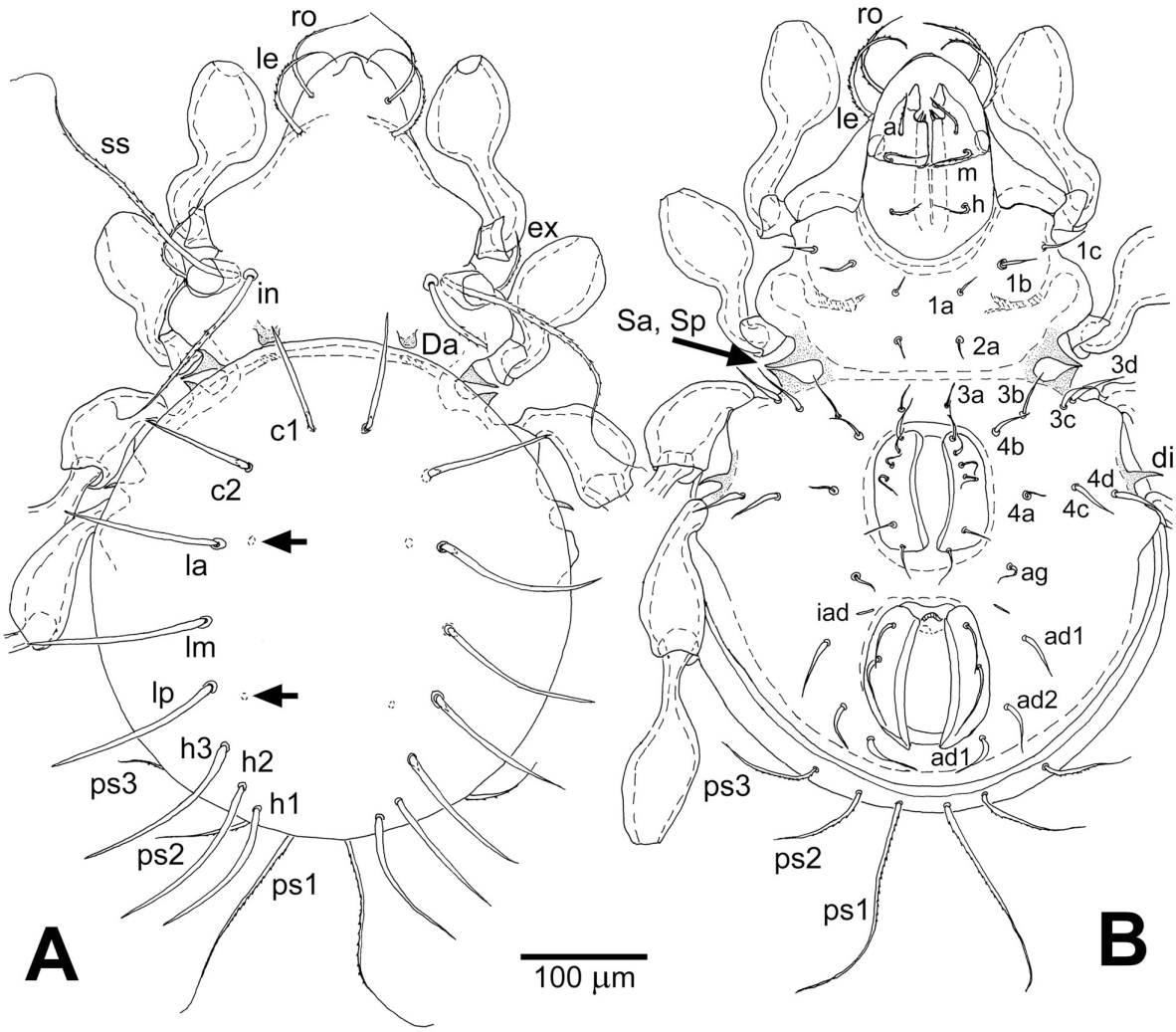


FIGURE 9. *Metabelba romandiolae* - specimen from S. Benedetto in Alpe. A - dorsal view, arrows point to light spots; B - ventral view. Legs only partly drawn, leg setae and cerotegument not drawn.

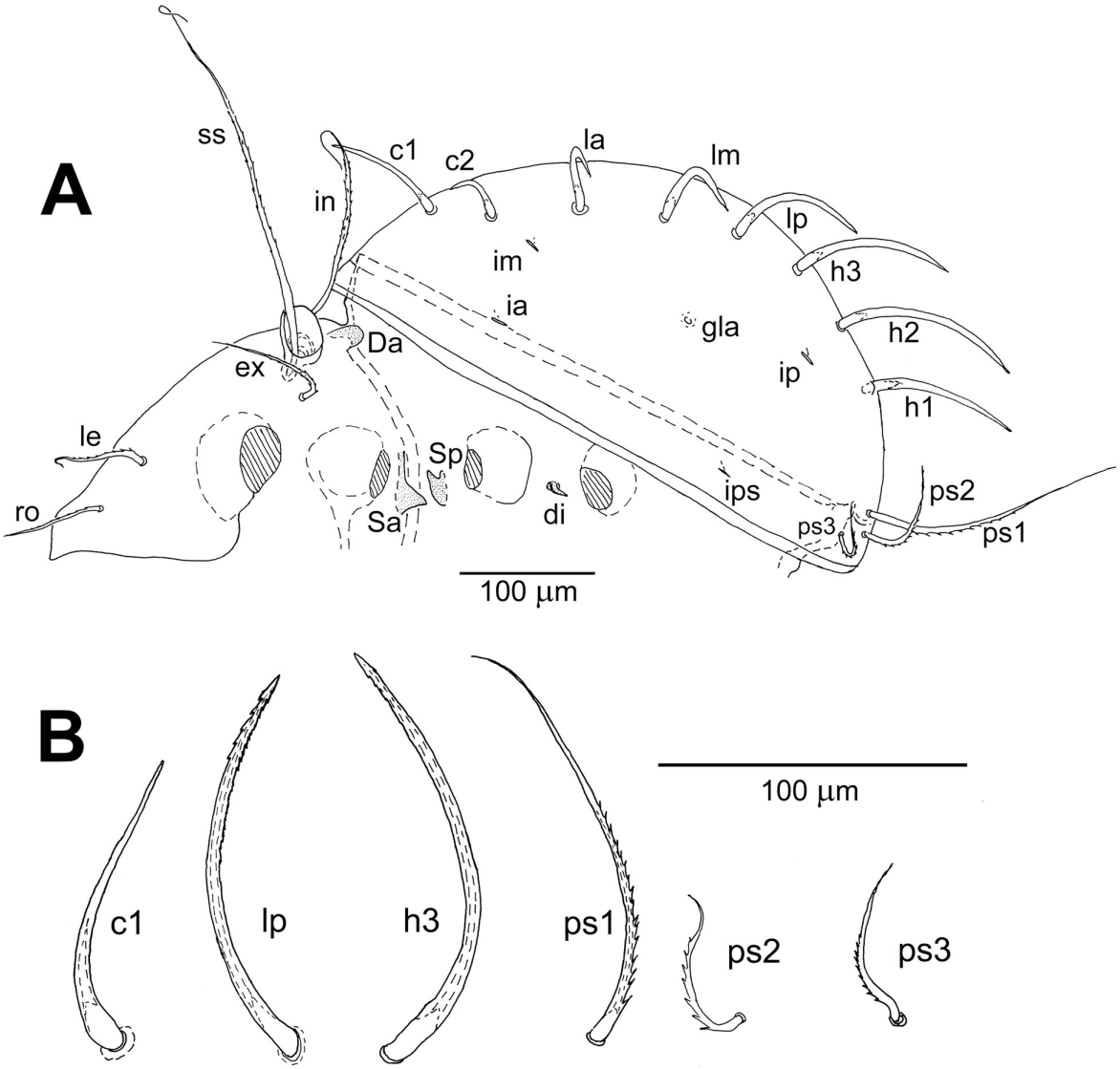


FIGURE 10. *Metabelba romandiolae.* A - specimen from S. Benedetto in Alpe, partial lateral view; B) specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym) - details of some notogastral setae. Cerotegument not drawn.

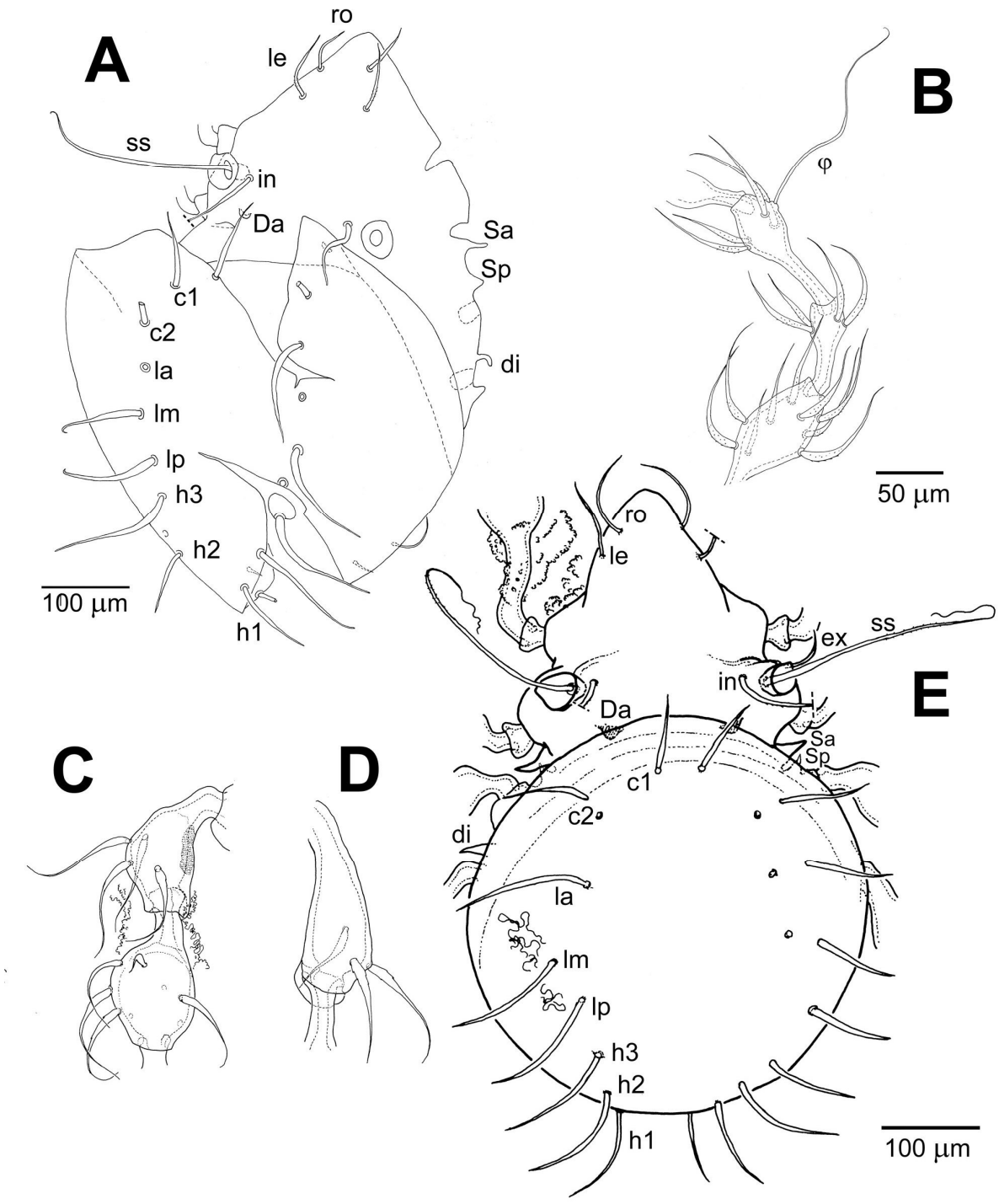


FIGURE 11. *Metabelba romandiolae.* - neotype, coll. of P. Zangheri, drawn by F. Bernini (A, B); specimen from coll. of C. Willmann, labelled as "*Belba setiger*", drawn by L. Miko (C, D, E). A - dorsolateral view; B - tibia, genu and distal part of femur IV; C - trochanter and femur III; D - trochanter IV; E - dorsal view. Cerotegument not drawn in A, B and partly drawn in C, D, E.

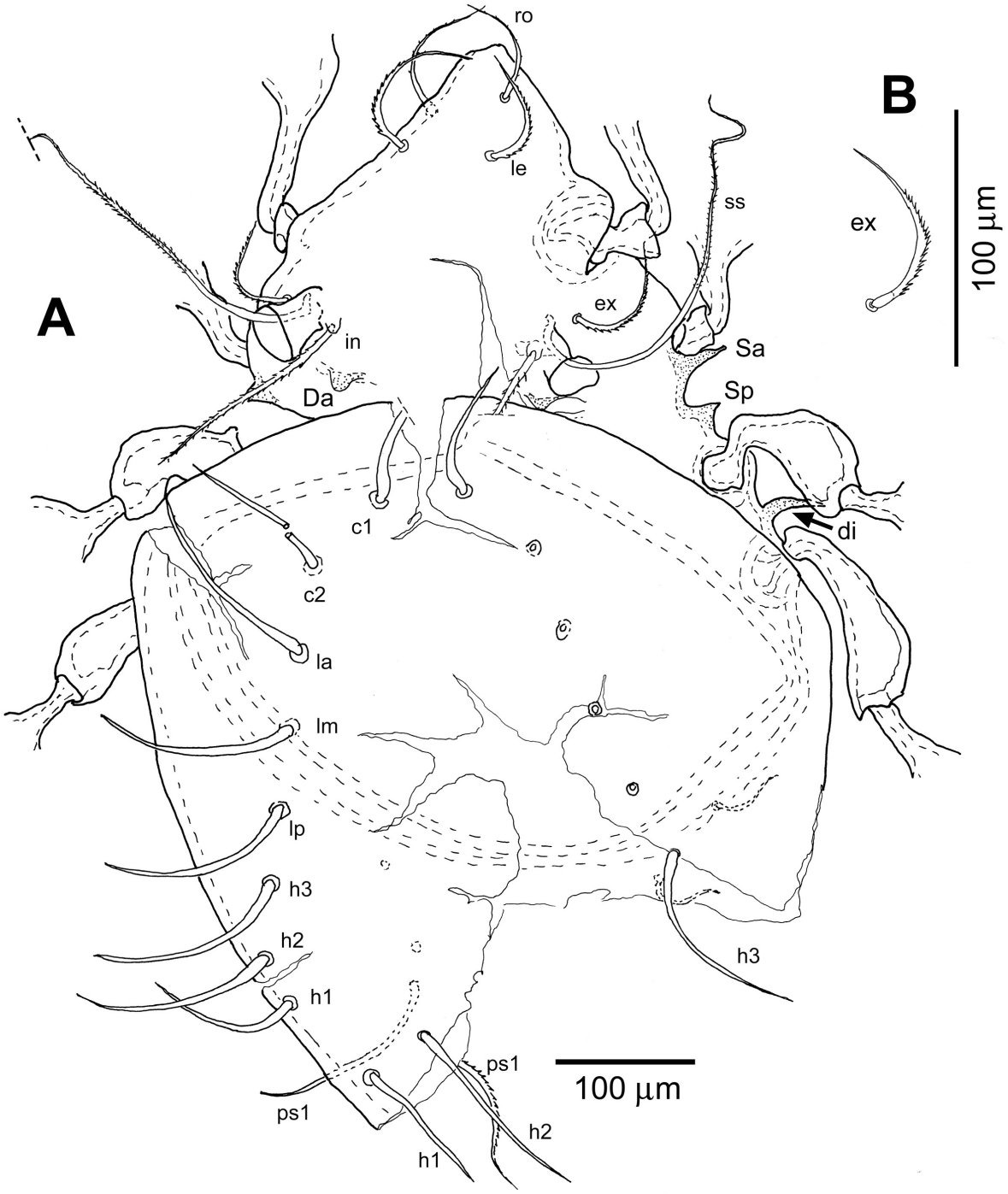


FIGURE 12. *Metabelba romandiolae* - specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym). A - dorsal view. Legs only partly drawn, leg setae and cerotegument not drawn. B - exobothridial seta in detail.

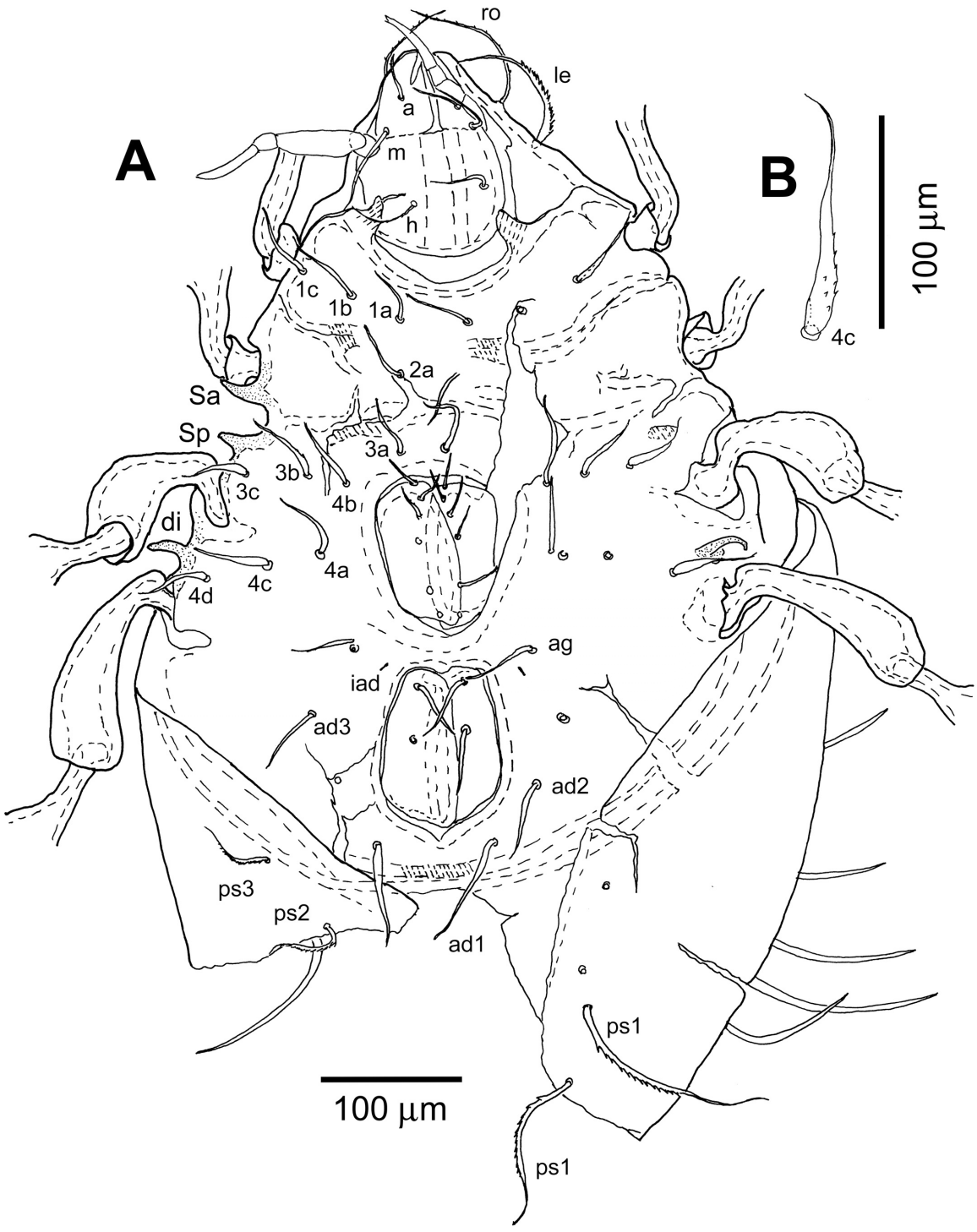


FIGURE 13. *Metabelba romandiolae* - specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym). A) ventral view in total. Legs only partly drawn, cerotegument and setae of legs and pedipalps not drawn; B) detail of epimeral seta *4c*.

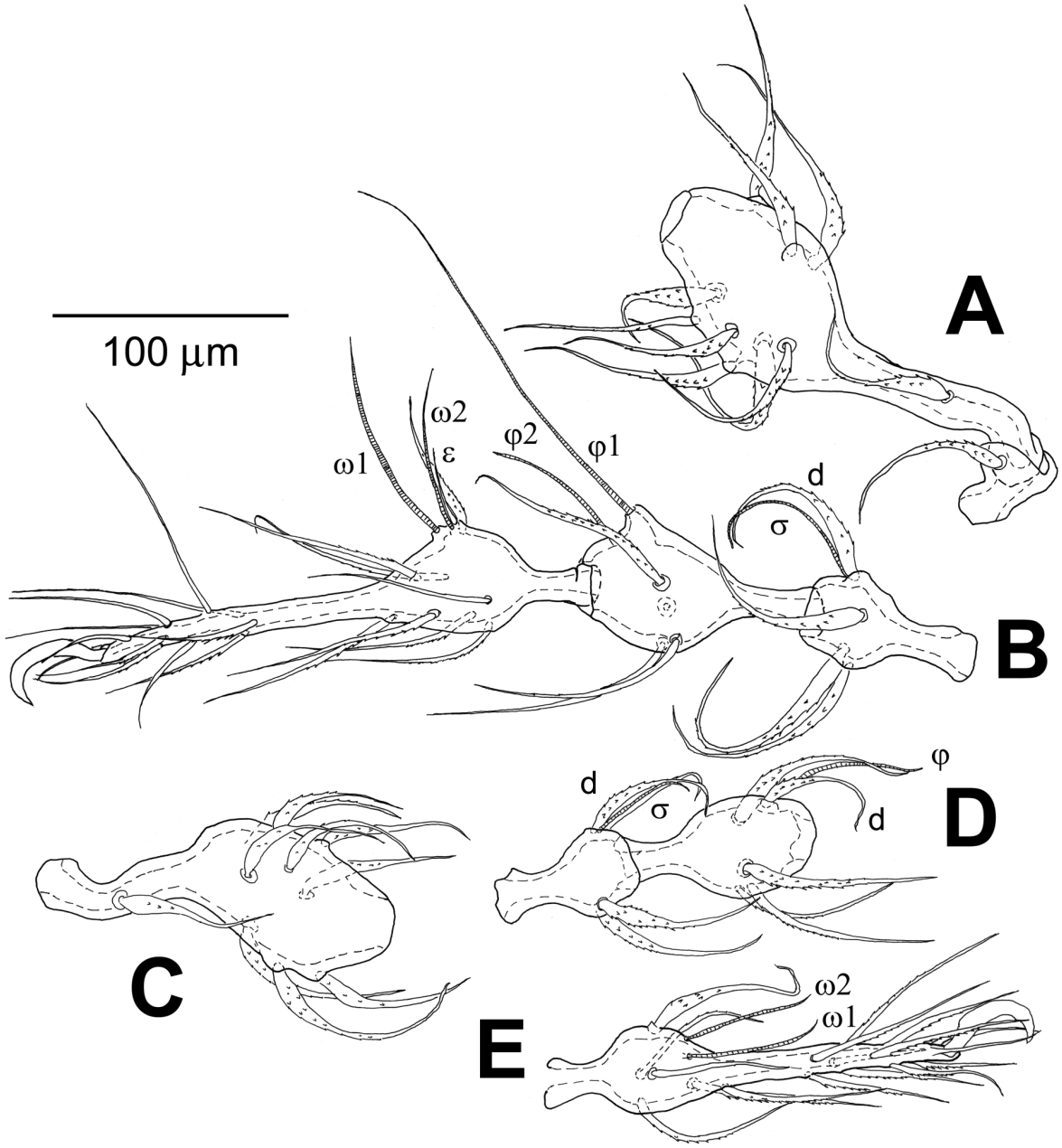


FIGURE 14. *Metabelba romandiolae* - - specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym) - leg I and II. A) left trochanter and femur I, antiaxial view; B) left genu, tibia and tarsus I, antiaxial view; C) left femur II, paraxial and slightly ventral view; D) left genu and tibia II, paraxial view; E) left tarsus II, paraxial view.

