

# Discovery of *Belba sculpta* MIHELČIČ, 1957 (Acari, Oribatida, Damaeidae) in an aeolian sand habitat of the Upper Rhine Rift Valley

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## Abstract

*Belba sculpta* was found in a xerothermic habitat on late Pleistocene aeolian sand deposits in the Dossenwald near Mannheim in Southern Germany. This oribatid mite species is so far unknown from Central Europe. The taxon is redescribed on the basis of the new material, and the larva and nymphs are documented for the first time. Aspects of the taxonomy, evolutionary systematics and ecology of *Belba sculpta* are discussed. The *Belba sculpta* species group is introduced.

## Kurzfassung

### Entdeckung von *Belba sculpta* MIHELČIČ, 1957 (Acari, Oribatida, Damaeidae) in einem Flugsandhabitat im Oberrheingraben

*Belba sculpta* wurde in einem xerothermen Habitat auf Pleistozänen Flugsandböden im Dossenwald bei Mannheim in Süddeutschland entdeckt. Diese Oribatidenart ist in Mitteleuropa bisher unbekannt. Die Beschreibung des Taxons wird auf der Basis des neuen Fundmaterials ergänzt, wobei die Larven- und Nymphenstadien zum erstenmal beschrieben werden. Einige Aspekte der Taxonomie, evolutionären Systematik und Ökologie von *Belba sculpta* werden diskutiert. Die *Belba sculpta*-Artengruppe wird vorgestellt.

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## 1 Introduction

*Belba* VON HEYDEN, 1826, is a genus within the species-rich oribatid mite family Damaeidae BERLESE, 1896. In the present publication, the discovery of *Belba sculpta* MIHELČIČ, 1957, in a xerothermic habitat on late Pleistocene aeolian sand deposits of the Upper Rhine Rift Valley is noted and commented on. This species has up to now not been known to occur in Central Europe (MIKO 2006, WEIGMANN et al. 2015, BECK et al. 2018) and is so far only reliably known from Spain, where it typically occurs in very warm, relatively dry habitats and has been recorded from Madrid (MIHELČIČ 1957), from the semiarid Sabinas Albares vegetation zone of the provinces Huesca and Valencia (ARRIBAS et al. 1984), from diverse

locations in Andalusia (KAHWASH et al. 1992) as well as from La Gomera of the Canary Islands (MORAZA & PEÑA 2005).

*Belba sculpta* was initially described together with two other species, *B. ignota* MIHELČIČ, 1957, and *B. aberrans* MIHELČIČ, 1957, in the same publication. Subsequently PÉREZ-ÍÑIGO (1970) re-examined the original material of MIHELČIČ deposited at the Museo Nacional de Ciencias Naturales in Madrid and concluded that the latter two species were synonyms of *Belba sculpta*. The account of the species by PÉREZ-ÍÑIGO (1970, 1997) is still incomplete, however.

In the present paper, the existing description of adults of *Belba sculpta* is supplemented on the basis of the new collection material. The juvenile stages are described for the first time, and some facets of the morphology, ecology and systematics of the species are commented on. The *Belba sculpta* species group is introduced and contrasted with the monophyletic cluster containing *B. corynopus* (HERMANN, 1804), the type species of the genus. A new diagnosis of the genus *Belba* is provided and a determination key to *Belba* species of the world is presented.

## 2 Material and methods

Specimens of *Belba sculpta* (27 adults, 3 tritonymphs, 1 deutonymph, 2 protonymphs, 2 larvae) were collected during May and June 2018 in the Dossenwald near Mannheim, Germany. The mites were predominantly collected from sandy soil in sun-exposed areas with a sparse vegetation cover. Some were also taken from ground dwelling foliose lichens, mostly *Cladonia portentosa* (DUFOUR) COEM. living on shallow sandy soil next to a stand of Scots pine (*Pinus sylvestris* L.). Mites were obtained from the soil samples with a combination of Berlese apparatus extraction using the sun as a heat and light source, and sand flotation. Specimens were fixed in ethanol, macerated with lactic acid and observed under a light microscope.

Descriptions and measurements are based on specimens mounted on temporary cavity slides or on permanent slides. Unless specifically mentioned, the descriptions refer to the adult stage. Nine adults of *Belba sculpta* were deposited as voucher specimens in the collection of the Department of Zoology of the State Museum of Natural History Karlsruhe in Germany.

The conventions of measurement used follow BEHAN-PELLETIER & NORTON (1983, 1985) and BAYARTOGTOKH (2000). Dimensions of body structures are given in micrometers, with the mean value followed by the range in parentheses where based on a sample of 10 or more individuals. Setal length measurements are based on at least 3 specimens. Ventral body length is measured in lateral view from the tip of the rostrum to the posterior edge of the ventral plate. Total body length is calculated from the tip of the rostrum to the posterior border of the notogaster. Maximum notogastral width is determined in dorsal view. Prodorsal width is measured from the left margin to the right margin of the proterosoma at the level of the acetabulae in dorsal perspective. Length of the notogaster is measured in lateral perspective from its anterior to its posterior margin along a line parallel to the circumgastric scissure. Maximum height of the notogaster is determined in lateral view from its ventral to its dorsal border at an angle perpendicular to the plane of the circumgastric scissure and does not include the height of the latter, so as to avoid ambiguities resulting from differential notogastral expansion. Body height, the maximum dorsoventral thickness of the hysterosoma, is measured in lateral view from the ventral rim of the ventral plate to the dorsal rim of the notogaster in postgenital transect. Leg length is measured on intact slide mounted legs in lateral aspect from the proximal margin of the trochanter to the base of the claw. Length of single leg segments is determined in lateral view from the most proximal sclerotized point to the most distal and includes the portion inserted in the following, more proximal segment. Distance between an adanal seta and the genital plate is measured between the setal insertion point and the closest point on the border of the genital plate. Distances between setae are determined between their central insertion points. Leg setation formulae present the number of setae present on a specific segment of legs I-IV. Leg associated setal formulae refer to the presence (1) or absence (0) of setae paired with solenidia on a specific segment of legs I-IV.

Leg solenidial formulae show the number of solenidia present on the genu, tibia and tarsus of any given leg. Palpal setation formulae give the number of setae present on the palp in the sequence: trochanter-femur-genu-tibia-tarsus. Epimeral setation formulae give the number of setae present unilaterally on epimeres I-IV. The general morphological terminology utilized in this paper bases on BEHAN-PELLETIER & NORTON (1983, 1985), and NORTON & BEHAN-PELLETIER (2009). The nomenclature of the epimeral enantiophyses largely adheres to GRANDJEAN (1960a) and NORTON (1978b). If only a single pair of prodorsal tubercles is present in the dorsosejugal region, these are termed apophyses Ba, after BEHAN-PELLETIER & NORTON (1985). The nomenclature of the leg chaetotaxy derives from NORTON (1977b), while that of the gnathosoma follows VAN DER HAMMEN (1968) and ALBERTI et al. (2011). An explanatory list of the abbreviations used in the text and illustrations is presented by LAMOS (2016).

### 3 Results

#### 3.1 Description of *Belba sculpta* from the Dossenwald

##### 3.1.1 Adult Diagnosis

Medium sized *Belba* with a total body length ranging from 526-598  $\mu\text{m}$  (mean 561  $\mu\text{m}$ ). Lamellar and rostral setae smooth; mutual distance between ro-ro > le-le. Sensillus (190-230  $\mu\text{m}$ ) and interlamellar setae (220-240  $\mu\text{m}$ ) both exceptionally long, smooth and distally flagellate. Postbothridial tubercles Ba, Bp and ventrosejugal tubercles Va, Vp well developed, subtriangular. Apophysis E2p of propodoventral enantiophysis slightly less well defined; E2a represented by a thickened ridge. Prodorsal tubercles Aa, Ap, Da, Dp, La, Lp absent. Parastigmatic apophysis Sa elongate, ceratiform, laterally directed and with a sharply pointed apex; Sp much shorter, subtriangular. Propodolateral apophyses and spinae adnatae absent.

Notogastral setae of c-, l- and h-series smooth and of medium length (55-68  $\mu\text{m}$ ), darkly pigmented except for the most proximal part. Notogaster without a compact mass of debris; rarely with nymphal scalps. Genital, anal and most epimeral setae barbed. Epimeral setation formula 3-1-3-4. Adanal setae ad1, ad2, ad3 smooth, flagellate; seta ad3 laterally displaced. Pseudanal setae ps1, ps2, ps3 marginally positioned, thin, smooth, flagellate; seta ps1 very long (80-110  $\mu\text{m}$ ). For-

mulae of leg setation, including famulus: leg I: (1-7-4-4-20); leg II: (1-6-4-5-17); leg III: (2-4-3-4-17); leg IV: (1-4-3-4-13). Solenidial formulae: I: (1-2-2); II: (1-1-2); III: (1-1-0); IV: (0-1-0). Solenidia of genera I-III and tibiae II-IV both coupled. Setae on trochanter and femur of legs I-IV slender, smooth, elongate except femur II paraxially with a conspicuous thick, short, hornlike seta I'. Setae d on femur IV, genu IV and tibia IV distally flagellate and extremely long, with seta d of tibia IV measuring 260  $\mu\text{m}$ . Setae I' of these segments similar in appearance and very elongate with seta I' of tibia IV attaining a length of 243  $\mu\text{m}$ . Leg IV measures 1,5 times the ventral body length.

### Body dimensions

Total body length 561 (526-598)  $\mu\text{m}$ . Ventral body length 523 (506-548)  $\mu\text{m}$ . Body width 347 (315-368)  $\mu\text{m}$ . A slight sexual dimorphism exists. Females are on the average 22  $\mu\text{m}$  longer than males (v. b. l., two tailed t-test,  $n = 17$ ,  $P < 0.01$ ). Ratio of ventral body length to body width 1,5:1. Body height 293  $\mu\text{m}$ . Length of proterosoma 209  $\mu\text{m}$ . Length of hysterosoma 312  $\mu\text{m}$ .

### Integument

Colour of adults chestnut-brown. Cuticle strongly sclerotized, finely granular in appearance with the microtubercles small, round in dorsal view, variable in size and spacing regionally. Microtubercles comparatively large and widely spaced on the central region of the notogaster and posterior prodorsal surface; smaller, less distinct on rostral tip, notogastral margin, genital and anal plates as well as on the surfaces of genuae, tibiae and tarsi. Medial to lyrifissure ia the diameter of the microtubercles is 0,1-0,2  $\mu\text{m}$ , and their density is 20/ $\mu\text{m}^2$ . Body markedly microtuberculate and strongly sclerotized on all enantiophyses. Epimeres I-IV without sizeable cuticular tubercles, alveoli or other significant sculpturing besides the apophyses and muscle scars. Cerotegument waxy, white in colour, covers most of external body surface. Cerotegumental particle aggregations mostly filamentous, but ranging from columnar to cottony in appearance. Individual cerotegumental filaments sometimes very elongate, reaching a length of up to 90  $\mu\text{m}$ . Cerotegument especially thick on prodorsum, sejugal region, epimeral region and proximal leg segments. Body and leg setae often covered with cerotegumental excrescences. Integument occasionally with loosely attached debris and fungal micelles. Notogaster never carrying a compact

mass of debris and usually without exuvial scalps but one newly moulted adult specimen transporting these on the notogaster.

### Prodorsum (Figs. 1, 3)

Prodorsum approximately triangular in dorsal perspective, narrowed in sejugal area. Maximum width of prodorsum 215 (207-233)  $\mu\text{m}$ . The length of the prodorsum, measured from the rostral tip to the dorsosejugal groove in lateral view, is about equal to its width. Rostral tectum broad, rounded anteriorly in dorsal view. Rostrum projecting anteroventrally in lateral view. Weakly developed, slightly elevated naso-like structure present, with a well demarcated oval semi-fenestrate area of lighter cuticle. Tectum of podocephalic fossa not ventrally projecting. Rostral and lamellar setae thin, smooth, slightly attenuate, curved laterad and then strongly inwards towards the sagittal plane. Seta le (80-90  $\mu\text{m}$ ) > ro (70-80  $\mu\text{m}$ ). Mutual distance between insertion points of setae le: 42  $\mu\text{m}$  < ro: 61  $\mu\text{m}$ . Exobothridial setae 60  $\mu\text{m}$  in length, setiform, without barbs, only slightly thinner than the lamellar setae. A small gland opening situated close to insertion of seta ex. Interlamellar setae smooth, slender, thickest in the proximal region, frequently undulating, distally very thin and flagellate, and very long (220-240  $\mu\text{m}$ ). Sensillus smooth and minimally thicker at its basis than the interlamellar setae. Sensillus initially relatively straight, distally flagellate, and very long (190-230  $\mu\text{m}$ ). Interlamellar setae and sensillus frequently with a broken-off distal part. Bothridium laterally directed, irregularly funnel shaped with a fairly large opening; proximally with internal ring-like ridges and distally with faint radiating bands of chitin, providing mechanical support to the weakly sclerotized distal bothridial funnel. Bothridial border entire. Postbothridial tubercles Ba and Bp large, subtriangular, well developed, with rounded tips. True postbothridial ridges and antebothridial ridges absent. Apophyses Aa, Ap of prodorsal enantiophysis, Da, Dp of dorsosejugal enantiophysis and La, Lp of laterosejugal enantiophysis absent. Prodorsum without conspicuous tuberculate or alveolar sculpturing. Propodolateral apophysis, lamellae, costulae, tutorium and areae porosae absent. Prodorsum elevated in the region of the larger internal muscle attachments. A noticeable field of muscle sigillae situated in the mid-sagittal plane just anterior to the dorsosejugal groove. Additional smaller sigillae located anterior and paraxial to apophysis Ba, and anterior, lateral and posterior

to each bothridium. Two further very large paired sigillary fields occur in the central region of the prodorsum. Distinct centropodorsal groove absent. Dorsosejugal furrow deep and fairly wide.

### **Notogaster** (Figs 1, 3)

Notogaster shield-like, covers most of hysterosoma. Observed from a viewpoint perpendicular to the circumgastric scissure, it is slightly oval, about 1,16 times as long as wide. Notogastral length 402 (370-431)  $\mu\text{m}$ , width 347 (315-368)  $\mu\text{m}$ . In lateral perspective notogaster hemispherical, robust and fairly flat, maximum height about 156  $\mu\text{m}$ , corresponding to 0,4 times the notogastral length. Dorsal notogastral margin in lateral view almost evenly rounded, only anteriorly slightly flattened. Area porosae between setae h1 absent. Spinae adnatae absent.

Eleven pairs of notogastral setae present. Setae of c-, l-, and h- series slender, smooth, curved in lateral aspect, approximately 55-68  $\mu\text{m}$  long; their alveoli arranged along two symmetrical longitudinal rows which are arched, in dorsal view. In well cleared notogasters a thin, brown line is visible paraxial to the insertion points of setae c2 to h2. Anterior to seta c2 the lines become indistinct. Posteriorly the lines are delimited by the oval sigillary field between setae h1 and ps1. Using only a light microscope and without employing histological methods, it was not possible to conclusively identify the exact nature of the linear structure and the region immediately medial to it. One hypothesis is that the line represents a shallow longitudinal groove, which forms the border of a lightly sclerotized strip or very low ridge on which the insertion points of setae c2 to h1 are located, with all of the alveoli being positioned paraxial to the groove.

Notogastral setae darkly pigmented except for the short proximal base part which is lighter in colour and also thinner than the adjoining more distal portion. Mutual distance between setae c1: 25  $\mu\text{m}$ , between setae lm: 174  $\mu\text{m}$ . Distance between setal pair c2 about 4 times that of c1. A diminutive lightly coloured spot present postero-medial to the insertion point of each seta la and lp. In dorsal perspective setae c1 directed towards the anterior, the remainder, c2-h3, radially directed. Pseudanal setae ps1, ps2, ps3 marginally positioned on posterior ventrolateral notogastral border, thin, smooth, finely attenuate and flagellate; ps1 very long (80-110  $\mu\text{m}$ ).

Sigillae along lateral and posterolateral margins of the notogaster form two long bands, ending an-

teriorad just posterior to insertion points of setae c2. Scattered but more or less regularly arranged sigillae also anteriorly in area between insertions of setae c1 and c2 and similarly posteriorly in the sector demarcated by insertions of setal pairs h1 and ps1. Lyrifissures ia, im, ip, ih and ips present, with latter two located on ventral border. Opening of latero-opisthonotal gland located midlaterally on notogastral margin between lyrifissure im and ip. Distance ia - im > im - ip.

### **Epimeral region** (Figs 2, 3)

The epimeral region consists of the contiguous epimeres I-IV, sclerotized coxal fields, each of which is associated with a pair of legs. Tubercle Sa of parastigmatic enantiophyses long, ceratiform, laterally directed and with a sharply pointed apex. Sp much shorter, subtriangular. Length of Sa 2,5-3x the length of Sp when observed in ventral perspective. Discidium elongate, conical to subtriangular, acute. On opposite sides of the ventrosejugal groove lie conspicuous, large tubercles Va and Vp of ventrosejugal enantiophysis, their tips rounded to subtriangular. Tubercle E2p of propodoventral enantiophysis slightly less well defined. E2a very indistinct, represented by a slightly thickened ridge. Formula for epimeral setation: 3-1-3-4. Epimeral setae 1a, 2a short (24-30  $\mu\text{m}$ ), the remainder measuring 38-57  $\mu\text{m}$  in length. Setae 1c, 3b, 3c, 4d smooth; all other epimeral setae with double rows of minute relatively widely spaced barbs. Seta 3b associated with tubercle Vp. Epimeres I and II have distinct areas of muscle scars, whereas the sigillary fields of epimeres III and IV are joined together into one large area. Significant alveolar or verrucose sculpturing absent.

