

Charles University in Prague
Faculty of Science
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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

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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 None of the nomenclatory acts proposed in the attached unpublished manuscripts is available until the works are published in ordinary way.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.).

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Prohlášení

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

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31. května 2010

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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 redescription 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.

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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 taxonomy 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 peer-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 the 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 Brachypyliina 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 Damaeioidea Berlese, 1896, whereas Gymnodamaeidae to Plateremaeoidea Trägårdh, 1931 (see Weigmann, 2006; Norton and Behan-Pelletier, 2009) or to monotypical superfamily Gymnodamaeioidea Grandjean, 1954 (see Balogh and Balogh, 1992; Subías, 2004).

The relations between different superfamilies within 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 gastronomic exuviae of previous ontogenetic stages ("scalps") on the dorsal side of the gastronomic region (Fig. 1). Another remarkable morphological feature (but probably not independent from the previous one) characterizing the Euphérédermés, is the reduction of some gastronomic 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 gastronomic exuviae ("scalps"), typical for nymphs of the oribatid section Euphérédermes.

Monophyly of Euphérédermés was not supported by Maraun et al. (2004), but it might be an effect of 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 gastronomic 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 gastronomic 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 gastronomic 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 gastronomic 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 redescrptions 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).

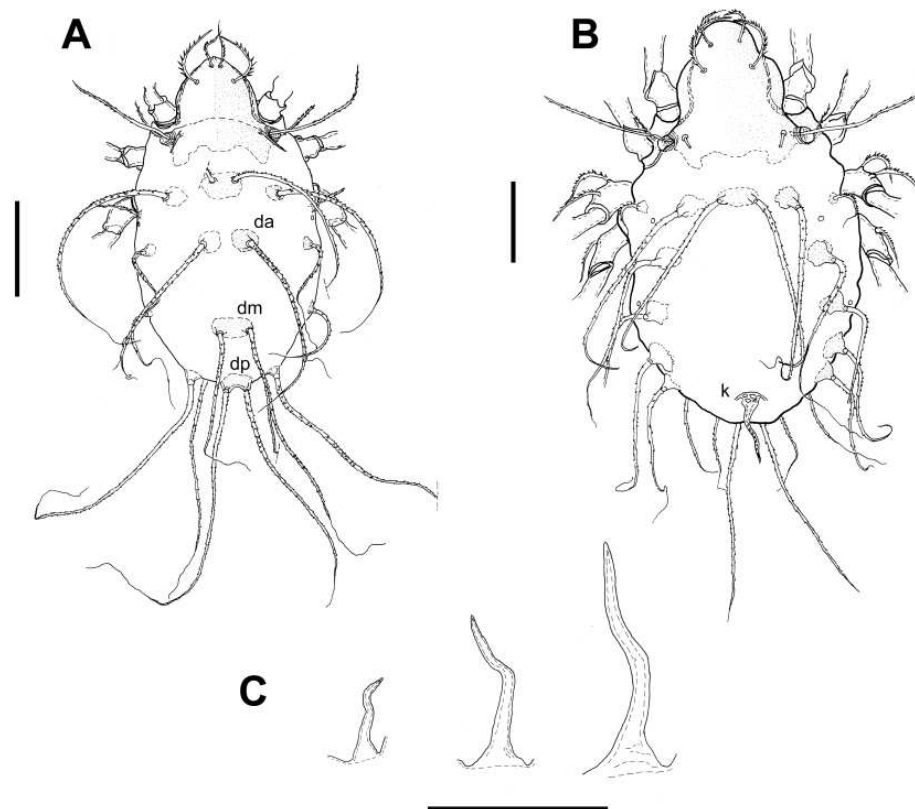


Fig. 3: *Spatiodamaeus verticillipes* (Damaeidae): A) larva in dorsal view; B) deutonymph in dorsal view; C) nymphal cornicles in lateral view, from left to right: protonymph, deutonymph, tritonymph. Scales: 100µm. Abbreviations: *da*, *dm*, *dp* - notogastral setae, present only in larva; *k* - cornicle.

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.)