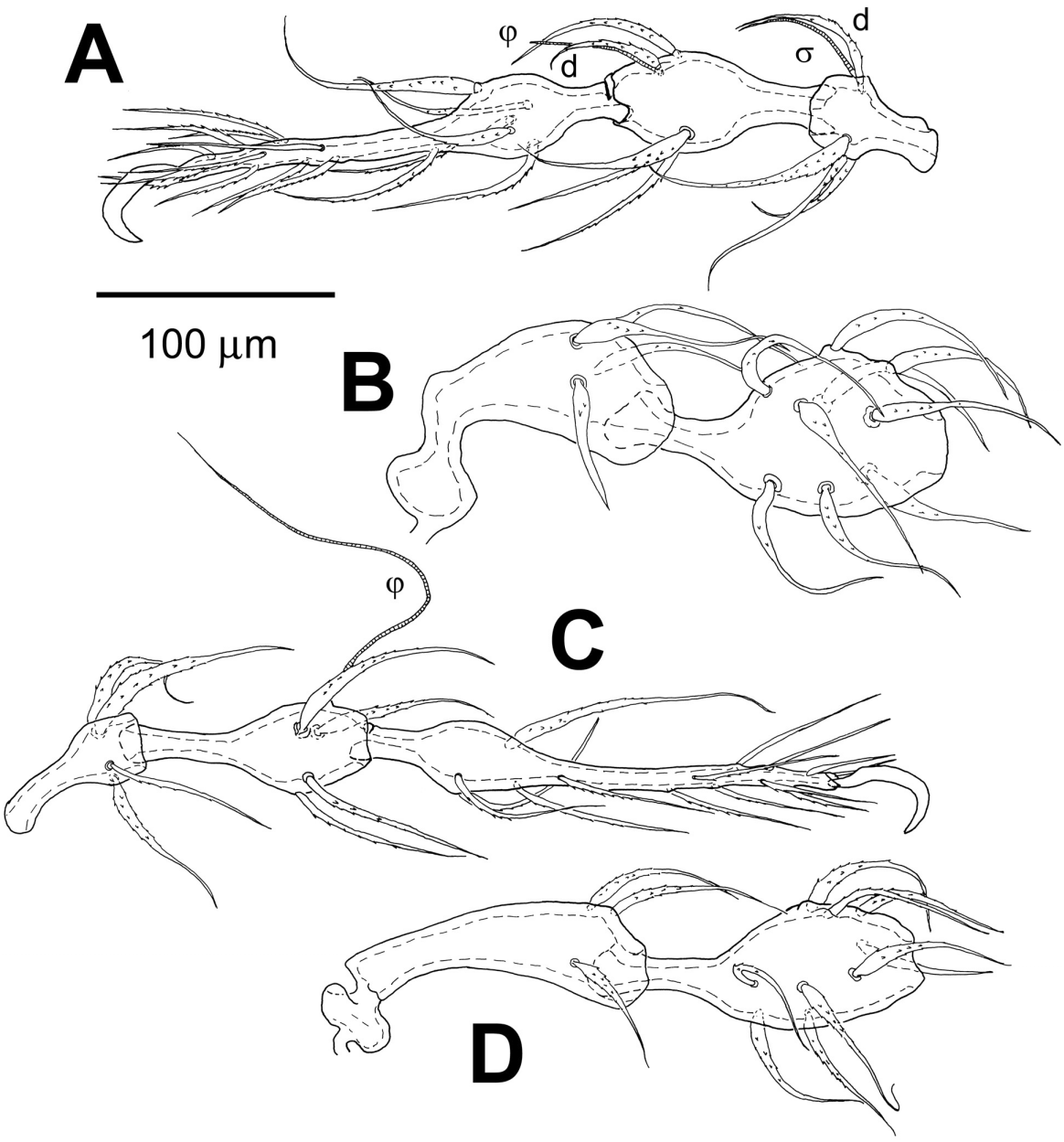


FIGURE 15. *Metabelba romandiolae* - specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym) - leg III and IV. A) right genu, tibia and tarsus I, antiaxial view; B) left trochanter and femur III, antiaxial and slightly ventral view; C) left genu, tibia and tarsus IV, antiaxial and slightly ventral view; D) left trochanter and femur IV, antiaxial and slightly ventral view.

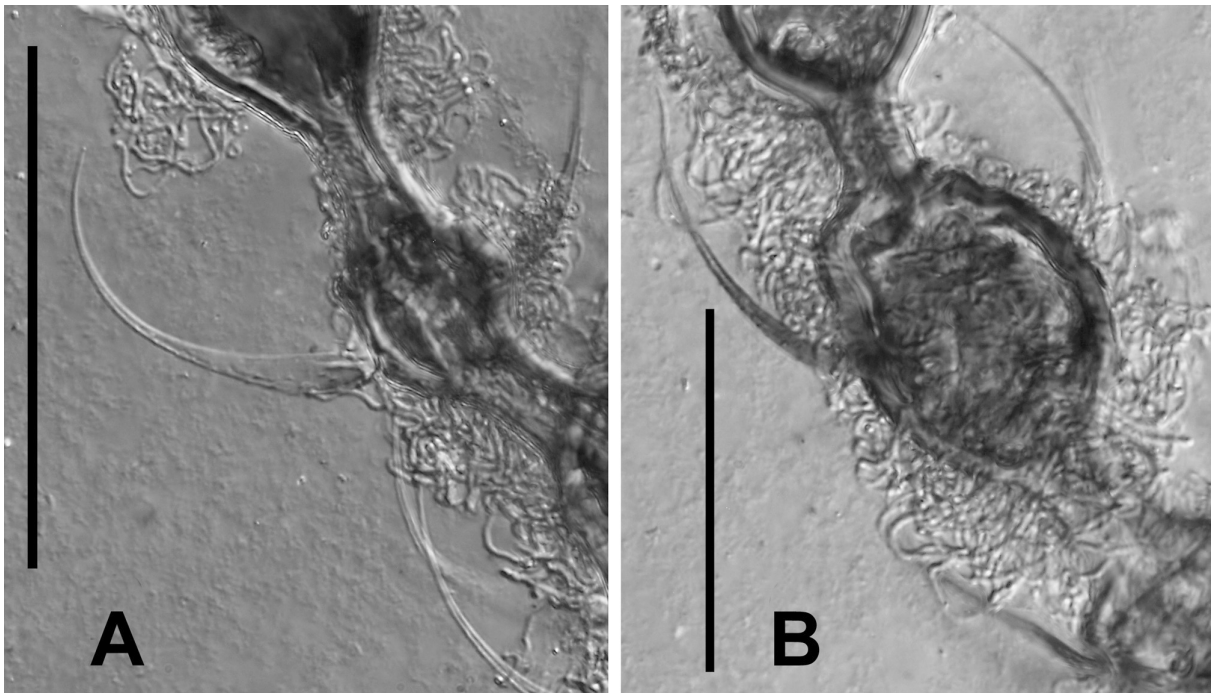


FIGURE 16. *Metabelba romandiolae* - - specimen from collection of F. Mihelčič labelled as "type of *Metabelba gladiator"* (junior synonym), light micrographs, Nomarski DIC. A) detail of genu III with typical leg setae; B) cerotegument on tibia IV. Scale bars: 100 μm.

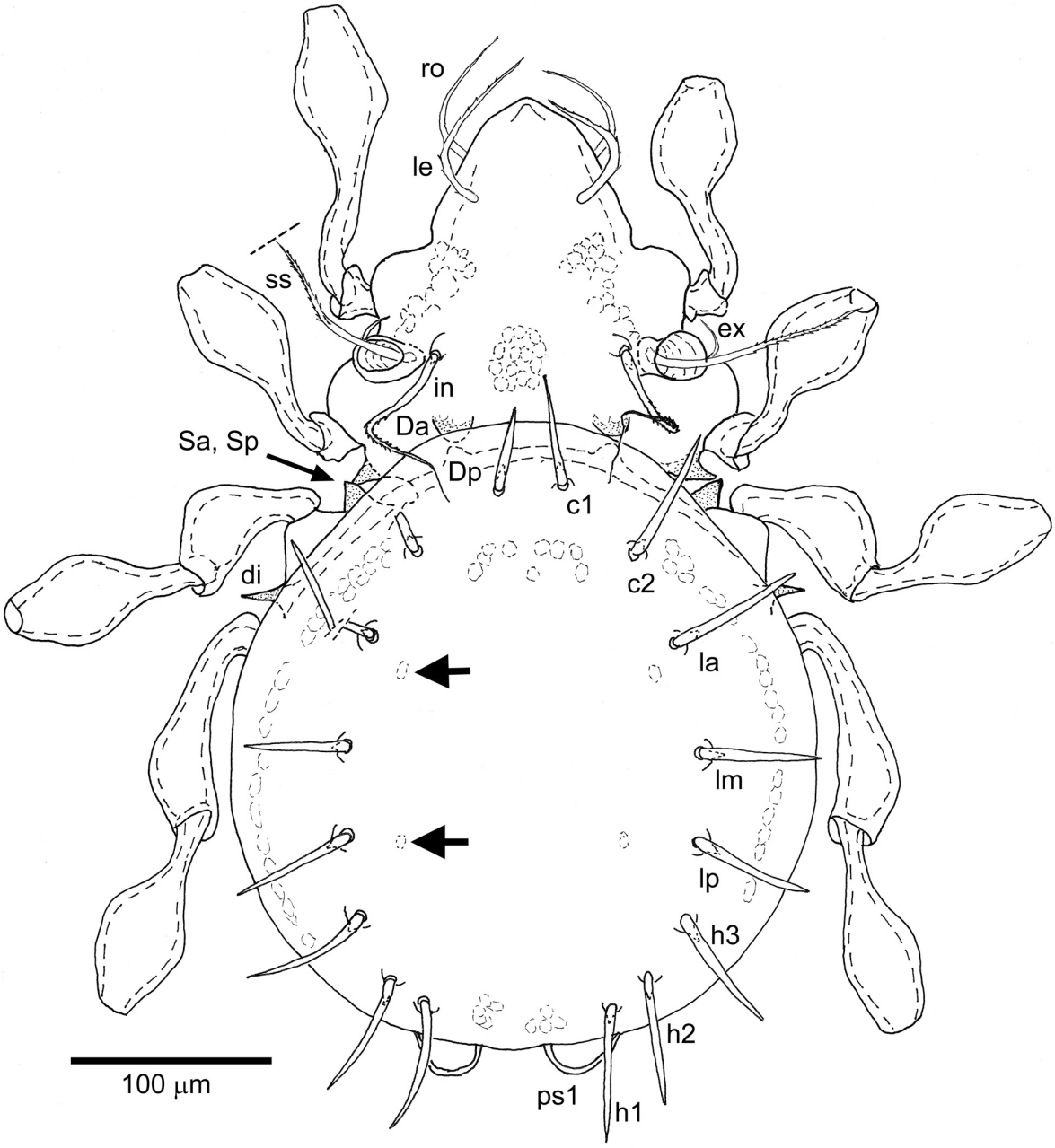


FIGURE 17. *Metabelba sphagni* - holotype, dorsal view. Short arrow points to light spots adjacent to setae *la* and *lp*. Legs only partly drawn, leg setae and cerotegument not drawn.

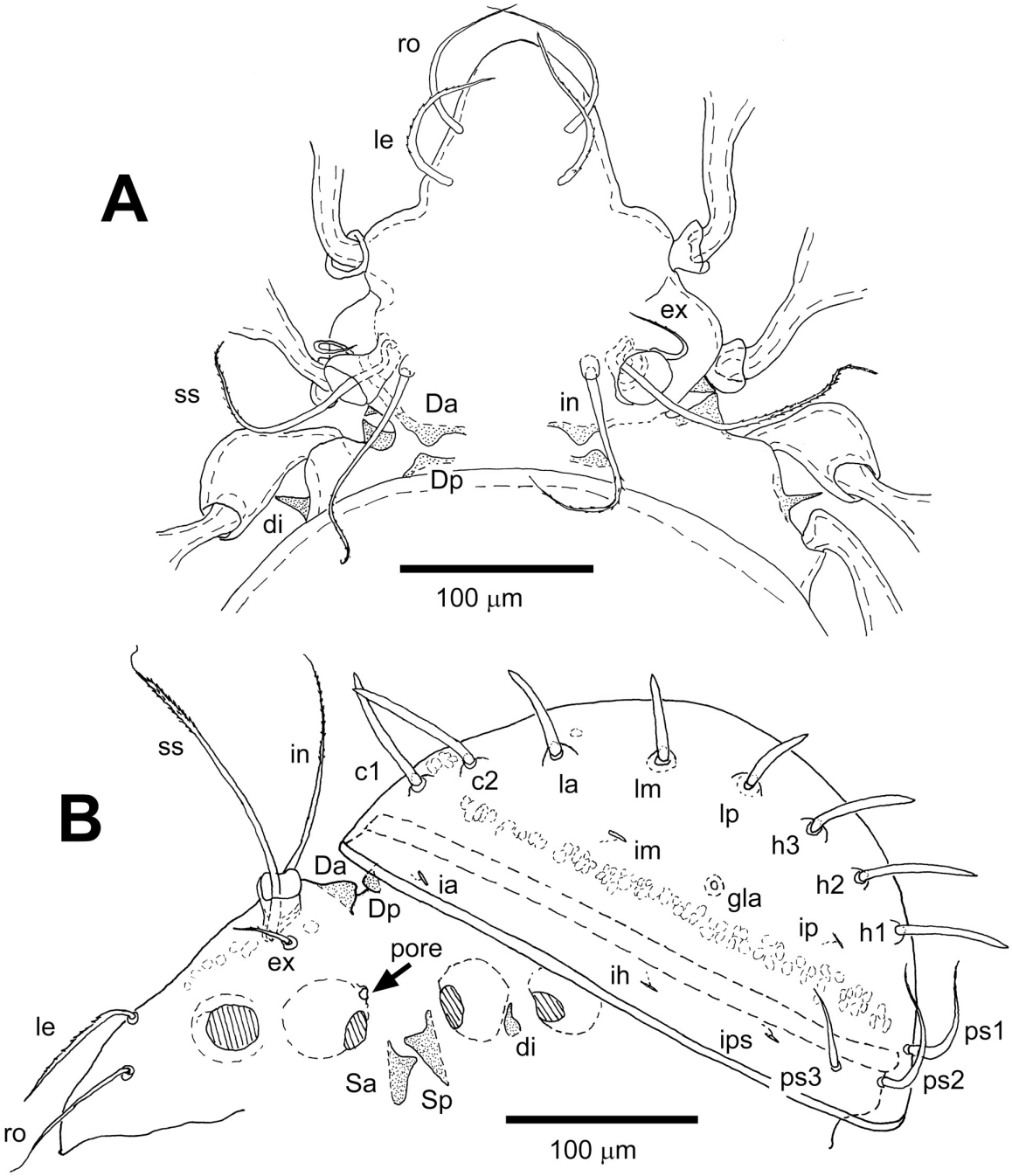


FIGURE 18. *Metabelba sphagni*. A - paratype, prodorsum in dorsal view B- specimen from Ruda, South Bohemia, ventral view. Legs only partly drawn, leg setae and cerotegument not drawn.

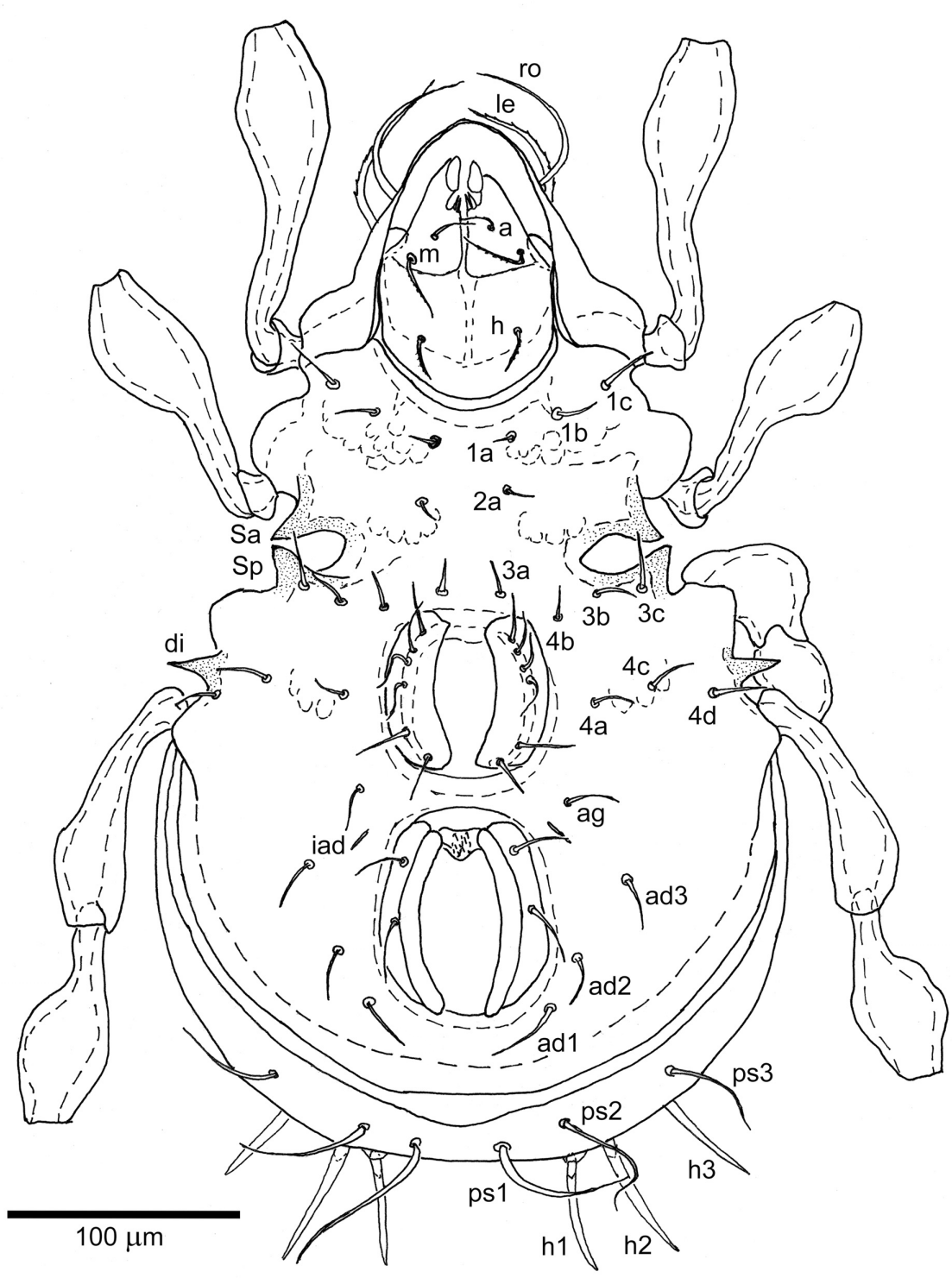


FIGURE 19. *Metabelba sphagni* - specimen from Ruda, South Bohemia, ventral view. Legs only partly drawn, leg setae and cerotegument not drawn.