### **Anogenital region** (Figs 2, 3)

Adanal setae ad1, ad2, ad3 smooth, flagellate, only slightly longer (48-63  $\mu\text{m}$ ) than the epimeral setae. Their insertion points form a straight line when seen in ventral perspective with seta ad3 being significantly laterally situated. Ratios of the distances of the insertion points of setae ad1, ad2, ad3 to the border of the anal plate are about 1: 2: 4.5 respectively. Genital and anal plates large and positioned close together. Anal opening distinctly longer and slightly wider than genital opening. Paired genital valves each with a row of six barbed slender setae, g1-g4 inserted close together, g5, g6 more distantly situated. Seta g1 slightly longer than the others. Posterior medial region of genital valves with sigillae. Paired anal

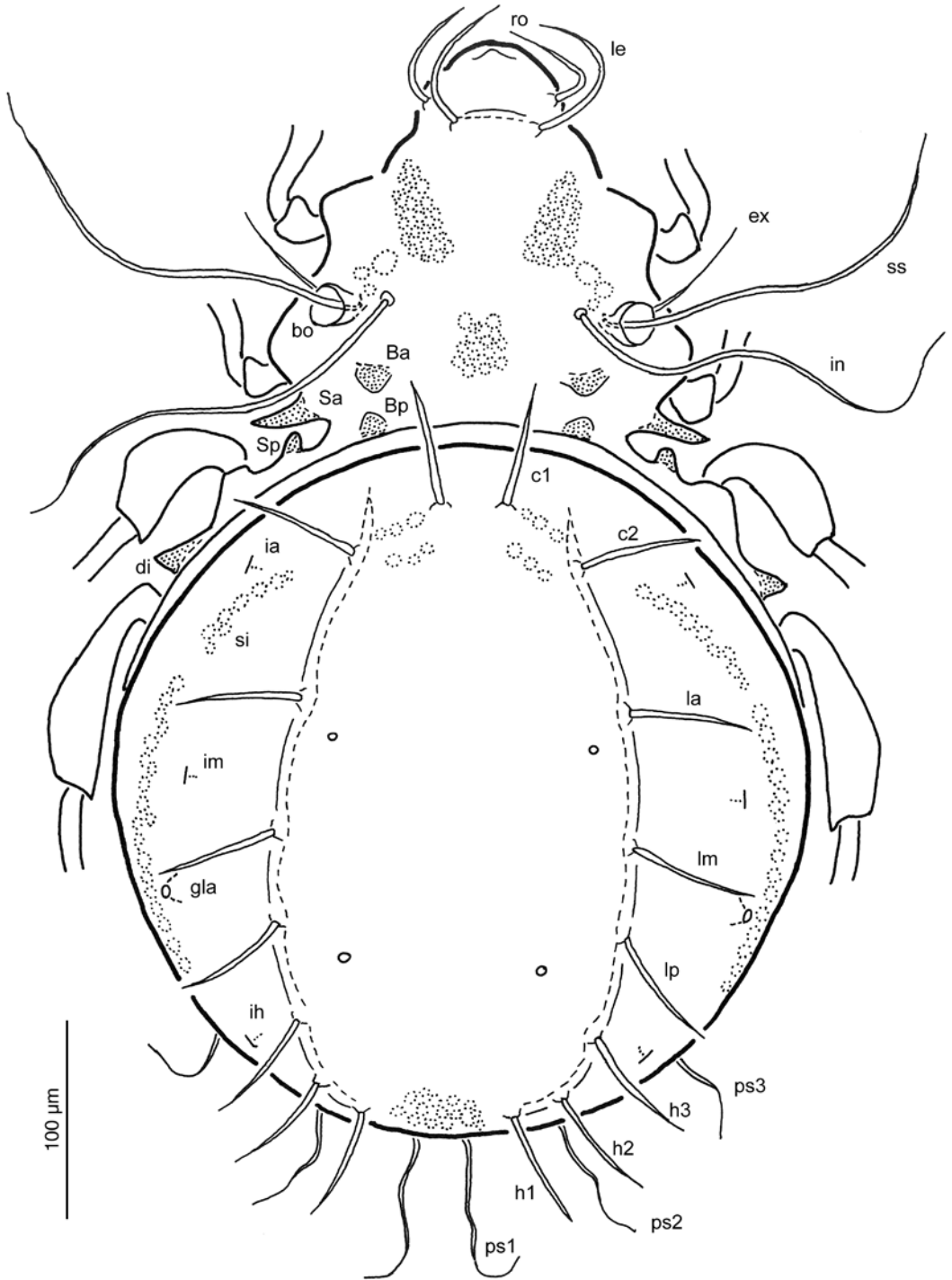


Figure 1. *Belba sculpta* adult, dorsal aspect.

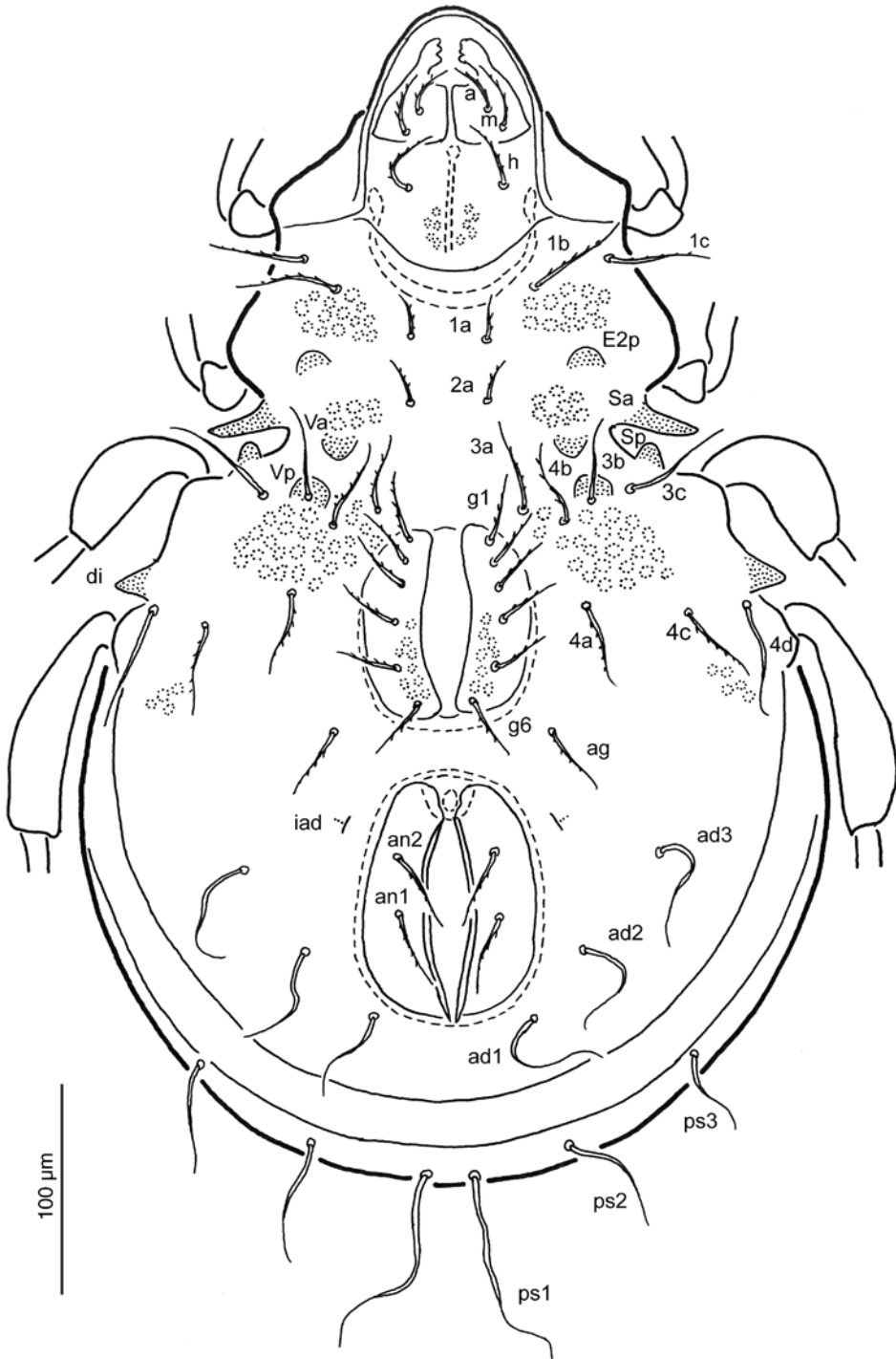


Figure 2. *Belba sculpta* adult, ventral aspect.

valves smooth, each with two sparsely barbed thin setae: an1, an2. Anal lyrifissure ian observable as a small slit in the anterolateral corner of each valve. Aggenital setae ag (36 μm) lateroventrad genital plates, similar in size and appearance to genital setae. Genital and anal cavities both surrounded by an externally reflexed rim. Anal plates with a well-defined medial carina. Anteriormost medial part of anal opening covered by unpaired preanal organ, which serves to retract the anal valves. Two articular sockets connect the preanal organ to the anterior border of the anal opening. Adanal lyrifissures iad oblique, anterolateral to the anal plates.

The pregenital chamber contains the genital papillae as well as either a spermatopositor or a ovipositor. Genital papillae Va, Vm, Vp lobe-like, approximately equal in shape and dimensions. Spermatopositor egg-shaped in ventral view, with seven hollow setal pairs: Ψ1, Ψ2, τ1, τ2, τ3, τ4, kx. Setae Ψ1, Ψ1, Ψ2, Ψ2 form a distinct group situated ventrally to a sclerotized strip lo-

cated along the midline of the spermatopositor when observed in ventral perspective. In similar view, setal group τ1, τ2, τ3, τ4, kx occurs in two clusters, one on each side of the sclerotized median strip. The spermatopositor serves to produce stalked spermatophores.

Ovipositor a short, tubular, hollow cylinder consisting of a proximal part Pp and a distal eversible portion subdivided into a base bDp and three conical eugenital lobes L1-L3. The latter encircle the eugenital opening through which the egg exits. Unpaired ventral lobe L1 with 4 setae, the apical setae Ψ1, Ψ1 and the proximal Ψ2, Ψ2. Paired dorsolateral ovipositor lobes L2 and L3 each with 4 setae: τ1 in an apical position, τa most proximal and setae τb, τc in between. The insertion points of setae τa, τb, τc of each lobe are grouped close together, approximately in the shape of an equilateral triangle. All setae on eugenital lobes thick, spinelike, eupathidial, about 18 μm in length. The surface of the lobes is smooth, while that of Pp and bDP is pleated. The ovipositor base bDp is

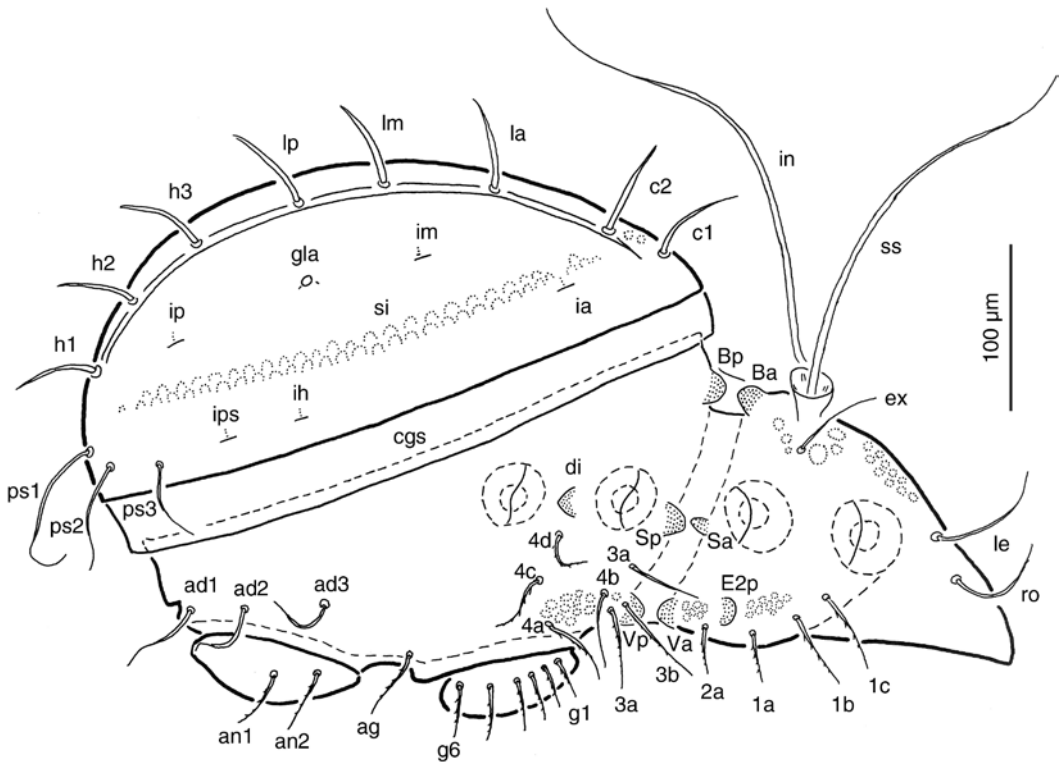


Figure 3. *Belba sculpta* adult, lateral aspect.

very broad, together with its short lobes it is only slightly longer (81  $\mu\text{m}$ ) than wide (57  $\mu\text{m}$ ) and bears six thornlike eupathidial setae k, each with a length of roughly 20  $\mu\text{m}$ .

### Gnathosoma (Figs 3, 7)

The gnathosoma consists of the infracapitulum, paired chelicerae and paired pedipalps. This unit resides within a cavity, the camerostome. Infracapitulum diarthric, with a transverse labio-genal articulation. Mentum quadrate in shape, slightly wider than long, medially with two slightly asymmetrical rows of sigillae of pharyngeal muscles. The posterior of the infracapitulum articulates via two grooves with a pair of condyles at the lateral base of the mentotectum. Genal notch absent. Genal carinae anteriorly bearing pedipalps and minute supracoxal seta e1. Infracapitular setae h, m, a bilaterally barbed, tapering, curved towards the midline and of medium length; relative lengths:  $h \geq m > a$ . Ventral surfaces of mentum and genuae microtuberculate. Anterolaterally each gena is separated by a dorsal manubrial area porosa from the rutellum. Rutella smooth, atelebasic, with a conspicuous distal hyaline swelling. Paraxial surface of each rutellum with rutellar brush. Labrum elongate, arrowhead-like in appearance, with an acute tip. An area porosa positioned on antiaxial side of the gena and also in the cheliceral groove. Lateral lips relatively broad, each anteriomedial with a long, triangular, membranous tip, distally with the adoral sclerite bearing slender, smooth, needle-like adoral setae or1 and or2. Mouth opening situated between the unpaired dorsal labrum and the two latero-ventral lateral lips.

Chelicerae robust, chelate-dentate and elongate (122  $\mu\text{m}$ ). Digitus fixus and digitus mobilis each with 3 large triangular teeth. Site of articulation of cheliceral digits situated ventral to insertion of seta chb. Seta cha inserted in a dorsal to somewhat paraxial position, directed anteriorly, long, evenly barbed, with a ventral bend in the distal half and tapering at the tip. Seta chb slightly shorter, antiaxially situated, barbed with the longest barbs in the distal third, where they form a distinct fringe which shortens strongly towards the tip. Paraxial cheliceral surface with three tiny chitinous spines sp posterior to seta cha. Body wall attaches obliquely to the proximal third of the chelicerae. A very large area porosa located antiaxially between approximately the distal line of attachment of the cheliceral sheath and the insertion point of seta chb. Ventral region of digitus

mobilis also with a small porose area. Lamellated organ located paraxially on principal segment of chelicera. Trägårdh's organ long, slender, tapering to a thin tip, on paraxial side. Coxal opx, ventral opv and paraxial oncophyyses op' present.

Pedipalpi slender, pentamerous, with a length of 201  $\mu\text{m}$ . Setal formula of pedipalps: 0-2-1-3-9(1). Solenidion  $\omega$  distally directed, with a rounded tip and laid dorsolaterally on the tarsal cuticle, not associated with the seta acm. Subulimal su, ulimal ul', ul'' and anteroculminal acm setae inserted distally on tarsus, eupathidial and approximately half the length of the solenidion. Inferior inf and superior sup seta of palpfemur, lateral seta l'' of palpgenu, and lateral l', l'' setae of palptibia distinctly barbed. Dorsal seta d of palpgenu as well as culminal cm, lateral l', l'', and ventral vt', vt'' setae of palptarsus smooth. All setae except eupathidia elongate, slender, acuminate. Palptarsus with a dorsoproximal lyrifissure.

### Legs (Tab. 1, Figs 4-6)

Legs with five free segments. Leg segments elongate, clavate, often with slightly wrinkled integument and muscle scars on bulbs, particularly the femora. Trochanter I and II short, straight. Trochanter III and IV both much longer, bent posteriorly at a right angle at the point where they emerge from the acetabulum, distally with a small antiaxial spur-like projection, a tectum, protecting articulation with femur. Femur I and II bent at a right angle just immediately distal to their articulation with the trochanter. Femur III and IV straight instead.