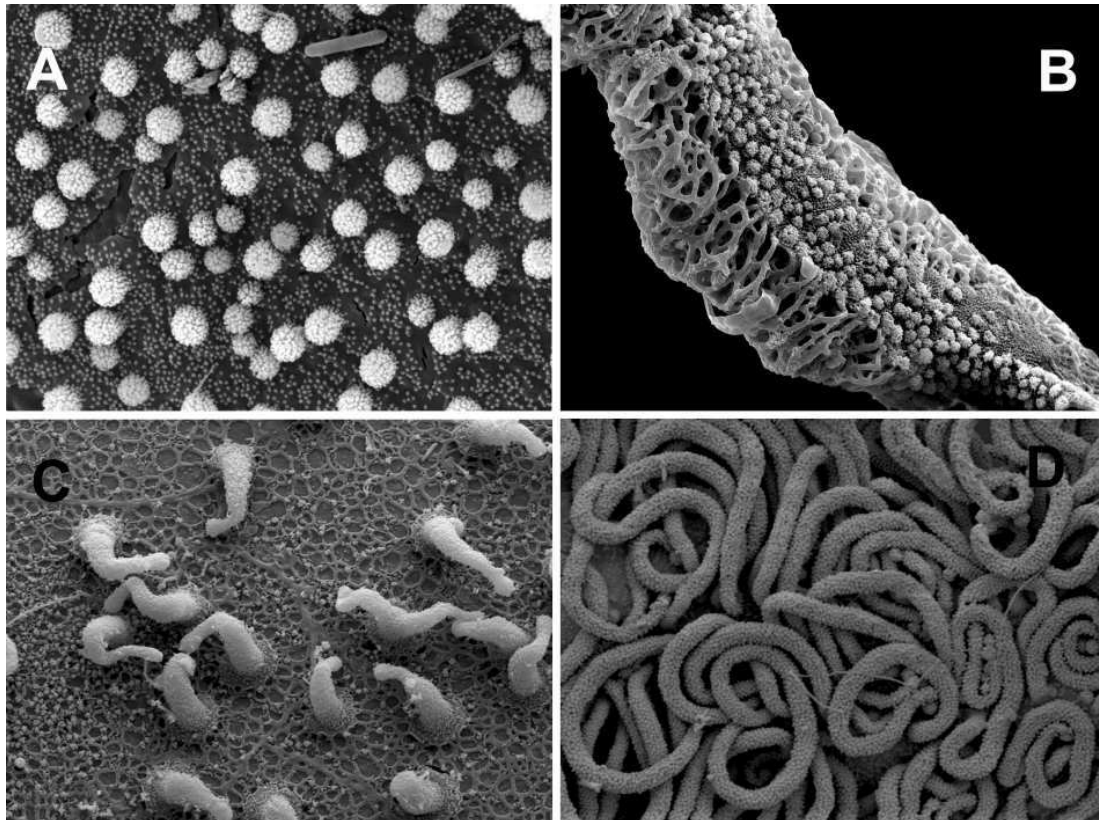


Fig. 4: Cerotegument details of selected adult Damaeidae. A) *Belba compta* - granular cerotegument on prodorsum; B) *Belba bartosi* - reticulate and granular cerotegument on femur I; C) *Damaeus onustus* - vermicular cerotegument with reticulate base layer on anterior part of notogaster; D) *Spatiodamaeus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

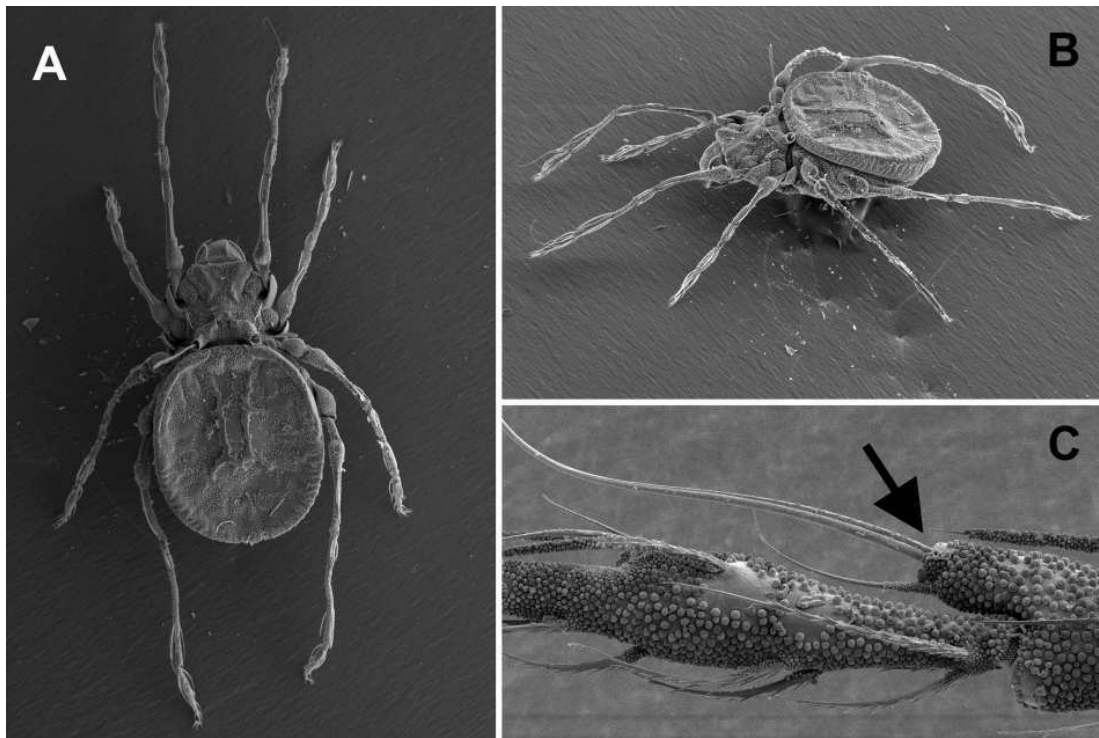


Fig. 5: Typical body form and characters of Gymnodamaeidae on the example of *Gymnodamaeus bicostatus*. A) adult in dorsal view; B) adult in dorsolateral view; C) proximal part of tarsus I and distal part of tibia I in lateral view with typical apophysis (arrow) bearing two solenidia and companion seta *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 artificial 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 structures may be often confused. The procuticular sculpture seems to be 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 microorganisms, 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 the above-mentioned authors.

Siepel and De Ruiter-Dijkman (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 ($^{15}\text{N}/^{14}\text{N}$ and/or $^{13}\text{C}/^{12}\text{C}$) 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 preferred 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 faeces (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 swollen 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 stages 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 faunistic 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*, *Eueremaes 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 optimisation 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.

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6 Aggreements of the co-authors

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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 conceived 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



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On behalf of the Faculty Commission

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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 conceived 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.

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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.

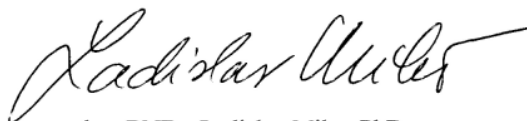
Mourek, J., Miko, L., Bernini, F. (*submitted*) Taxonomy of European Damaeidae (Acari: Oribatida) IV. Partial revision of *Metabelba* Grandjean, 1936 with proposal of one new subgenus, one new species and redescrptions of two known species.

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



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