

THE NYMPHS OF *MICREREMUS BREVIPES*
(ACARI: ORIBATIDA) AND
COMPLEMENTARY REMARKS ON THE ADULT

PFINGSTL, T. and KRISPER, G.

*Institute of Zoology, Karl-Franzens University
Universitaetsplatz 2, A-8010 Graz, Austria; e-mail: tobias.pfingstl@gmx.at*

The nymphs of the arboricolous oribatid mite *Micreremus brevipes* are described in detail. Following characters are considered as specific for the juveniles of this species: 1) darker sclerotized pygidial zone, 2) no setae on genu III in all stages and 3) solenidia ϕ on tibiae II and IV microcephalic. A comparison with other known immatures of the family Micreremidae indicates that the present placement of *Phylleremus* and *Phylloribatula* within this family is not justified. Additionally the legs of the adults of *M. brevipes* are depicted and characterized for the first time, whereas the existence of porose areas on trochanter III and IV, all femora and tarsi could be demonstrated.

Key words: porose organs, arboricolous, Cymbaeremaeoidea, Licneremaeoidea

INTRODUCTION

The family of Micreremidae was established by GRANDJEAN (1954) and consists at present of five genera with a cosmopolitan distribution (SUBÍAS 2011). In Europe only two species of the genus *Micreremus* BERLESE, 1908 are known whereas SUBÍAS (2004) synonymized these two taxa, namely *M. brevipes* (MICHAEL, 1888) and *M. gracilior* WILLMANN, 1931 and accepted only *M. brevipes* as valid species. There were no data published that confirm such a synonymy, and following WEIGMANN (2006) both taxa are separated clearly by several characters. *Micreremus brevipes* is one of the most common arboreal mites in occidental Europe (GRANDJEAN 1954) and is supposed to be associated with lichens and mosses (SEYD & SEAWARD 1984). Although there are diverse extensive descriptions of the adults of this species (GHILAROV & KRIVOLUCKIJ 1975, MAHUNKA 1963, PEREZ-IÑIGO 1997, WEIGMANN 2006), detailed information on the morphological features of the legs are lacking. Concerning the ontogeny, MICHAEL (1888) presented the first depiction of a *M. brevipes* nymph and GRANDJEAN (1933, 1947, 1949, 1953, 1954, 1955 and 1961) provided important information on the immatures of *M. brevipes* and the genus respectively on several occasions. WUNDERLE (1992) investigated the development of *M. brevipes* and detected a one year life cycle with protonymphs being the main overwintering stage. Nevertheless, data on

the juveniles of this species is widely incomplete and the knowledge about many morphological characters is scarce up to the present. Therefore this paper presents morphological details of the nymphs of *M. brevipes* and amends the existing descriptions of the adults by the addition of important features of the legs.

MATERIAL AND METHODS

Specimens were sampled from bark of field maple (*Acer campestris*), Hradec Králové (Czech Republic), 23/4/2009, leg. G. Krisper.

Adults and nymphs of *M. brevipes* were collected by hand from the bark samples using a binocular stereomicroscope; no larvae were found. Sampled adults were determined using WEIGMANN'S identification key (2006). For investigation in transmitted light specimens were preserved in ethanol (70%) and then embedded in Berlese mountant. Observations, drawings and photographs were conducted with a differential interference contrast microscope (Olympus BH-2) equipped with a drawing attachment. Image stacks of nymphs and adult were obtained by an Olympus Camedia C4040 zoom digital camera and layered with the software Combine ZP.

RESULTS

Nymphs – common features

Habitus – The nymphs are dorsoventrally flattened. Integument slightly plicate, folds on anterior third orientated longitudinally and transversally on middle of gastronomic region. Thin layer of cerotegument showing small granules, distributed more densely on posterior half. Color yellowish white to light brown, whereas the pygidial posterior third of hysterosoma stronger sclerotized resulting in a definite brown color with a clod like pattern.

Prodorsum – Interlamellar setae (*in*) long, slightly thickened and spinose. Lamellar setae (*le*) half as long as (*in*), slightly thickened and spinose. Rostral setae (*ro*) prominent, same length as (*in*), dorsally dentate and arcuated ventrally. One pair of short, smooth and spiniform exobothridial setae (*ex*) located laterad of bothridia. Bothridia circular, borders slightly projecting. Sensilla short and capitate, surface slightly spinose. Medially a single large porose area posterior to interlamellar setae, reaching dorsal sejugal furrow.

Subcapitulum – diarthric, dentate rutella with three teeth (Fig. 1); first one spoon-like, second tooth triangular and acute, third tooth smallest with slightly rounded tip. Setae *a* and *m* smooth and spiniform, seta *h* thin and also spiniform. Pedipalp pentamerous, chaetome 0–2–1–3–10 (solenidion included) (Fig. 2). Tip of solenidion touching eupathidium *acm* forming an incomplete “corne double”.

Ventral region of idiosoma – All apodemes and cotyloid walls porose. A pair of elliptic porose areas laterad of genital opening. Concave paired porose areas laterally on a level with anterior border of anal valves, near orifice of opisthotal glands *gla*. Another pair of large porose areas flanking anal opening. Paraproctal atrichosy to deutonymph.