Leg lengths, based on a sample of 5 individuals, are: I: 551  $\mu\text{m}$ , II: 423  $\mu\text{m}$ , III: 528  $\mu\text{m}$ , IV: 783  $\mu\text{m}$ . Relative lengths of legs I to IV are: 1: 0,77: 0,96: 1,42. Leg IV 1,5 times the ventral body length. Setae on trochantera, femora and genua mostly slender, smooth and relatively long. Femur II paraxially with very conspicuous smooth, thick,

Table 1. Leg segment lengths of *Belba sculpta* adults, n = 5 (in  $\mu\text{m}$ ).

Segment	Leg I	Leg II	Leg III	Leg IV
trochanter	–	–	80	117
femur	197	145	146	203
genu	72	57	56	87
tibia	99	77	95	161
tarsus	205	172	208	263



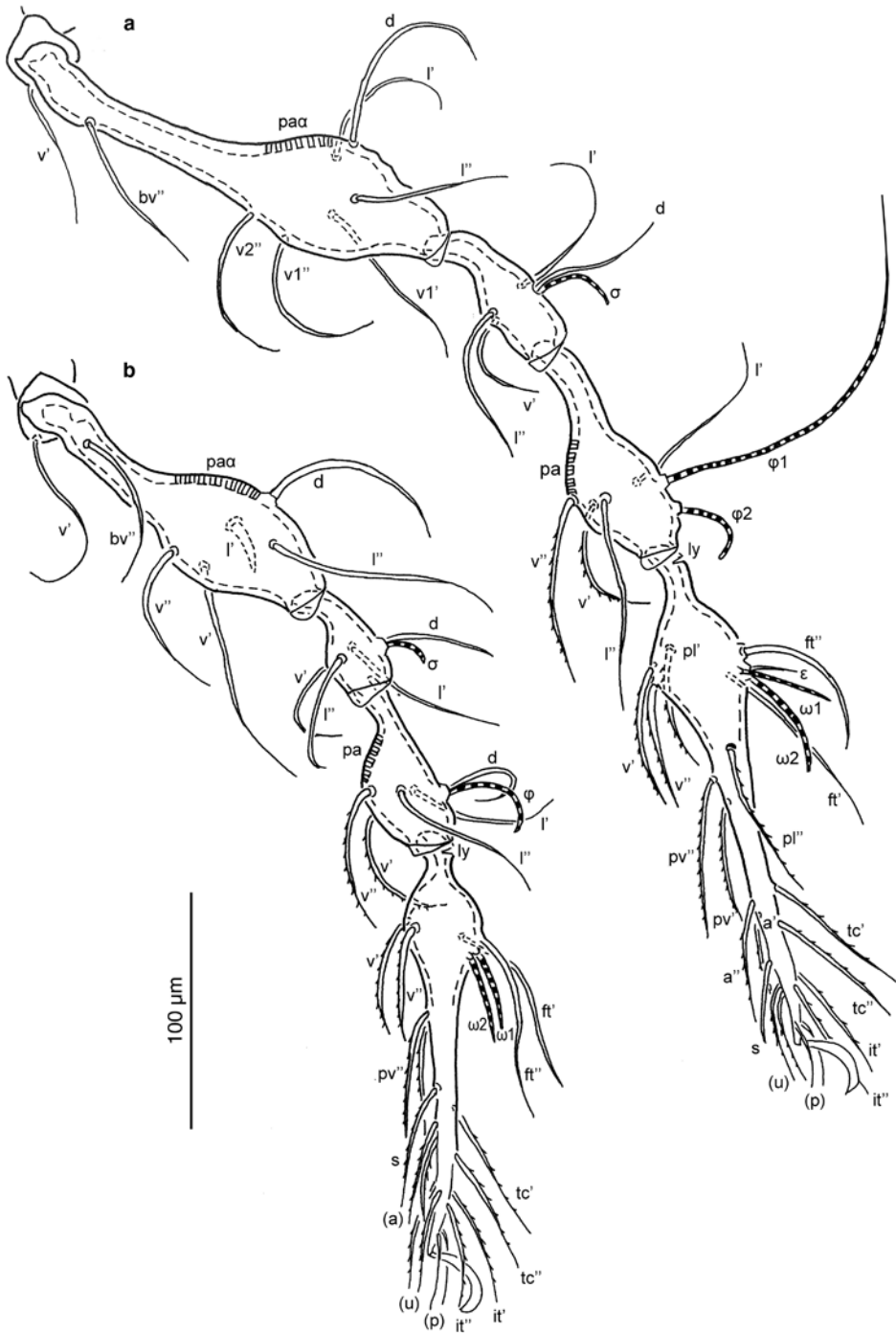


Figure 4. *Belba sculpta* adult. a) femur to tarsus of leg I, antiaxial view. b) femur to tarsus of leg II, antiaxial view.

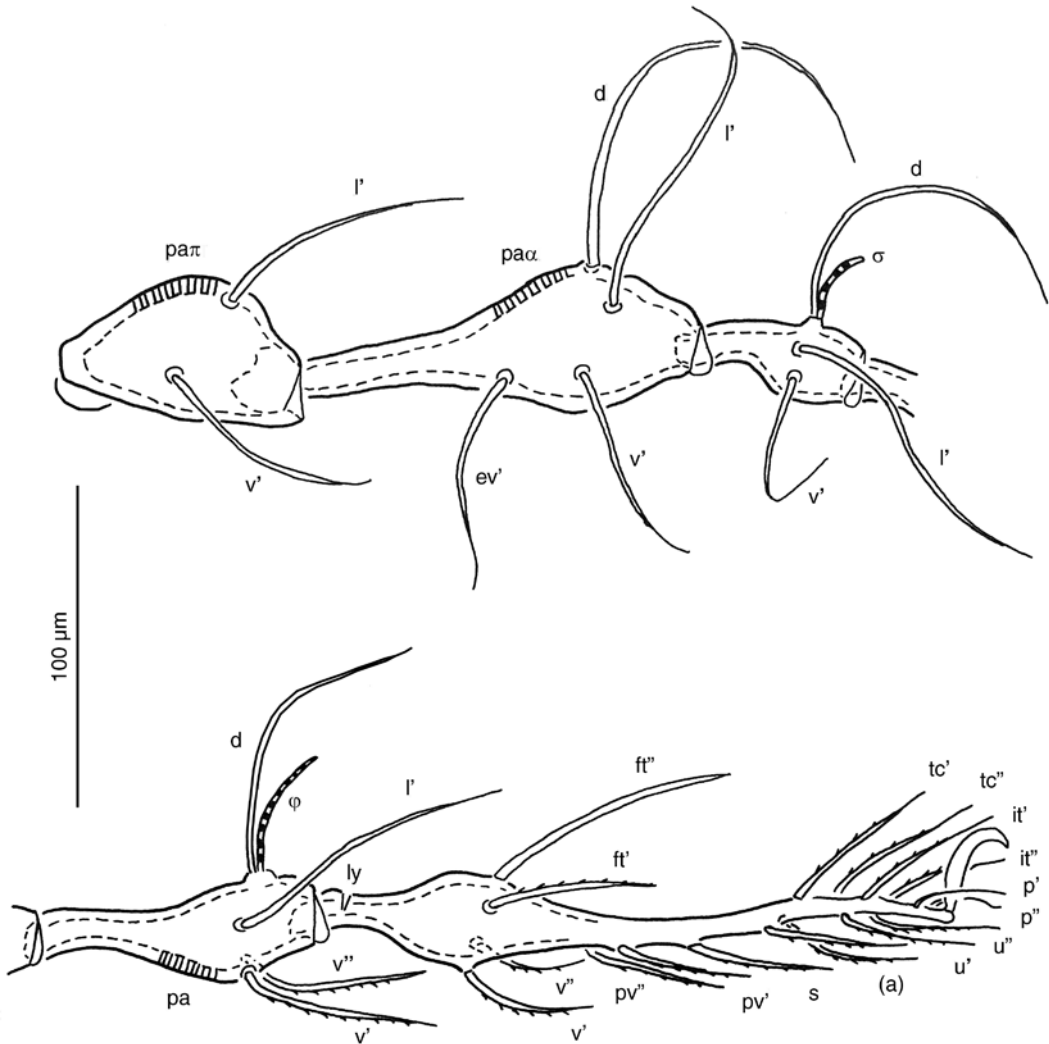


Figure 5. *Belba sculpta* adult, leg III, antiaxial aspect.

short (25 μm), hornlike seta l'. Seta d on femur IV slender, distally flagellate, very long (239 μm). Seta d on genu IV slender, flagellate distally and extremely long (260 μm); seta l' slightly shorter (243 μm). Setae d and l' of tibia similar in appearance to those of genu with a length of 251 μm and 162 μm, respectively. Setae d on genu I thicker and longer, on genua II-III considerably longer than their coupled solenidia σ. Solenidia φ of tibiae II-IV shorter than their associated setae d. On tibiae I-III: ventral v',

v'' and lateral l', l'' setae with rows of spines. On tibia IV ventral setae v', v'' with barbs, lateral seta l' smooth. Dorsal setae on tibiae II-IV unbarbed. On tarsi I-IV: fastigial setae ft', ft'' smooth, strong and long; tectal setae tc', tc'' and iterals it', it'' inconspicuously barbed; prorals p', p'' smooth and thin; unguinals u', u'', primiventrals pv', pv'' and anterolaterals a', a'' with strong spines projecting from their convex sides. The unpaired subunguinal seta s is smooth on leg I, but barbed on legs II-IV. Only tibial solenidium φ1 on leg I, and

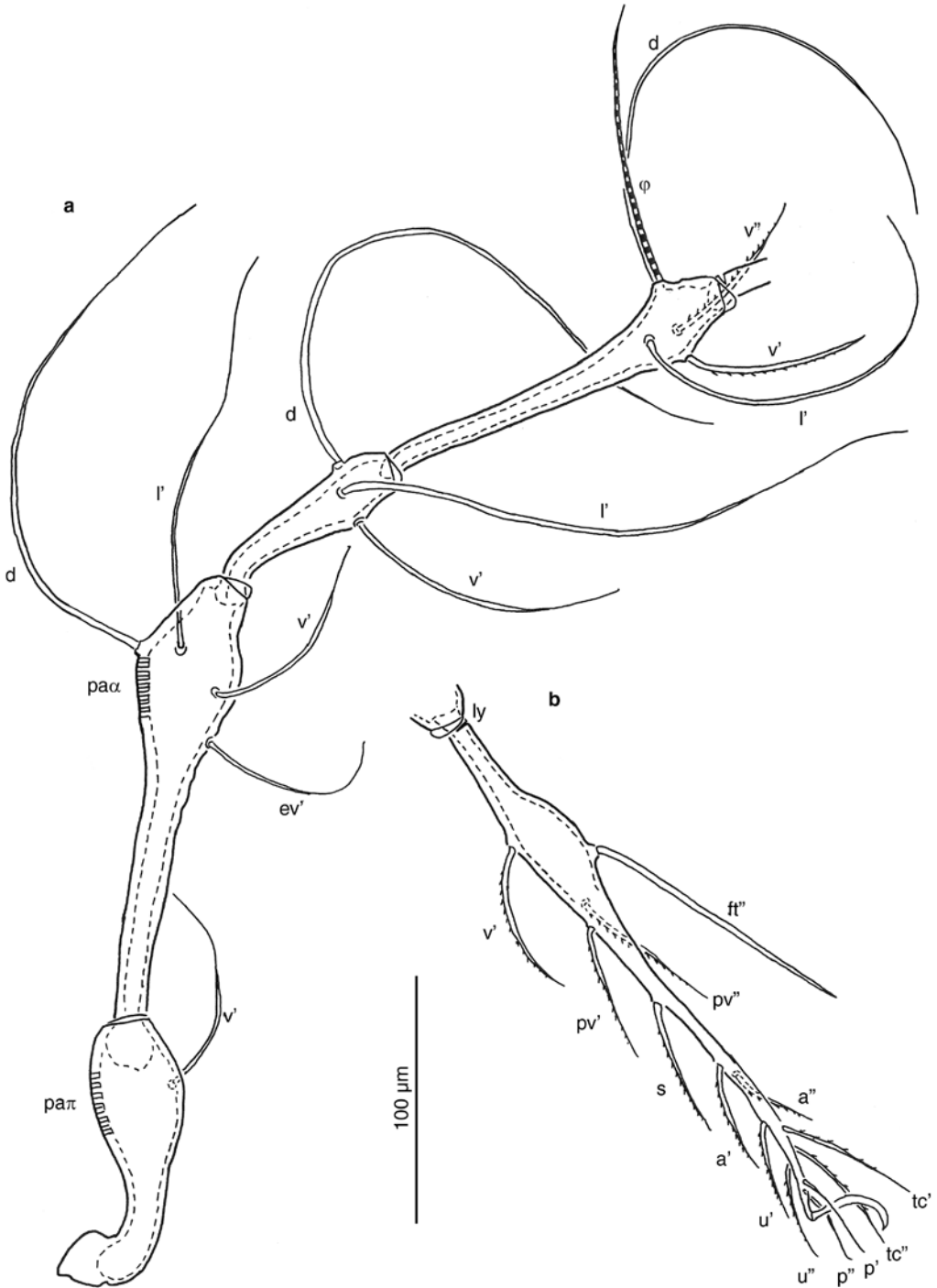


Figure 6. *Belba sculpta* adult. a) trochanter to tibia of leg IV, antiaxial view. b) tarsus of leg IV, antiaxial aspect.

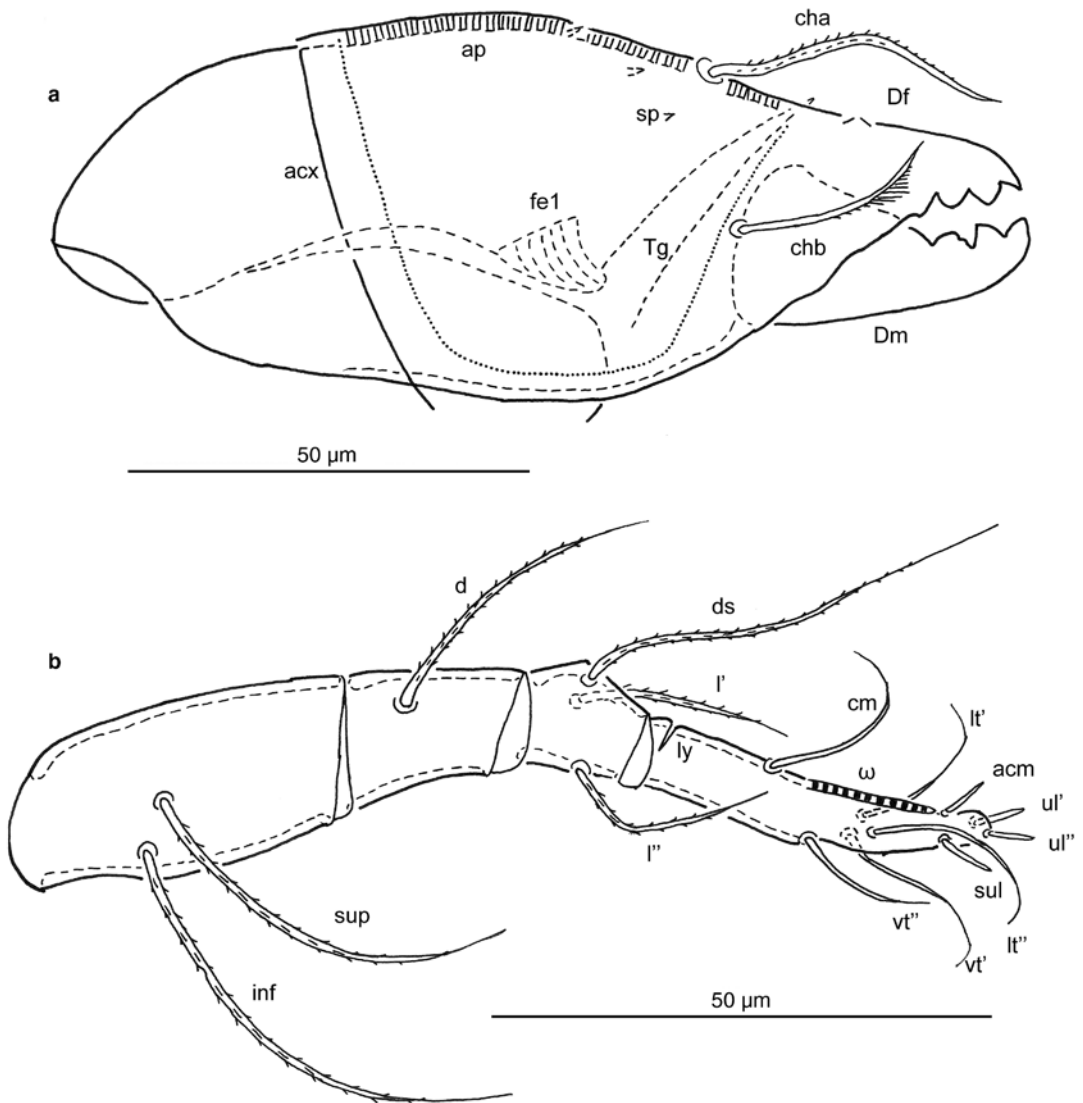


Figure 7. *Belba sculpta* adult. a) chelicera, antiaxial view. b) palp, antiaxial view.