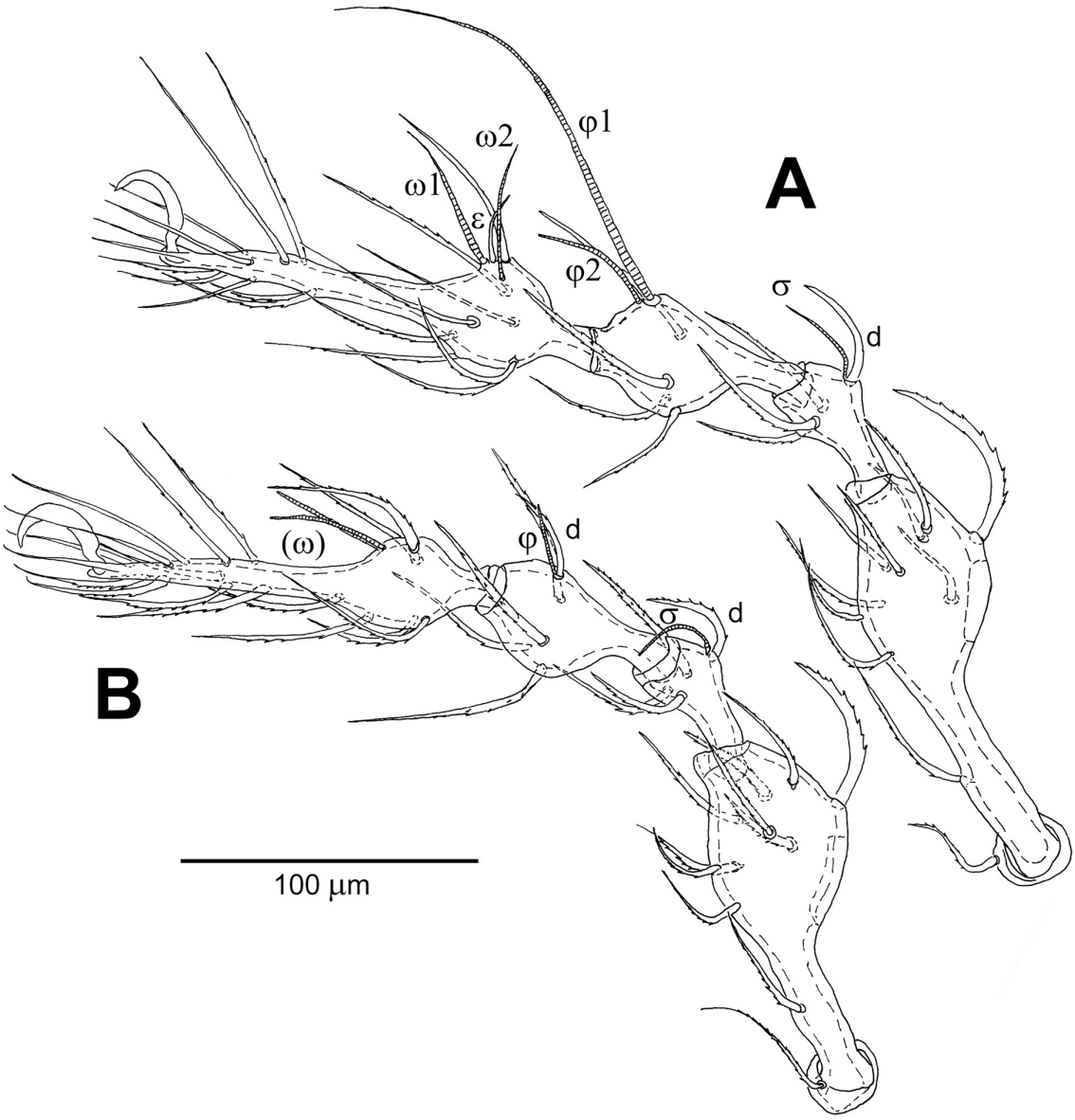


FIGURE 20. *Metabelba sphagni* - specimen from Ruda, South Bohemia, leg I and II. A - leg I, antiaxial view; B - leg II, antiaxial view. Cerotegument not drawn.

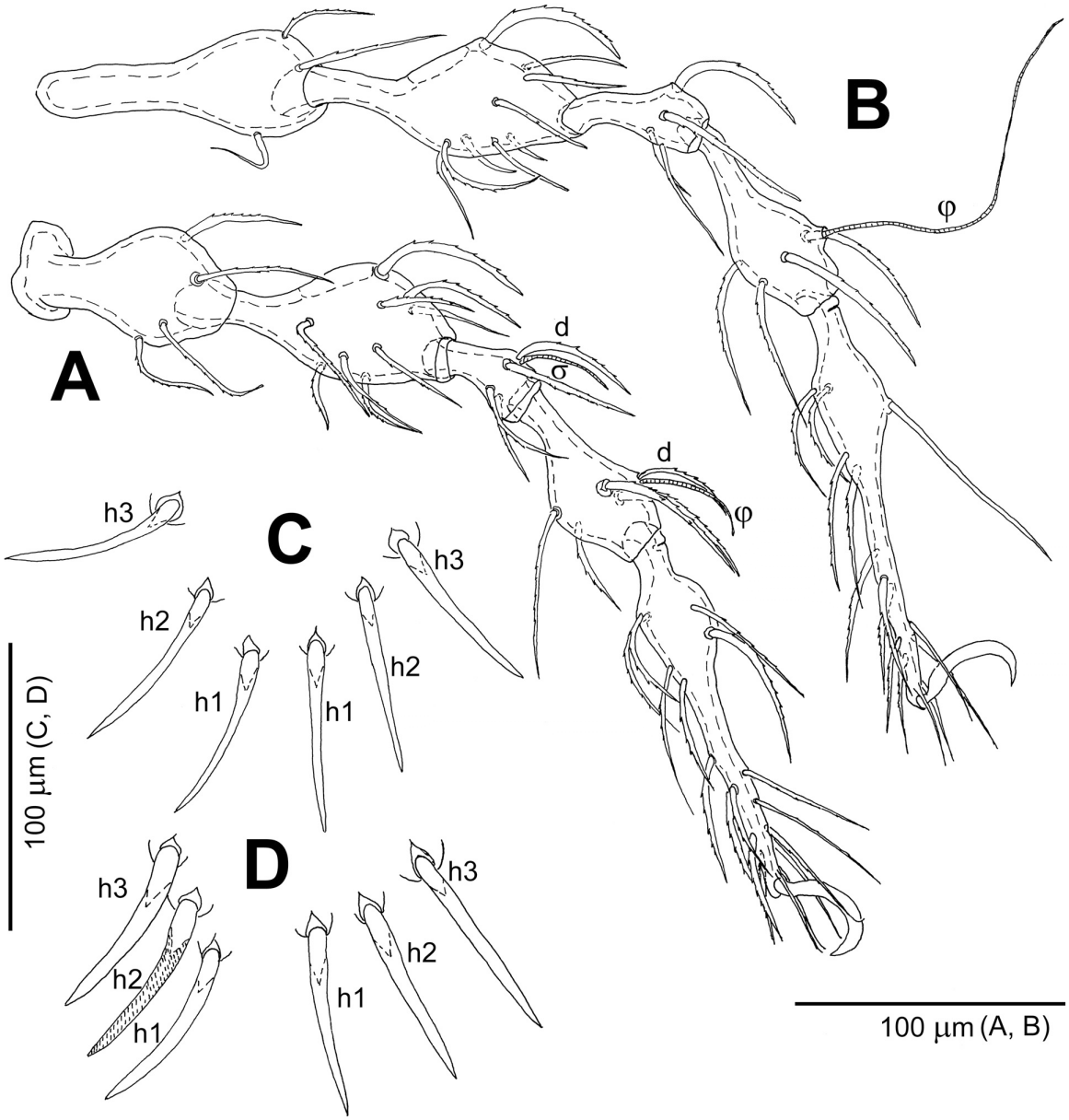


FIGURE 21. *Metabelba sphagni* - leg III and IV and details of some notogastral setae. Specimen from Ruda, South Bohemia (A, B), holotype (C); specimen from Velký Tisý South Bohemia, coll. of M. Kunst (D), labelled as "*Metabelba lanceolata*". A - leg III, antiaxial view; B - leg II, antiaxial view. C, D - details of notogastral setae *h1* - *h3* from both sides of the body of a given specimen mounted in permanent slide, relative distance between setae not maintained. Cerotegument not drawn.

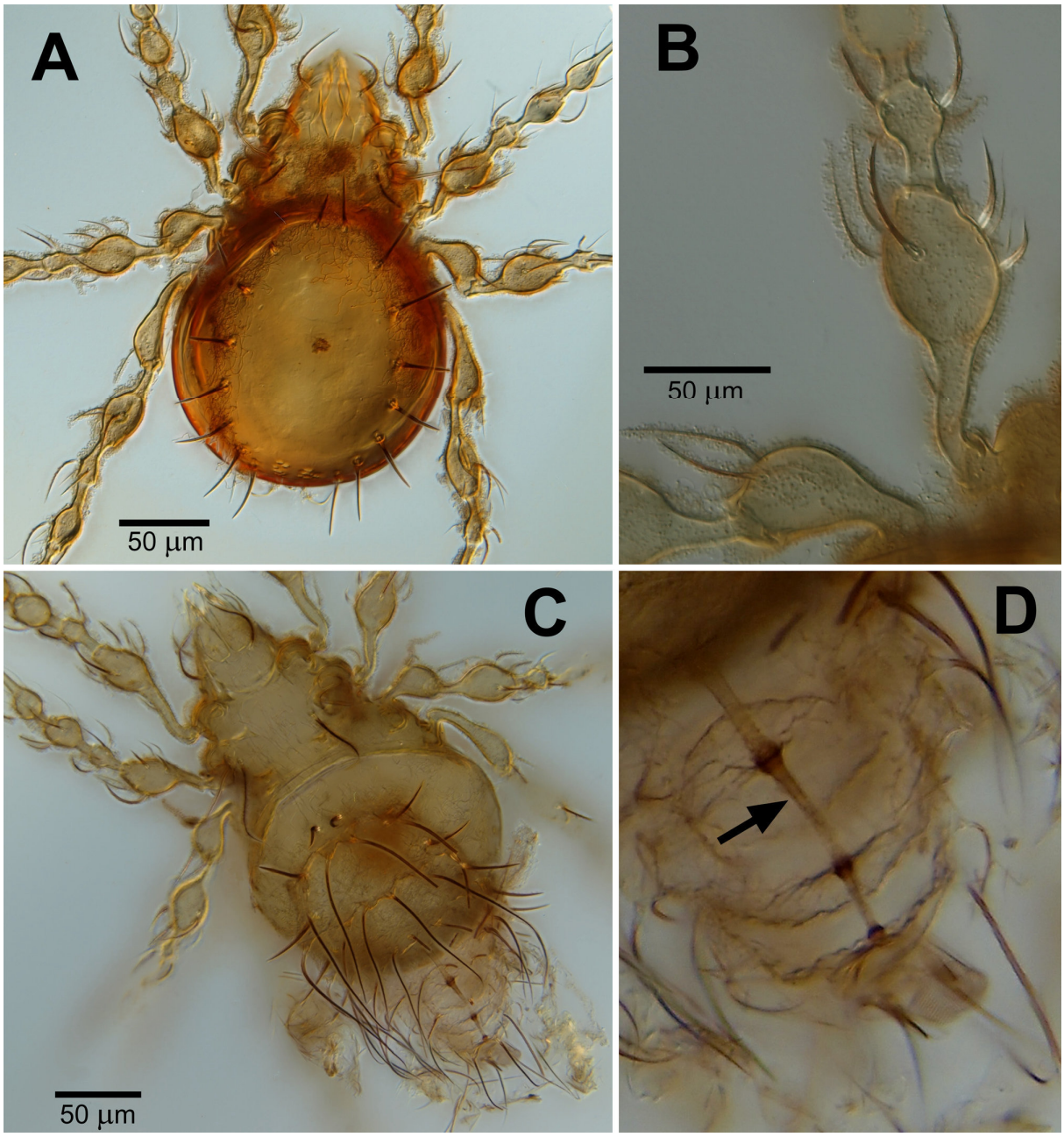


FIGURE 22. *Metabelba sphagni* - light micrographs, Nomarski DIC. A - holotype, dorsal view; B - paratype, proximal segments of leg II and III with cerotegument; C - paratype with gastronotic exuvia, anterodorsal view; D - paratype - detail of gastronotic exuviae, arrow points to cornicle *k* of deutonymphal exuvium.

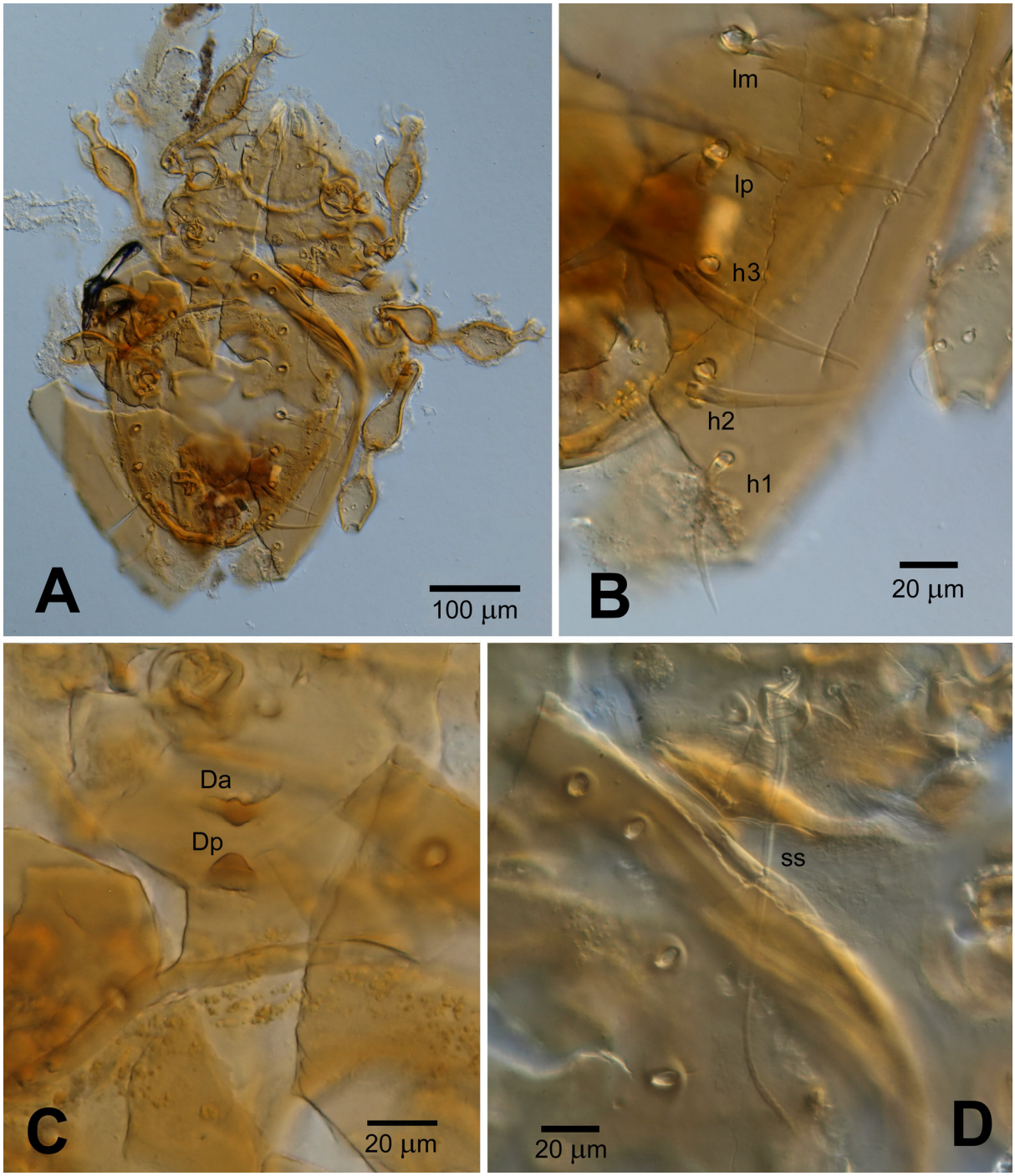
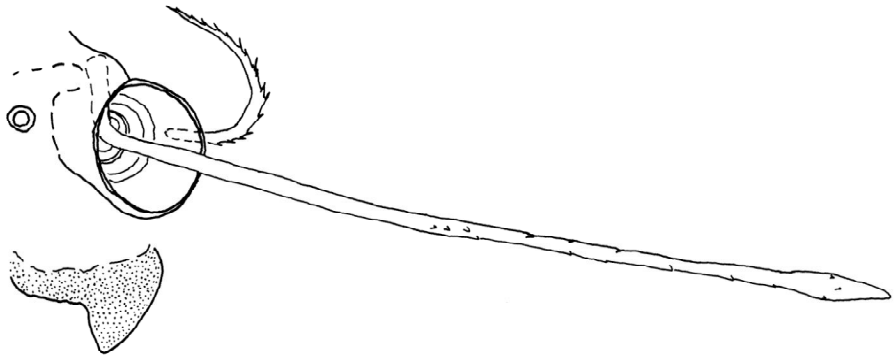


FIGURE 23. *Metabelba sphagni* - specimen from collection of L. van der Hammen labelled as "holotype of *Metabelba lanceolata"* (new synonymy), light micrographs, Nomarski DIC. A - dorsal view in total; B - detail of some notogastral setae; C - detail of centrodorsal tubercles (*Da*, *Dp*) on prodorsum; D - detail of sensillus and insertions of anterior notogastral setae.

Contribution 1.5

Mourek, J., Miko, Skubała, P. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) V. Redescription of *Epidamaeus bituberculatus* (Kulczynski, 1902).



TAXONOMY OF EUROPEAN DAMAEIDAE (ACARI: ORIBATIDA) V. REDESCRIPTION OF *EPIDAMAEUS BITUBERCULATUS* (KULCZYNSKI, 1902)

Jan Mourek[1,2] Ladislav Miko[3]and Piotr Skubała[4]

1. Charles University, Faculty of Science, Department of Zoology and Dept. of Teaching and Didactics of Biology, Viničná 7, CZ-128 44 Prague, Czech Republic (e-mail: jan_mourek@yahoo.co.uk), coresponding author;

2. Charles University, Faculty of Education, Department of Biology and Environmental Studies, M. D. Rettigové 4, CZ-116 39 Prague 1, Czech Republic

3. European Commission, DG Environment, Avenue de Beaulieu 9, 1160 Auderghem, Brussels, Belgium (e-mail: ladislav.miko@ec.europa.eu)

4. University of Silesia, Department of Ecology, 40-007 Katowice, Bankowa 9, Poland (e-mail: piotr.skubala@us.edu.pl)

ABSTRACT - *Epidamaeus bituberculatus* (Kulczynski, 1902)—type species of the genus *Epidamaeus* Bulanova-Zachvatkina 1957—is redescribed and illustrated in detail based on adult specimens collected in dead wood and tree hollows in natural forest in Upper Silesia, Poland. The species is characterized mainly by single pair of postbothridial tubercles (*Ba*) on prodorsum; comparatively strong sensillus evenly strong throughout withblunt tip; fully developed propodoventral (*E2a*, *E2p*) and ventrosejugal (*Va*, *Vp*) enantiophyses. The neotype is designated, because the original type series is presumably lost. The species seems to be comparatively rare and remained poorly known until present. At least part of published records is probably based on confusion with other species of the genus.

Key words - Acari, Oribatida, Damaeidae, taxonomy, neotypus, redescription, dead wood, Poland, Central Europe

INTRODUCTION

The genus *Epidamaeus* Bulanova-Zachvatkina, 1957b with the type species *Epidamaeus bituberculatus* (Kulczynski, 1902) represents a diverse and morphologically heterogeneous group of oribatid mites of the family Damaeidae Berlese, 1896. With more than 70 included named species (Bayartogtokh, 2000b, 2001; Subías, 2004, 2009) it is one of the largest genera of the family.

The genus is distributed mostly on Northern Hemisphere, with the highest diversity in Palaearctic and Nearctic regions (Norton, 1979a; Behan-Pelletier and Norton, 1983, 1985; Bayartogtokh, 2000a, 2000b, 2000c, 2001; Subías, 2004, 2009). In the Southern Hemisphere, only several species have been described from Neotropical region (Norton, 1979b).

The concept and diagnosis of the genus has changed since its original proposal (Bulanova-Zachvatkina, 1957a, 1957b) as was reviewed by Bayartogtokh (2000b) and Miko (2006) and is not stabilised yet. Norton (1978) distinguished two subgenera, *Epidamaeus* sensu stricto having spinae adnatae present and a new subgenus *Epidamaeus* (*Akrodamaeus*) Norton, 1978 with spinae adnatae absent, fully reduced. Subías (2004) recombined the later subgenus as *Metabelbella* (*Akrodamaeus*), but he did not provide any reasons or reference to any previous work to substantiate such combination.

At present, the genus is defined by characters of *Damaeus* sensu lato (companion seta d absent and solenidion φ free on tibia II-IV, leg IV longer than body, famulus of

immatures sunken in sclerotized cup and minute), combined with absence of propodolateral apophysis P and absence of additional ventral setae *v2´´* on tarsi I and IV, with variable set of prodorsal and ventral tubercles, interlamellar setae clearly shorter than sensillus and usually well developed spinae adnatae (see Miko, 2006; Miko and Mourek, 2008). Nevertheless, there are exceptions from almost all of these characters.

In our view, *Epidamaeus* is in need of complete critical revision, because the genus seems to be poorly defined and many included older species were insufficiently described. Taxonomic position of some of the species included in *Epidamaeus* by Subías (2004, 2009) is in our view rather uncertain, because their original descriptions lack important diagnostic characters. Miko (2006) provided a diagnostic key to Central European species with detailed illustrations and transferred some of the known species into a new genus *Kunstidamaeus* with the type species *Kunstidamaeus lengersdorfi* (Willmann, 1932), which was treated in detail by Miko and Mourek (2008). Some further species included and recently mostly placed within *Epidamaeus* were described or redescribed by Miko (2010).

Miko and Mourek (2008) indicated that even *Epidamaeus* sensu stricto comprises in fact of several morphologically well-defined species groups that could be very probably distinguished as new genera or subgenera. Unfortunately, immature stages have been described only for part of the species and one of the main diagnostic characters on the genus level—ontogeny of the famulus—is thus known only in some of them (Norton, 1978; Mourek and Miko 2009; Ermilov and Łochyńska 2009).

Further problem, preventing the revision of supraspecific classification of the genus *Epidamaeus*, has been the poor knowledge of the type species *Epidamaeus bituberculatus* (Kulczynski, 1902). The type series is presumably lost. All studied specimens originally determined as *E. bituberculatus* from various museum collections as well as from the material provided by other colleagues belonged to other species (Miko, 2006). Therefore the only base remained the original description by Kulczynski (1902), providing a relatively good illustration of dorsal side, but lacking information about the ventral side and details of the leg setation.

In this situation, the only solution was to try to get topotypical material for the study. Precise location of Kulczynski´s localities in Silesia, Poland (within the municipalities Krzeszowice and Grzegórzki—now part of Cracow) is not completely clear, and at least some of them most probably do not exist any more because of urbanisation, or they were transformed to an intensive forest plantations. Nevertheless, at least some quasi-natural forests in the broader area of Upper Silesia (Poland) still could be visited and material collected. Recently, P. Skubała () rediscovered *E. bituberculatus* in three forest localities of this region, during the study of oribatid mites inhabiting decaying wood and tree hollows (Skubała and Duras, 2008; Skubała and Gurgul, subm.; Skubała and Marzec, in prep.) . One of the localities—reserve „Gora Chełm"—is located in the south-west part of Jura Krakowsko-Częstochowska mts. in the distance of only about 45 km from the Kulczynski's locality Krzeszowice. The specimens are in good accordance with the original illustrations and description by Kulczynski (1902) and we consider them to be conspecific with Kulczynski´s species. In the present work we therefore provide a detailed redescription and illustrations of adult *E. bituberculatus* based on this material and designate the neotype. Without more detailed information about other species of the genus, we believe it is not appropriate to provide revised genus definition and we do not attempt to do it here. Redescriptions of some other European species and revision of the supraspecific classification of *Epidamaeus*, including redefinition of the genus, will follow in subsequent parts of this series.