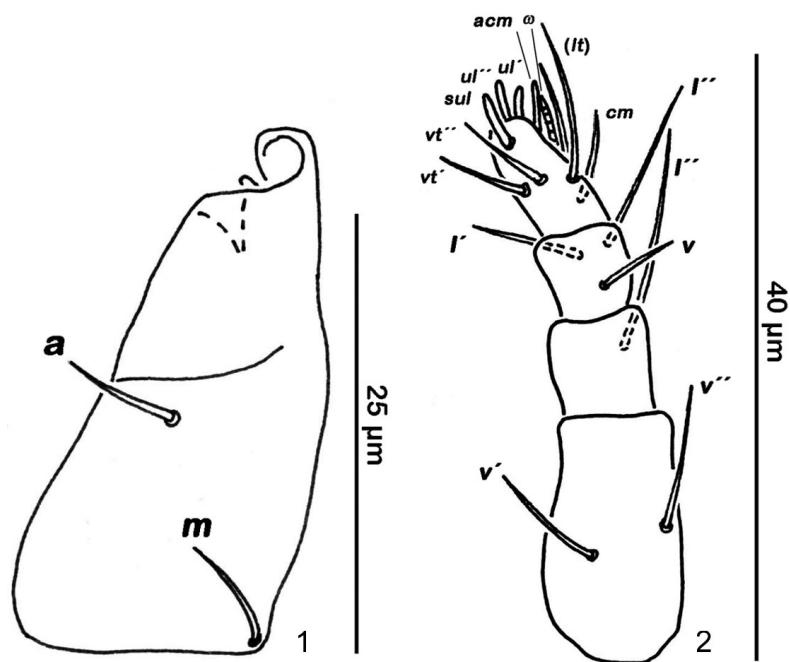
Legs – monodactylous; large claws, dorsally slightly dentate and inserting on an elongated ambulacral stalk. All femora with circular or elliptic porose areas on ventral paraxial side. No famulus on tarsus I detectable.

Protonymph

Protonymph (N = 10) – Body length 188–228 μm , average 212 μm .

Gastronotic region (Fig. 3) – 15 pairs of notogastral setae; setae c_{1-3} , *da*, *dm*, *dp*, *la* and *lm* slightly lanceolate and spinose, setae *lp*, h_{2-3} fusiform and spinose and setae h_1 and p_{1-3} thin and spiniform, whereas p_2 slightly spinose. Cupule *im* located between seta *lm* and *lp*.

Ventral region of the idiosoma (Fig. 4) – epimeral setation (3–1–2–1), setae *1a-c*, *2a*, *3a-b* and *4a* thin, smooth and spiniform. One pair of thin genital setae lo-



Figs 1–2. *Micreremus brevipes* deutonymph: 1 = left rutellum, ventral view, 2 = left pedipalp, ventrolateral view

Table 1. *Micreremus brevipes*, leg setation from protonymph to adult. First development of setae characterized by letters; () = pair of setae; – = no change with regard to the preceding stage.

	Instars	Troch anter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	Protonymph		<i>d, bv''</i>	<i>d, σ</i>	<i>l', (v), φ</i>	<i>pv'', (a), (u), (p), (tc), (ft), ω₁, ω₂</i>	0–2–1–3–11	1–1–2
	Deutonymph		–	–	φ ₂	–	0–2–1–3–11	1–2–2
	Tritonymph		–	–	–	(<i>it</i>)	0–2–1–3–13	1–2–2
	Adult		<i>v</i>	–	–	–	0–3–1–3–13	1–2–2
Leg II	Protonymph		<i>d, bv''</i>	<i>l', σ</i>	<i>l', v', φ</i>	<i>pv'', (a), (u), (p), (tc), ft', ω</i>	0–2–1–2–10	1–1–1
	Deutonymph		–	–	–	–	0–2–1–2–10	1–1–1
	Tritonymph		–	–	<i>v''</i>	(<i>it</i>)	0–2–1–3–12	1–1–1
	Adult		<i>v</i>	–	<i>l''</i>	–	0–3–1–4–12	1–1–1
Leg III	Protonymph		<i>d, ev'</i>		<i>v', φ</i>	<i>pv', (u), (p), (tc)</i>	0–2–0–1–7	0–1–0
	Deutonymph		–	–	–	–	0–2–0–1–7	0–1–0
	Tritonymph		–	–	–	(<i>it</i>)	0–2–0–1–9	0–1–0
	Adult		<i>l'</i>	–	<i>v''</i>	–	1–2–0–2–9	0–1–0
Leg IV	Protonymph					<i>pv', (u), (p), ft''</i>	0–0–0–0–6	0–0–0
	Deutonymph		<i>d, ev'</i>	<i>d</i>	<i>v', φ</i>	(<i>it</i>)	0–2–1–1–8	0–1–0
	Tritonymph		–	–	–	–	0–2–1–1–8	0–1–0
	Adult		<i>v'</i>	–	<i>v''</i>	–	1–2–1–2–8	0–1–0

cated on anterior third of genital valves. Cupule *ips* in paraanal position, *ip* between *h*₂ and *p*₁; cupule *ih* untraceable.

Legs (Figs 5–8) – Solenidia ω_{1–2} on tarsus I long reaching distal end of the claw. Solenidion φ on tibia II microcephalic, showing a spoon-like broadened tip. Setation and solenidia see Table 1.

Deutonymph

Deutonymph (N = 18) – Body length 243–280 μm, average 265 μm.

Gastronotic region (Figs 9, 11) – 15 pairs of notogastral setae; same positions and shapes as in protonymph.

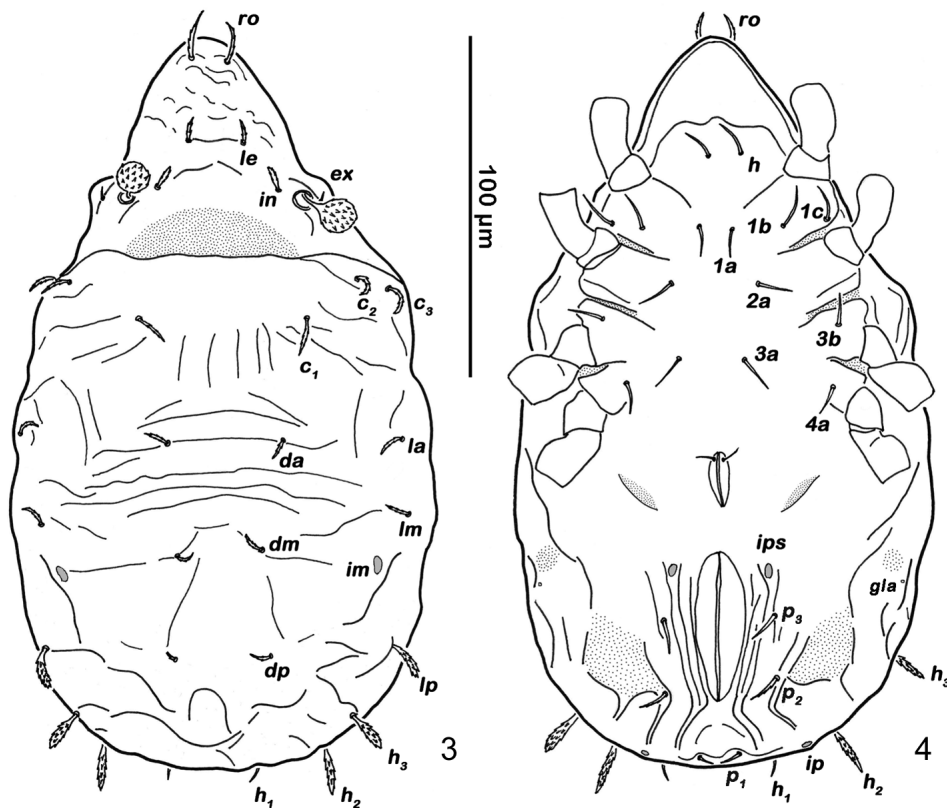
Ventral region of the idiosoma (Figs 10, 12) – epimeral setation (3–1–2–1), same positions and shapes as in protonymph. Two pairs of genital setae; first pair close to anterior border of genital aperture, second pair next to posterior end of genital opening. Cupule *iad* in paraanal position, cupule *ips* from this stage untraceable. Three pairs of short and spiniform adanal setae ad_{1-3} , whereas ad_1 slightly barbed. Porose areas flanking anal opening removed from laterad of setae p_{2-3} to area between setae ad_{1-3} and p_{2-3} .