$\phi$  on leg IV long and tactile. Solenidia  $\sigma$ I,  $\phi$ 2I,  $\sigma$ II,  $\phi$ II,  $\sigma$ III short, ceratiform, curved towards the ambulacrum, tarsal solenidia  $\omega$ 1I,  $\omega$ 2I,  $\omega$ 1II,  $\omega$ 2II short, rod-like. Solenidium  $\omega$ 1 longer than  $\omega$ 2 on the tarsus of leg I. Famulus short, strongly tapering.

Formulae of leg setation, including famulus: leg I: (1-7-4-4-20); leg II: (1-6-4-5-17); leg III: (2-4-3-4-17); leg IV: (1-4-3-4-13). Solenidial formulae: I: (1-2-2); II: (1-1-2); III: (1-1-0); IV: (0-1-0). Soleni-

dia of genua I-III and tibiae II-IV coupled. The variability of the leg chaetotaxy was investigated in detail in 5 individuals. No variation in leg setation or solenidiotaxy was observed.

An area porosa positioned dorsally to mediodorsally on the proximal region of the bulbs of femur I-IV and on trochanter III and IV. Additional smaller porose areas situated ventrally, proximal to the ventral setae, on tibia I-IV. A slit-like lyrifissure is present dorsoproximally on the bulbs of

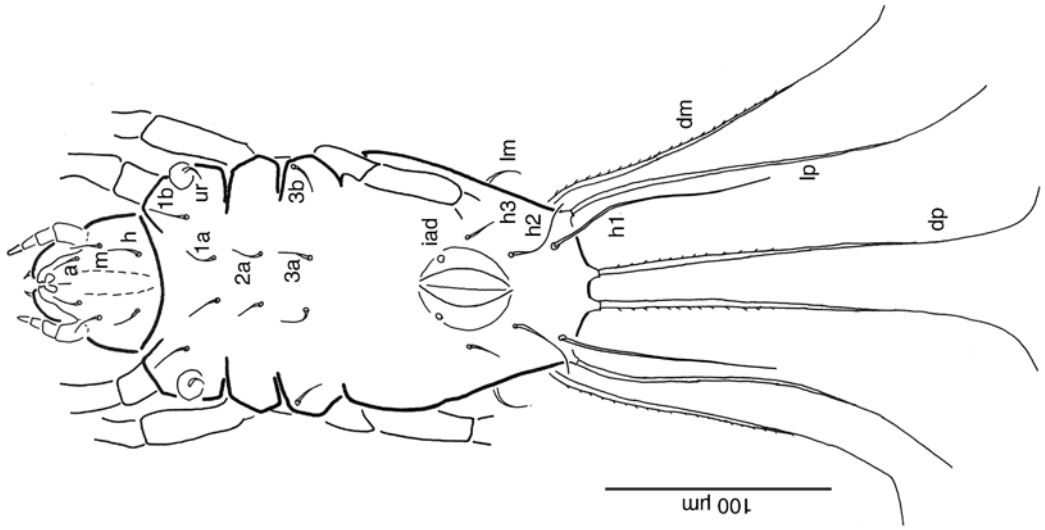


Figure 9. *Belba sculpta* larva, ventral view.

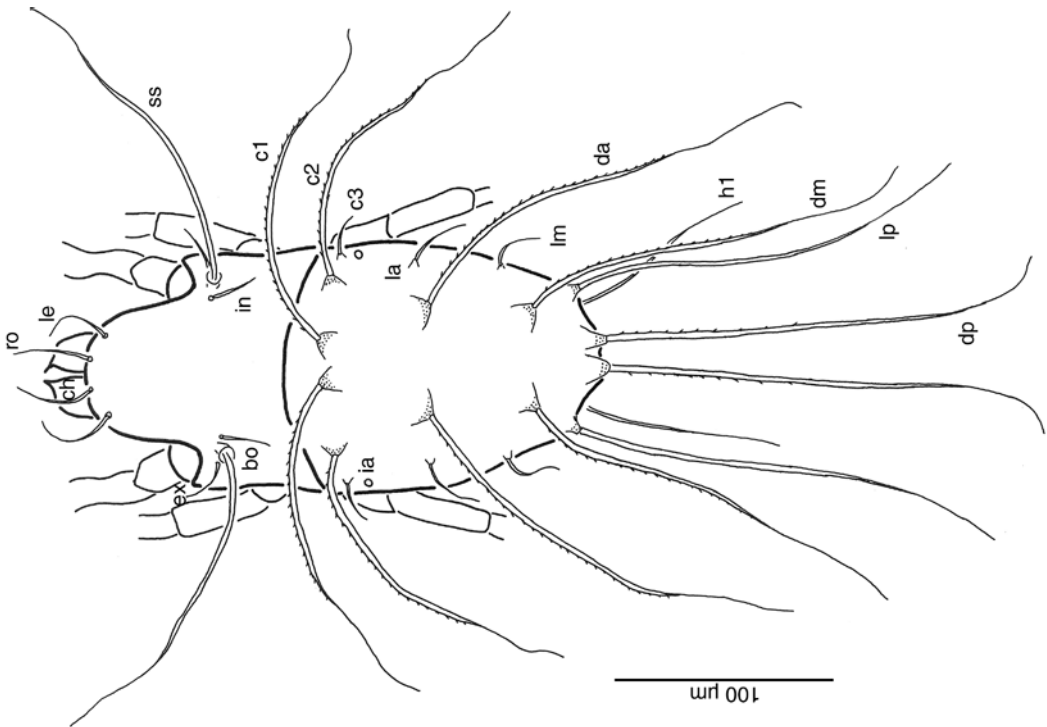


Figure 8. *Belba sculpta* larva, dorsal view.

tarsi I-IV close to the tibio-tarsal joint. Claws monodactyl, with a length of about 30  $\mu\text{m}$  on all tarsi, with smooth, sickle-shaped ungues. A diminutive area porosa visible, immediately proximal to the ambulacrum, in ventral location, on all tarsi. Setae p', p'' and s eupathidial on tarsus I.

### 3.1.2 Larva and nymphs

#### Body dimensions

Larva: length 250  $\mu\text{m}$ , width 114  $\mu\text{m}$ , height 121  $\mu\text{m}$ . Protonymph: length 294  $\mu\text{m}$ , width 145  $\mu\text{m}$ , height 140  $\mu\text{m}$ . Deutonymph: length 403  $\mu\text{m}$ , width 194  $\mu\text{m}$ , height 203  $\mu\text{m}$ . Tritonymph: length 510  $\mu\text{m}$ , width 268  $\mu\text{m}$ , height 250  $\mu\text{m}$ . Body length of larva measures about 0,45 x, and that of tritonymph 0,93 x the adult total body length. Ratio of body length to width about 2,2:1 in the larva and 2:1 in the three nymphal stages.

#### Integument

Cuticle of body smooth, transparent and white in colour. Gnathosoma, legs, some setal apophyses and sclerites lightly sclerotized, light to dark brown. The extent and degree of sclerotization are greatest in the tritonymph and least in the larva. Cerotegument a continuous thin film with

more or less regularly spaced hemispherical granules or tubercles. Granules spherical in dorsal view, tuberculate to conical in lateral view, generally with a diameter of 1-2  $\mu\text{m}$  or less. Cerotegument generally very thick, covering most of body and legs and also setal bases. Cerotegument more strongly developed, with slightly larger granules in tritonymph than in preceding stages. Setae of prodorsum, notogaster and legs light to very dark brown, possessing a hyaline base. Amount of pigmentation least in ventral setae.

#### Prodorsum (Figs 8, 10, 11, 13)

Prodorsum short, measuring about half the length of the notogastral region in lateral view. Rostrum broadly rounded. Prodorsal apophyses absent. Interlamellar seta fairly short (23  $\mu\text{m}$ ), smooth and attenuate in larva; extremely short (tritonymph 14  $\mu\text{m}$ ), without barbs, and truncate in nymphs. Sensillus long (larva 167  $\mu\text{m}$ ; tritonymph 224  $\mu\text{m}$ ), smooth, distally flagellate. Bothridia funnel-shaped. Exobothridial seta smooth, of moderate length in the larva (45  $\mu\text{m}$ ) and tritonymph 53  $\mu\text{m}$ ), Rostral setae of larva smooth, about similar in length (44  $\mu\text{m}$ ) to the unbarbed lamellar setae (48  $\mu\text{m}$ ). In later ontogenetic stages setae ro similarly without barbs,

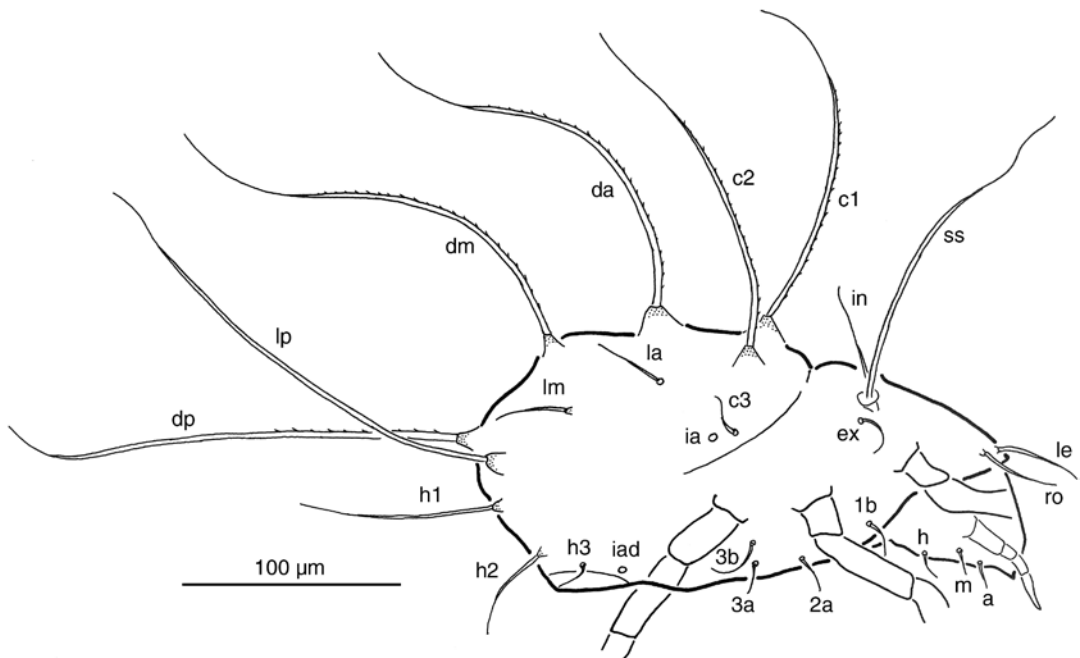


Figure 10. *Belba sculpta* larva, lateral view.

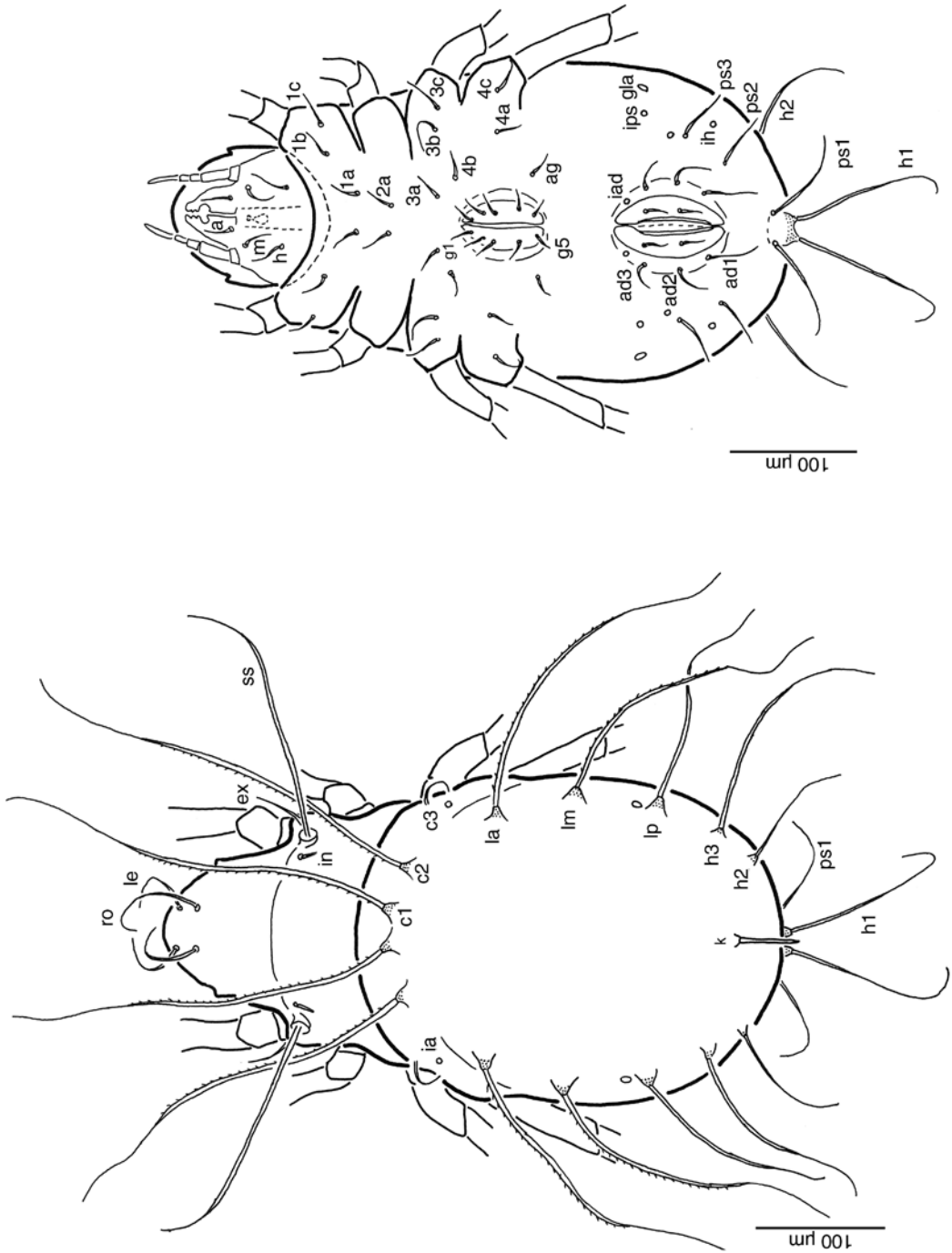


Figure 12. *Belba sculpta* tritonymph, ventral view.

Figure 11. *Belba sculpta* tritonymph, dorsal view.

somewhat shorter (tritonymph 77  $\mu\text{m}$ ) than the smooth setae la (tritonymph 102  $\mu\text{m}$ ). Larval lamellar setae relatively much more laterally inserted than those of nymphs. The ratio of the distance of the insertion points of the setal pairs le-le : ro-ro: is 2,5:1 in the larva and roughly 1:1 in the tritonymph.

### Notogaster (Figs 8, 10, 11, 13)

Larval setation unidifferent, with 12 pairs of notogastral setae which reveal a considerable variety in size and form. Setae c1 (181  $\mu\text{m}$ ), c2 (165  $\mu\text{m}$ ), da (206  $\mu\text{m}$ ), dm (185  $\mu\text{m}$ ), lp (201  $\mu\text{m}$ ) and dp (220  $\mu\text{m}$ ) are thick, elongate, dark in colour, barbed and with flagellate tips which are frequently broken off. Setae c3 (23  $\mu\text{m}$ ), la (30  $\mu\text{m}$ ) and lm (28  $\mu\text{m}$ ) differ from these in being thinner, shorter, not displaying distinct flagellate tips, in

missing barbs and in that they insert on considerably smaller setal sclerites which are set on apophyses. They share the dark brown colour of the former. Setae h1 (100  $\mu\text{m}$ ), h2 (38  $\mu\text{m}$ ) are smooth and thin with h3 (12  $\mu\text{m}$ ) being minute, without barbs and very slender.