MATERIALS AND METHODS

Following material, collected in Upper Silesia region of Poland, was used for this redescription:

- *Beskid Zywiecki Mountains, reserve "* Śrubita *"*, 850 m a.s.l. 49°28'N 19°02'E, tree hollow in a fir tree (*Abies alba*), 1 adult (female), 24. 09. 2006, P. Skubała leg. We designate this specimen as the **neotype.**
- *Jura Krakowsko-Czestochowska, reserve "Parkowe"*, 300 m a.s.l. 50°43'N 19°27'E., dead wood of a beech stump and tree hollow in a beech tree (*Fagus sylvatica*), 2 adults, 14. 11. 2005, P. Skubała leg.
- *Jura Krakowsko-Czestochowska, reserve " Gora Chełm "*, 420 m. a.s.l.; 50°27'N, 19°31'E beech logs (3rd class of decay), under bark, 2 adults, 28. 09. 2005, P. Skubała leg. All specimens unmounted, preserved in glycerole.

The neotype will be deposited in Acarological Collections of Senckenberg Museum für Naturkunde Görlitz (Germany). One of the remaining specimens will be deposited in National Museum of Natural History Naturalis, Leiden (Netherlands), two specimens will be kept in the collection of J. Mourek and one in the collection of L. Miko.

In the present paper we follow the morphological terminology and abbreviations developed by Grandjean (1960) and modified by subsequent authors (see Miko and Mourek 2008 for complete references and a list of abbreviations) and Grandjean´s notation of leg setae reviewed by Norton (1977). Setal formulas of appendages are given as numbers per segment (from trochanter to tarsus), famulus included, solenidia in parentheses. Epimeral setal formulas are given as numbers per podosomal segment (I-IV).

All observations and measurements were done on specimens cleared in pure lactic acid and mounted in temporary microscopic slides with a central excavation.

The drawings were made with a compound microscope equipped with a camera lucida. All measurements are given in micrometers (μm) as a range, usually followed with a mean in parentheses and number of measured specimens (n). Instead of the total body length we used the ventral length, measured in lateral view from the tip of the rostrum to the posterior edge of the ventral plate (see also Bayartogtokh and Norton, 2007). The maximal notogastral width was measured in dorsal view. Legs I and II were measured without trochantera, legs III and IV were measured including the trochantera. The length of individual leg segments was measured including the proximal part immersed in the previous segment and the total length of a given leg is given as a sum of all measured segments (including the immersed proximal parts).

Family Damaeidae Berlese 1896

Epidamaeus bituberculatus (Kulczynski)

Epidamaeus bituberculatus (Kulczynski, 1902): 36-38, Figs. 20, 21, 56, 57

Synonymy - *Oribata bituberculata* Kulczynski, 1902; Sellnick (1928). *Belba bituberculata*: Willmann(1931); Sellnick (1960); *Epidamaeus bituberculatus*: Bulanova-Zachvatkina (1957b); Bulanova-Zachvatkina (1967); Bulanova-Zachvatkina (1975); Schatz (1983); Olszanowski et al. (1996)

Type localities – Krzeszowice, Grzegorzki (Poland, Upper Silesia, NW from Krakow), see Kulczynski (1902)

Neotype locality – reserve "Srubita", Beskid Zywiecki Mountains, (Poland, Upper Silesia), 850 m, 49°28'N 19°02'E

Diagnosis - *Epidamaeus* with one pair of distinct postbothridial tubercles (*Ba*) on prodorsum behind bothridia. Sensillus long, sparsely covered with minute barbs, straight, with weakly indicated subterminal expansion and blunt tip. Interlamellar seta (*in*) shorter than 0,5 of the length of sensillus, strong, erect with blunt tip, sparsely covered with minute barbs. Spinae adnatae strong, slightly curved mediad in dorsal view and ventrad in lateral view. Notogastral setae strong, erect, slightly curved, slightly overreaching insertions of respective successive seta, covered with minute barbs; setae *c1* and *c2* directed anterolaterad; setae *la* - *h1* directed posteriad or posterolaterad. Propodoventral enantiophyses (*E2a* and *E2p*) and ventrosejugal enantiophyses (*Va*, *Vp*) present, well developed.

REDESCRIPTION OF ADULT

(immatures not available)

Measurements - Kulczynski (1902) indicated body size about 0.6 mm. Our specimens had ventral body length 448 - 489 (474) μm and maximal notogastral width 284-339 (318) μm, detailed measurements of legs and individual leg segments in Table 1.

Integument - Body colour yellowish brown to medium brown. Most of body,legs and setae covered with distinct cerotegument with filamentous excrescences. Filamentous excrescenses dense on legs (except for distal parts of tarsi), on prodorsum and in sejugal area, loose on notogaster and on anogenital region. Cerotegument excrescences granular in lateral and posterior parts of membranous cuticle connecting notogaster and ventral plate. Cuticle after removal of cerotegument mostly smooth, apophyses and other emergent structures faintly microtuberculate. No exuvial "scalps" (gastronotic exuviae) observed on notogaster of studied adults.

Prodorsum - Fig. 1A, 2A. Prodorsum of roughly triangular shape in dorsal view, maximum width slightly behind the level of bothridia, about 0.64 of notogastral width. Length of prodorsum about 0.57 of the notogastral length. Rostrum with weakly developed dorsal protuberance. Propodolateral apophysis (*Pa*) absent. Postbothridial tubercle (*Ba*) present, well developed; tubercles *Bp*, *Da*, *Dp* and *La* absent. Parastigmatic apophyses long, narrow, subparallel and subequal in length, *Sa* being only slightly longer than *Sp*, tip of *Sa* directed slightly anterolaterad, tip of *Sp* directed laterad. All prodorsal setae shortly barbed. Rostral (*ro*) and lamellar (*le*) seta comparatively long, both distinctly overreaching the rostrum, curved anteromediad; *le* slightly longer than *ro*. Interlamellar seta (*in*) comparatively short, strong, erect, with blunt tip, sparsely covered with minute barbs. Exobothridial seta fine, comparatively long, arched anteromediad, sparsely covered with minute barbs on outer curvature. Sensillus long, sparsely covered with minute barbs, straight, with weakly indicated subterminal expansion and blunt tip. Bothridium funnel-like, with slightly expanded rim, the rim is more developed in posterolateral side. Pair of short sclerotized elevations, not longer than diameter of bothridium, directed anteromediad, visible anterior to bothridia in dorsal view.

Notogaster - Fig 1A, 1B. Outline of notogaster broadly oval to almost circular in dorsal view; evenly rounded in lateral view, with maximum height only slightly posterior of center, slightly flattened in lateral view: notogastral height smaller than half notogastral length. Spinae adnatae strong, slightly curved mediad in dorsal view and ventrad in lateral view. Notogastral setae strong, erect, slightly curved, slightly overreaching insertions of respective successive seta, covered with minute barbs; setae *c1* and *c2* directed anterolaterad. Setae *la* - *h1* directed posteriad or posterolaterad. Posterior notogastral setae *ps1*-*ps3* comparatively long, *ps1* > *ps2* > *ps3*, slightly finer than *h1*-*h3*.

Ventral region - Fig 1B. Medial pit *cp* on coxisternum I well developed as closed circular structure. Anterior tectum of podocephalic fossa laterally with sharp angle, but without projecting tip. Weakly defined transverse ridge directed posterolaterad present on anterior tectum of podocephalic fossa; Propodoventral enantiophysis (*E2a* and *E2p*) and ventrosejugal enantiophysis (*Va, Vp*) complete, well developed, tubercular, *Vp* being the largest. Apodeme between epimeres I and II distinct only in lateral parts; apodeme between epimere II and III complete. Discidium well developed as a distinct, strong beak-form spine, pointing posterolaterad, distinctly prominating from body outline in dorsal view. Ventral setation as usual in Damaeidae (Grandjean 1960; Norton 1977b); epimeral setal formula (from epimere 1 to epimere 4): 3-1-3-4; genital *g*: 6; aggenital *ag*: 1; anal *an*: 2; adanal *ad*: 3. Ventral setae comparatively long, fine, most with more or less distinct minute barbs on outer curvature; part of them inserted on minute apophyses. Seta *1c* inserted on a short and narrow lateral ridge visible in ventral view; seta *3b* more or less on tubercle *Vp* and seta *4b* at its base.

Gnathosoma - Fig 1B, 2B. Generally normal for family, subcapitulum with three pairs of setae (*a*, *m*, *h*), all of them distinctly barbed on outer curvature. Setation of the pedipalp (from trochanter to tarsus, solenidia in parentheses) as follows: 0-2-1-3-8(1). Palptarsal solenidion ω procumbent, long about 0.46 of the tarsal length. Chelicera and cheliceral setae of normal shape for the family.

Legs (Fig. 3, 4) - Legs monodactylous, moderately long, leg IV longer than body, legs I and III approximately as long as body, leg II shorter than body; detailed measurements of legs and leg segments in Table 1. Leg setae comparatively long and thin, most with distinct short barbs on outer curvature. Setal formulas of legs as follows (from trochanter to tarsus, famulus included, solenidia in parentheses): I: 1-7-4(1)-4(2)-20(2); II: 1-6-4(1)-4(1)-17(2); III: 2-4-3(1)-3(1)-17; IV: 1-4-3-3(1)-14. All tarsi with only two posterior ventral accessory setae, seta *v2´´* absent. Seta *d* absent from all tibiae, solenidia on all tibiae free, as usual within the genus. Solenidia of genua I-III with companion seta *d*, all genual solenidia distinctly shorter than their respective companion setae. Famulus normal, emergent in adult.

Distribution and ecology - The species has been reported from numerous localities in Palearctic region. However, it is nearly impossible to assess the real area of distribution of the species from literature records since many of them are probably based on wrong identification. L. Miko (unpubl.) studied numerous specimens from collections of different authors, originally identified as *E. bituberculatus*. None them agreed with the original description of Kulczynski (1902) and they were most often either *E. kamaensis* or *Kunstidamaeus tecticola*. Also demand for recent specimens passed to working acarologists did not result in any new individuals. It was not found in a large material of Damaeidae collected in numerous localities in Central Europe by L. Miko and J. Mourek. P. Skubała did not find *E. bituberculatus* in 30 soil samples collected in forest sites on the original type locality Krzeszowice in 2008, which are now mostly transformed into intensive production forests. The species therefore seems to be indeed comparatively rare as already noted by Kulczynski (1902).

The ecology of the species is unclear. Original records by Kulczynski (1902) are from mosses on roofs in Krzeszowice and from brushwood near Grzegórzki ("in muscis tectorum in pago Krzeszowice " and "in virgultis pagi Grzegórzki " respectively, in Latin original). The recent findings of P. Skubała (Skubała and Duras, 2008; Skubała and Gurgul, subm.; Skubała and Marzec, in prep.) suggest, that the species might prefer dead wood and tree hollows in natural beech and fir forests.

DISCUSSION

As mentioned above, we have no doubts about identity of our specimens of *E. bituberculatus*, which match very well the original description by Kulczynski (1902). In fact, the only two known Central European species with single pair of prodorsal tubercles are *E. bituberculatus* and *E. berlesei* (Michael 1898). Nevertheless, *E. berlesei* is easily distinguished by very long flagellate sensillus, thin and irregularly curved notogastral setae, absence of epimeral and ventrosejugal tubercles and very long legs. The prodorsal tubercles of *E. berlesei* are positioned more medial—posterior from insertions of interlamellar setae—and their homogeny with *Ba* is questionable, some authors may assign them rather to *Da*. The misidentification of other species as *E. bituberculatus* may be caused by lower visibility or overlooking of posterior tubercles (*Bp*), or more laterally positioned tubercles *La* in the case of *Kunstidamaeus* species. *Epidamaeus bituberculatus* has very similar general shape of prodorsum and also overall body shape with much more common species *E. tatricus* (Kulczynski, 1902) and *E. setiger* (Kulczynski, 1902). Nevertheless, both of the species clearly differ by radial arrangement of notogastral setae and by absence of prodorsal tubercles (*E. tatricus*) or presence of full set of tubercles *Ba*, *Bp* and *Da* (*E. setiger*). Based on body shape, arrangement of setae and a presence of very distinct and well visible tubercles *Ba*, the species *Epidamaeus kamaensis* (Sellnick, 1926) may be often misidentified as *E. bituberculatus*. Presence of *E. kamaensis* in Central Europe was apparently often overlooked, as it was originally described from North-East part of the continent. Nevertheless, this species has present, even if sometimes weakly developed, posterior tubercles *Bp*, and in rare cases also reduced remnants of *Da* and *La* may be present (see Miko, 2006). The most striking difference is apparent in development of ventral side, which was not presented by Kulczynski (1902): *E. kamaensis* lacks distinct ventral tubercles in sejugal area (see Miko, 2006). Other smaller differences are related to the form and size of spinae adnatae, development of medial pit *cp* on coxisternum I, length of epimeral setae etc. Another species, often misidentified as *E. bituberculatus*, is *Kunstidamaeus tecticola* (Michael, 1888). The similarities are again in presence of distinct tubercles *Ba*, general body shape and also arrangement of notogastral setae in two subparallel rows. Nevertheless, *K. tecticola* has also well developed tubercles *La* (typical character of *Kunstidamaeus*), small but distinct apophysis *P* and spinae adnatae bent laterad. The notogastral setae are longer, and only pair *c1* is directed anteriad. On the ventral side, strong *Va* tubercle is present, but *Vp* is missing. Summing up, none of the known species present in a broader (Central) European area closely resembles *E. bituberculatus* in details. Several species were nevertheless described from other parts of the world, being apparently more closely related.

Epidamaeus crassisensilatus Bayartogtokh, 2000b was described from litter of larch forest (*Larix sibiricus*) in mountains of Central Mongolia. The species is very similar to *E bituberculatus*, differing only in several minute characters. Notogastral setae of *E. crassisensilatus* seem to be slightly shorter with more attenuate tips. Notogastral setae *ps2* and *ps3*, interlamellar setae and all of the setae on ventral side are smooth, whereas in *E. bituberculatus* they are sparsely barbed. Lateral part of podosoma and of exobothridial area of *E. crassisensilatus* are distinctly granulated (granulation not apparent in *E. bituberculatus*), and ventral tubercles *E2p* and *Va* are connected by distinct ridge (in *E. bituberculatus* ridge absent). Only study of broader material of both species (Mongolian species was decribed on the base of 3 individuals) may show if there is variability in the mentioned characters, which would make a differentiation of the two species difficult. Also the body size of *E crassisensilatus* is similar to our material of *E. bituberculatus*, but the former species seems to have slightly shorter legs in absolute values as well as in relation

to body length (see Table 1). Because of the relatively minor differences described above, we consider *E crassisensilatus* to be a closely related, but separate species from *E. bituberculatus*.

Other two species belonging to the same group as *E. bituberculatus* are easier to distinguish. Both *E. culterisetosus* Bayartogtokh, 2000a from Mongolia and *E. chukchi* Behan-Pelletier and Norton, 1985 from North-East Russia have similarly developed set of prodorsal and ventral tubercles, basically having all ventral tubercles present, a pair of distinct tubercles *Ba* on prodorsum, and strong, long and slightly converging spinae adnatae present. They nevertheless clearly differ by the shape and arrangement of notogastral setae and form of sensillus. *Epidamaeus culterisetosus* has notogastral setae arranged radially, having a special knife-like shape, and sensillus long and slightly expanded distally. *E. chukchi* has notogastral setae very short and bladelike, sensillus with short flagellate ending, and in addition a transversal ridge present on the place of tubercles *Bp*.

ACKNOWLEDGEMENTS

The study was partially financially supported by the Grant Agency of the Charles University, Prague (grant *GAUK 217/2004/B-BIO/PrF*). The first author is very grateful to Prof. Jaroslav Smrž (Charles University, Faculty of Science, Prague, Czech Republic) for his steady support and kind advice during the postgraduate study.

REFERENCES

Bayartogtokh, B. 2000a. New oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. Species Diversity 5: 183-200.

Bayartogtokh, B. 2000b. Two new species of oribatid mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. Acarina 8: 65-78.

Bayartogtokh, B. 2000c. Two species of damaeid mites (Acari: Oribatida: Damaeidae) from Mongolia, with notes on distribution of the genera *Epidamaeus* and *Dyobelba*. Biogeography 2: 67-79.

Bayartogtokh, B. 2001. Three new soil mites of the genus *Epidamaeus* (Acari: Oribatida: Damaeidae) from Mongolia. Zoosystema 23: 29-49.

Bayartogtokh, B., R. A. Norton. 2007. The *Dyobelba tectopediosa* species-group (Acari: Oribatida: Damaeidae) from the Southeastern USA, with a key to world species of *Dyobelba* and notes on their distribution. Zootaxa 1591: 39–66.

Behan-Pelletier, V. M., R. A. Norton. 1983. *Epidamaeus* (Acari: Damaeidae) of arctic western North America and extreme northeast, U.S.S.R. Canadian Entomologist 115: 1253-1289.

Behan-Pelletier, V.M., R. A. Norton. 1985. *Epidamaeus* (Acari: Damaeidae) of subarctic western North America and extreme northeastern USSR. Canadian Entomologist 117: 277-319.

Bulanova-Zachvatkina, E. M. 1957a. Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Soobschchenije I. Zoologicheskij Zhurnal 36: 1167-1186. (in Russian)

Bulanova-Zachvatkina, E. M. 1957b. Bulavonogije pancirnyje kleschchi semejstva Damaeidae Berl. Rod *Epidamaeus*, gen. n. (Acariformes, Oribatei). Soobschchenije II. Zoologicheskij Zhurnal, 36: 1792–1801. (in Russian).

Bulanova-Zachvatkina, E. M. 1967. Pancirnije kleschtschi - Oribatidy. Vysshaya Shkola, Moscow. 254 pp. (in Russian).

Bulanova-Zachvatkina, E. M. 1975. Nadsemejstvo Belboidea Dubinin, 1954 (=Damaeoidea Balogh, 1961). pp. 120-143. *In*: Gilijarov, M. S., Krivolutskij, D. A. (Eds): Opredelitel obitaiustschich v potschve kljeschtschei. Nauka, Moskva. (in Russian).

Ermilov S. G., M. Łochyńska. 2009. Morphology on juvenile stages of *Epidamaeus kamaensis* (Sellnick, 1925) and *Porobelba spinosa* (Sellnick, 1920) (Araci:Oribatida: Damaeidae). Annales Zoologici (Warszawa) 54: 527-544.

Grandjean, F. 1960. *Damaeus arvernensis* n. sp. (Oribate). *Acarologia*, 2, 250-275.

Kulczynski, V. 1902. Species Oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. Diss. Math. Phys. Acad. Litt. Cracov ser. B., Cracov. 42: 10-56.

Michael, A.D. 1888. British Oribatidae. vol. II. - Ray Society, London. 337-657.

Miko, L. 2006. Damaeidae. pp 179-207. In: Weigmann, G.: *Hornmilben (Oribatida)*, Die Tierwelt Deutschlands 76, Goecke&Evers Publ.

Miko, L. (2010) Taxonomy of European Damaeidae (Acari: Oribatida) III. Species of the *Kunstidamaeus tenuipes* (Michael, 1885) group, with a description of *Kunstidamaeus fraterculus* n. sp. from East Slovakia. Zootaxa 2327: 51–64

Miko, L. and Mourek J. (2008) Taxonomy of European Damaeidae (Acari: Oribatida). I. *Kunstidamaeus* Miko, 2006 with comments on *Damaeus* sensu lato. Zootaxa 1820: 1–26.

Mourek, J., Miko, L. (2009) Ontogeny of the famulus in selected members of Damaeidae (Acari: Oribatida) and its suitability as a phylogenetic marker. In: Bruin J. and Sabelis M. W. (eds.): *Trends in Acarology*. Proceedings of the International Congress of Acarology (ICA-12, Amsterdam, August 2006), published on CD-ROM. 31-36.

Norton, R. A. 1977. A review of J.Grandjean's system of leg chaetotaxy in the Oribatei and its application to Damaeidae. pp. 33-62. *In*: Dindal, D. L. (Ed.), Biology of oribatid mites, 33, SUNY College of Environmental Science and Forestry, Syracuse, New York.

Norton, R. A. 1978. Generic concepts in the Damaeidae (Acari, Oribatei). I. Three taxa based on species of Nathan Banks. Acarologia 20: 603-621.

Norton, R. A. 1979a. Aspects of the biogeography of Damaeidae sensu latu (Oribatei), with emphasis on North America. pp. 535-540. *In:* Rodriguez, J.G. (Ed.): Recent Advances in Acarology, vol. 2.

Norton, R. A. 1979b. Damaeidae (Acari: Oribatei) collected by the Hungarian Soil Zoological Expedition to South America. Folia Entomologica Hungarica 32: 55-64.

Olszanowski, Z., Rajski, A., Niedbala, W. 1996. Roztocze Acari - Mechowce Oribatida. - Katalog Fauny Polski - Catalogus faunae Poloniae, Poznán, Poland, 34(9): 243 pp.

Schatz, H. 1983. U.-Ordn. Oribatei, Hornmilben. Catalogus faunae Austriae. Ein systematisches Verzeichnis aller auf osterreichischem Gebiet festgestellten Tierarten, 9, Österreichische Akadademie der Wissenschaften, Wien, 118 pp.

Sellnick M. 1926. Novye russkie Oribatidae. - Izv. Biol. Nauk. Issled. Inst. Permsk, gosud. univ. Perm, 4: 339-342.

Sellnick M. 1928. Formenkreis: Hornmilben, Oribatei. In: Brohmer P., Ehrmann P., Ulmer H. (Hrsg.) Die Teirwelt Mitteleuropas 3, 4. Lief. (Teil 9). Quelle & Meyer, Leipzig: 1-41.

Sellnick M. 1960. Formenkreis: Hornmilben, Oribatei. Nachtrag. pp. 45-134. *In:* Brohmer, P. Ehrmann P. and Ulmer G. (eds.): Die Tierwelt Mitteleuropas, Leipzig, 3(4).

Skubała P., Duras M. 2008. Do decaying logs represent habitat islands? Oribatid mite communities in dead wood. Annales Zoologici 58: 453-466.

Skubała P., Gurgul B. (subm.) Importance of tree hollows for biodiversity of mite (Acari) fauna in the forest reserve „Śrubita".

Skubała P., Marzec A. (in prep.) Microarthropod communities with emphasis on oribatid mites in different forms of dead wood and on the forest floor in a beech forest

Subías, L.S. 2004. Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1758-2002). *Graellsia* 60: 3–305.

Subías, L. 2009. [internet] Listado sistematico, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (Excepto fósiles). last changes in April 2009. 547 pp. [; cited 24. 4. 2010] Available from: http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf

Willmann, C. 1931. Moosmilben oder Oribatiden (Cryptostigmata). pp. 79-200. *In:* Dahl, F. (Ed.): Die Tierwelt Deutschlands, Bd. 22, vol. 5, Gustav Fischer, Jena:

TABLE 1. Measurements of *Epidamaeus bituberculatus* in comparison with *E. crassisensillatus* (values from Bayartogtokh, 2000b). All measurements are given in μm. Legs I and II were measured without trochantera, whereas legs III and IV were measured with trochantera.