Legs (Figs 13–16) – Solenidion ϕ on tibia II and IV microcephalic. Chaetome and solenidia see Table 1.

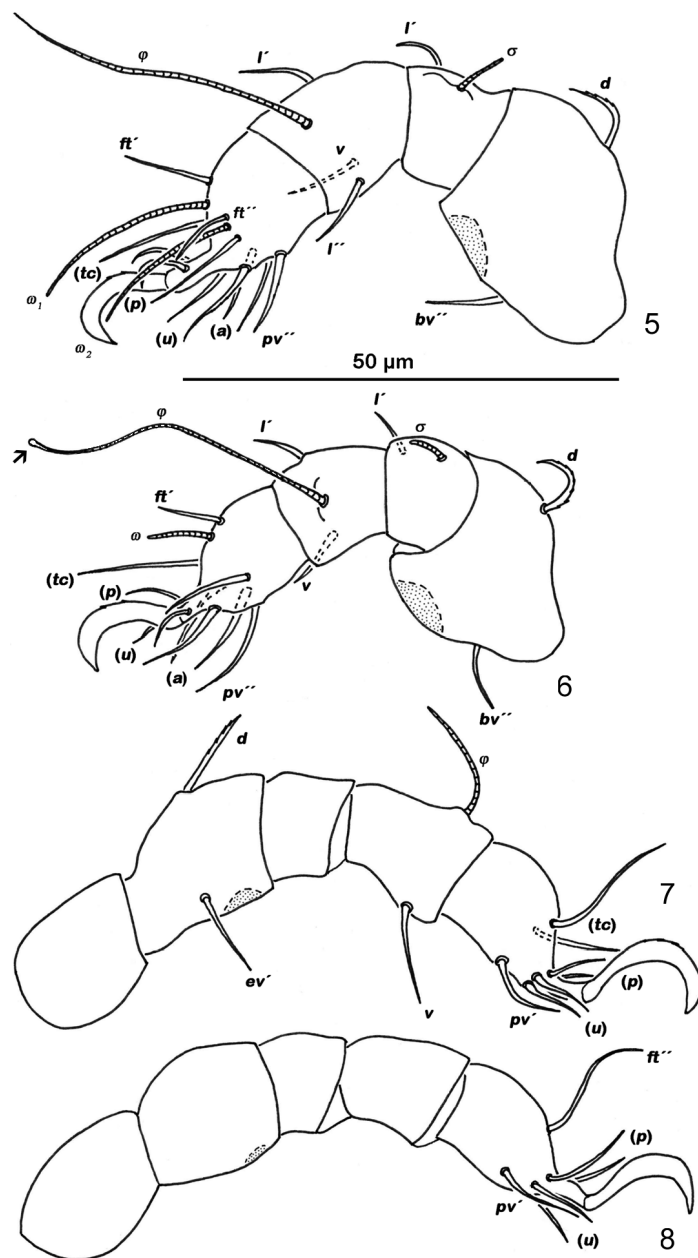
Tritonymph

Tritonymph (N = 1) – Body length 310 μm .

Gastronotic region – 15 pairs of notogastral setae.



Figs 3–4. *M. brevipes* protonymph (legs omitted): 3 = dorsal view, 4 = ventral view



Figs 5–8. *M. brevipis* protonymph left legs antiaxial view: 5 = leg I (trochanter omitted), 6 = leg II (trochanter omitted), 7 = leg III, 8 = leg IV

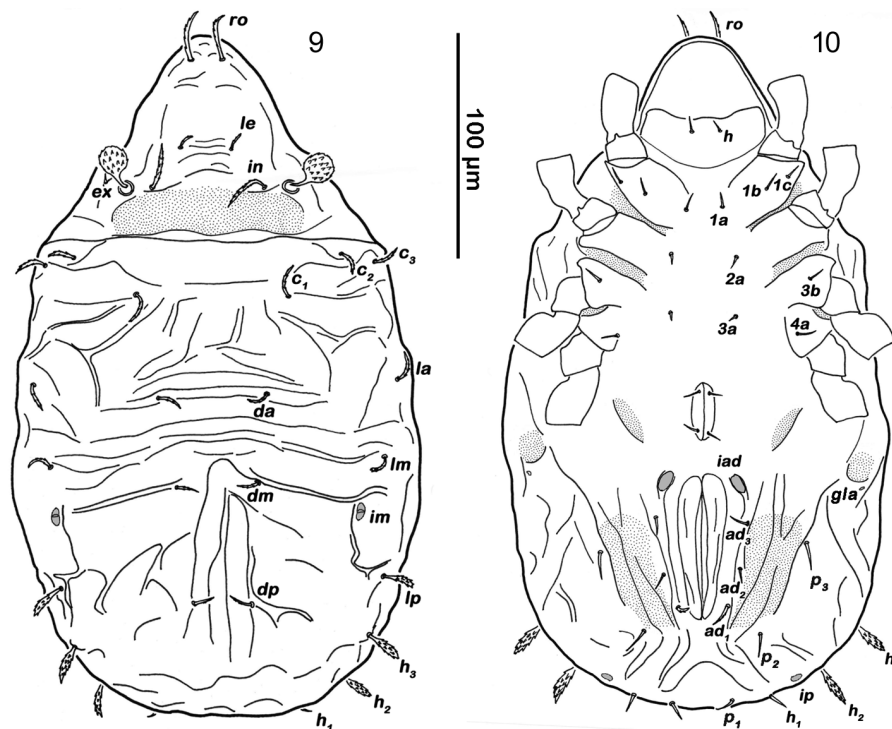
Ventral region of the idiosoma – epimeral setation (3–1–2–1). Three pairs of genital setae, emerged pair located in the middle of genital valves. Two pairs of smooth and spiniform anal setae an_{1-2} located on the anterior half of anal valves. Porose areas flanking anal opening in same position as in deutonymph. Cupule *ian* in paraanal position.