The nymphal setation contrasts to that of the larva in that it is quadridifferent with the pseudanal setae ps1, ps2 and ps3 present and the three dorsocentral setae not being developed instead. In addition, setae la and lm are very much longer and seta lp shorter relative to the body length in the nymphal stages than in the larva. Nymphal setae c1, c2, la, lm are thick, elongate, dark coloured with a hyaline base, minutely barbed and with flagellate tips. Setae c3, lp, h3, h2, h1 are significantly shorter and very generally without any barbs. The dark brown strongly sclerotized

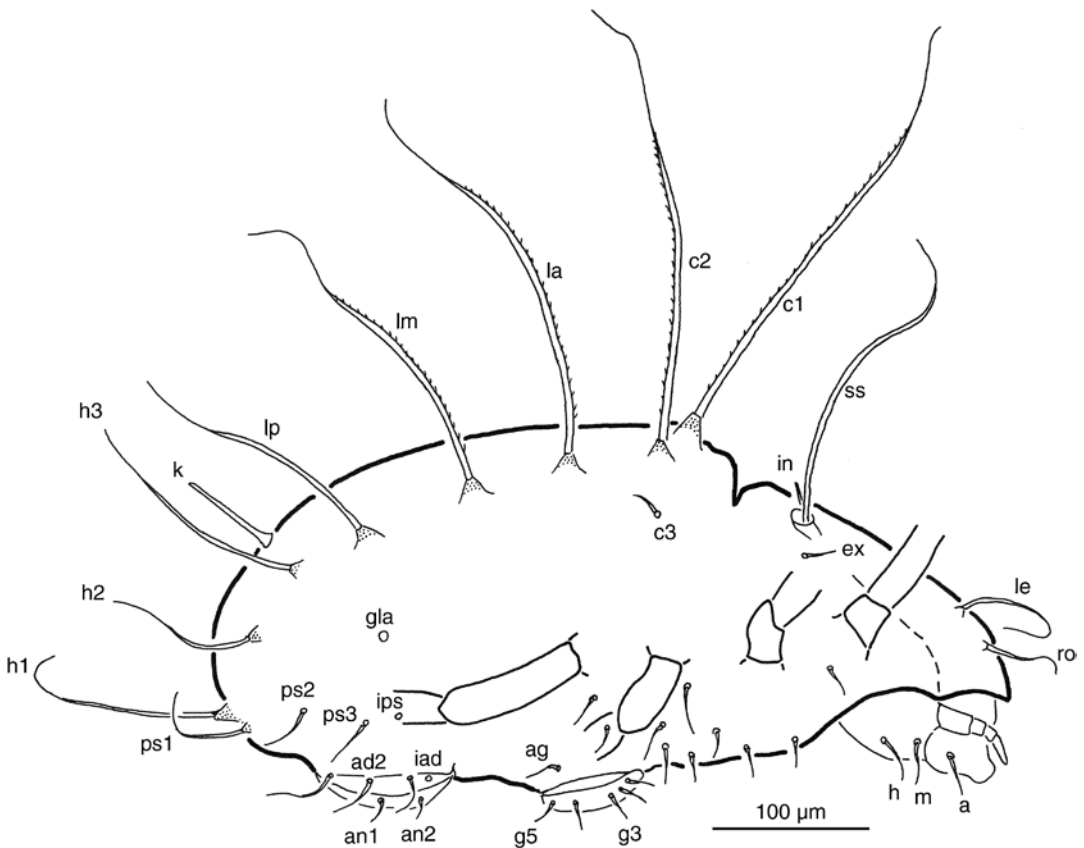


Figure 13. *Belba sculpta* tritonymph, lateral view.



setal sclerites are fairly small, largest on the longest notogastral setae and positioned on distinct apophyses. Setal pair c1 is located on a single basally fused sclerite in nymphs. Setal pair h1 similarly inserted on a larger common sclerite. Setal lengths for the tritonymph are as follows: c1 (329  $\mu\text{m}$ ), c2 (326  $\mu\text{m}$ ), c3 (39  $\mu\text{m}$ ), la (273  $\mu\text{m}$ ), lm (252  $\mu\text{m}$ ), lp (175  $\mu\text{m}$ ), h3 (161  $\mu\text{m}$ ), h2 (105  $\mu\text{m}$ ), h1 (154  $\mu\text{m}$ ), ps1 (101  $\mu\text{m}$ ), ps2 (46  $\mu\text{m}$ ), ps3 (42  $\mu\text{m}$ ). Seta c3 gets lost in the adult.

Nymphs eupheredermous with a thin, relatively straight cornicle k present. Each lightly sclerotized nymphal cornicle inserts into the cornicle of the scalp of the preceding stage, thereby connecting the scalps. Cornicle is absent in larva, but a functionally equivalent internal indentation in the larval scalp exists. Nymphs carry the exuvial scalps of the previous ontogenetic stages on their notogaster in a conspicuous stacked fashion resembling a pagoda. They never transport a compact mass of organic debris. Adult without cornicle k. Cupules ia, im, ip and ih are present in the larva, with ips added in the protonymph, and iad in tritonymph. The latero-ophistonotal gland occurs in all stages.

#### Anogenital region (Figs 9, 12)

Genital, aggenital, adanal and anal setal formulae are: larva 0-0-0-0; protonymph 1-0-0-0; deutonymph 3-1-3-2; tritonymph 5-1-3-2. In the adult, a single genital seta is added on each genital valve. Number of papillae in the genital chamber: larva 0; protonymph 1; deutonymph 2; tritonymph 3. Larva without genital aperture. Ovipositor and spermatopositor absent in juveniles. Lyrifissure ian present in tritonymph, missing in earlier stages.

#### Epimeral region (Figs 9, 10, 12, 13)

Epimeral setation of larva 3-1-2, of protonymph 3-1-2-1, of deutonymph 3-1-2-2 and of tritonymph 3-1-3-3. Urstigma or Claparede's organ present on epimere I in larva, absent in later stages. Seta 3c of larva modified as a broad scale covering Claparede's organ (included in setal formula). Epimeres lightly sclerotized, except for a longitudinal median strip, particularly in the tritonymph. Epimeral region without sclerotized tubercles. Tracheal vestibules absent.

#### Gnathosoma

Palp setal formulae: larva 0-1-1-3-9 + 1 $\omega$ ; nymphs 0-2-1-3-9 + 1 $\omega$ . Seta inf of the palpfemur first found in the protonymph. Chelicerae and in-

fracapitulum of larva and nymphs very similar to those of the adult, excepting some differences in size and proportion. Suture of labio-genal articulation occurs in the form of an integumental fold in the larva and nymphs.

#### Legs (Tabs 2-4, Figs 14 - 17)

Five segments present. Leg shapes in the larva simple, almost cylindrical. The leg segments of the tritonymph are already more similar to that of the adult in shape and character and possess more clearly defined bulbs. Legs are not or only slightly sclerotized. Leg IV absent in larva, present in nymphs. Legs I-III are relatively short with leg I being about equal in length to the total body length (b.l.) in each stage. Leg II measures about 0,7-0,8 b.l. and leg III slightly less than the body length in all developmental stages. Leg IV achieves about 1,14 times the body length when it first arises in the protonymph. In the tritonymph it already reaches a length of 1,4 b.l., very similar to that of the adult leg IV which measures 1,45 b.l. Arranged according to length, the order of the legs in the nymphs is L4 > L1 > L3 > L2.

Porose areas located distally on the ventral femora of the legs in the tritonymph. During ontogeny these are displaced so that in the adult they are positioned approximately dorsally on the posterior region of the bulb instead. In the larva and nymphs, setae on trochantera- and femora I-IV slender, smooth, long to very long. Genual seta d of larva regressed, extremely short, with its associated solenidion  $\sigma$  strongly bent towards the segment surface and longer than the seta. In nymphs, seta d of genua I-III elongate, longer than their coupled solenidion  $\sigma$ , with the latter being erect. In the tritonymph, seta d on genu IV slender, smooth, flagellate distally and exceptionally long, l' similar in appearance and only minimally shorter. Setae d and l' of tibia IV of tritonymph smooth, flagelliform and extremely long. The relative lengths of the individual leg setae

Table 2. Leg lengths of ontogenetic stages of *Belba sculpta* (in  $\mu\text{m}$ ).

Stage	Leg I	Leg II	Leg III	Leg IV
larva	244	189	213	–
protonymph	319	247	287	338
deutonymph	406	270	362	497
tritonymph	485	341	458	705
adult	536	406	510	770

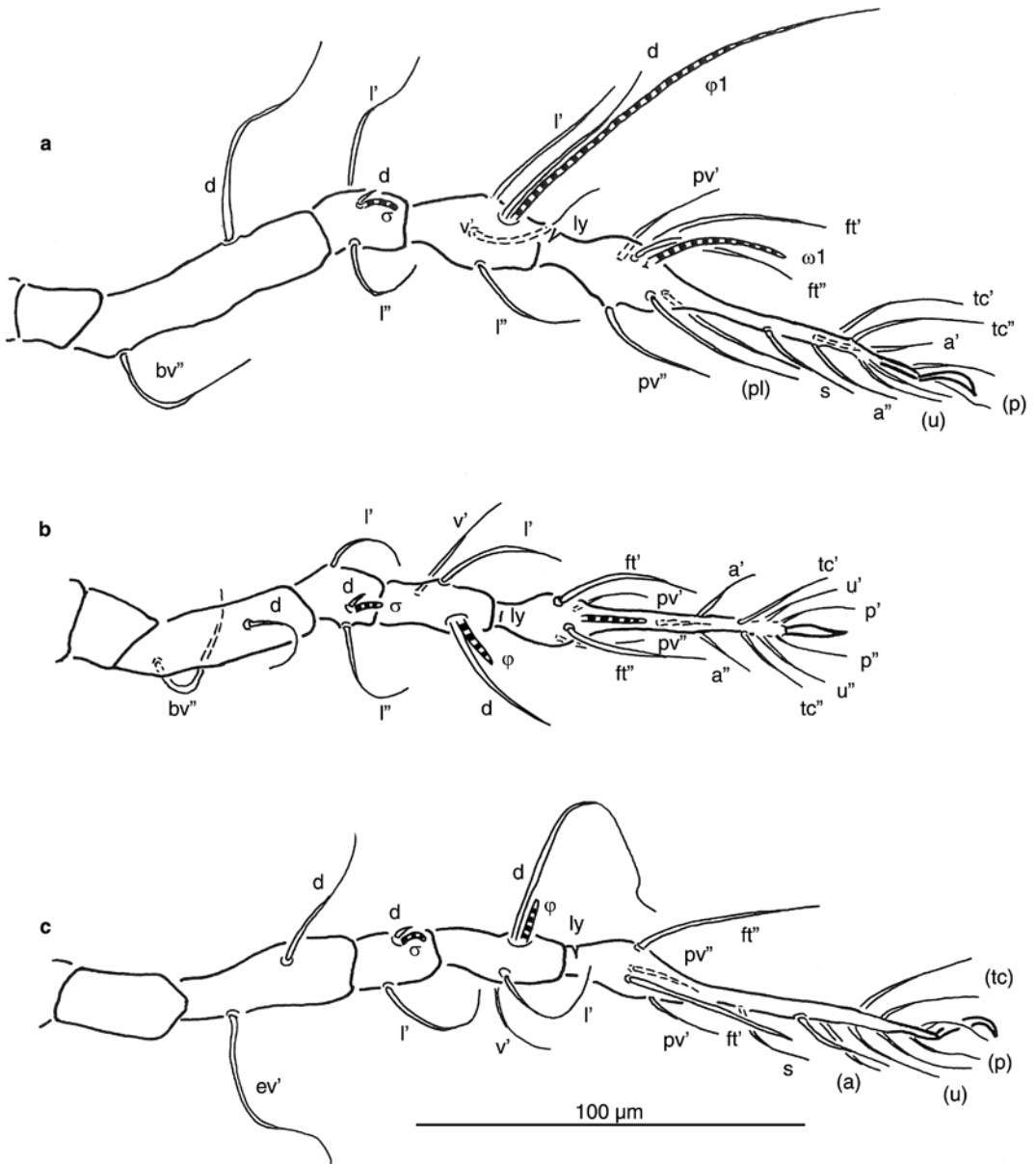


Figure 14. *Belba sculpta* larva. a) leg I, antiaxial view. b) leg II, dorsal view. c) leg III, antiaxial view.

and their general appearance in the tritonymph already show a remarkable resemblance to that of the adult.

Unpaired subunguinal seta *s* of tarsus I barbed, non-eupathidial, and inserted proximally to anterolateral setae in larva and nymphs. In adult, seta

*s* is eupathidial and has its point of origin distally to the anterolateral setae. Setae *pl*'', *pv*'', *pv*'' of leg I experience a distinct distalward shift during ontogeny, not inserting on the tarsal bulb in the adult. Famulus regressive, extremely short and sunken in a sclerotized cup in immatures.

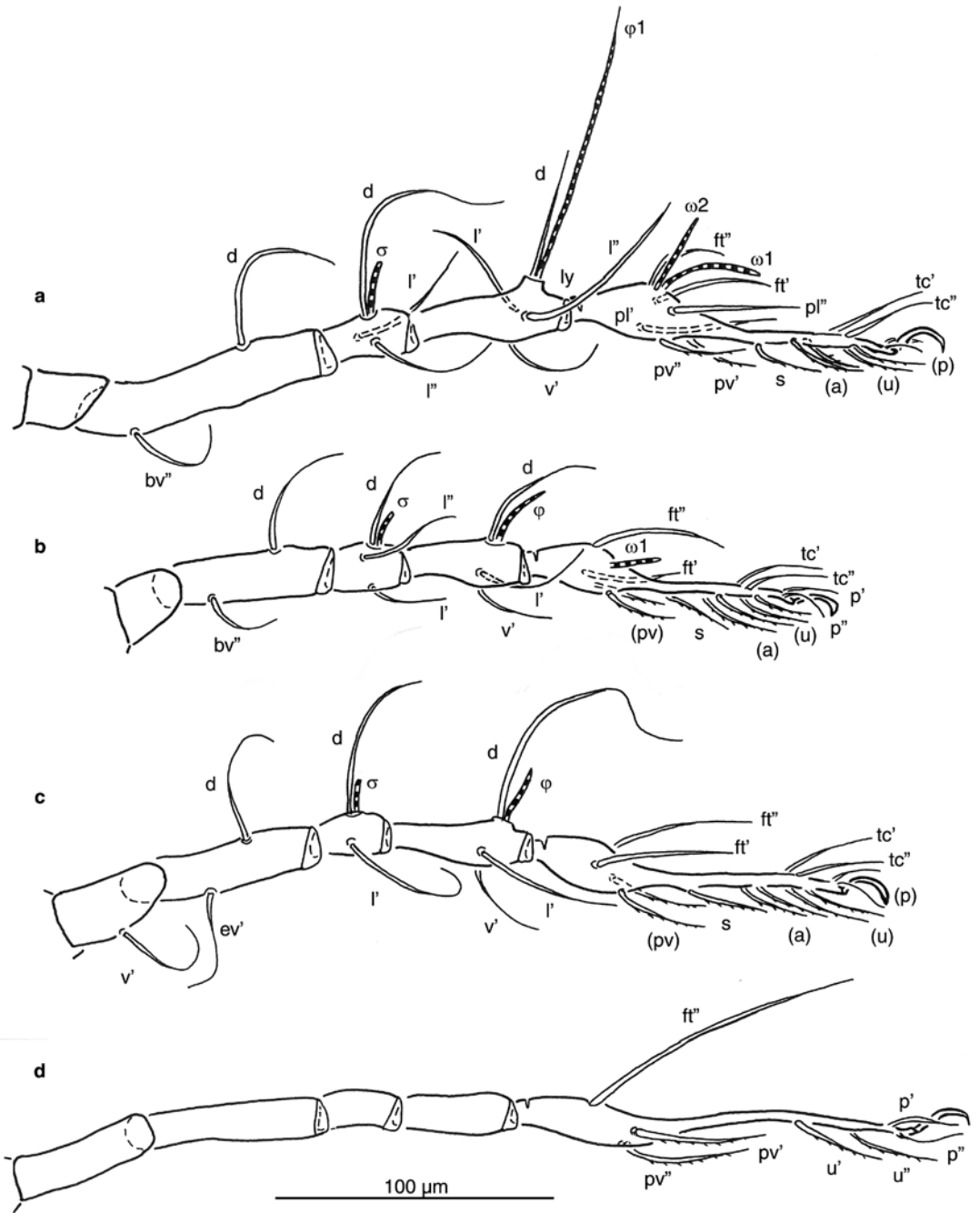


Figure 15. *Belba sculpta* protozyte. a) leg I. b) leg II. c) leg III. d) leg IV. All in antiaxial view.

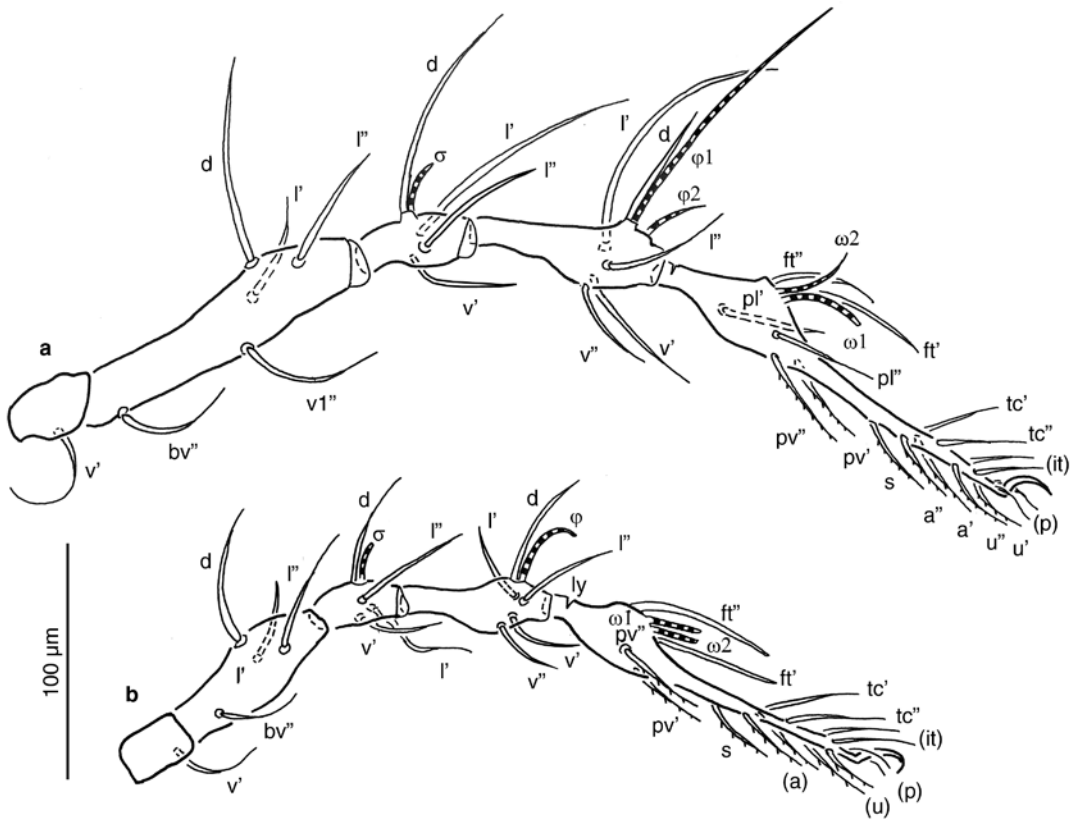


Figure 16. *Belba sculpta* tritonymph. a) leg I, antiaxial view. b) leg II, antiaxial view.