	E. bituberculatus (n=5)			***E. crassisensillatus*** (n=3 for body measurements; n=1 for leg segments)
	mean	**min**	**max**	
ventral body length	**474**	**448**	**489**	**442 - 477 (460)**
maximum notogastral width	**318**	**284**	**339**	**269 - 380 (274)**
leg I	**489**	**470**	**515**	**440**
leg I : ventral body length	**1.03**	**1.00**	**1.06**	**0.96**
femur I	158	150	168	147
genu I	63	59	68	58
tibia I	75	70	79	68
tarsus I	194	186	206	167
leg II	**416**	**384**	**444**	**362**
leg II : ventral body length	**0.88**	**0.85**	**0.91**	**0.79**
femur II	130	114	147	109
genu II	56	52	59	48
tibia II	63	58	68	58
tarsus II	167	160	174	147
leg III	**507**	**470**	**535**	**462**
leg III : ventral body length	**1.07**	**1.05**	**1.09**	**1.00**
trochanter III	76	68	85	73
femur III	111	106	115	96
genu III	54	52	59	48
tibia III	79	74	82	73
tarsus III	187	170	197	172
leg IV	**641**	**602**	**685**	**564**
leg IV : ventral body length	**1.35**	**1.29**	**1.40**	**1.23**
trochanter IV	113	104	124	106
femur IV	134	126	144	129
genu IV	68	62	74	63
tibia IV	102	90	115	94
tarsus IV	226	216	235	172

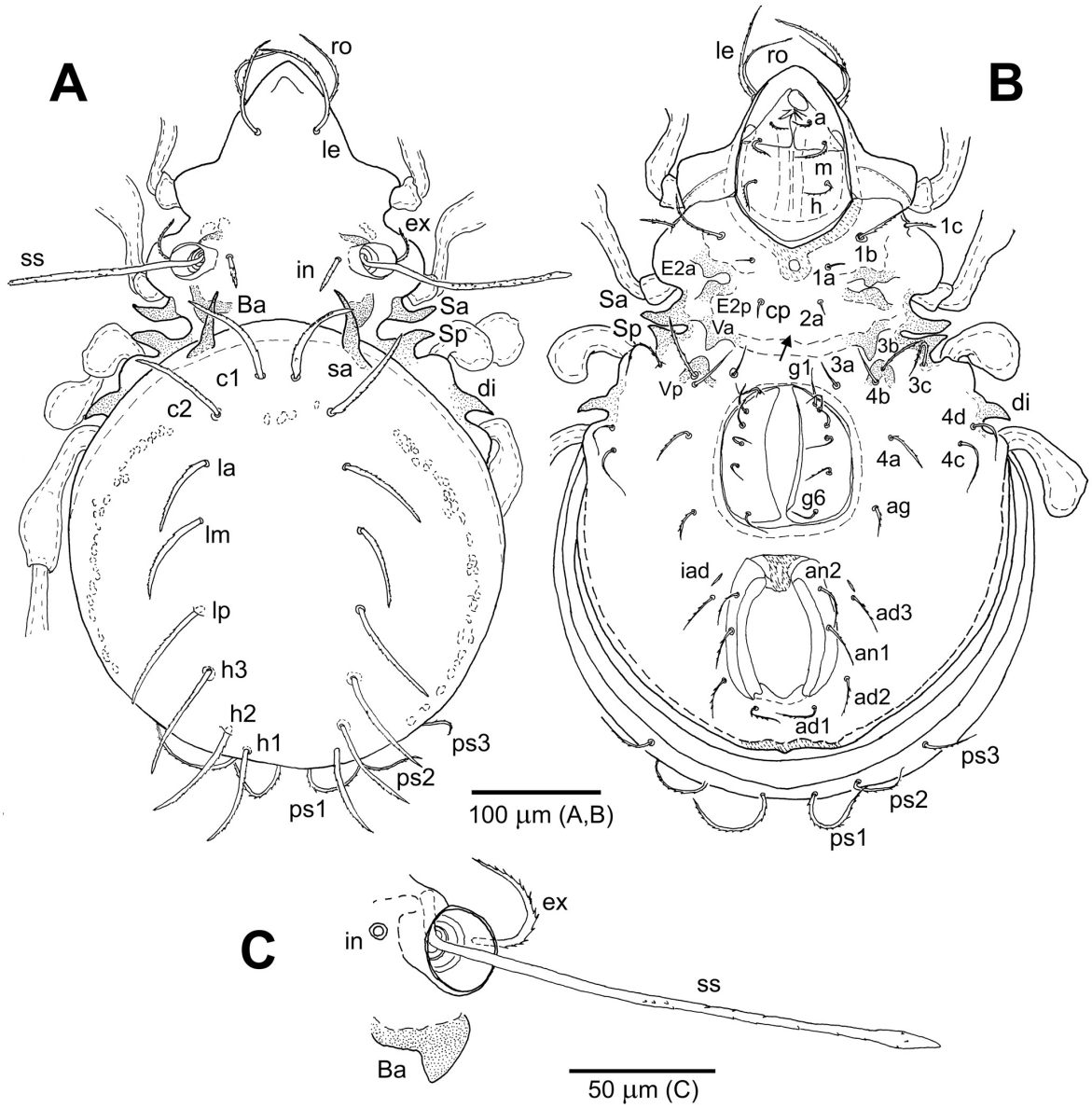


FIGURE 1. *Epidamaeus bituberculatus* - A, dorsal view; B, lateral view; C, detail of bothridium with sensillus, exobothridial seta and postbothridial tubercle *Ba* in dorsal view. Legs only partly drawn, leg setae and cerotegument not drawn.

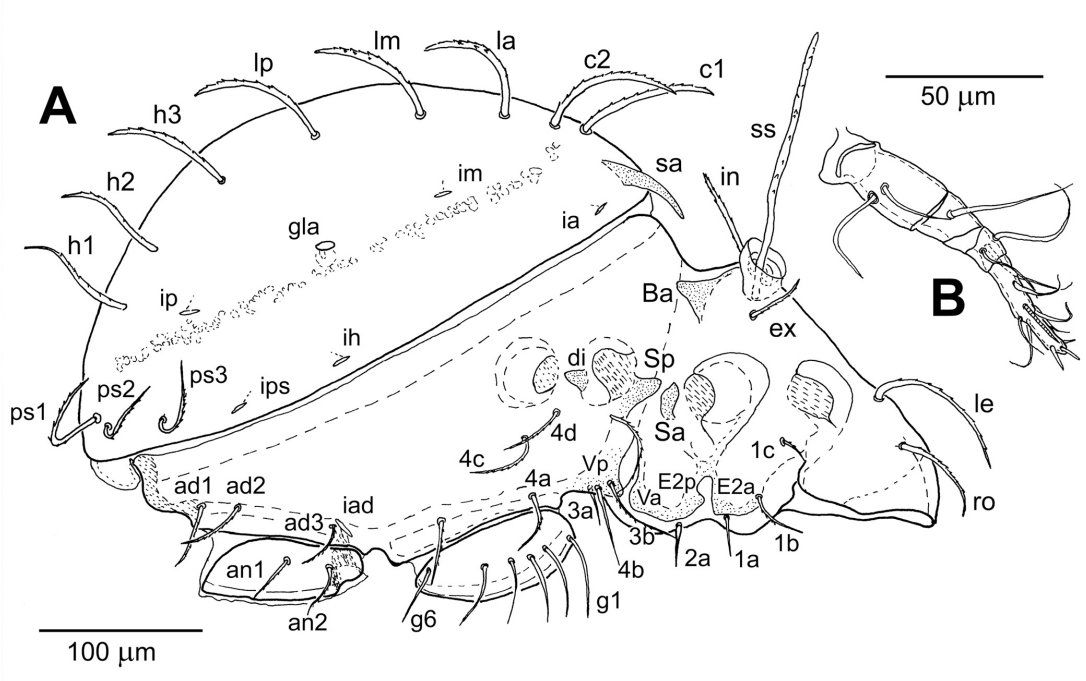


FIGURE 2. *Epidamaeus bituberculatus* - A, lateral view without legs; B, pedipalp in antiaxial view. Cerotegument not drawn.

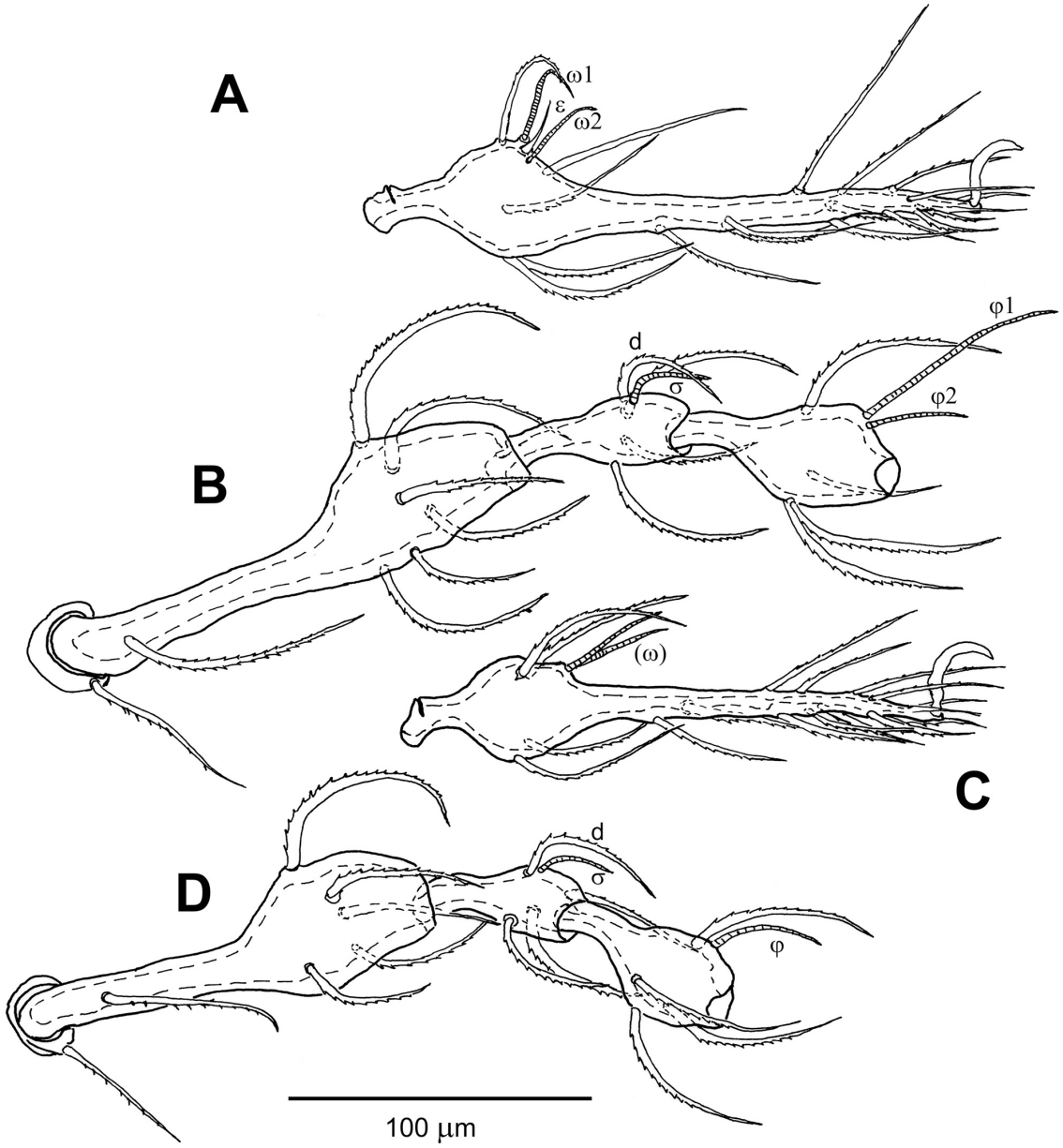


FIGURE 3. *Epidamaeus bituberculatus* - leg I and II, antiaxial view. A) tarsus I; B) trochanter, femur, genu and tibia I; C) tarsus II; D) trochanter, femur genu and tibia II; Cerotegument not drawn.

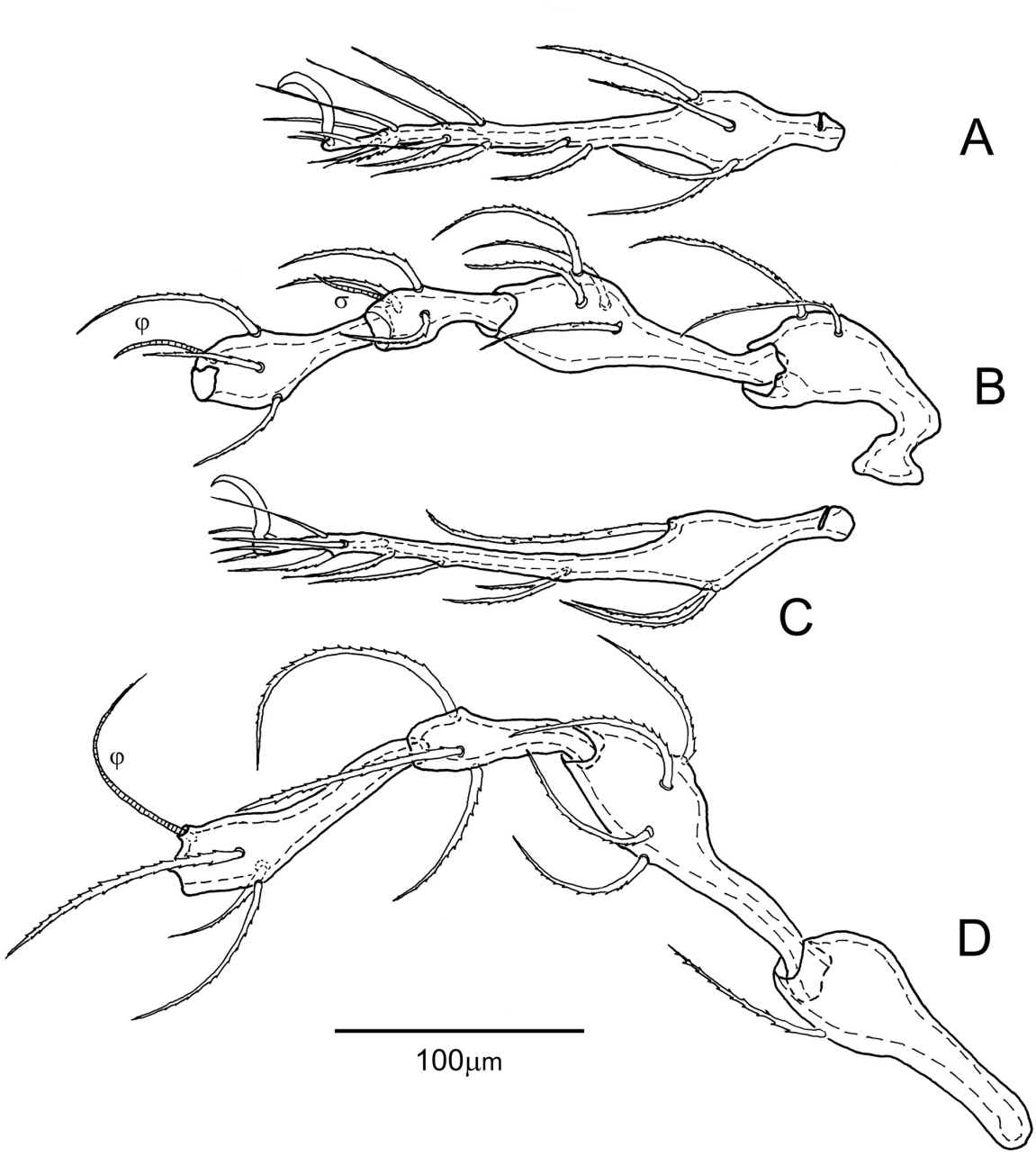


FIGURE 4. *Epidamaeus bituberculatus* - leg III and IV, antiaxial view. A, tarsus III; B, trochanter, femur, genu and tibia III; C, tarsus IV; D, trochanter, femur genu and tibia IV. Cerotegument not drawn.

Contribution 2.1

Koukol O., **Mourek, J.**, Janovský Z., Černá K. (2009) Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? *Soil Biology and Biochemistry*. 1124-1131.

Soil Biology & Biochemistry 41 (2009) 1124–1131

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous *vs.* specialized saprotrophic fungi from pine litter?

Ondřej Koukol [a,*], Jan Mourek [b,c], Zdeněk Janovský [a], Kristýna Černá [a]

[a] Charles University, Faculty of Science, Department of Botany, Benátská 2, CZ-128 44 Prague, Czech Republic
[b] Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44 Prague, Czech Republic
[c] Charles University, Faculty of Education, Department of Biology and Environmental Education, M. D. Rettigové 4, CZ-116 39 Prague 1, Czech Republic

ARTICLE INFO

Article history:
Received 14 November 2008
Received in revised form
4 February 2009
Accepted 9 February 2009
Available online 12 March 2009

Keywords:
Feeding preferences
Scots pine litter
Oribatid mites
Saprotrophic fungi
Feeding niches

ABSTRACT

Previous studies of oribatid mite feeding preferences for different saprotrophic fungi were limited to ubiquitous fungal species, whereas saprophytes specialized to decompose particular substrates have been neglected. We examined the preference of seven oribatid mite species (*Adoristes ovatus*, *Eniochthonius minutissimus*, *Eueremaeus silvestris*, *Nothrus silvestris*, *Oppiella subpectinata*, *Porobelba spinosa* and *Spatiodamaeus verticillipes*) for nine autochthonous saprotrophic fungi from Scots pine litter (*Pinus sylvestris*). Among the fungal species offered were specific coniferous litter colonizers (*Allantophomopsis lycopodina*, *Ceuthospora pinastri*, *Hormonema dematioides*, *Scleroconidioma sphagnicola*, *Verticicladium trifidum*, *Marasmius androsaceus* and *Sympodiella acicola*) and two ubiquitous species (*Cladosporium herbarum* and *Oidiodendron griseum*). The fungi were inoculated on fragments of pine needles and offered simultaneously and separately to the mites. Our main hypothesis, that oribatid mites (usually occurring in more than one type of ecosystems) would prefer the ubiquitous fungal species rather than those specific to pine litter, was supported only partly. The ubiquitous *C. herbarum* was highly preferred by all studied mites, but most of them preferred one or more of the specialized fungi with similar intensity. The basidiomycete *M. androsaceus* along with sterile needles were consistently avoided by all mites in all experiments. Our results do not support the hypothesis, that the "true" fungivorous oribatid mites in traditional sense are more selective fungal feeders than are the "unspecialized" panphytophagous ones. We observed no gradation in preference of fungi for oribatid mites as a group, but rather a discontinuous and dynamic mosaic with particular mites preferring particular fungal species. This heterogeneous mosaic shapes the feeding niches occupied by particular oribatid mite species and probably reduces competition for food source among numerous species coexisting in a given habitat and time.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The heterogeneous habitat of coniferous forest litter offers sufficient time and space for interactions between numerous species of microarthropods (mainly oribatid mites and collembolans) and fungi (particularly ascomycetes and basidiomycetes). Knowledge of microarthropod feeding preferences is essential for understanding this rather complex system (Schneider et al., 2004a). In Scots pine (*Pinus sylvestris* L.) forest soil more than 100 oribatid mite species may coexist (Mourek, unpubl.) in total densities up to 425,000 ind/m^2 (Wallwork, 1983). The number of fungal species known from pines was assessed to 890 (Hawksworth, 2001), but the figure may be one order higher.

The classification of oribatid mite feeding habits into guilds or trophic groups (Schuster, 1956; Luxton, 1972; Siepel and De Ruiter-Dijkman, 1993) is useful in describing general patterns and may reflect the role of a given mite species in decomposition, though it does not reflect real diversity of species-specific features, such as the differences in selectiveness for fungal species. In contrast to the generally considered low degree of food resource partitioning in oribatid mites (Maraun et al., 2003; Schneider et al., 2004a), the results of stable isotope analyses (^{15}N/^{14}N and/or ^{13}C/^{12}C) indicated distinct niche separation among different oribatid species (Schneider et al., 2004b; Erdmann et al., 2007).

Most oribatid mite species can feed on a variety of fungal species (Maraun et al., 1998; Schneider and Maraun, 2005; Schneider et al., 2005) and even the species considered being predominantly macrophytophagous often ingest some amount of fungal material (Behan-Pelletier and Hill, 1983). The spectra of fungi preferred by different mites partly overlap and it is still unknown to what extent

* Corresponding author. Department of Botany, Charles University in Prague, Faculty of Science, 128 41 Prague 2, Czech Republic. Tel.: +42 221 951 650.
E-mail address: o.koukol@seznam.cz (O. Koukol).

0038-0717/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2009.02.018

the interspecific differences contribute to the coexistence of high number of mite species (Maraun et al., 1998; Schneider and Maraun, 2005).

There remain significant gaps in our knowledge, which are caused not only by the huge microorganism diversity in the soil systems, but also by the prevalent "zoocentric" experimental approach. Firstly, most of the studies aimed on the oribatid feeding preferences omitted the role of fungal physiology. With rare exceptions (Kaneko et al., 1995) the fungi offered in preference tests were cultivated on agar media, not on natural substrates. Substrate quality affects the growth and physiology (e.g. the production of volatile compounds) of both the saprotrophic and ectomycorrhizal fungi and this may bias the microarthropods' preferences, as was shown in collembolans (Klironomos, 1992; Kaneko et al., 1995; Sadaka-Laulan et al., 1998).

Secondly, in numerous studies only part of the fungi used were determined to species level. For example in the study of Schneider and Maraun (2005), half of the species were identified to the generic level only. Other authors (e.g. Luxton, 1972; Kaneko et al., 1995; Maraun et al., 1998) employed even unidentified sterile fungal strains in feeding preference tests. The deficiency in fungal identification makes difficult comparison of different studies and interpretation of their results. Similarly, omitting autecology of undetermined fungal species largely robs us of an important source of understanding of the system.

Thirdly, the fungal species hitherto offered in feeding preference tests were mostly ubiquitous species, whereas fungi restricted to a particular substrate (microhabitat) have been almost entirely neglected so far. Numerous saprotrophic fungal species occur e.g. only on leaf litter of particular plant species. Their substrate specificity ("preference") contrasts with distribution of soil oribatid mite species, which are rarely confined to a given habitat (e.g. to litter of one tree species or to a particular forest type) and usually inhabit a wider spectrum of ecosystems (Weigmann and Kratz, 1981; Weigmann, 2006).