Legs – Small porose areas on the proximal ventral side of all tarsi. Setation and solenidia see Table 1.

Supplementary data on the morphology of adults (Fig. 17)

Body – No axillary saccule at the base of pedipalp; epimeral setation 3–1–2–1, all setae thin and spiniform; opening of opisthonotal gland posterior and next to seta *lp*.

Legs (Figs 18–21) – Cerotegument slightly granular. Elongated ambulacral stalks bearing claws. Tridactylous, homodactylous, claws dorsally slightly dentate. All claws ventrally with a small incision close to forefront, resulting in an ad-



Figs 9–10. *M. brevipes* deutonymph (legs omitted): 9 = dorsal view, 10 = ventral view

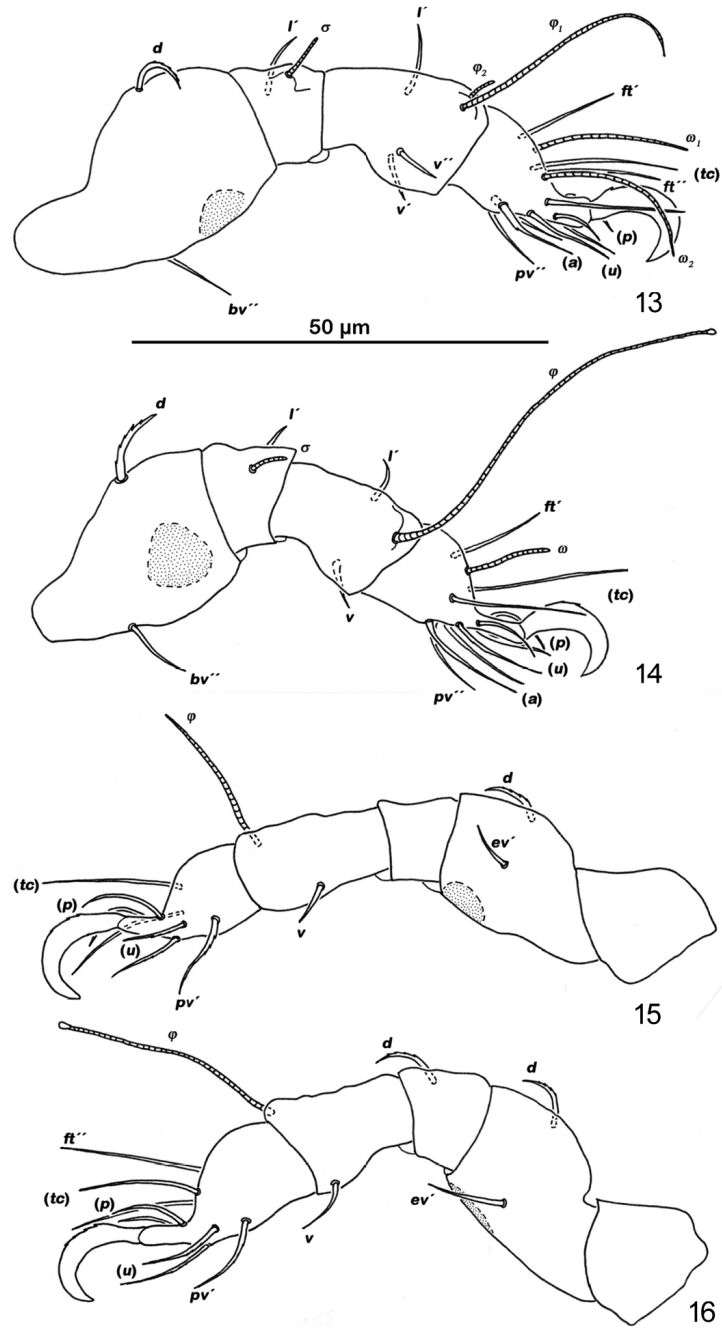
ditional ventral tooth. Setae *d* on femora dorsally barbed. All ventral setae on tibiae and tarsi ventrally barbed. Femora I and II with large porose areas paraxially. Femora III and IV with two paraxial porose areas, distal one close to seta *d* and proximal one close to trochanter. Trochanter III and IV dorsally with a small porose area paraxially. All tarsi equipped with small ventral porose areas located close to tibia. Solenidia ϕ on tibia II and IV microcephalic.