Table 3. Setal and solenidial counts on the legs of *Belba sculpta* during ontogeny.

	Setae	Solenidiae		Setae	Solenidiae
<b>Leg I</b>			<b>Leg III</b>		
larva	0-2-3-4-16	1-1-1	larva	0-2-2-3-13	1-1-0
protonymph	0-2-3-4-16	1-1-2	protonymph	1-2-2-3-13	1-1-0
deutonymph	1-4-4-5-16	1-2-2	deutonymph	2-3-3-4-13	1-1-0
tritonymph	1-5-4-5-18	1-2-2	tritonymph	2-3-3-4-15	1-1-0
adult	1-7-4-4-20	1-2-2	adult	2-4-3-4-17	1-1-0
<b>Leg II</b>			<b>Leg IV</b>		
larva	0-2-3-3-13	1-1-1	protonymph	0-0-0-0-7	0-0-0
protonymph	0-2-3-3-13	1-1-1	deutonymph	0-2-2-3-12	0-1-0
deutonymph	1-4-4-4-13	1-1-2	tritonymph	1-3-3-4-12	0-1-0
tritonymph	1-4-4-5-15	1-1-2	adult	1-4-3-4-13	0-1-0
adult	1-6-4-5-17	1-1-2			

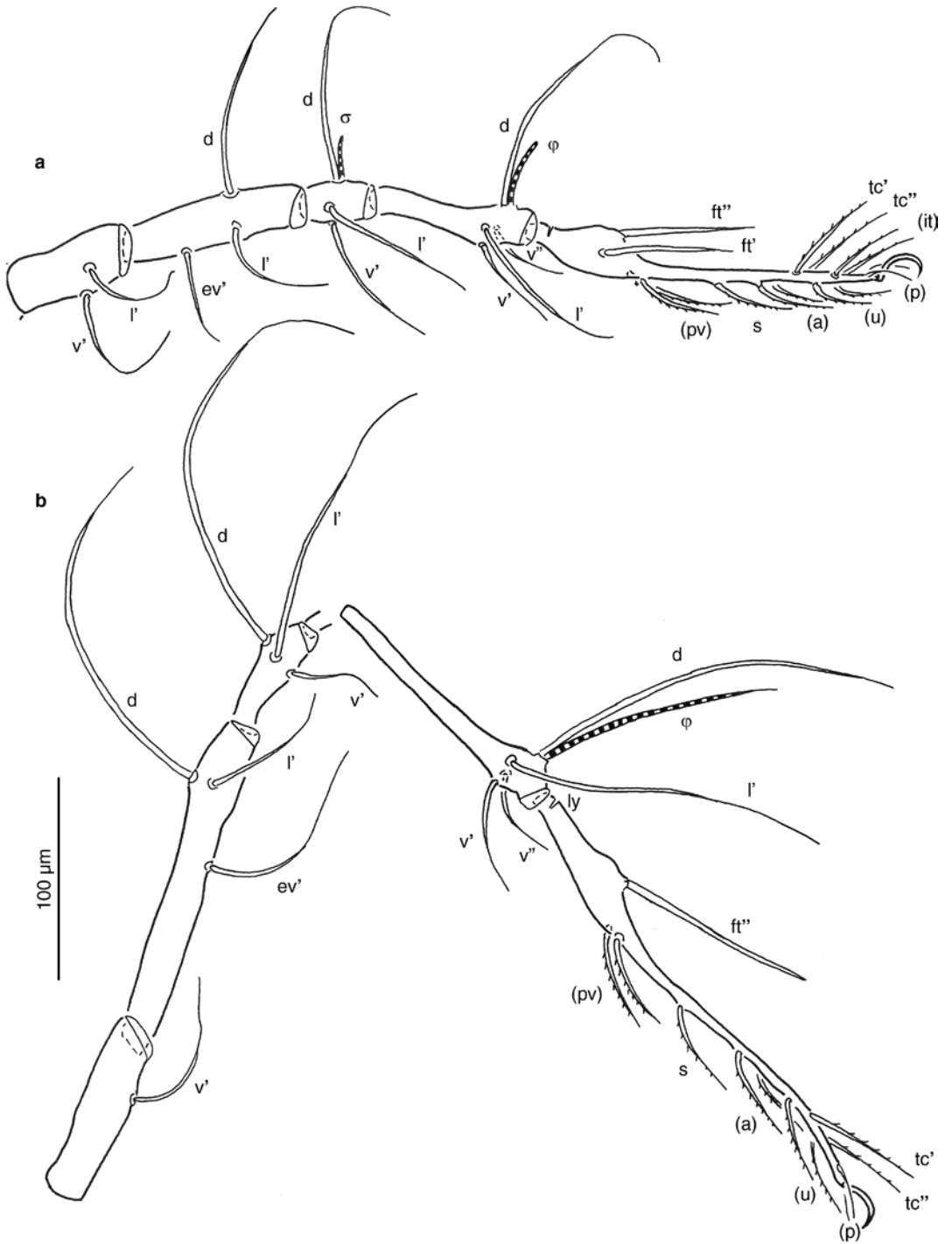


Figure 17. *Belba sculpta* tritonymph. a) leg III, antiaxial view. b) leg IV, antiaxial view.

Table 4. Ontogeny of leg chaetotaxy in *Belba sculpta*.

	Trochanter	Femur	Genu	Tibia	Tarsus
<b>Leg I</b>					
larva	–	d, bv <sup>o</sup> ,	dσ, (l)	dφ1, (l), v <sup>o</sup>	(ft), (pl), (pv), (tc), (a), (u), (p), s, e, ω1
protonymph	–	–	–	–	ω2
deutonymph	v <sup>o</sup>	(l)	v <sup>o</sup>	v <sup>o</sup> , φ2	–
tritonymph	–	v1 <sup>o</sup>	–	–	(it)
adult	–	v1 <sup>o</sup> , v2 <sup>o</sup>	–	d lost	(v)
<b>Leg II</b>					
larva	–	d, bv <sup>o</sup>	dσ, (l)	dφ, l', v <sup>o</sup>	(ft), (pv), (tc), (a), (u), (p), s, ω1
protonymph	–	–	–	–	–
deutonymph	v <sup>o</sup>	(l)	v <sup>o</sup>	l <sup>o</sup>	ω2
tritonymph	–	–	–	v <sup>o</sup>	(it)
adult	–	(v)	–	–	(v)
<b>Leg III</b>					
larva	–	d, ev <sup>o</sup>	dσ, l'	dφ, l', v <sup>o</sup>	(ft), (pv), (tc), (a), (u), (p), s
protonymph	v <sup>o</sup>	–	–	–	–
deutonymph	l'	l'	v <sup>o</sup>	v <sup>o</sup>	–
tritonymph	–	–	–	–	(it)
adult	–	v <sup>o</sup>	–	–	(v)
<b>Leg IV</b>					
protonymph	–	–	–	–	ft <sup>o</sup> , (pv), (u), (p)
deutonymph	–	d, ev <sup>o</sup>	d, l'	dφ, l', v <sup>o</sup>	(tc), (a), s
tritonymph	v <sup>o</sup>	l'	v <sup>o</sup>	v <sup>o</sup>	–
adult	–	v <sup>o</sup>	–	–	v <sup>o</sup>

In table 4, the setal structures are indicated at the stage where they are first added, and are assumed present in the later stages unless noted otherwise. A dash indicates that no additions occur. Roman letters refer to setae, Greek letters to solenidia. Setae coupled with solenidia are shown as dσ or dφ.

The solenidia σ on genu I-III, φ on tibia II-III, φ1 on tibia I as well as ω1 on tarsus I-II are larval in origin. Solenidium ω2 on tarsus I is first visible in the protonymph. Solenidia φ2 on tibia I, φ on tibia IV, and ω2 on tarsus II, are all deutonymphal in appearance. The larva displays the fundamental setae: femur I-II: d, bv<sup>o</sup>; femur III: d, ev<sup>o</sup>; genu I-II: d, (l); genu III: d, l'; tibia I: d, (l), v<sup>o</sup>; tibia II-III: d, l', v<sup>o</sup>; tarsus I: (ft), (tc), (p), (u), (a), s, (pv), (pl), e; tarsus II-III: (ft), (tc), (p), (u), (a), s, (pv). This corresponds to the typical damaeid pattern.

Setae first arising in the protonymph are trochanter III: v<sup>o</sup>; tarsus IV: ft<sup>o</sup>, (p), (u), (pv). Setae initially found in the deutonymph are: trochanter I, II: v<sup>o</sup>; trochanter III: l'; femur I-II: l', l<sup>o</sup>; femur III: l'; femur IV: d, ev<sup>o</sup>; genu I-III: v<sup>o</sup>; genu IV: d, l'; tibia I, III: v<sup>o</sup>; tibia II: l<sup>o</sup>; tibia IV: d, l', v<sup>o</sup>; tarsus IV: (tc), (a), s. Of tritonymphal origin are setae trochanter IV: v<sup>o</sup>; femur I: v1<sup>o</sup>; femur IV: l<sup>o</sup>; genu IV: v<sup>o</sup>; tibia II, IV: v<sup>o</sup>; tarsus I-III: (it). Setae arising in the adult are: femur I: v1<sup>o</sup>, v2<sup>o</sup>; femur II: v<sup>o</sup>, v<sup>o</sup>; femur III-IV: v<sup>o</sup>; tarsus I-III: (v); tarsus IV: v<sup>o</sup>. The adult has lost the associated seta d on tibia I.

### 3.2 Discussion

#### Identity of the *Belba* from the Dossenwald

Among the presently known species of the genus *Belba* only *Belba dubinini* BULANOVA-ZACHVATKINA, 1962, *B. meridionalis* BULANOVA-ZACHVATKINA,

1962, *B. prasadi* BAYARTOGTOKH, 2000, *B. sasakawai* ENAMI, 1989, and *B. sculpta* resemble the *Belba* species discovered in the Dossenwald in possessing: 1) slender, relatively long, smooth notogastral setae of the c-, l- and h- series; 2) long flagellate pseudanal seta ps1; 3) smooth, flagellate, elongate to very elongate sensillus and interlamellar seta; 4) clavate legs with smooth, flagellate, elongate to very elongate setae d and l' on genu IV.

*Belba sasakawai*, which shares with the Dossenwald *Belba* specimens the possession of well-defined tubercles Ba, Bp, Va, Vp, is distinguishable from the latter by the extremely long setae ps1 (148-190 µm), notogastral setae of c-, l-, and h-series with a distinct middle vein and bilateral vanes, and a smaller body size with a mean length of merely 395 µm in Japan (ENAMI 1989) and 450 µm in China (WANG & NORTON 1995). This species is known only from Japan (ENAMI 1989) and the southern provinces of China (WANG & NORTON 1995).

*Belba dubinini* as described by BULANOVA-ZACHVATKINA (1962, 1967, 1975) differs from the Dossenwald *Belba* in the following characteristics: being considerably larger with a body length of 680-760 µm; lacking the postbothridial tubercles Bp; having the mutual distance between the insertion points of lamellar setae le exceed that of the rostral setae ro; parastigmatic tubercle Sa short, triangular in dorsal view with a lateral extension not considerably exceeding that of tubercle Sp; seta l' on femur II setiform and normally developed, instead of short, thick, ceratiform; possessing only 3 setae on femur IV; leg IV measuring 2x the body length. The type locality of *Belba dubinini* is the Crimean (BULANOVA-ZACHVATKINA 1962) but there are also collection records from Georgia (MURVANIDZE et al. 2018), Poland (ZALEWSKA 1983), the Ukraine (YAROSHENKO 2009, ERMILOV et al. 2012) and the Russian Far East (KRIVOLUTSKY 1995). The species needs to be redescribed.

Using the account in BAYARTOGTOKH (2000), *Belba prasadi* from Mongolia can be distinguished from the Dossenwald *Belba* as follows: postbothridial tubercles Bp absent, shorter posterior notogastral seta ps1, interlamellar setae and sensillus both much shorter, seta l' of femur II elongate and slender, smaller size with a ventral body length of 406-441 µm.

The *Belba* specimens from Mannheim show a very close overall resemblance in their morphological features to *Belba sculpta* from Spain. With

a maximum body length of 526-598 µm and a width of 315-368 µm they are slightly smaller than individuals from Madrid for which PÉREZ-ÍÑIGO (1970) indicates a length of 580-640 µm and a width of 370-420 µm. KAHWASH et al. (1992) give a length of 525-575 µm and a width of 312-375 µm for *Belba sculpta* specimens collected in various locations in Andalusia, which agree excellently with the dimensions of the material from the Dossenwald. The above authors do not specify the criteria used in their body length measurements, but it is most likely that they refer to the total body length.

PÉREZ-ÍÑIGO (1970, 1997) mentions that *Belba sculpta* possesses a little projecting and rounded propodolateral apophysis. The illustrations he provides (PÉREZ-ÍÑIGO 1970, p. 275, figs 32, 33; 1997, p. 134; fig. 46), as well as the earlier contribution by MIHELČIČ (1957) demonstrate, however, that an apophysis P is absent in this species, agreeing with the results of the present study.

The Dossenwald *Belba* differ from the Spanish specimens of *Belba sculpta*, based on the description of the latter by PÉREZ-ÍÑIGO (1970, 1997) in possessing: I) a short, thick, thorn-like seta l' paraxially on femur II instead of seta l' setiform, thin and of normal appearance; II) barbed genital, anal and epimeral setae instead of these all being smooth; III) epimeral setation formula 3-1-3-4 instead of 3-1-4-4; IV) tarsal setation 20-17-17-13 instead of 21-18-18-15.

The barbs on the epimeral setae of the Dossenwald specimens are not easily seen. It is likely that they were overlooked or deemed to be of no significance by PÉREZ-ÍÑIGO (1970, 1997) in the *Belba sculpta* from Spain. A degree of intraspecific variability in the number of setae of epimere III is relatively common in oribatids. The tarsal setal formula of 21-18-18-15 has up to now not reliably been noted to occur in any species of *Belba* and is instead characteristic of taxa such as *Damaeus* KOCH, 1835, and *Tectodamaeus* AOKI, 1984 (LAMOS 2016). Since tarsal setal counts in damaeid mites are often not easy to determine correctly under a light microscope, especially in slide mounted holotype specimens, it is probable that the tarsal setation formula presented by PÉREZ-ÍÑIGO (1970, 1997) for *Belba sculpta* is the result of a slight inaccuracy in counting.

The spinelike seta on femur II in the Dossenwald specimens is possibly a significant distinction between the specimens from Mannheim and the Spanish *Belba sculpta*, since this highly unusual trait has up to now only been found in some

*Belba* species from Central Asia (BULANOVA-ZACHVATKINA 1962, TOLSTIKOV 1996, TOLSTIKOV & LYASHCHEV 1996). No reference to such a seta is made by either MIHELČIČ (1957) or PÉREZ-ÍÑIGO (1970, 1997). With reference to the femora of *Belba sculpta*, PÉREZ-ÍÑIGO (1970, p. 277) states: "todos los pelos son finas y flexuosus". Again it is conceivable that the short stubby character of seta l' may have been overlooked or disregarded, because it may have been considered a broken off seta. Since the legs of *Belba sculpta* were not adequately illustrated in either MIHELČIČ (1957) or PÉREZ-ÍÑIGO (1970, 1997), it is not possible to have absolute certainty in the matter. Even if it would be demonstrated that the *Belba sculpta* from Spain do not possess the highly modified ceratiform femoral seta l', this distinction alone would not justify recombining the Dossenwald *Belba* with a species other than *B. sculpta*, or possibly erecting a new species level taxon for them.

Although I consider it highly likely that the Dossenwald *Belba* does indeed belong to *Belba sculpta*, possibly being a subspecies of the latter, this still demands formal proof which requires the reexamination and detailed redescription of the type material of *Belba sculpta*, *B. aberrans* and *B. ignota*. The question of character variability will also have to be addressed in various populations of *Belba sculpta* originating from both Spain and Germany.

The *Belba* cf. *sculpta* collected at the Pollino Massif in the Apennine mountains in southern Italy differs from the Spanish *Belba sculpta* in possessing more medially inserted rostral setae and a non-flagellate sensillus, based on BERNINI et al. (1987). It accordingly differs in the same way from the Dossenwald *Belba sculpta*.

*Belba meridionalis* from Turkmenistan, initially described by BULANOVA-ZACHVATKINA (1962), is a second species which shows a strong similarity to the *Belba* specimens from Mannheim. Shared characters in addition to those mentioned already include: 1) a short, thick, thorn-like seta l' paraxially on femur II; 2) a relatively broadly rounded rostrum 3) tubercle Sa of parastigmatic enantiophyses long, laterally directed and with a sharply pointed apex, tubercle Sp much shorter, subtriangular; 4) mutual distance between rostral setae greater than between lamellar setae; 5) distance between insertions of notogastral setal pair c2 about 4 times that of c1.