We attempted to bridge the above-mentioned gaps and employed nine saprotrophic fungi autochthonous to pine litter (two of them ubiquitous and seven with specificity to coniferous needles) and seven oribatid mite species inhabiting the same biotope into a series of preference and consumption tests. Most of these fungal species have not been used yet in any preference test, though they are among the most frequent colonizers of pine litter. Our main goal was to find out if ubiquitous fungal species are more attractive as food source for oribatid mites than specific mycoflora in pine litter. Further, we examined the reliability of two different methods for determining oribatid feeding preference and whether the preferences are stable over time. Last, we wanted to determine whether the predominantly mycophagous oribatid species are more selective ("choosier") towards particular fungal species than the "generalists" feeding both on fungal and plant material (panphytophages sensu Luxton, 1972).

2. Material and methods

2.1. Localities

Oribatid mites and fungi used in the trials originated from a single locality in a Scots pine (*Pinus sylvestris* L.) forest in the National Park Bohemian Switzerland in North Bohemia (Czech Republic). Litter for fungal isolations and oribatid extraction was collected in November, 2006 and April and August, 2007, respectively. Collections were taken from study plots located about 3 km west from Doubice village on the top of sandstone rock massive "Růžová zahrada," about 450 m a.s.l. (50°53′20.28″N, 14°24′53.82″E). The forest (plant association *Dicrano–Pinetum*) has interspersed birch trees (*Betula pendula* Roth), and the herb layer is patchy and composed mainly of *Vaccinium vitis-idaea* L. and *V. myrtillus* L. The soil is sandy and very shallow (10–45 cm) and the humus form is a typical mor.

2.2. Fungal species

Saprotrophic fungal species were isolated on 1.5% malt agar following surface sterilization of litter needles by 30% hydrogen peroxide (90 s on horizontal shaker). Nine fungi were selected based on their distribution patterns. All fungal strains were identified based on their morphology and further confirmed by alignment of the ITS sequence with databases sequences (NCBI). Codes in brackets refer to strain numbers in the Culture Collection of Fungi (Charles University in Prague, Faculty of Science) or in the Culture Collection of Basidiomycetes (Institute of Microbiology, Academy of Sciences of the Czech Republic). *Sympodiella acicola* W.B. Kendr. (CCF 3736) was included as a species colonizing only litter needles of *P. sylvestris* (Tokumasu et al., 1994; Koukol, 2007). *Verticicladium trifidum* Preuss (CCF 3739) and *Ceuthospora pinastri* (Fr.) Höhn. (CCF 3740) represented ascomycetes colonizing only litter needles of conifers (*Pinaceae*) (Minter, 1981; Maanen and Gourbière, 1997; Przybył et al., 2007). *Hormonema dematioides* Lagerb. & Melin (CCF 3734) colonizes both coniferous wood and litter (Hermanides-Nijhof, 1977). *Allantophomopsis lycopodina* (Höhn.) Carris (CCF 3738) and *Scleroconidioma sphagnicola* Tsuneda, Currah & Thormann (CCF 3735) were frequently isolated from pine litter needles in the studied area (Koukol unpubl.) but the former may colonize also decaying clubmoss stems and ericaceous plants (Carris, 1990) and the latter was also recorded from peat moss (Tsuneda et al., 2000). The only basidiomycete included – *Marasmius androsaceus* (L.) Fr. (CCBAS 859/I), is a key decomposer of coniferous litter (Gourbière and Corman, 1987). Two ubiquitous ascomycetes were employed in order to relate our study to literature results: *Cladosporium herbarum* (Pers.) Link (CCF 3741) is a widespread species colonizing dead organic matter and various soil types and *Oidiodendron griseum* Robak (CCF 3840) is a soil species not restricted to any soil type (Domsch, 2007).

2.3. Oribatid mite species

Samples from the litter and fermentation layer were stored in plastic bags in the dark at 5 °C. Living mites were extracted by heat in modified Berlese–Tullgren funnels and collected in plastic jars with moistened plaster of Paris about 1 week before the start of the experiments. They were sorted under dissecting microscope using a fine brush and identified to species level according to Weigmann (2006). Extracted individuals were fed with coccal green alga (*Desmococcus* spp.), which is accepted as food by most oribatid mites and is often used as a rearing diet in laboratory cultures (see e.g. Hubert et al., 2001), and then starved for 2 days before the experiments.

We employed adults of the following seven oribatid mites that belong to the dominant species in pine forests in the studied area (Mourek, unpubl.). *Eueremaeus silvestris* (Forsslund, 1956) (Eremaeidae), *Porobelba spinosa* (Sellnick, 1920) (Damaeidae), *Spatiodamaeus verticillipes* (Nicolet, 1855) (Damaeidae) and *Oppiella subpectinata* (Oudemans, 1900) (Oppiidae) represent species feeding mainly on fungi (Schuster, 1956; Luxton, 1972; Siepel and De Ruiter-Dijkman, 1993). *Eniochthonius minutissimus* (Berlese, 1903) (Eniochthoniidae) is probably also predominantly fungivorous (Luxton, 1972; Pande and Berthet, 1973; Schneider et al., 2004b), but may feed on decomposing plant material as well (Wallwork, 1967). *Adoristes ovatus* (C.L. Koch, 1839) (Liacaridae) in adult stage feeds on fungal and higher plant material (Schuster,

1956; Wallwork, 1967; Luxton, 1972; Trávníček, 1989), whereas its immature stages feed inside decomposing plant tissues (Trávníček, 1989; Hågvar, 1998). *Nothrus silvestris* Nicolet, 1855 (Nothridae) is an unspecialized feeder, grazing on fungi as well as on various plant materials (Schuster, 1956; Luxton, 1972; Siepel and De Ruiter-Dijkman, 1993). Results of stable isotope study (Schneider et al., 2004b) further revealed that *N. silvestris* may feed also on living and dead animal bodies.

2.4. Feeding preference tests ("Cafeteria I and II")

We adopted a modified conventional multiple choice feeding preference test ("cafeteria") derived from the work of Kaneko et al. (1995), in which all fungal species were simultaneously offered to a given mite species. Sterile *P. sylvestris* needle fragments (2 cm length, sterilized in autoclave) were precolonized with a desired fungal strain growing on 1.5% malt agar for 1–4 weeks depending on the growth rate of a particular fungal species. All fungal species intensively colonized needle fragments at the beginning of each experiment. They formed either dense and sporulating mycelium (*S. acicola*, *C. herbarum*, *O. griseum*, *H. dematioides*, *S. sphagnicola*), dense mycelium with numerous pycnides (*C. pinastri*, *A. lycopodina*) or dense sterile mycelium (*M. androsaceus*, *V. trifidum*). *M. androsaceus* produced also several rhizomorphs per colonized needle throughout the run of all experiments.

2.4.1. Cafeteria I

Six needle fragments (one fragment per fungal species) colonized by *C. pinastri*, *C. herbarum*, *M. androsaceus*, *O. griseum*, *S. acicola*, *V. trifidum* and a sterile control fragment were placed radially at regular distances into a Petri dish with plaster of Paris (3–5 mm thick layer) at the bottom moistened with sterile distilled water. Six replicates were performed for a given mite species. The relative position of fragments varied among experiments to minimize the effect of a neighboring fungal strain.

Twenty adults of a given mite species per dish were allowed to move and consume fungi. Relative preference of the mite species for the particular fungal strain was measured by counting the individuals on needle fragments or in their close vicinity (within 2 mm). Individuals found in the remaining space were enumerated as "wanderers". Dishes were kept in the dark at 16 °C and counts made thrice at 24 h intervals, with the last count after 72 h.

2.4.2. Cafeteria II

We used the same design as in Cafeteria I, but with a modified set of seven fungal species offered (*A. lycopodina*, *C. pinastri*, *H. dematioides*, *M. androsaceus*, *S. sphagnicola*, *S. acicola*, *V. trifidum*). The dishes were examined and counts made only once, after 3 days. Along with counting of individuals, the number of fecal pellets deposited on a given needle fragment or in its close vicinity was used as a second measure of feeding preference for mite species *A. ovatus*, *E. silvestris*, *N. silvestris*, *P. spinosa* and *S. verticillipes*. This was not possible for the other mite species due to their very small fecal pellets, which could not be reliably distinguished from various fungal structures (e.g. microsclerotia of *S. sphagnicola*).

2.5. Consumption test

To test the consumption rate of a given oribatid mite species on a particular fungal species, seven adults were kept in a plastic chamber together with one fungal species as a food source. This test was performed for three mite species (*S. verticillipes*, *A. ovatus* and *E. silvestris*) and for all nine fungal species used in previous experiments. Cylindrical plastic chambers (3 cm in diam., 3.5 cm high) with a layer of plaster of Paris (8–10 mm thick) at the bottom moistened with sterile distilled water were supplied with three needle fragments (2 cm length) precolonized by one fungal strain (same technique as in Cafeteria I and II). Chambers were kept in the dark at 16 °C. Fecal pellets were counted after 4, 11 and 18 days.

2.6. Data analysis

The counts of mites on needles and in their close vicinity together with the number of "wanderers" (Cafeteria I and II) were analyzed by means of generalized linear models with mixed effects (GLMM). The analysis of the fecal pellets numbers deposited on needles and in their close vicinity (Cafeteria II) followed the same technique. A Poisson distribution of the counts variables was assumed, so the Poisson family with log link-function was applied. Counts of individuals in different time intervals within a Petri dish (Cafeteria I) were set as a random effect. If necessary, over-dispersion was treated by refitting the model with the quasipoisson family. After fitting the saturated model, simplification and model comparison was performed. The simplification was done by stepwise merging of the factor levels with closest values of model coefficients. This procedure yielded in the end several (2–4) groups of fungi for each mite species. Fungi (together with sterile control fragments and "wanderers") that have been grouped together did not have significantly different numbers of mites on them. The computations were done by using the *lmer* procedure from the *lme4* package (Bates, 2007) of the *R 2.6.1* statistical environment (R Development Core Team, 2007).

We believe that our approach handles the problems in this kind of data better than the often-used MANOVA (see e.g. Hubert et al., 2001; Schneider et al., 2005; Schneider and Maraun, 2005). We see advantages especially in the ability to handle the hierarchical nature of data (several countings in different times from the same Petri dish and also variability at the Petri dish level) and in the ability to use the more appropriate Poisson distribution (in contrary to the MANOVA's assumption of normality of the response variables). However the intercorrelation of the observations within the Petri dish, due to the finite number of mites there, remains a problem sometimes causing the underdispersion of the model.

In order to assess the level of congruence between the datasets on counts of individuals and fecal pellets from Cafeteria II, we also performed multivariate analysis using the programme CANOCO 4.5 (ter Braak, 1988). We used the data on numbers of fecal pellets as response variables ("species data") and the data on occurrence of individuals as explanatory variables ("environmental data"). The preliminary DCA analysis showed that the longest gradient in dataset is shorter than 2, therefore we further used the linear model (Lepš and Šmilauer, 2003). We performed PCA to inspect the main trends within the fecal pellets dataset and subsequently we performed constrained ordination by means of RDA with occurrences on all needles as explanatory variables. Samples were standardized in both analyses in order to account for different rate of pellet production by each mite species. Significance of the canonical axes in RDA was tested by using the implemented permutation test (4999 permutations).

The results of the Consumption test were analyzed by using the linear mixed effect models (LME), since the numbers of fecal pellets in chambers were high enough to justify (together with subsequent normality tests, data not shown) the approximation of Poisson distribution with the Normal one. The raw data were standardized before the analysis by dividing the increase between counts by the mean of surviving individuals at the beginning and end of the interval. This standardization was necessary, since towards the end of experiment some of the oribatid individuals died. Counts of fecal pellets in different time intervals within a chamber were again set as a random effect. The following procedure of model fitting,

simplification and model comparison was done in the same way as for Cafeteria I and II. In order to explore the non-linear trends in time the polynomial contrasts of the "time of counting" variable were examined. The computations were done by using the same *lmer* procedure from the above cited R package.

3. Results

3.1. Cafeteria I

The ubiquitous fungus *C. herbarum* belonged to the most preferred fungi for all seven mite species employed, the preference being most distinct for *O. subpectinata* and *E. minutissimus*, which preferred only this fungus (Table 1). The preferences for the remaining fungi differed among individual mites: *A. ovatus* and *N. silvestris* most preferred *C. herbarum* and *C. pinastri*; *P. spinosa* most preferred both ubiquitous fungi, *C. herbarum* and *O. griseum*; *S. verticillipes* most preferred *C. herbarum* and *V. trifidum*; whilst *E. silvestris* preferred *C. herbarum* and *S. acicola*. Needles with *M. androsaceus* and the sterile control needles were regularly the least occupied. The numbers of individuals found on the plaster during counting ("wanderers") greatly differed among the mite species (Table 1).

Within the time frame of observation (3 days) we did not observe any qualitative change in the mite preferences. There was a significant interaction with time ($p < 0.05$) for three mite species. In *O. subpectinata* and *A. ovatus*, the number of "wanderers" increased, whilst the counts on *C. herbarum* and *C. pinastri* simultaneously dropped. On the other hand, the decrease in number of *S. verticillipes* "wanderers" (from 62% to 29%) was connected with increased number of mites on *C. herbarum* and *V. trifidum*.

3.2. Cafeteria II

3.2.1. Occurrence of individuals

Elimination of the two ubiquitous fungi *C. herbarum* and *O. griseum* from the set of offered fungi and inclusion of three new species resulted in some changes in the groups formed on the basis of occurrence of oribatid individuals on needle fragments (Table 1). The newly included fungus *A. lycopodina* was highly preferred by *O. subpectinata*, *E. silvestris* and *A. ovatus*. Moreover *E. silvestris* preferred also *S. acicola* as in Cafeteria I. *A. ovatus* and *N. silvestris*

Table 1
Average proportion of individulas or faecal pellets deposited by oribatid mite species on a given fungus (counted from all replicates and time intervals). Groups of fungi and control sterile needles with the same letters have insignficant difference in preference of given mite (GLMM, $P < 0.05$). The category "wanders" indicates mites walking on plaster. Abbrevation: NA - the catagory was excluded from the analysis because of singularity in data

Fungal species	Oribatid mite species						
	A. ovatu s (%)	*S. verticillipes (%)*	*E. silvestris (%)*	*P. spinosa (%)*	*N. silvestris (%)*	*E. minutissimu (%)s*	*O. subpectinata (%)*
Cafeteria I. - individuals							
C. herbarum	19.1^{a}	17.3^{a}	16.8^{a}	35.2^{a}	22.1^{a}	26.2^{a}	49.7^{a}
O. griseum	1.4^{c}	4.8^{b}	3.2^{b}	39.8^{a}	2.7^{c}	9.7^{b}	4.5^{b}
C. pinastri	19.4^{a}	5.7^{b}	5.5^{b}	2.8^{c}	24.8^{a}	5.5^{b}	2.9^{b}
V. trifidum	6.1^{b}	16.2^{a}	5.8^{b}	7.8^{b}	11.1^{b}	8.8^{b}	10.5^{b}
S. acicola	4.4^{b}	7.7^{b}	13.3^{a}	2.2^{c}	5.3^{c}	4.7^{b}	5.4^{b}
M. androsaceus	0.6^{c}	0.9^{c}	0.9^{c}	2.5^{c}	3.4^{c}	2.3^{c}	5.4^{b}
sterile needle	2.4^{d}	2.0^{c}	1.5^{c}	0NA	0NA	4.2^{c}	0.6^{c}
"wanderers"	46.7	45.4	53.2	9.7	30.5	38.5	21.1
Cafeteria II. - individuals							
C. pinastri	5.1^{b}	10.4^{b}	4.3^{c}	9.4^{b}	1.0^{d}	6.6^{c}	11.0^{b}
A. lycopodina	16.2^{a}	9.4^{b}	23.4^{a}	4.3^{b}	4.9^{c}	6.6^{c}	28.0^{a}
H. dematioides	20.5^{a}	12.5^{b}	3.2^{c}	5.1^{b}	28.4^{a}	11.3^{b}	14.6^{b}
S. sphagnicola	10.3^{b}	3.1^{c}	10.6^{b}	6.8^{b}	13.7^{b}	9.4^{b}	6.1^{c}
V. trifidum	6.0^{b}	43.8^{a}	13.8^{b}	24.8^{a}	13.7^{b}	17.9^{a}	11.0^{b}
S. acicola	8.5^{b}	18.8^{b}	20.2^{a}	35.0^{a}	14.7^{b}	4.7^{c}	13.4^{b}
M. androsaceus	0%^{NA}	0NA	4.3^{c}	0.9^{c}	1.0^{d}	3.8^{c}	2.4^{c}
sterile needles	2.6^{c}	1.0^{c}	0NA	0NA	1.0^{d}	0NA	1.2^{c}
"wanderers"	30.8	1.0	20.2	13.7	21.6	39.6	12.2
Cafeteria II. - faecal pellets							
C. pinastri	4.1^{d}	13.5^{b}	11.7^{b}	6.2^{c}	5.4^{c}		
A. lycopodina	15.4^{c}	16.3^{b}	16.8^{a}	8.1^{c}	7.2^{c}		
H. dematioides	35.0^{a}	17.1^{b}	16.8^{a}	5.7^{c}	52.4^{a}		
S. sphagnicola	21.7^{b}	3.6^{c}	11.7^{b}	14.2^{b}	16.3^{b}		
V. trifidum	3.6^{d}	32.0^{a}	8.8^{b}	8.1^{c}	6.6^{c}		
S. acicola	17.2^{c}	16.8^{b}	25.5^{a}	56.9^{a}	8.4^{c}		
M. androsaceus	1.9^{e}	0.6^{d}	8.0^{b}	0.5^{d}	0.6^{d}		
sterile needles	1.0^{f}	0.3^{d}	0.7^{c}	0.5^{d}	3.0^{d}		
Consumption - faecal pellets							
C. herbarum	17.2^{a}	20.2^{a}	8.3^{c}				
O. griseum	5.4^{c}	13.8^{b}	4.2^{c}				
C. pinastri	10.2^{b}	12.0^{b}	8.5^{b}				
A. lycopodina	14.4^{a}	8.7^{c}	22.5^{a}				
H. dematioides	11.8^{b}	12.1^{b}	21.2^{a}				
S. sphagnicola	15.3^{a}	5.6^{c}	14.6^{b}				
V. trifidum	4.2^{c}	7.2^{c}	8.2^{c}				
S. acicola	12.2^{b}	12.5^{b}	7.7^{c}				
M. androsaceus	4.7^{c}	2.0^{d}	1.1^{d}				
sterile needles	4.4^{c}	6.0^{c}	3.6^{c}				

preferred the newly added *H. dematioides*. *S. verticillipes* preferred *V. trifidum* even more distinctly than in Cafeteria I. *E. minutissimus* preferred *V. trifidum* in the second set of fungi, whereas it was not preferred in Cafeteria I. *P. spinosa* (whose both preferred fungi from Cafeteria I were eliminated in Cafeteria II), occurred predominantly on *S. acicola* and *V. trifidum*. The last added fungal species, *S. sphagnicola*, was preferred intermediately by *E. silvestris*, *N. silvestris* and *E. minutissimus*.

As in Cafeteria I, *M. androsaceus* and sterile control needles remained mostly unoccupied. Therefore they had to be often excluded from analysis due to zeros at all measurements and subsequent singularities in the model. The percentage of "wanderers" (ranging from 12% to 39%) was more balanced among the mites than in Cafeteria I, with the exception of *S. verticillipes*, where only about 2% individuals walked around.

3.2.2. Distribution of fecal pellets

The main features of results based on the distribution of fecal pellets were similar to those based upon occurrence of individuals (Table 1). The lowest numbers of pellets were regularly deposited on control fragments and on those colonized by *M. androsaceus*. The only substantial differences were observed for *A. ovatus* and *E. silvestris*. Analysis of pellet distribution of *A. ovatus* revealed high preference for *H. dematioides* and intermediate for *A. lycopodina*, though occurrence of individuals indicated high preference for both of these fungi. Similarly, analysis of pellets of *E. silvestris* revealed that *H. dematioides* scored in the most preferred group, but it was the least preferred fungus as measured by occurrence of individuals.

3.2.3. Congruence between the occurrence of individuals and distribution of fecal pellets

Through constrained ordination (RDA) we were able to explain approximately two thirds of the variability in number of fecal pellets by the first two ordination axes in comparison to amount of variability explainable in unconstrained PCA in first two axes (35.1% and 52.4%, respectively). Basically, there seems to be good agreement between the two types of data in revealing fungi that some of the mite species showed clear preference for (*H. dematioides*, *S. acicola*, *V. trifidum* and less *S. sphagnicola*). The occurrence of individuals on the first three fungi also explained most variation when using the forward selection of variables ($P < 0.05$, data not shown). On the other hand, the remaining counts showed only weak or no correlation with corresponding numbers of fecal pellets. Especially they were uncorrelated in *C. pinastri* and *M. androsaceus*.

3.3. Consumption test

A. ovatus had the highest production of fecal pellets per chamber (mean = 187.87; SE = 21.73), *S. verticillipes* had somewhat less (mean = 156.00; SE = 13.97) and *E. silvestris* had the least (mean = 64.83; SE = 7.29). The means were calculated based upon the raw unstandardized and untransformed counts at the last counting, pooled for all fungal species.

During the test, we did not observe any contamination on fragments precolonized with a desired fungal species. However, in most cases the sterile needle fragments used as control were sparsely overgrown by fungal mycelium (not identified) from the time of the second counting (11 days), probably due to contamination with fungal propagules brought by mites. Therefore, the fecal pellets produced on this diet resulted probably from grazing on fungal contaminants rather than on needle tissues.

The results of pellet production in *A. ovatus* roughly corresponded to the preference tests, but the counts were more balanced among the fungal species (Fig. 1). Two of the preferred fungi from Cafeteria I and II – *C. herbarum* and *A. lycopodina* – were most consumed together with *S. sphagnicola*. The remaining two preferred fungi from Cafeteria I and II – *C. pinastri* and *H. dematioides* – ranked in the second most preferred group. *S. verticillipes* produced most pellets on *C. herbarum*, which corresponds well with preference of this mite in Cafeteria I. However, it consumed *V. trifidum* only intermediately although this fungus, together with *C. herbarum*, was preferred in Cafeteria I and was the most preferred one in Cafeteria II. *E. silvestris* produced most pellets on *A. lycopodina* and *H. dematioides*, whereas *C. herbarum* and *S. acicola* (fungi preferred most in Cafeteria I by this mite) ranked only in the lower intermediate group.