DISCUSSION

There are many constant features in the ontogenetic development of *M. brevipes*. The epimeral setation does not change from protonymph to adult, the shape of all notogastral setae is non-varying in the nymphs and all porose areas are already present in the protonymphal stage, whereas they become more distinct from stage to stage. The ventral tarsal porose areas are the exception as they can



Figs 11–12. *M. brevipes* deutonymph LM-micrographs, scale bar = 100 μ m: 11 = dorsal view – layered from 13 images, 12 = ventral view – layered from 11 images



Figs 13–16. *M. brevipes* deutonymph right legs antiaxial view: 13 = leg I (trochanter omitted) solenidion ϕ_1 appears perspectively foreshortened, 14 = leg II (trochanter omitted), 15 = leg III, 16 = leg IV

only be detected in the tritonymph and the adult. The porose areas flanking the anal opening are already present in the protonymph, but there is a change in the relative position of these areas. In the protonymphal stage they are located in the pseudanal segment, laterad of setae p_{2-3} and in the deuto- and tritonymphal stage they are positioned in the adanal segment, laterad of setae ad_{1-3} . In the latter two stages no trace of porosity could be found in the pseudanal segment, this means that these porose areas are completely displaced in the deutonymph and that the protonymphal areas are not homologous with that of the following stages. Furthermore this observation indicates that a position close to the anal aperture is necessary for the function of these areas, whereas it is not known whether the function is respiratory or secretory.

The comparison of the present study shows in large part conformity with the data on *Micreremus* juveniles provided by GRANDJEAN (1933, 1947, 1949, 1953, 1954, 1955 and 1961). The only diverging aspect concerns the emergence of tactile microcephalic solenidia. GRANDJEAN (1954) stated that the microcephaly of the solenidia ϕ on tibia II and IV is developed for the first time in the deutonymph.

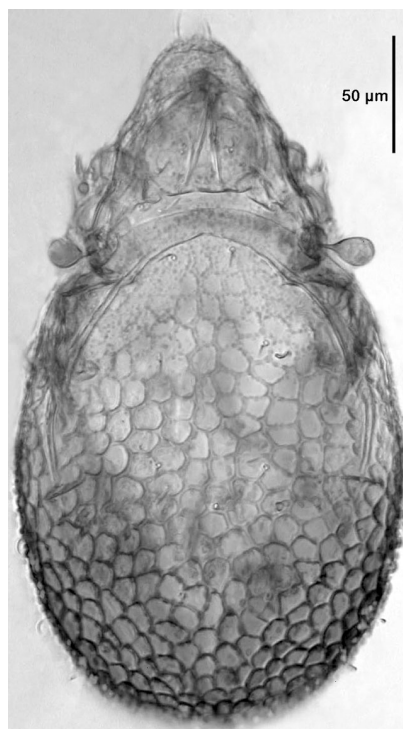
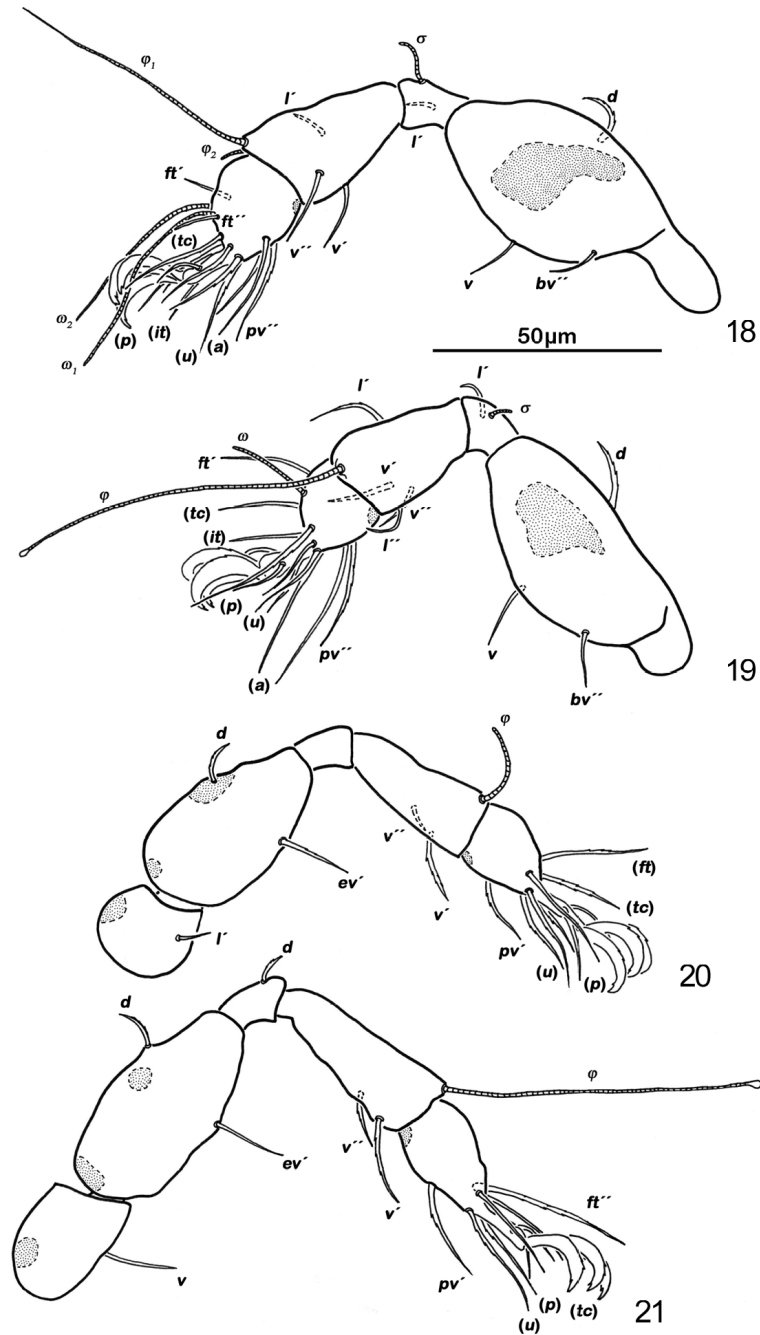


Fig. 17. *M. brevipes* adult dorsal view, LM-micrograph layered from 12 images



Figs 18–21. *M. brevipis* adult left legs antiaxial view: 18 = leg I (trochanter omitted), 19 = leg II (trochanter omitted), 20 = leg III, 21 = leg IV

Table 2. Comparison of the occurrence of microcephalic tibial solenidia (ϕ) in the adults of different brachypylinae oribatid taxa (compiled from literature).