Based on the text and illustrations in BULANOVA-ZACHVATKINA (1962, 1967, 1975), *Belba meridionalis*

differs from the Dossenwald *Belba sculpta* in the following: 1) postbothridial tubercle Bp absent; 2) presence of only 6 setae on femur I; 3) equal length of solenidion and seta d on tibia III; 4) tibia of leg IV twice as long as tibiae I-III; 5) much shorter setae d and l' on genu IV relative to the length of this segment; 6) much shorter setae d and l' on tibia IV relative to the length of this segment; 7) more marginal placement of insertions of notogastral setae c2-h3; 8) adult mites carry nymphal scalps on notogaster; 9) a greater body size of 620-660 µm.

The very brief documentation of *Belba meridionalis* by BULANOVA-ZACHVATKINA (1962, 1967, 1975) does not give sufficient information on the ventral characters and on the leg setation other than that of the femur II, genu IV and tibia IV. Clearly the species should be redescribed. However, the holotype of *Belba meridionalis* does unfortunately no longer exist in the collection of the museum of the Institute for Animal Systematics and Ecology in Novosibirsk, which houses the damaeid mite collection of BULANOVA-ZACHVATKINA (TOLSTIKOV & LYASHCHEV 1996). The latter authors carried out a very thorough search for any other material of *Belba meridionalis* in several collections in Russia and Uzbekistan and found only two microscope slides labelled *B. meridionalis*. These contained other *Belba* species, however, namely *B. bulanovae* SUBIAS, 2016 (corresponding to *B. minuta* BULANOVA-ZACHVATKINA, 1962), and *B. lammeisetosa* TOLSTIKOV & LYASHCHEV 1996, respectively. Although it cannot be ruled out that the mites from Mannheim may well belong to *Belba meridionalis*, based on what little we know about this taxon, and only if we assume an inaccurate description by BULANOVA-ZACHVATKINA (1962, 1967, 1975), there is no way at present to verify this due to a complete absence of material and the highly incomplete description of *B. meridionalis*. TOLSTIKOV & LYASHCHEV (1996: p. 3) write: "The existence of *B. meridionalis* B.-Z., 1962 remains questionable". At the present time *Belba meridionalis* may be considered as being effectively a species inquirenda. BERNINI et al. (1995) mention collection records of an as yet undescribed *Belba* cf. *meridionalis* from Sicily in their checklist of the Italian acarofauna.

### Morphology of *Belba sculpta*

A pair of minute light spots is found on the notogaster of *Belba sculpta* posteriomedial the insertion points of setae la, and another similar pair is located posteromedial setae lp. These



were illustrated by PÉREZ-ÍÑIGO (1970, 1997), who comments in the first contribution that they were visible on all specimens of *B. aberrans*, *B. ignota*, and *B. sculpta* which he had examined. They were also evident in all the representatives of the latter which I collected in Mannheim. Two pairs of notogastral light spots clearly homologous to those of *Belba sculpta* have so far been noted for some species of *Metabelba* GRANDJEAN, 1936 (HAMMEN & STRENZKE 1953, MOUREK et al. 2011), including *Metabelba (Neobelba) pseudopapillipes* BULANOVA-ZACHVATKINA, 1967 (MIKO & KOLESNIKOV 2014).

The function of the spots is unclear. It may be that the anterior pair differs functionally from the more posterior one, as they are dissimilar in structure when observed under high magnification in a light microscope. This is also suggested by the fact that in a few species such as *Belba paracorynopus* BULANOVA-ZACHVATKINA, 1962 (MIKO et al. 2017) the anterior pair of spots is situated in an identical position on the notogaster relative to the notogastral setae as in *B. sculpta*, whereas the second pair is instead located posterior-medial seta Im. It is conceivable that at least the posterior light spots are actually muscle sigillae. A conspicuous oval cuticular sculptured area, with a diameter only slightly less than that of the bothridial opening, is present together with some similar smaller ones anterior and slightly medial to the bothridium of *Belba sculpta*. MIKO & KOLESNIKOV (2014) interpret an identical structure in *Metabelba (Neobelba) pseudopapillipes* as being an area porosa. I view it as being a small sigillary field instead.

Distinct ridges or other linear structures associated with the insertions of the notogastral setae, like they are present in *Belba sculpta*, have seldomly been depicted or mentioned in descriptions of Damaeidae. Since these are not easy to perceive, I suspect that they are much more common in the family than is suggested by their scarce occurrence in the literature. Three species known for displaying such a ridge system are *Damaeus onustus* KOCH, 1844 (ABD-EL-HAMID 1966), *Epidamaeus conjugenus* XIE et al., 2011 (XIE et al. 2011) and *Spatiodamaeus conjugenus* XIE et al., 2016 (XIE et al. 2016). BAYARTOGTOKH (2000) notes that in *Belba crassisetosa* setae c1 and c2 are each situated on a weakly developed longitudinal ridge. From a biomechanical perspective it appears that the function of the cuticular ridges is to provide structural support to the notogastral setae at their site of insertion and to stabilise

the dome-like notogaster against impinging compressional and torsional forces.

GRANDJEAN (1960), in one of the most detailed documentations yet of a damaeid mite, illustrates and describes the notogaster of *Damaeus arvernensis* GRANDJEAN, 1960. He does not mention any notogastral ridges associated with setae, but instead comments on two longitudinal notogastral grooves. The “grand sillon” (GRANDJEAN 1960, p. 258) of *Damaeus arvernensis* appears to be homologous to the “line” associated with the notogastral seta insertions of the Dossenwald *Belba*. The second groove mentioned by GRANDJEAN (1960), which runs closer to the sagittal plane than the outer groove and is approximately parallel to the latter, is indistinct and weakly developed in *Belba sculpta*. More research is needed before the notogaster of *Belba sculpta* and other damaeid mites is fully understood.

The ovipositor has been investigated in only a handful of species of Damaeidae such as *Damaeus arvernensis* by GRANDJEAN (1960), *D. riparius* NICOLET, 1855 by ERMILOV (2010b), *Belbodamaeus indicus* ERMILOV, KALUZ & WU, 2013, by ERMILOV et al. (2013) and *Belba cornuta* WANG & NORTON, 1995, by ERMILOV (2018). The ovipositor of *Belba sculpta* is similar to the one of these species in possessing two possibly derived traits that are apparently absent in all other higher oribatid mites except *Hungarobelba* BALOGH, 1943 (MIKO & TRAVÉ 1996), although they are known from the Trhypochthoniidae within the Macropyliina (ERMILOV 2011), namely 1) a short, wide appearance with a broad ovipositor base bDp which is only slightly longer than wide, and very short lobes L1-L3, and 2) an arrangement of the insertions of the setae ra, rb, rc of both eugenital lobes L2 and L3 in the approximate shape of an isosceles triangle. These character states may be synapomorph for the Damaeidae and Hungarobelbidae. It should be noted though, that the ovipositor of *Protodamaeus* SUBÍAS, 2019, within the Hungarobelbiae MIKO & TRAVÉ, 1996, is not described and that virtually no research has been done on the ovipositor of the Ameroidea BULANOVA-ZACHVATKINA, 1957.

The presence of a tiny vestigial famulus sunken in a sclerotized cup in the nymphs of *Belba sculpta* is highly unusual, since this trait is so far unknown in published descriptions of species of *Belba* (NORTON 1979c, NORTON & PALACIOS-VARGAS 1982, SENICZAK et al. 2013) and similarly not present in species of possibly related genera such as *Caenobelba* (NORTON 1980) and *Tokukobelba* LAMOS, 2016 (SENICZAK & SENICZAK 2013, LAMOS

2016), both of which possess a normal sized emergent nymphal famulus. Species of the *Metabelba* cluster of genera such as *Metabelba glabriseta* (ERMILOV et al. 2010), *Metabelba papillipes* (ERMILOV 2010a), *Metabelbella interlamellaris* (SENICZAK & SENICZAK 2013) and *Metabelbella tichonravovi* (ERMILOV & KHAUSTOV 2011) differ from *Belba sculpta* in that although the famulus in these is minute, it is not situated in a sclerotized cup. The character state of *Belba sculpta* instead is characteristic of species within genera such as *Damaeus* (GRANDJEAN 1954, NORTON 1978a), *Spatiodamaeus* BULANOVA-ZACHVATKINA, 1967 (MIKO & MOUREK 2010), *Epidamaeus* BULANOVA-ZACHVATKINA, 1957 (ERMILOV & LOCHYNSKA 2009, SENICZAK et al. 2013) and *Kunstdamaeus* MIKO, 2006 (MIKO & MOUREK 2008), all of which display a tibial associated setation of 0-0-0-0 and typically also possess spinae adnatae.

### 3.3 Evolutionary systematics and phylogenetics of *Belba sculpta*

#### 3.3.1 Biphyletic nature of *Belba*

The major diagnostic traits of *Belba* such as the trochanteral setation of 1-1-2-1 or 1-1-2-2, a genual setation of 4-4-3-3, a genual associated setation of 1-1-1-0, a tibial associated setation of 0-1-1-1 and possibly also the general absence of spinae adnatae may be considered as being plesiomorph for the Damaeidae. The genus *Belba* misses strong derived defining characteristics and its heterogeneous species composition has been commented on by several authors such as NORTON (1979a, 1979b), WANG & NORTON (1995) and LAMOS (2016). The monophyly of *Belba*, as it is presently conceived of in the literature (SUBIAS 2019) is questionable. In the following, I will present morphological evidence which indicates that *Belba* may be biphyletic.

#### 3.3.2 Species groups within *Belba*

The subgenus *Belba* (*Belba*) is here seen as consisting of two morphologically very distinct species clusters, the *Belba corynopus* species group and the *Belba sculpta* species group, both of which differ from *Belba* (*Protobelba*) NORTON, 1979, in the absence of spinae adnatae. The *Belba corynopus* group encompasses the species *Belba paracorynopus*, *B. pseudocorynopus* MÄRKEL & MEYER, 1960, *B. patelloides* (MICHAEL, 1890) and *B. unicornis* ENAMI, 1994, as well as the namegiving type species of the genus, *Belba corynopus*.

The *Belba sculpta* group differs from the *B. corynopus* group in:

- 1) Postbothridial tubercle Ba not extremely laterally positioned.
- 2) Bothridia more medially positioned, not located at lateral margin of prodorsum.
- 3) Notogaster of normal height (height to length ratio is about 0,4:1) instead of notogaster high in lateral perspective (ratio of notogaster height to length is 0,55:1-0,7:1).
- 4) Notogaster usually without nymphal scalps and always without a compact mass of detritus instead of notogaster carrying nymphal exuviae and a compact mass of debris.
- 5) Seta ad3 much more laterally inserted.
- 6) Cerotegument mainly filamentous instead of mostly reticulate.
- 7) Epimere II with only 1 seta instead of epimeral neotrichy with presence of 3 or 4 setae on epimere II.
- 8) Nymphs without porose apodemes instead of nymphs with porose sejugal apodeme and sac-like porose vestibules from apodemes I and II, where known.
- 9) Nymphal famulus regressed, sunken in a sclerotized cup, instead of nymphal famulus of normal length, emergent, where known.
- 10) Femoral setation formula 7-6-4-4 versus 7-7-5-5.
- 11) Associated seta d of tibia IV smooth and always longer than solenidion, frequently twice as long as the solenidion instead of barbed and shorter than solenidion.

Character states 1, 2, 3, 4, 7, 8 and 10 of the *corynopus* group may be considered as being derived within the Damaeidae. In the traits 5, 9 and 11 the character state of the *sculpta* group represents the derived one instead, with that of the *corynopus* grouping being the plesiomorph state. A reticulate and a filamentous cerotegument are both derived with respect to the plesiomorph ontogenetically earlier granular one.

The *Belba sculpta* species group is a Eurasian clade consisting of altogether 13 described species, namely *Belba sculpta*, *B. aurata* KULLJEV, 1967, *B. bulanovae*, *B. cornuta*, *B. daghestanica* BULANOVA-ZACHVATKINA, 1962, *B. dubinini*, *B. flammeisetosa*, *B. heterosetosa* BAYARTOGTOKH, 2004, *B. meridionalis*, *B. prasadi*, *B. sarvari* TOLSTIKOV, 1996, *B. sasakawai* and *B. tenuisetosa* BULANOVA-ZACHVATKINA, 1962.

The exact phylogenetic affinities of the Dossenswald *Belba sculpta* within the *sculpta* group are not resolved. The species shares a strong syna-

pomorphy, the spine-like seta l' on femur II with *B. bulanovae*, *B. daghestanica*, *B. flammeisetosa*, *B. meridionalis* and *B. sarvari*. It additionally possesses the derived smooth, flagellate, elongate to very elongate setae d and l' on both genu IV and tibia IV which are also found in *B. aurata*, *B. bulanovae*, *B. dubinini*, *B. flammeisetosa*, *B. meridionalis*, *B. prasadi* and *B. sasakawai*. The apomorphic long seta ps1 may be interpreted as being a synapomorphy of *B. meridionalis*, *B. sasakawai* and *B. sculpta*.

In two early pioneer papers, NORTON (1979a, 1979b) already suggested an at least biphyletic origin for the genus *Belba*, based on his studies of the North American damaeid fauna, and identified a “*corynopus* group” and a “*jacoti* group” in the species of the genus. With regard to their defining characters, these species groups agree very well with those identified by me. A slight difference between the classification system of NORTON (1979a, 1979b) and that of the present publication is that NORTON includes the subgenus *Protobelba* within the *corynopus* group, whereas I do not. The morphology of the representatives of the *jacoti* group, based on NORTON (1979a, p. 531), approximately corresponds to that of the members of the *Belba sculpta* species group in that they show: cerotegument granular or filamentous, epimeral setation 3-1-3-4, nymphs without porose apodemes, and notogaster does not carry a compact mass of debris. It is notable that the representatives of the *jacoti* group possess an apomorphic nymphal regressed famulus sunken in a sclerotized cup (NORTON 1979a), similar to the one of the Dossenwald *Belba sculpta*. The “two or three species” (NORTON 1979b, p. 537) of the *jacoti* group occur in southern North America, especially in Florida and some Caribbean islands (NORTON, 1979b). It is possible that they comprise a clade distinct from the Eurasian members of the *sculpta* group. Since *Belba jacoti* WILSON, 1936, whose original description is partly inaccurate and does not even suffice to locate the genus in *Belba*, has not yet been formally redescribed and I also have not seen any collection material of this taxon, I prefer to employ the name “*Belba sculpta* species group” for the cluster of Eurasian *Belba* species related to *Belba sculpta*.

Although they do not belong to the *corynopus* group, it is somewhat unclear whether or not the species *Belba clavasensilla* NORTON & PALACIOS-VARGAS, 1982, *B. crassisetosa* BAYARTOGTOKH, 2000, and *B. rossica* BULANOVA-ZACHVATKINA,

1962, belong to the *sculpta* group. The nymphs of the arboreal *Belba clavasensilla* from Mexico display a plesiomorph emergent famulus (NORTON & PALACIOS-VARGAS, 1982), while the two last named closely related species differ from those in the *sculpta* group in their femoral setation of 7-7-5-5, based on the descriptions in BAYARTOGTOKH (2000) and WANG & NORTON (1995), respectively.

### 3.3.3 Evolutionary systematics of the *Belba sculpta* species group

The morphological differences between members of the *Belba sculpta* species group and representatives of the genera *Belbodamaeus* BULANOVA-ZACHVATKINA, 1967, *Dameobelba* SELLNICK, 1928, and *Subbelba* BULANOVA-ZACHVATKINA, 1967, are slight.

The genus *Subbelba* is assumed by numerous authors such as NORTON (1977a) and MIKO (2006) to possess a degree of femoral neotrichy comparable to *Metabelba*, displaying 9 or 10 setae on each of femora I and II as well as 8 or 9 setae on each of femora III and IV. However, the illustration of femur II of *Subbelba partiocrispa* BULANOVA-ZACHVATKINA, 1967, the type species of the genus, presented by BULANOVA-ZACHVATKINA (1975: p. 138, fig. 272) shows only 6 setae. The proportions of the segment and the details of the setation show an excellent correspondence to that of *Oribata montanus* KULCZYNSKI, 1902 (cf. MIKO 2006: p. 205, fig. 109b). KULCZYNSKI (1902: tab. IV, fig. 69) presents a precise drawing of leg IV of this species in which it is shown to possess only 4 setae on femur IV, namely the usual d, l', v' and ev'. BULANOVA-ZACHVATKINA (1967) noticed the great similarities between *Subbelba partiocrispa* and *Oribata montanus*, suggesting that the latter may also belong to *Subbelba*. At one place in her contribution (1967: p. 230), she actually refers to KULCZYNSKI's species as *Subbelba montana*.

With *Subbelba* not showing any femoral neotrichy, the status of *Caenobelba* NORTON, 1980, may be challenged. It is highly likely that *Subbelba partiocrispa* shares the normal femoral setation of 7-6-4-4 shown by *Caenobelba alleghaniensis* NORTON, 1980. Additionally, the type species of *Subbelba* and *Caenobelba* share a trochanteral setation of 1-1-2-2, a genual setation of 4-4-3-3, a tibial associated setation 0-1-1-0, absence of spinae adnatae, absence of the propodolateral apophysis, short apophyses Sa and Sp and other features, based on the initial accounts of BULANOVA-ZACHVATKINA (1967, 1975)

and NORTON (1980). Since *Subbelba* possesses priority and no differences between the two type species are known which would justify a separation at generic level, I view *Caenobelba* as a junior synonym of *Subbelba*, at least until the type of the latter is redescribed. It should be noted that I here use a concept of *Subbelba* that is quite different from that of SUBÍAS (2019) in that I do not see *Dyobelba* NORTON, 1979, and *Quatrobella* NORTON, 1980, as being subgenera of *Subbelba* but instead view them as being distinct genera. The members of the *Belba sculpta* species group can therefore be differentiated from *Subbelba* only in the presence of an associated seta d on the tibia of leg IV.