The production of fecal pellets slackened after the second counting for all three mites (data not shown). We even recorded a nett decrease in pellet counts in some chambers, but never consistently in all three replicates of a given fungal species. It indicates that the mites started to feed on their own fecal pellets.

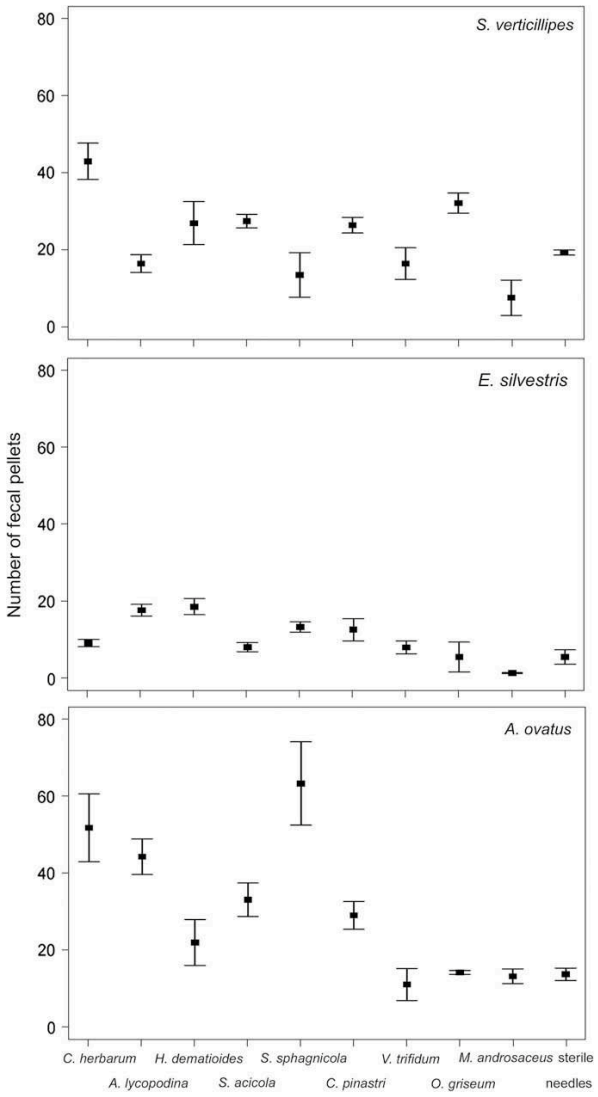


Fig. 1. Counts of fecal pellets produced by *Spatiodamaeus verticillipes*, *Eueremaeus silvestris* and *Adoristes ovatus* in the Consumption test after 18 days (means ± SE, $n = 3$).

4. Discussion

4.1. What is the best indicator of oribatid mite feeding preference?

We suppose that the two widely used methods to quantify the oribatid feeding preference (counting of individuals present on particular food items and counting of fecal pellets deposited on or in close vicinity to the food) have their limits. Firstly, it is little known about the intensity of mite mobility within the time frame of several days in laboratory conditions. Secondly, the fecal pellets may not be deposited exactly in the same place where mites have grazed, due to a comparatively long gut-passage time (Luxton, 1972). Thirdly, preferences revealed in multiple choice tests may be seriously affected by the spectrum of food items offered: inclusion of a highly preferred fungus, such as *C. herbarum* in Cafeteria I, might lure the mites away from other fungi that would be readily grazed if offered separately. Neither of the methods can be considered superior if results are contradictory, since each is only a proxy measure of feeding preference. We recommend simultaneous use of both techniques, which we view as complementary in identifying the most preferred fungal species.

Consumption of fecal pellets by the mites, revealed in later phases of the Consumption test, might affect the results of laboratory studies based solely on counts of fecal pellets, especially of long-term experiments.

4.2. Do oribatid mites prefer ubiquitous fungi?

The mites included in our study, like most oribatid mites in temperate zones, have a wide geographic distribution and inhabit several types of habitats (Weigmann and Kratz, 1981; Weigmann, 2006). Therefore, we hypothesized that they would prefer ubiquitous fungal species. In general, they preferred *C. herbarum* more highly than *C. pinastri*, *S. sphagnicola* and *M. androsaceus*. However, some mite species (*S. verticillipes* and *E. silvestris*) preferred *V. trifidum* and *S. acicola* just as well, even in Cafeteria I with *C. herbarum* present.

The high attractiveness of *C. herbarum*, supposedly the commonest fungal species on live and dead plant material (Domsch, 2007), could be related to its fast growth, massive production of spores and limited antimicrobial activity, typical characteristics of r-selected fungi (Carlile et al., 2001). The species is also known to produce only one endotoxin toxic to mammals (Domsch, 2007). Therefore it might be a suitable and favorite part of diet especially for oribatid mite species, which is accessible "anytime and anywhere". *C. herbarum* and closely related *C. cladosporioides* were also highly preferred by numerous oribatid mites, including adults of *Adoristes ovatus* (Hartenstein, 1962; Trávníček, 1989), as well as by some astigmatid mites (Hubert et al., 2004). *C. cladosporioides* was also isolated from the body surface of oribatid mites (Renker et al., 2005) and together with *C. herbarum* it is frequently carried on the body surface of astigmatid mites in stored grain (Hubert et al., 2003). The amply germinating dry spores of *C. herbarum* are carried easily through the air (Domsch, 2007), but the dispersion via oribatid surface may be beneficial within the soil profile. We suggest that the high attractiveness of *C. herbarum* and *C. cladosporioides* to oribatid mites as a food source might be a general autecological characteristic of both fungal species.

Unlike *C. herbarum*, *O. griseum* was highly preferred only by *P. spinosa*. Other oribatid mite species rather neglected this widespread fungus or showed only weak preference. The genus *Oidiodendron* encompasses morphologically uniform species that often share the same habitat, but differ distinctly in attractiveness to particular oribatid mites and other microarthropods (Kiefer and Cancela da Fonseca, 1971).

4.3. Do oribatid mites prefer fungi colonizing a narrow range of substrate?

Unlike the ubiquitous species, *S. acicola* is a saprotrophic fungus colonizing only litter of *P. sylvestris* (Tokumasu et al., 1994; Koukol, 2007). It also differs from the other pine litter colonizers used in our study, because it grows on the surface of needles, forming a distinct dark net of melanized mycelium and sparse patches of conidiophores. Kendrick and Burges (1962) hypothesized that fungi forming such a superficial mycelial net may attract microarthropods. Initially, *S. acicola* seemed to be a promising model fungus to test mite preference for a specific surface colonizer of litter needles. However, it was preferred only by *E. silvestris* when offered together with the highly preferred *C. herbarum* (Cafeteria I). It became highly preferred by *P. spinosa* and moderately preferred by three other mite species but only when *C. herbarum* was excluded (Table 1). Thus, though it is continually exposed to the mites and other microarthropods on the needle surface, it does not seem to attract a wide spectrum of oribatid mite species to litter needles.

The other fungi colonizing coniferous litter used in our trials are internal colonizers. In natural conditions their vegetative mycelia are immersed in the needle interior, but pycnides (*C. pinastri* and *A. lycopodina*), conidiophores (*V. trifidum*) and rhizomorphs (*M. androsaceus*) protrude through the epidermis or stomata and are exposed. However, in our trials, their mycelium formed dense masses also on the needle surface and so could be grazed. *V. trifidum* was strongly preferred by *S. veriticillipes*, which intensively grazed its mycelium (conidiophores were not produced during the tests). *V. trifidum* was also preferred by *P. spinosa* in Cafeteria II, but only when measured by mite counts. In natural conditions in the litter, one needle may host a community of several fungal species either partitioning the needle or sharing the same space (van Maanen and Gourbière, 1997). This coexistence of several species in a very minute space may represent a food source for various oribatid mite species with different preferences. Surprisingly, this fundamental feature of the coniferous litter has not been considered in previous studies of oribatid feeding preferences.

4.4. What makes a fungal species preferred and/or palatable?

Identification of the principle causes of fungal palatability for microarthropods remains elusive. No one has tested whether oribatid mites are attracted by fungal volatiles, or examined the possibility that mites are actively attracted by fungi, though these phenomena are known for collembolans (Bengtsson et al., 1988) and may even play an important role in nutrient cycling (Klironomos and Hart, 2001).

The other clues to the cause of attractiveness come from morphology of the mycelium and spores. The mycelium is highly variable among our fungal species, reaching different levels of melanization and width (3–12 μm) according to its age. Though the spores are also in the same order of magnitude (length less than 15 μm), spores of some fungi are protected by specific structures. We suppose that the pycnides of *C. pinastri* and *A. lycopodina* prevent conidia from being grazed. Though these two fungal species were grazed moderately during the experiments, their pycnides producing masses of conidia were completely untouched.

As noted above, the latter two fungal species together with *V. trifidum* are interior needle colonizers under natural conditions. Thus, the palatable mycelium may be normally reached only by oribatids tunneling inside decomposing plant material (namely Phthiracaridae, Euphthiracaridae and immatures of Liacaridae including *Adoristes ovatus*; see Wallwork, 1958; Trávníček, 1989; Hågvar, 1998). This conclusion is consistent with observations that

their digestive tract frequently contains fungal material as well as that of plants (Behan-Pelletier and Hill, 1983). *S. verticillipes* preferred *V. trifidum* in our experiments, but it may not feed upon the mycelium of this fungus in nature, because the mite does not tunnel in dead plant matter.

4.5. Why are saprotrophic basidiomycetes not preferred by oribatids?

There was a consistently low incidence of individuals and production of pellets on the basidiomycete *M. androsaceus* by all our oribatid mite species, irrespective of whether it was offered separately or together with other fungi. We suspect that some type of chemical repellence is responsible for its low suitability as a food source, though Newell (1984) found that *M. androsaceus* was intensively consumed and preferred by the collembolan *Onychiurus latus* (Gisin, 1956). Similarly to our results, Schneider et al. (2005) recorded low palatability of *Agrocybe gibberosa* (Fr.) Fayod for three oribatid mite species. So far, *M. androsaceus* and *A. gibberosa* have been the only saprotrophic members of Agaricomycetes used for feeding preference tests with oribatids. This is rather bewildering considering the key role of saprotrophic basidiomycetes in decomposition and nutrient cycling in forest ecosystem (Cairney, 2005). As partial explanation, there may be bias in study designs; priority is often given to collembolans in studies of microarthropod interaction with wood- and litter-decomposing basidiomycetes (Kampichler et al., 2004; Tordoff et al., 2008; see Gange, 2000 for critique on selection of collembolan species).

4.6. Are the "true" fungivores choosier than the panphytophages?

Our results are only partly consistent with the hypothesis that the oribatid mites feeding mainly on fungal material (*S. verticillipes*, *P. spinosa*, *O. subpectinata* and *E. silvestris*) have a better ability to discern among fungal species and would be thus more selective than the "unspecialized" species (*A. ovatus* and *N. silvestris*), which consume both fungal and higher plant material (panphytophages sensu Luxton, 1972); the latter possibly also living and dead soil invertebrates (Schneider et al., 2004b). In Cafeteria I, *O. subpectinata* appeared to be the most selective species, preferring *C. herbarum* only. For *E. minutissimus*, which seems mainly fungivorous, but also feeds on plant detritus to some extent (Wallwork, 1967; Schneider et al., 2004b), we observed a similar pattern, but the preference for *C. herbarum* was less pronounced. However, the other predominantly fungivorous oribatid mites, *S. verticillipes*, *P. spinosa* and *E. silvestris*, were not more selective than the panphytophages, preferring two of the fungal species offered in Cafeteria I. This indicates that one feeding guild can harbor species with different strategies regarding the selection of fungal species. Moreover, the degree of selectiveness differed between Cafeteria I and II for some oribatid species and thus seems to change with the spectrum of available fungi.

4.7. Conclusions

We observed no gradation in preference of fungi for oribatid mites as a group, but rather a discontinuous and dynamic mosaic with particular mite species preferring particular fungal species. This heterogeneous mosaic shapes the feeding niches occupied by particular oribatid mite species and ensures that numerous species may coexist in a given habitat and time without strong competition for food resources. Thus, our results are incongruent with the prevalent opinion that the differences in preference for fungi are rather small among soil microarthropods and therefore cannot explain the high diversity of coexisting microarthropod species (Maraun et al., 1998; Schneider and Maraun, 2005; Tordoff et al., 2008). Considering the tremendous fungal diversity in soil, this latter opinion may only reflect the very limited number of fungal species that have been studied.

Acknowledgements

We thank the administration of the National Park Bohemian Switzerland (Czech Republic) for allowing us to collect the samples for our experiments and to Ivana Marková for help during the collection. We are indebted to Roy A. Norton (Syracuse, USA) and to the two anonymous reviewers for valuable comments on our manuscript. The study was financially supported by project of the Grant Agency of the Academy of Science of the Czech Republic.

References

Bates, D., 2007. lme4: Linear Mixed-effects Models Using S4 Classes. R package version 0.99875-9.
Behan-Pelletier, V.M., Hill, S.B., 1983. Feeding habits of sixteen species of Oribatei (Acari) from an acid peat bog, Glenamoy, Ireland. Revue d'Écologie et de Biologie du Sol 20, 221–267.
Bengtsson, G., Erlandsson, A., Rundgren, S., 1988. Fungal odour attracts soil Collembola. Soil Biology and Biochemistry 20, 25–30.
Cairney, J.W.G., 2005. Basidiomycete mycelia in forest soils: dimensions, dynamics and roles in nutrient distribution. Mycological Research 109, 7–20.
Carlile, M.J., Watkinson, S., Graham, G., 2001. The Fungi. Elsevier, Amsterdam, 588 pp.
Carris, L.M., 1990. Cranberry black rot fungi: *Allantophomopsis cytisporea* and *Allantophomopsis lycopodina*. Canadian Journal of Botany 68, 2283–2291.
Domsch, K.H., 2007. Compendium of soil fungi. IHW Verlag. Eching, 672 pp.
Erdmann, G., Otte, V., Langel, R., Scheu, S., Maraun, M., 2007. The trophic structure of bark-living oribatid mite communities analysed with stable isotopes (^{15}N, ^{13}C) indicates strong niche differentiation. Experimental and Applied Acarology 41, 1–10.
Gange, A.C., 2000. Arbuscular mycorrhizal fungi, collembola and plant growth. Trends in Ecology and Evolution 15, 369–372.
Gourbière, F., Corman, A., 1987. Decomposition des aiguilles d'*Abies alba*: hétérogénéité du substrat et de la mycoflore, role de *Marasmius androsaceus*. Soil Biology and Biochemistry 19, 69–75.
Hågvar, S., 1998. Mites (Acari) developing inside decomposing spruce needles: biology and effect on decomposition rate. Pedobiologia 42, 358–377.
Hartenstein, R., 1962. Soil oribatei I: feeding specificity among forest soil oribatei (Acarina). Annals of the Entomological Society of America 55, 202–206.
Hawksworth, D.L., 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycological Research 105, 1422–1432.
Hermanides-Nijhof, E.J., 1977. *Aureobasidium* and allied genera. Studies in Mycology 15, 141–177.
Hubert, J., Žilová, M., Pekár, S., 2001. Feeding preferences and gut contents of three panphytophagous oribatid mites (Acari: Oribatida). European Journal of Soil Biology 37, 197–208.
Hubert, J., Stejskal, V., Kubátová, A., Münzbergová, Z., Váňová, M., Žd'árková, E., 2003. Mites as selective fungal carriers in stored grain habitats. Experimental and Applied Acarology 29, 69–87.
Hubert, J., Jarošík, V., Mourek, J., Kubátová, A., Žd'árková, E., 2004. Astigmatid mite growth and fungi preference (Acari: Acaridida): comparisons in laboratory experiments. Pedobiologia 48, 205–214.
Kampichler, C., Rolschewski, J., Donnely, D.P., Boddy, L., 2004. Collembolan grazing affects the growth strategy of the cord-forming fungus *Hypholoma fasciculare*. Soil Biology and Biochemistry 36, 591–599.
Kaneko, N., McLean, M.A., Parkinson, D., 1995. Grazing preferences of *Onychiurus subtenuis* (Collembola) and *Oppiella nova* (Oribatei) for fungal species inoculated on pine needles. Pedobiologia 39, 538–546.
Kendrick, W.B., Burges, A., 1962. Biological aspects of the decay of *Pinus sylvestris* leaf litter. Nova Hedwigia 4, 313–342.
Kiefer, E., Cancela da Fonseca, J.P., 1971. Sur les rapports entre microarthropodes et micromycètes d'un sol forestier. Zentralblatt für Bakteriologie und Parasitologie. Abteilung II 126, 510–520.
Klironomos, J.N., 1992. Feeding preferences of the collembolan *Folsomia candida* in relation to microfungal succession on decaying litter. Soil Biology and Biochemistry 24, 685–692.
Klironomos, J.N., Hart, M.M., 2001. Animal nitrogen swap for plant carbon. Nature 410, 651–652.
Koukol, O., 2007. Effect of Pinus strobus L. invasion on the mycoflora of pine litter needles in the Bohemian Switzerland National Park (Czech Republic). In:Härtel, H. et al., (Eds.), Sandstone Landscapes. Academia, pp. 229–233.
Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge, 282 pp.
Luxton, M., 1972. Studies on the oribatid mites of a Danish beech wood soil, I. Nutritional biology. Pedobiologia 12, 434–463.

Maanen, van A., Gourbière, F., 1997. Host and geographical distribution of *Verticicladum trifidum*, *Thysanophora penicillioides* and similar fungi on decaying coniferous needles. Canadian Journal of Botany 75, 699–710.

Maraun, M., Migge, S., Schaefer, M., Scheu, S., 1998. Selection of microfungal food by six oribatid mite species (Oribatida, Acari) from different beech forests. Pedobiologia 42, 232–240.

Maraun, M., Martens, H., Migge, S., Theenhaus, A., Scheu, S., 2003. Adding to 'the enigma of soil animal diversity' fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85–95.

Minter, D.W., 1981. Microfungi on needles, twigs and cones of pinus in ČSSR. Česká Mykologie 35, 90–101.

Newell, K., 1984. Interaction between two decomposer Basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. Soil Biology and Biochemistry 16, 235–239.

Przybył, K., Karolewski, P., Oleksyn, J., Łabędzki, A., Reich, P., 2007. Fungal diversity of Norway spruce litter: effects of site conditions and premature leaf fall caused by bark beetle outbreak. Microbial Ecology 10, 999–1018.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org.

Renker, C., Otto, P., Schneider, K., Zimdars, B., Maraun, M., Buscot, F., 2005. Oribatid mites as potential vectors for soil microfungi: study of mite-associated fungal species. Microbial Ecology 50, 518–528.

Sadaka-Laulan, N., Ponge, J.F., Roquebert, M.F., Bury, E., Boumezzough, A., 1998. Feeding preferences of the collembolan *Onychiurus sinensis* for fungi colonizing holm oak litter (*Quercus rotundifolia* Lam.). European Journal of Soil Biology 34, 179–188.

Schneider, K., Maraun, M., 2005. Feeding preferences among dark pigmented fungal taxa (''Dematiacea'') indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). Pedobiologia 49, 61–67.

Schneider, K., Renker, C., Scheu, S., Maraun, M., 2004a. Feeding biology of oribatid mites: a minireview. Phytophaga 14, 247–256.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004b. Trophic niche differentiation in oribatid mites (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$. Soil Biology and Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Scheu, S., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67–72.

Schuster, R., 1956. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. Zeitschrift für Morphologie und Ökologie der Tiere 45, 1–33.

Siepel, H., De Ruiter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on their carbohydrase activities. Soil Biology and Biochemistry 25, 1491–1497.

ter Braak, C.J.F., 1988. CANOCO – a FORTRAN Program for Canonical Community Ordination by [partial] [detrended] [canonical] Correspondence Analysis, Principle Components Analysis and Redundancy Analysis. Technical report: TNO Institute Wageningen, 95 pp.

Tokumasu, S., Aoki, T., Oberwinkler, F., 1994. Fungal succession on pine needles in Germany. Mycoscience 35, 29–37.

Tordoff, G.M., Boddy, L., Jones, T.H., 2008. Species-specific impacts of collembola grazing on fungal foraging ecology. Soil Biology and Biochemistry 40, 434–442.

Trávníček, J., 1989. Laboratory cultivation and biology of mites in the family Liacaridae (Acari: Oribatida). Acta Universitatis Carolina – Biologica 33, 69–80.

Tsuneda, A., Thormann, M.N., Currah, R.S., 2000. *Scleroconidioma*, a new genus of dematiaceous Hyphomycetes. Canadian Journal of Botany 78, 1294–1298.

Wallwork, J.A., 1958. Notes on feeding behaviour of some forest soil Acarina. Oikos 9, 260–271.

Wallwork, J.A., 1967. Acari. In: Burges, A., Raw, F. (Eds.), Soil Biology. Academic Press, London, pp. 362–395.

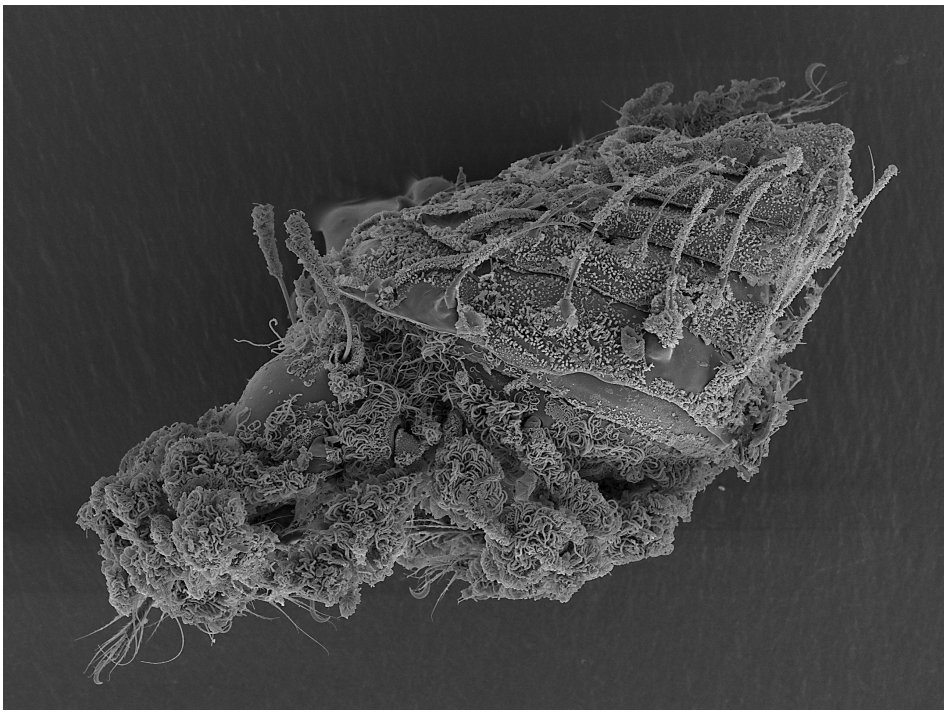
Wallwork, J.A., 1983. Oribatids in forest ecosystems. Annual Review of Entomology 28, 109–130.