Microcephalic solenidia ϕ on tibia	I	II	III	IV
Ameronothroidea				
<i>Capillibates stagaardi</i> HAMMER, 1966			+	+
Cymbaeremaeoidea				
<i>Bulleremaeus reticulatus</i> HAMMER, 1966	+		+	
Licneremaeoidea				
<i>Micreremus brevipes</i> (MICHAEL, 1888)		+		+
<i>Fenichelina porosa</i> (MAHUNKA, 1985)	+	+	+	+
Oripodoidea				
<i>Siculobata leontonycha</i> (BERLESE, 1910)			+	+
<i>Vesiculobates silvaticus</i> HAMMER, 1979			+	+
<i>Nasozetes sumatrensis</i> SELLNICK, 1930		+	+	+
<i>Parapirnodus coniferinus</i> BEHAN-PELLETIER, CLAYTON et HUMBLE, 2002			+	+
<i>Symbioribates aokii</i> KARASAWA & BEHAN-PELLETIER, 2007	+	+	+	+
Ceratozetoidea				
<i>Trichoribates spatulosestosus</i> REEVES, 1967		+	+	+

This is true for ϕ IV but the present investigation shows that ϕ II exhibits this special character state already in the protonymph.

Although nine species of the genus *Micreremus* are described so far (SUBÍAS 2011), only the juveniles of *M. brevipes* are known. The complete lack of information about the immatures of the remaining eight species as well as of related genera makes the definition of genus specific ontogenetic characteristics difficult. Following characters in juveniles of *M. brevipes* are remarkable: 1) darker sclerotized pygidial zone, 2) no setae on genu III in all stages and 3) solenidia ϕ on tibiae II and IV microcephalic. Characters 2 and 3 are also present in the adult stage and therefore specific for the adults of this species, too. Microcephalic solenidia were also found in some species of the superfamilies Oripodoidea and Ceratozetoidea (see KARASAWA & BEHAN-PELLETIER 2007), as well as in genera of Ameronothroidea, Cymbaeremaeoidea, and Licneremaeoidea (see WOAS 2002). The expression of such specialised solenidia on tibiae is different among the species (Table 2). Furthermore, *Bulleremaeus reticulatus* HAMMER, 1966 (Cymbaeremaeidae) possesses microcephalic solenidia ω_1 and ω_2 on tarsus I, additionally.

The comparison with data on juvenile morphology of other arboreal living members of Micreremidae, Lamellareidae, Dendroeremaeidae, Adhaesozetidae, and Cymbaeremaeidae shows a mosaic distribution of most characters (Table 3).

BEHAN-PELLETIER and WALTER (2007) already stated that distinct prodorsal, ag-genital and adanal porose areas as well as porose areas surrounding the opening of opisthonotal glands exist in ameronothroid and cymbaeremaeoid species (within Adhaesozetidae) and among Licneremaeoidea they can be found in Dendroeremaeidae and Micreremidae. These porose areas are present in *Micreremus brevipes* and *Phylleremus* (BEHAN-PELLETIER & WALTER 2007) but are lacking in *Phylloribatula* (MARTINEZ & PALACIOS-VARGAS 1998). *Phylleremus* was originally placed within the family of Adhaesozetidae by BEHAN-PELLETIER and WALTER (2007), whereas SUBÍAS (2011; update of "Listado sistemático" 2004) transferred *Phylleremus* to Micreremidae. According to the scattered distribution of such porose areas, this character does not indicate a close relationship of the supposed micreremid genera. BEHAN-PELLETIER and WALTER (2007) provided strong arguments for the placement of *Phylleremus* within Adhaesozetidae and the present comparison also demonstrates that *Phylleremus* shares more juvenile characteristics with the Adhaesozetidae than with Micreremidae. Therefore we agree with BEHAN-PELLETIER and WALTER (2007) classifying *Phylleremus* as an adhaesozetid genus. SUBÍAS (2004) also subsumed the family Fenicheliidae (following BALOGH & BALOGH 1998), containing *Phylloribatula*, under Micreremidae, and NORTON and BEHAN-PELLETIER (2009) affirmed this taxonomic rearrangement. Although nothing is known about the juveniles of the genus *Fenichelia*, the adult morphology indicates a close relationship with *Micreremus* and therefore supports this taxonomic change. *Phylloribatula* juveniles share several ontogenetic characters with *Micreremus* immatures, as for example notogastral unideficiency, genital setation, loss of solenidion ω_2 on tarsus II and reduction of primilateral setae on tarsus I, but there are certain obvious and important differences contradicting its placement within Micreremidae. MARTINEZ and PALACIOS-VARGAS (1998) mentioned the presence of porose eccentric microsclerites at the bases of all setae in all immature stages of *Phylloribatula* and this is an important taxonomic character which typically characterizes the members of the Oripodoidea (NORTON & BEHAN-PELLETIER 2009). Further the aspis of *Phylloribatula* juveniles (MARTINEZ & PALACIOS-VARGAS 1998) is developed as a complete rostral tectum which is very short only covering the bases of the chelicerae. A similar aspis can be found outside the Licneremaeoidea in *Domitorina plantivaga* (GRANDJEAN, 1951); moreover, there is a striking similarity in the habitus of the immatures of *Domitorina* and *Phylloribatula*. According to these facts the present placement of *Phylloribatula* within the Micreremidae and even within the Licneremaeoidea cannot be supported and this genus should be transferred to the Oripodoidea.

The adult morphology of *M. brevipes* is well documented (GRANDJEAN 1954, 1964, GHILAROV & KRIVOLUCKIJ 1975, MAHUNKA 1963, PEREZ-IÑIGO 1997,

Table 3. Comparison of ontogenetic characters of arboreal genera. Vertical lines separating taxa Licnermaeidae, Cymbaeremaeidae and Oripodoidea. Developmental formulas listed from protonymph to adult. ? = no information available, + = present, - = absent. Data taken from literature: *Phylleremus* (BEHAN-PELLETIER & WALTER 2007), *Phylloribatula* (MARTINEZ & PALACIOS-VARGAS 1998), *Tenuelamellarea* (MARTINEZ *et al.* 1995), *Dendroeremaeus* (BEHAN-PELLETIER *et al.* 2005), *Adhaesozetes* (WALTER & BEHAN-PELLETIER 1993) and *Cymbaeremaeus* (PFINGSTL & KRISPER 2011).

	Micreremidae			Lamella-	Dendroere-	Adhaeso-	Cymbaere-	Oripo-
	<i>Micre-</i> <i>remus</i>	<i>Phylle-</i> <i>remus</i>	<i>Phyllori-</i> <i>battula</i>	reidae <i>Tenuela-</i> <i>mellarea</i>	maeidae <i>Dendroere-</i> <i>maeus</i>	zetidae <i>Adhaeso-</i> <i>zetes</i>	maeidae <i>Cymbaere-</i> <i>maeus</i>	doidea <i>Phyllori-</i> <i>battula</i>
notogastral setae (La-Ny-Ad)	12-15-14	12-14-9	12-15-14	11-14-9	12-15-10	10-13-13	12-15-13	12-15-14
genital setae	1-2-3-4	1-3-5-6	1-2-3-4	1-2-3-4	1-3-5-6	1-3-5-6	1-3-5-6	1-2-3-4
aggenital setae	0-0-0-0	0-1-1-1	0-0-0-1	0-0-0-0	0-1-1-1	0-1-1-1	0-1-1-1	0-0-0-1
adanal setae	0-3-3-3	0-2-2-2	0-3-3-3	0-2-2-2	0-3-3-3	0-3-3-3	0-3-3-3	0-3-3-3
anal setae	0-0-2-2	0-0-2-2	0-0-2-2	0-0-1-1	0-0-2-2	0-0-2-2	0-0-3-3	0-0-2-2
prodorsal porose area/median	+	+	-	-	-	+	+	-
prodorsal porose area/lateral	-	+	-	-	+	+	+	-
aggenital porose areas	+	+	-	-	+	+	+	-
adanal porose areas	+	+	-	-	+	-	+	-
porose areas near <i>gla</i>	+	+	-	-	+	+	+	-
tibia I apophysis	-	-	+	+	+	+	+	+
dorsal companion setae / legs	-	-	-	?	-	-	+	-
porose areas on femora	+	+	-	?	+	+	+	-
protonymphal leg IV	0-0-0-0-6	0-0-0-0-7	?	?	0-0-0-0-7	0-0-0-0-7	0-0-0-0-7	?
solenidion ω on tarsus II	-	+	-	-	+	-	-	-
primitalar tarsal setae (leg I)	-	+	-	-	+	-	-	-
subunguinal pulvillus	-	+	-	-	+	+	+	-
elongated ambulacrum	+	+	+	+	+	+	+	+

WEIGMANN 2006) but porose areas on certain leg segments have never been mentioned. The present investigation though confirmed the existence of these characters in this species. Adults of most *Brachypylina* have porose areas on the legs whereas these organs can also be developed as saccules, brachy-, platytracheae or tracheae in different groups (NORTON *et al.* 1997). Within Cymbaeremaeoidea and Licneremaeoidea simple, not internalized, porose areas on the legs of adults are known to occur in *Micreremus*, *Phylleremus* (BEHAN-PELLETIER & WALTER 2007), Dendroeremaeidae (BEHAN-PELLETIER *et al.* 2005) and Adhaesozetidae (WALTER & BEHAN-PELLETIER 1993). Among these taxa subdivided femoral porose areas are unique to *M. brevipes*, but in some Zetorchestidae (TRAVÉ 1963) and Eremaeidae (BEHAN-PELLETIER 1993) similar divided organs can be found. In the latter two taxa this femoral porose area is apportioned in a ventral and a dorsal part, whereas in *M. brevipes* a proximal and a distal part are present. As many descriptions of other members of Licneremaeoidea lacking information on the legs (e.g. BALOGH & BALOGH 1998), a clear statement about the real distribution of porose organs is not possible at present.

The mosaic distribution of juvenile characteristics among the compared arboreal taxa (compare Table 3) does not allow associating characters unequivocally to the arboreal lifestyle. A subunguinal pulvillus, absent in *Micreremus*, is present in *Phylleremus*, Dendroeremaeidae, Adhaesozetidae and Cymbaeremaeidae. BEHAN-PELLETIER and WALTER (2007) already stated that this structure may have evolved independently many times and appears to be correlated with the arboreal ecology. Elongated ambulacral stalks occur in all compared taxa and therefore may also relate to the arboreal lifestyle.

WUNDERLE (1992) reported that the pharate juveniles of *M. brevipes* show tendency to take cover in exuviae of older stages of the same species. This behaviour could be confirmed during the observations of the present study. WALTER and BEHAN-PELLETIER (1993) observed similar behavioural strategies in *Adhaesozetes polyphyllos*. Adult females of this species used the empty exuviae of nymphs and larva as sites for oviposition. The authors assumed that this behaviour may represent a means of airborne dispersal and protection against desiccation. The latter function is more likely in *M. brevipes* juveniles, as exuviae are always found in crevices under the bark.

*

Acknowledgements – We thank the reviewers, especially VALERIE BEHAN-PELLETIER, for their valuable comments and remarks.