Weigmann, G., 2006. Hornmilben (Oribatida). – Die Tierwelt Deutschlands 76. Goecke & Evers, Keltern, 520 pp.

Weigmann, G., Kratz, W., 1981. Die deutschen Hornmilbenarten und ihre ökologische Charakteristik. Zoologishe Beiträge 27, 459–489.

Contribution 2.2

Koukol O., Janovský Z., Černá K., **Mourek J.** (*submitted*) The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes.



The effect of oribatid mites on the dispersal potential of two anamorphic ascomycetes

Koukol Ondřej[1], Janovský Zdeněk[1], Černá Kristýna[1] and Mourek Jan [2,3]
[1]Charles University, Faculty of Science, Department of Botany, Benátská 2, CZ-128 44 Prague, Czech Republic
[2]Charles University, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44 Prague, Czech Republic
[3]Charles University, Faculty of Education, Department of Biology and Environmental Education, M. D. Rettigové 4, CZ-116 39 Prague 1, Czech Republic

Address:
Charles University in Prague, Faculty of Science
Department of Botany
Benátská 2, CZ-128 44 Prague
Czech Republic

E-mail: o.koukol@seznam.cz
Tel.: +420 221 951 650

Abstract
Changes in the number of propagules (conidia and hyphal fragments) potentially used for the dispersal of two anamorphic ascomycetes were determined after grazing by two mycophagous oribatid mites at two mite densities. Fragments of pine litter needles precolonised by *Sympodiella acicola* and *Fusicladium cordae* were exposed to grazing by *Porobelba spinosa* and *Spatiodamaeus verticillipes*. The number of propagules was determined as the number of fungal colonies on agar plates originating from a suspension made by washing the surface of individual needle fragments. Lower density grazing by *Spatiodamaeus verticillipes* resulted in higher number of propagules of both fungal species and reversed the decrease in the number of propagules in the control treatment. In contrast, both oribatid mites at the higher density significantly decreased the number of colonies. Simultaneously, allochthonous fungi were introduced by the mites into the needle fragments. Our results indicate that *Spatiodamaeus verticillipes* and *Porobelba spinosa* may represent an important force affecting the dispersal of particular fungal species and the composition and structure of fungal communities in pine litter, with the effects being mite-density dependent.

Descriptors: oribatid mites, anamorphic ascomycetes, hyphal fragments, conidia, dispersion, allochthonous fungi, *Sympodiella acicola*, *Fusicladium cordae*, *Spatiodamaeus verticillipes*, *Porobelba spinosa*

Key words: ascomycetes; oribatid mites; dispersion; colonisation; allochthonous fungi

Introduction

Anamorphic ascomycetes produce large numbers of conidia (asexual spores) to disperse over a large area, but these species can also disperse by hyphal fragments following the mechanical disruption of mycelia (Carlile *et al*. 2001). Both conidia and mycelia are utilised as nutrition sources by numerous soil-dwelling arthropods, especially oribatid mites (Acari: Oribatida) and collembolans (Hexapoda: Collembola). Oribatid mites include, in addition to other feeding strategies, numerous fungal feeders that graze primarily on ascomycetes and show a distinct preference within this group of fungi (Schneider & Maraun 2005; Koukol *et al*. 2009). The overall negative effect of grazing could be offset by enhanced dispersion of the fungi. Mite faeces often contain a large proportion of undamaged fungal spores and fragments of hyphae (Smrž & Norton 2004), and these propagules, together with those attached to surface of the mite bodies, may contribute to the dispersion of fungi within litter and soil (Behan & Hill 1978; Maraun *et al*. 1998; Renker *et al*. 2005). The effect of grazing by oribatid mites on fungal colony has not been tested in experimental conditions yet. Therefore, it is not known, how compensatory these opposing effects (grazing vs. enhanced dispersion) are for particular fungal species. Several studies showed that grazing by collembolans may have not only negative effect, but it may increase fungal respiration and hyphal coverage of basidiomycete and zygomycete, respectively (Bengtsson & Rundgren 1983, Bretherton *et al*. 2006).

In the present study, we exposed two anamorphic ascomycetes *Fusicladium cordae* Koukol (*Venturiaceae*, Dothideomycetes) and *Sympodiella acicola* W.B. Kendr. (Ascomycota *inc. sed*.) to grazing by two fungal feeding oribatid mites *Porobelba spinosa* (Sellnick) and *Spatiodamaeus verticillipes* (Nicolet) (both Damaeidae) in two different densities. Though *Porobelba spinosa* and *Spatiodamaeus verticillipes* are closely related, they differ in body size (345-420 μm and 670-735 μm, respectively). In a previous study (Koukol *et al*. 2009) we have demonstrated that these species intensively grazed

anamorphic ascomycetes during multiple-choice preference tests. The aims of the present study were 1) to evaluate the effect of grazing by oribatid mites at two different densities on the number of fungal propagules and 2) to determine if oribatid mites can introduce new fungal species into a previously colonised substrate. We supposed that these two mite species would have different effect and this effect would depend on their densities. We further hypothesised that fungi may benefit from lower grazing intensity through an increase in their dispersal potential.

Materials and Methods

Both oribatid mite species (adults) and the fungal strains originated from the litter and the fermentation layer from a pine (*Pinus sylvestris* L.) forest in the same locality in the Bohemian Switzerland NP (Czech Republic). Needles for fungal isolations were collected in November, 2006; litter for oribatid extraction was collected in October 2008. Collections were taken from study plots located about 3 km west from Doubice village on the top of sandstone rock massive with pine forest (plant association *Dicrano–Pinetum*); see Koukol *et al*. (2009) for locality details. *Sympodiella acicola* represents a common fungal species that colonises the surface of litter needles of *Pinus sylvestris* and is therefore accessible to grazing by various soil arthropods. *Fusicladium cordae* is less frequent, but colonises also the surface of pine litter needles. *Fusicladium cordae* and *Sympodiella acicola* produce a large number of cylindrical conidia that are roughly similar in shape and size. *Sympodiella acicola* and *Fusicladium cordae* were subcultured on agar slants with 2% malt agar (MA, 2% w/v saccharose, 18 g agar, Himedia, India) (Fassatiová 1986) for 4 weeks. Two slants per fungal species were supplied with 3 ml sterile water and were shaken vigorously for 15 min using an IKA HS 260 shaker (IKA, Staufen, Germany) to obtain a suspension for inoculation. Sterile needle fragments (sterilised in an autoclave for 20 min) were soaked in the suspension and were shaken at low intensity for 30 min. For each treatment, six needle fragments were placed radially at regular distances in a Petri dish (6 cm in diam.) with plaster of Paris (3-5 mm thick) on the bottom, moistened with sterile distilled water and incubated for 28 d in the dark at 25˚C, by which time mycelia had evenly colonised the needle fragments. Living mites were extracted by heat in modified Berlese–Tullgren funnels about 7 d before the start of the experiments and were hand sorted with a fine brush. Each mite species was stored separately in sterile polypropylen plastic chambers with a layer of moistened plaster of Paris on the bottom and fed *ad libitum* with a culture of coccal green alga (*Desmococcus* spp.), which is commonly used as a rearing diet for oribatid mites (Hubert *et al.*, 2001, Smrž & Norton, 2004). Two days before the experiment, the mites were transferred into new sterile damp chambers and starved until the beginning of the experiment. This was done to minimize the amount of allochthonous fungal propagules in their digestive tract. Two runs of the experiment were performed in sequence with both fungal species, using either the lower (four individuals per Petri dish) or the higher (seven individuals) mite density. For each run, three treatments with nine Petri dishes each were carried out for both fungal species. These treatments were 1) grazing by *Porobelba spinosa*; 2) grazing by *Spatiodamaeus verticillipes*; and 3) ungrazed control. Each treatment was assigned randomly amongst the Petri dishes. The numbers of fungal propagules of *Sympodiella acicola*, *Fusicladium cordae* and allochthonous fungi introduced by the mites were determined after 7, 14 and 21 d. At each time point, three Petri dishes per treatment were harvested. Each needle fragment was vigorously shaken in 3 ml sterile distilled water for 5 min using a horizontal shaker, and then 100 µl of suspension (optimised for the Petri dish) was pipetted onto a Petri dish (6 cm in diam.) containing 2% MA and was evenly distributed with a sterile glass rod. The malt agar medium is a nonselective medium routinely used for isolation of various

saprotrophic fungi (Mueller *et al*. 2004). The dishes were incubated at 25˚C in the dark. Colonies of *Sympodiella acicola* and *Fusicladium cordae* originating from the washed propagules were counted after 4-6 d. Allochthonous fungi, whose propagules were introduced by *Porobelba spinosa* and *Spatiodamaeus verticillipes* and grew on the agar plates, were identified based on morphological characteristics. The frequencies of allochthonous fungal species were counted as the ratio of the number of colonies of particular fungal species to the total number of all colonies of allochthonous species obtained from all Petri dishes in the run.

The resulting data were analysed by means of generalised linear models (GLM) with an assumed Poisson distribution of the dependent variable and a logarithm as the canonical link function. The prevalent overdispersion was treated by refitting to a quasi-Poisson family, and subsequent tests of model comparisons were made using the F-test. The minimal adequate models were obtained by means of backward selection. Runs of each density were analysed. All computations were performed in the R statistical environment, version 2.10.0 (R Development Core Team, 2009).

Results and Discussion

Effect of grazing

The outcome of grazing in our experiments depended primarily on the mite species identity and secondarily on its density. The identity of the fungal species was of less importance. The control treatments of the two runs showed different patterns (Fig. 1 a-d), though time and experimental conditions (humidity, temperature) were held constant in both runs. This indicates that some other condition (for example slightly different quality of needle) altered the fitness and the physiological state of the fungal strains between the two runs and that either mycelium senescence, waning of conidia production or loss of conidia viability were occurring in different intensity. This variability made our results difficult to interpret in terms of mite influence, but it should be attributed to natural fungal variability.

In the first run with lower mite density (Fig. 1 a, b), the number of propagules continuously decreased with time in the control treatments of both *Sympodiella acicola* and *Fusicladium cordae*. The effect of mites differed. *Porobelba spinosa* had no effect on the number of fungal colonies. *Spatiodamaeus verticillipes* reversed the decreasing trend with time (interaction mite:time $p=0.04$), but this apparent positive effect on the number of fungal propagules, should only be regarded in comparison to the decreasing control (Fig. 1 a, b). The increased propagule amount could be explained by rejuvenation of senescent mycelium through mite grazing and fragmentation of hyphae. The former phenomenon is well known for plants, where herbivore grazing may promote growth by production of growth promoters and by decreasing competition for light and nutrients from the soil (Agrawal 2000). The positive effect of arthropod grazing on fungal vegetative growth has been recorded in the literature only rarely. Periodic grazing by collembolans increased the respiration of the zygomycete *Umbelopsis isabellina* (Oudem.) W. Gams (Bengtsson & Rundgren 1983). Bretherton *et al*. (2006) observed a positive effect of collembolan grazing on the hyphal coverage of saprotrophic basidiomycete *Phanerochaete velutina* (DC.) Parmasto.

In the second run of our experiments with the higher mite density (Fig. 1 c, d), the number of colonies in the control treatment increased over time, reflecting probably continuous production of new conidia. Both species of oribatid mites caused a significant decrease in the number of new colonies (interaction mite:time $p<0.001$). *Sympodiella acicola* was almost completely grazed down, and no colonies were retrieved from some of the needles exposed to *Spatiodamaeus verticillipes*. The smaller species, *Porobelba*

spinosa, had lower impact (Fig 1 c, d). This result clearly shows a detrimental effect of intensive grazing of mites in a high population density on the growth and sporulation of fungi and on their ability to colonise other needles.

Introduction of allochthonous fungal species by the mites

The presence of viable propagules of microfungi on oribatid mite body surfaces and within their faeces are well-known phenomena (Renker *et al.* 2005) that, for example, help to recover microbial communities after a disturbance (Maraun *et al*. 1998). We suppose that allochthonous fungi introduced in our experiments were delivered on the body surface of the mite species. Their faeces should not contain fungal material because the mite species were fed several days by alga and then starved prior to the experiments. The body surfaces of *Spatiodamaeus verticillipes* and *Porobelba spinosa* are covered with a thick layer of filamentous cerotegument (Miko 2006, 2008). This type of cerotegument seems to be very suitable for the attachment of fungal spores; we frequently observed attached fungal spores at both mite species (Mourek, unpubl.). The number of colonies of allochthonous fungi introduced by the mites increased considerably at the higher mite density, with *Spatiodamaeus verticillipes* introducing more fungal propagules than *Porobelba spinosa* ($p<0.001$). The number also increased over time, which suggests that either some fungi were continuously detached from the mites' surfaces or that these fungi established sporulating colonies on needles (Fig 1 e, f). In total, 15 fungal species were isolated. *Penicillium janthinellum* Biourge, *Acremonium* sp. and *Verticillium* sp. were distributed by both mites and reached a frequency of colonies greater than 20%. *Acrodontium crateriforme* (J.F.H. Beyma) de Hoog was recorded at a frequency of 20%, but was distributed only by *Spatiodamaeus verticillipes*. Other fungal species were recorded mostly as singletons, including *Alternaria alternata* (Fr.) Keissl., *Acremonium butyri* (J.F.H. Beyma) W. Gams, *Chaetomium funicola* Cooke, *Chalara longipes* (Preuss) Cooke, *Eurotium repens* de Bary, *Geomyces pannorum* (Link) Sigler & J.W. Carmich., *Lecanicillium evansii* Zare & W. Gams, *Oidiodendron rhodogenum* Robak, *Trichoderma* sp. and two unidentified coelomycetes producing pycnides.

The number of fungal species introduced onto the needles by *Spatiodamaeus verticillipes* and *Porobelba spinosa* was comparable to the 16 species isolated from the surface of ten individuals of four mite species by Renker *et al*. (2005). Most of the fungal species recorded and identified in our study belong to unspecialised soil saprotrophic fungi (Domsch 2007). *Acrodontium crateriforme* was characterised as an entomophilic saprotroph by Miętkiewski *et al.* (2000).

Summary

Our laboratory study demonstrated that oribatid mites affected the number of fungal propagules giving rise to new colonies. The oribatid mites *Spatiodamaeus verticillipes* and *Porobelba spinosa* may represent an important force affecting the composition and structure of fungal communities in pine litter, with the effects being mite-density dependent. At higher densities, the mites were able to locally suppress particular fungal species while introducing new fungal species into the grazed space. At lower mite densities, grazing by *Spatiodamaeus verticillipes* increased the number of fungal propagules and thus enhanced the distribution potential of the studied fungal species.

Acknowledgements

We thank the administration of the Bohemian Switzerland National Park (Czech Republic) for permission to collect the samples for our experiments. We would also like to thank Ivana Marková for help during the collection. The study was financially supported by a project of the Grant Agency of the Academy of Science of the Czech Republic, Nr. KJB601110718.

References

Agrawal AA, 2000. Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends in Plant Science* **5**: 309-313

Behan VM, Hill SB, 1978. Feeding habits and spore dispersal of Oribatid mites in the North American Arctic. *Revue d'Écologie et de Biologie du Sol* **15**: 497-516.

Bengtsson G, Rundgren S, 1983. Respiration and growth of a fungus, *Mortierella isabellina*, in response to grazing by *Onychiurus armatus* (Collembola). *Soil Biology & Biochemistry* **15**: 469-473.

Bretherton S, Tordoff M, Hefin Jones T, Boddy L, 2006. Compensatory growth of *Phanerochaete velutina* mycelial systems grazed by *Folsomia candida* (Collembola). *FEMS Microbiology Ecology* **58**: 33-40.

Carlile M, Watkinson SC, Gooday GW, 2001. *The Fungi*. Second Edition, Elsevier, Amsterdam.

Domsch KH, 2007. *Compendium of soil fungi*. IHW Verlag, Eching.

Fassatiová O, 1986. *Moulds and filamentous fungi in technical microbiology*. Elsevier, Amsterdam.

Hubert J, Žilová M, Pekár S, 2001. Feeding preferences and gut contents of three panphytophagous oribatid mites (Acari: Oribatida). *European Journal of Soil Biology* **37:** 197-208.

Koukol O, Mourek J, Janovský Z, Černá K, 2009. Do oribatid mites (Acari: Oribatida) show a higher preference for ubiquitous vs. specialized saprotrophic fungi from pine litter? *Soil Biology & Biochemistry* **41**: 1124-1131.

Maraun M, Visser S, Scheu S, 1998. Oribatid mites enhance the recovery of the microbial community after a strong disturbance. *Applied Soil Ecology* **9**: 175-181.

Miętkievski R, Bałazy S, Tkaczuk C, 2000. Mycopathogens of mites in Poland – a review. *Biocontrol Science and Technology* **10**: 459-465.

Miko L, 2006. Damaeidae. In: Weigmann G, *Die Tierwelt Deutschlands, Vol. 76 Hornmilben (Oribatida)*, Goecke & Evers, Keltern, pp. 179-207.

Miko L, 2008. Taxonomy of European Damaeidae (Acari: Oribatida) II. *Porobelba weigmanni* n. sp. (Oribatida, Damaeidae), from East Slovakia, with comments on other known species of the genus. *Zootaxa* 1844: 55-62.

Mueller GM, Bills GF, Foster MS, 2004. *Biodiversity of Fungi*. Elsevier, San Diego.

R Development Core Team, 2009. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Renker C, Otto P, Schneider K, Zimdars B, Maraun M, Buscot F, 2005. Oribatid mites as potential vectors for soil microfungi: study of mite-associated fungal species. *Microbial Ecology* **50**: 518-528.

Schneider K, Maraun M, 2005. Feeding preferences among dark pigmented fungal taxa "Dematiacea" indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). *Pedobiologia* **49**: 61-67.

Smrž J, Norton RA, 2004. Food selection and internal processing in *Archegozetes longisetosus* (Acari: Oribatida). *Pedobiologia* **48**: 111-120.

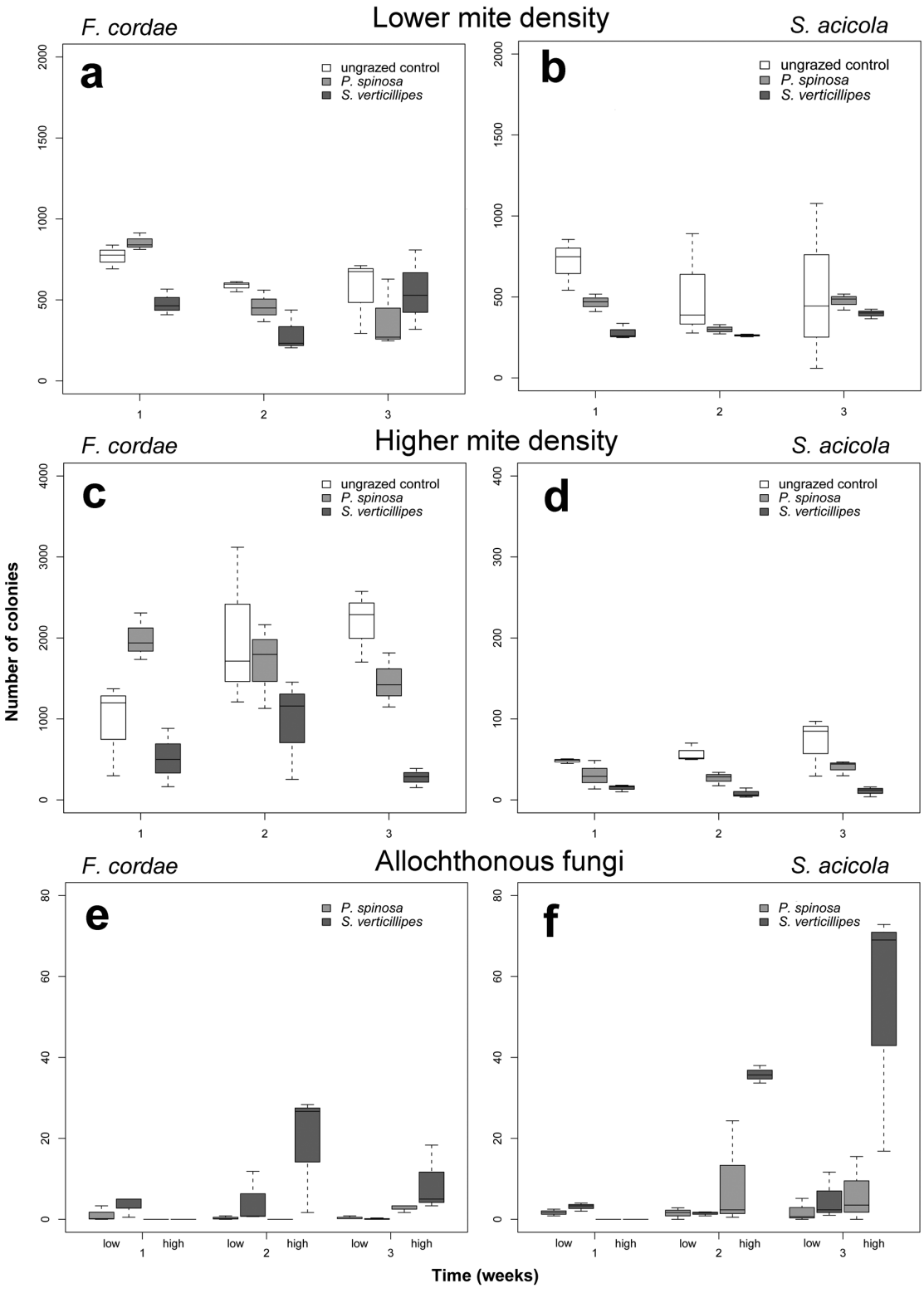


Fig 1 – Number of colonies of *Fusicladium cordae* (a, c) and *Sympodiella acicola* (b, d) growing from propagules in suspension from washed precolonised needles after grazing of the needles by mites at lower (a, b) and higher (c, d) density. Number of colonies of allochthonous fungi introduced by the mites to needles precolonised by *F. cordae* (e) and *S. acicola* (f). Note different scale of vertical axis used in particular plots.