REFERENCES

- BALOGH, J. & BALOGH, P. (1998) On the family Micreremidae Grandjean, 1954 (Acari, Oribatida). *Opuscula Zoologica Budapest* **31**: 17–23.
- BEHAN-PELLETIER, V. M. (1993) Eremaeidae (Acari: Oribatida) of North America. *Memoirs of the Entomological Society of Canada* **168**: 1–193.
- BEHAN-PELLETIER, V. M. & WALTER D. E. (2007) Phylleremus n. gen., from leaves of deciduous trees in eastern Australia (Oribatida: Licneremaeoidea). *Zootaxa* **1386**: 1–17.
- BEHAN-PELLETIER, V. M., EAMER, B. & CLAYTON, M. (2005) Dendroremaeidae n. fam., from forest trees in western North America (Acari: Oribatida: Licneremaeoidea). *Acarologia* **45**: 321–339.
- BERLESE, A. (1908) Elenco di generi e specie nuove di Acari. *Redia* **5**: 1–15.
- GHILAROV, M. S. & KRIVOLUTSKY, D. A. (1975) *Opredelitel' obitajuschtschich w potschwe kleschtschej, Sarcopiformes*. Nauka, Moskva, 492 pp.
- GRANDJEAN, F. (1933) Etude sur le développement des Oribates. *Bulletin de la Société Zoologique France* **58**: 30–61.
- GRANDJEAN, F. (1947) Observations sur les Oribates (18^e série). *Bulletin du Muséum nationale d'Histoire naturelle Paris* **19**: 395–402.
- GRANDJEAN, F. (1949) Formules anales, gastronomiques, génitales et aggénitales du développement numérique des poils chez les Oribates. *Bulletin de la Société Zoologique France* **74**: 201–225.
- GRANDJEAN, F. (1951) Sur deux espèces du genre “Dometorina” n. g. et les mœurs de “D. plantivaga” (Berl.) (Acariens, Oribates). *Bulletin de la Société Zoologique France* **75**: 224–242.
- GRANDJEAN, F. (1953a) Essai de classification des Oribates (Acariens). *Bulletin de la Société Zoologique France* **78**: 421–446.
- GRANDJEAN, F. (1953b) Sur le genres «Hemileius» Berlese et «Siculobata» n. g. (Acariens, Oribates). *Mémoires du Muséum nationale d'Histoire naturelle Série A, Zoologie* **6**: 117–138.
- GRANDJEAN, F. (1954) Observations sur les Oribates (29^e série). *Bulletin du Muséum nationale d'Histoire naturelle Paris* **26**: 334–341.
- GRANDJEAN, F. (1955) Observations sur les Oribates (32^e série). *Bulletin du Muséum nationale d'Histoire naturelle Paris* **27**: 212–219.
- GRANDJEAN, F. (1961) Considérations numériques sur les poils genitiaux des Oribates. *Acarologia* **3**: 620–636.
- GRANDJEAN, F. (1964) La solénidiotaxie des Oribates. *Acarologia* **6**: 529–556.
- KARASAWA, S. & BEHAN-PELLETIER, V. M. (2007) Description of a sexually dimorphic oribatid mite (Arachnida: Acari: Oribatida) from canopy habitats of the Ryukyu Archipelago, Southwestern Japan. *Zoological Science* **24**: 1051–1058.
- MAHUNKA, S. (1963) Neue Angaben zur Kenntnis der Oribatiden-Fauna Ungarns (Acari). *Folia Entomologica Hungarica* **16**: 227–238.
- MARTINEZ, P. A., VELIS, G. J., EGUARAS, M. J. & FERNANDEZ, N. A. (1995) La famille Lamellareidae dans la République Argentine. *Tenuelamellarea argentinensis* n. sp. *Acarologia* **36**: 354–363.
- MARTINEZ, P. A. & PALACIOS-VARGAS, J. G. (1998) A new species of Phylloribatula Balogh & Mahunka (Acari: Oribatei: Fenichelidae) from Argentina. *Acarologia* **39**: 165–171.
- MICHAEL, A. D. (1888) *British Oribatidae. Vol. II*. Ray Society London.
- NORTON, R. A., ALBERTI, G., WEIGMANN, G. & WOAS, S. (1997) Porose integumental organs of oribatid mites (Acari, Oribatida): 1. Overview of types and distribution. *Zoologica* **146**: 1–31.
- NORTON, R. A. & BEHAN-PELLETIER, V. M. (2009) Suborder Oribatida. Pp. 430–564. In: KRANTZ, G. W. & WALTER, D. E. (eds): *A manual of Acarology*. Third edition. Texas Tech University Press, Lubbock, Texas.

- PEREZ-IÑIGO, C. (1997) Acari: Oribatei, Gymnonota. Pp. 1–374. In: RAMOS, M. A. (ed.): *Fauna Iberica*. Vol. 9. Museo Nacional de Ciencias Naturales, Madrid.
- PFINGSTL, T. & KRISPER, G. (2011) Juvenile stages of the arboricolous mite *Cymbaeremaeus cymba* (Nicolet, 1855) (Acari: Oribatida: Cymbaeremaeidae). *International Journal of Acarology* **37**: 175–189.
- SEYD, E. L. & SEAWARD, M. R. D. (1984) The association of oribatid mites with lichens. *Zoological Journal of the Linnean Society* **80**: 369–420.
- SUBÍAS, L. S. (2004) Listado sistemático, sinónimo y biogeográfico de los ácaros oribátidos (Acariformes: Oribatida) del mundo. *Graellsia* **60**: 3–305.
- SUBÍAS, L. S. (2011) Listado sistemático, sinónimo y biogeográfico de los ácaros oribátidos (Acariformes: Oribatida) del mundo. <http://www.ucm.es/info/zoo/Artropodos/Catalogo.pdf>
- TRAVÉ, J. (1963) Oribates (Acariens) des Pyrénées Orientales (2^e série Zetorchestidae) (1^{re} partie): *Saxicolestes pollinivorus* n. sp. *Vie et Milieu* **14**: 449–455.
- WALTER, D. E. & BEHAN-PELLETIER, V. M. (1993) Systematics and ecology of *Adhaesozetes polyphyllos* sp. nov. (Acari: Oribatida: Licneremaeoidea), a leaf-inhabiting mite from Australian rainforests. *Canadian Journal of Zoology* **71**: 1024–1040.
- WEIGMANN, G. (2006) *Hornmilben (Oribatida)*. *Die Tierwelt Deutschlands, begründet 1925 von Friedrich Dahl*. 76. Teil. Goecke & Evers, Keltern, 520 pp.
- WILLMAN, C. (1931) Moosmilben oder Oribatiden (Cryptostigmata). Pp. 79–200. In: DAHL, F. (ed.): *Die Tierwelt Deutschlands*. Band 22. Fischer Verlag, Jena.
- WOAS, S. (2002) 4.1. Acari: Oribatida. Pp. 21–291. In: ADIS, J. (ed.) *Amazonian Arachnida and Myriopoda*. Pensoft Publishers, Sofia–Moscow.
- WUNDERLE, I. (1992) Die Oribatiden-Gemeinschaften (Acari) der verschiedenen Habitate eines Buchenwaldes. *Carolinea* **50**: 79–144.

Revised version received April 18, 2011, accepted October 3, 2011, published October 28, 2011