Two of the four presently known species of the genus *Belbodamaeus*, namely *Belbodamaeus rarituberculatus* BAYARTOGTOKH, 2004, and *B. indicus* differ from members of the *Belba sculpta* species group only in the presence of spinae adnatae. From a phylogenetic perspective, a strong argument may be made for transferring these two species to *Belba*. The “*Belba* species B” of WALTER et al. (2016) appears to be a typical representative of the *sculpta* group, except that it shows spinae adnatae.

*Belbodamaeus marginatus* KULIJEW, 1967, not listed in BULANOVA-ZACHVATKINA (1975), is in all likelihood a *Porobelba spinosa* (SELLNICK, 1920) instead, based on its description. The type species of the genus, *Belbodamaeus tuberculatus* BULANOVA-ZACHVATKINA, 1967, is very incompletely portrayed. It is characterized by large spinae adnatae, presence of prodorsal tubercles Ba and Da, absence of a propodolateral apophysis, trochanteral setation 1-1-2-1, and a tibial associated setation of 0-1-1-1 (BULANOVA-ZACHVATKINA 1975). No other information about the setal formulae of the leg segments or the ventral structures is provided by its author. *Belbodamaeus tuberculatus* requires redescription from topotypic material before any other species can reliably be situated in the genus.

The location of the holotype of *Belbodamaeus tuberculatus* is not specified by BULANOVA-ZACHVATKINA (1967, 1975), and *Belbodamaeus* is not listed in the species catalogue of the Siberian Zoological Museum, which houses a substantial damaeid collection, including numerous types of species named by BULANOVA-ZACHVATKINA. At the present time the classification of species of Damaeidae possessing both spinae adnatae and a tibial associated setation of 0-1-1-1 is problematic.

In numerous contributions, including virtually all major diagnostic keys of the Damaeidae published so far, it is stated that *Dameobelba minutissima* (SELLNICK, 1920), displays small spinae adnatae (SELLNICK, 1960; BULANOVA-ZACHVATKINA 1967, 1975; BALOGH 1972; BALOGH & BALOGH 1992) or that the development of these structures is intraspecifically variable (PÉREZ-ÍÑIGO 1997, MIKO 2006). These assumptions appear to be based on an early publication by GRANDJEAN (1936, p. 67), who noted that the genus possesses spinae adnatae, but that these were minute. However, subsequently this author re-examined specimens from several locations in France, and also a paratype from Germany sent to him by SELLNICK and concluded: “En 1936 j’ai probablement confondu les lyrifissures *ia* avec des spinae adnatae” (GRANDJEAN 1955: p. 212). Already NORTON (1977a) was aware of this passage in which GRANDJEAN concluded that spinae adnatae are not present in the species. In all specimens of *Dameobelba minutissima* examined by me, these structures were similarly not detectable. Spinae adnatae have also not been detected in this species by WILLMANN (1931), NORTON (1977a) or KRATZMANN (1993). *Dameobelba* may be distinguished from members of the *Belba sculpta* species group by its highly coiled spiral setae c1 and c2 which hold the exuviae of the immature stages.

The morphological similarity of species in the *Belba sculpta* group to species in genera such as *Belbodamaeus*, *Dameobelba* and *Subbelba* together with the pronounced differences between the *sculpta* and *corynopus* groups suggest that *Belba* may be biphyletic. A monophyly of *Belba* cannot be ruled out, however. The existence of two very distinct lineages of *Belba*, with no species having a set of intermediate or mixed characteristics, is remarkable. It would be worthwhile to investigate the phylogeny of species of *Belba* and of related genera with molecular data.

### 3.4 Diagnosis of the genus *Belba*

#### *Belba* VON HEYDEN, 1826

*Belba* VON HEYDEN, 1826. Isis, Jena 1(6): 611.

**Type species:** *Notaspis corynopus* HERMANN, 1804. Mem. Apt. p. 89; plate IV, fig 2.

**Locus typicus:** Strasbourg, France.

**Type depository:** Type or neotype not designated.

### Diagnosis

With the general characteristics of the family Damaeidae. Apophyses Ba of postbothridial enantiophysis mostly present, Bp usually absent. Prodorsal apophyses Aa and Ap absent. Dorsosejugal and laterosejugal enantiophysis absent. Propodolateral apophyses mostly absent, if present small and tip-like. Spinæ adnatae generally absent, if present then epimere II with 3 setae. Notogastral setae c1 and c2 not extremely long and not with multiple coils. Notogastral areae porosae between setal pairs h1 and ps1 absent. Apophyses Va, Vp of ventrosejugal enantiophysis present or absent. Apophyses E2a, E2p of propodoventral enantiophysis mostly absent. Epimeral setation 3-1-3-4 or with three or more setae on epimeres I-IV. Trochanteral setation 1-1-2-1 or 1-1-2-2. Femoral setation 7-6-4-4, 7-7-4-4 or 7-7-5-5. Genua setation usually 4-4-3-3, exceptionally 4-4-4-4. Genua associated setal formula 1-1-1-0. Tibial setation 4-4-5-4. Tibial associated setal formula 0-1-1-1. Tarsal setation generally 20-17-16-13, 20-17-17-13 or 20-17-17-14, including famulus. Tarsus of legs I-IV without setae v2'. Tarsus of leg I without seta v2".

### Comments

This diagnosis bases on earlier ones by BULANOVA-ZACHVATKINA (1962, 1967, 1975), NORTON (1979c), BAYARTOGTOKH (2000) and MIKO (2006). It considers recent developments in damaeid systematics and allows a clear distinction between *Belba* and the genera *Belbodamaeus*, *Dameobelba*, *Porobelba* GRANDJEAN, 1936, and *Tokukobelba*.

Several very different concepts of the genus *Belba* presently exist. They contrast strongly in the placement of the monotypic genus-level categories *Caenobelba* and *Protobelba*. SUBÍAS (2004, 2019) treats *Caenobelba* as a subgenus of *Belba*. This disagrees with the concepts of *Belba* of NORTON (1979c), BAYARTOGTOKH (2000), MIKO (2006), WALTER et al. (2014) and LAMOS (2016). None of the latter authors establish any link between *Belba* and *Caenobelba*, and they see them as being distinct genera.

In the traditional classification as supported by NORTON (1979c), BAYARTOGTOKH (2000), WALTER et al. (2014), and LAMOS (2016), *Protobelba*, which displays spinæ adnatae, is seen as being a subgenus of *Belba*. Alternative classificatory systems are employed by SUBÍAS (2004), who removes *Protobelba* from *Belba* and locates it as a subgenus of *Belbodamaeus*, as well as by MIKO & ERMILOV (2017) and SUBÍAS (2019) who

view *Protobelba* as being a full genus without any special phylogenetic sister group relationship to *Belba*.

The morphological evidence such as the shared epimeral neotrichy and the similarly shared nymphal porose sejugal apodeme and sac-like porose vestibules of apodemes I and II (NORTON 1979a, 1979c) suggests that *Protobelba californica* (BANKS, 1904) is allied to the *Belba corynopus* species group. Furthermore, the *Belba sculpta* species group appears to be phylogenetically much more distant to the *corynopus* clade than is *Protobelba*. Therefore, I have included *Protobelba* within *Belba*. The question that then raises itself is how one would classify species possessing both a *sculpta* group morphology and spinæ adnatae. Subsuming them under *Belba* appears to overstretch the diagnosis of the genus category *Belba*, especially considering that the *sculpta* group is morphologically so far removed from the *corynopus* group. The present paper accordingly follows BAYARTOGTOKH (2004), ERMILOV et al. (2013) and SUBÍAS (2019) in excluding *Belba*-like species with spinæ adnatae but without epimeral neotrichy from *Belba*, locating them in *Belbodamaeus* instead.

I have decided against establishing a new genus level category for the *Belba sculpta* species group because of the substantial number of older genera which may possibly be interpreted as being synonymous with such a genus or subgenus. Any one of the genera *Belbodamaeus*, *Dameobelba*, *Dasybelba* WOOLLEY & HIGGINS, 1979, *Subbelba* or *Tokukobelba*, for example, may be broadened in its diagnosis so as to include the *sculpta* group. If one were to subsume the *Belba sculpta* species group under *Subbelba*, one would have a concept of *Belba* similar to that of SUBÍAS (2019) with respect to his positioning of *Caenobelba*, a probable synonym of *Subbelba*, as subgenus of *Belba*.

### 3.5 Key to *Belba* species of the world

The last comprehensive keys to the genus *Belba* were published by BULANOVA-ZACHVATKINA (1962, 1975) a very long time ago. Since then several new species of the genus have been discovered, some have been redescribed (MIKO et al. 2017, ERMILOV 2018) while others have been transferred to genera such as *Kunstidamaeus* (MIKO 2010) and *Tokukobelba* (LAMOS 2016). Due to the incomplete descriptions of a lot of the species listed below, and also because of the almost total absence of data on the geographical variation of

the morphological characters used, the following key to adults of *Belba* is provisional.

- 1 Spinæ adnatae present; epimere II with 3 setae; trochanter IV with 2 setae; body length 724-884 µm; distribution Canada, USA. . . . . ***Belba (Protobelba) californica*** (BANKS, 1904)
- Spinæ adnatae absent. . . . . 2
- 2(1) Notogaster high, with a height to length ratio of 0,55-0,7 : 1; epimere II with 3 or more setae . . . . . 3
- Notogaster low, with a height to length ratio of about 0,4 : 1; epimere II with 1 seta . . . . . 7
- 3(2) Cornicle k present; tubercles Ba not situated at lateral prodorsal margin; setae of c-, l-, and h-series short, smooth, with setae c2, la longest; solenidion φ1 of tibia I longer than tarsus I; mean body length 523 µm; distribution: Japan, South Korea . . . . . ***Belba (Belba) unicornis*** ENAMI, 1994
- Cornicle k absent; tubercles Ba extremely laterally situated. . . . . 4
- 4(3) Notogastral setae smooth, setae c1, c2 shorter and thinner than la, lm; genu I with axial seta about 3 times length of other setae; solenidion φ1 of tibia I shorter than tarsus I; body length 670-830 µm; distribution: Europe . . . . . ***Belba (B.) corynopus*** (HERMANN, 1804)
- Setae c1, c2 approximately similar in length to la, lm, lp . . . . . 5
- 5(4) Solenidion φ1 of tibia I much shorter than tarsus I; axial seta similar in length to other setae on genu I; rostral setae ro and la marginally inserted; body length 690 µm; distribution: Europe . . . . . ***Belba (B.) pseudocorynopus*** MÄRKEL & MEYER, 1960
- Solenidion φ1 of tibia I of same length or slightly longer than tarsus I . . . . . 6
- 6(5) Notogastral setae c1 shorter and thinner than c2; seta d similar in length and width to other setae on genu I; body length 660 µm; distribution: Algeria, Spain . . . . . ***Belba (B.) patelloides*** (MICHAEL, 1890)
- Setae c1 and c2 similar in size to setae la, lm, lp; solenidion of tibia I as long as tarsus I; genu I with axial seta about 2,5 to 3 times length of other setae; body length 680 µm; distribution: China, Russia . . . . . ***Belba (B.) paracorynopus*** BULANOVA-ZACHVATKINA, 1962
- 7(2) Sensillus short, clavate with a thick globose, smooth, black head; body length 616-674 µm; distribution: Mexico . . . . . ***Belba (B.) clavassensilla*** NORTON & PALACIOS-VARGAS, 1982
- Sensillus of other appearance. . . . . 8
- 8(7) Propodolateral apophysis present. . . . . 9
- Propodolateral apophysis absent . . . . . 11
- 9(8) Femur II without a thick spinelike seta; notogastral setae of c-, l-, and h-series smooth, vaned willow-leaf-like with middle vein; postbothridial tubercles Ba, Bp absent (mainland China) or both present (Taiwan); sensillus and interlamellar setae smooth, distally flagellate; body length 355 µm . . . . . ***Belba (B.) cornuta*** WANG & NORTON, 1995
- Femur II with a thick spinelike seta; notogastral setae not vaned; tubercle Ba present, Bp absent . . . . . 10
- 10(9) Notogastral setae of c-, l-, and h-series smooth, thin, hairlike, of equal size; body length 434 µm; distribution Uzbekistan . . . . . ***Belba (B.) sarvari*** TOLSTIKOV, 1996
- Notogastral setae with short stalk and flame-like thickening with short barbs; setae c1, c2, h1 twice the length of la, lm, lp; body length 463 µm; distribution Tajikistan, Uzbekistan . . . . . ***Belba (B.) flammeisetosa*** TOLSTIKOV, 1996
- 11(8) Seta c1 2x to 3x length of setae c2 to h1; body length 478-547 µm; distribution: Mongolia . . . . . ***Belba (B.) heterosetosa*** BAYARTOGTOKH, 2004
- Seta c1 shorter relative to c2 . . . . . 12
- 12(11) Interlamellar setae very long: 150-300 µm . . . . . 13
- Interlamellar setae < 90 µm, clearly shorter than sensillus . . . . . 17
- 13(12) Parastigmatic tubercle Sa short, triangular in dorsal view with a lateral extension not exceeding that of tubercle Sp; interlamellar setae smooth, extremely long (300 µm); tubercle Ba present, Bp absent; notogastral setae smooth, long (100 µm); body length 680-760 µm; distribution: Poland, Ukraine, Russia . . . . . ***Belba (B.) dubinini*** BULANOVA-ZACHVATKINA, 1962
- Tubercle Sa long, laterally directed, with a sharply pointed apex . . . . . 14
- 14(13) Postbothridial apophyses Ba, Bp present . . . . . 15
- Postbothridial apophyses Ba present, Bp absent . . . . . 16
- 15(14) Pseudanal seta ps1 smooth, flagellate,

- measuring 150-200 µm; body length 378-480 µm; distribution: China, Japan. . . . . ***Belba (B.) sasakawai*** ENAMI, 1989
- Seta ps1 smooth, flagellate with a length of 70-110 µm; body length 500-640 µm; distribution: Germany, Spain. . . . . ***Belba (B.) sculpta*** MIHELČIČ, 1957
- 16(14)** Femur II paraxially with a thick, spinelike seta; body length 620-660 µm; distribution: Pakistan, Turkmenistan. ***Belba (B.) meridionalis*** BULANOVA-ZACHVATKINA, 1962
- Femur II without such a spinelike seta; body length 406-441 µm; distribution: Mongolia. . . . . ***Belba (B.) prasadi*** BAYARTOGTOKH, 2000
- 17(12)** Femur II with 7 setae; body length 330 µm; distribution: Azerbaijan. . . . . ***Belba (B.) aurata*** KULJUEV, 1967
- Femur II with 6 setae. . . . . **18**
- 18(17)** Trochanteral setation 1-1-2-1, femoral setation 7-6-4-4. . . . . **19**
- Trochanteral setation 1-1-2-2. . . . . **20**
- 19(18)** Femur II with a thick, spinelike seta; body length 420-492 µm; distribution: Russia, Tadjikistan, Uzbekistan. . . . . ***Belba (B.) bulanovae*** SUBÍAS, 2016
- Femur II without spinelike seta; body length 582 µm; distribution: Kirghizia (Russia). . . . . ***Belba (B.) tenuisetosa*** BULANOVA-ZACHVATKINA, 1962
- 20(18)** Chaetotaxy of genu I-IV: 4(1)-4(1)-4(1)-4; apophysis Ba present; sensillus rod-like, 2-3x length of interlamellar seta; body length 480 µm; distribution: Russia. . . . . ***Belba (B.) limasetosa*** BULANOVA-ZACHVATKINA, 1962
- Chaetotaxy of genu I-IV: 4(1)-4(1)-3(1)-3, apophysis Ba absent, femoral setation 7-7-5-5. . . . . **21**
- 21(20)** Sensillus smooth, distally flagellate; notogastral, interlamellar, lamellar and rostral setae smooth; body length 549-671 µm; distribution: Mongolia. . . . . ***Belba (B.) crassisetosa*** BAYARTOGTOKH, 2000
- Sensillus barbed, rod-like; notogastral, interlamellar, lamellar and rostral setae distinctly barbed; body length: 520-770 µm; distribution: China, Europe, Pakistan, Russia. . . . . ***Belba (B.) rossica*** BULANOVA-ZACHVATKINA, 1962

### Comments

*Belba pseudocorynopus* and *Belba bartosi* WINKLER, 1955 are seen as junior synonyms of *Belba*

*patelloides* by SUBÍAS (2019), while MIKO (2006) treats *B. pseudocorynopus* as a junior synonym of *B. bartosi*, without viewing either species as being a synonym of *B. patelloides*. I here follow BECK et al. (2018) in rejecting all of these synonymies. While the morphology of *B. pseudocorynopus* is well documented by MÄRKEL & MEYER (1960), the description of *B. bartosi* is very patchy and leaves out critical details. The leg setation in particular, with the exception of femur IV, is neither discussed nor illustrated in WINKLER (1955, 1957). In the latter, more detailed contribution, only 6 pairs of dorsal notogastral setae are mentioned in the text and are visible in the illustration of the dorsal aspect, while a seventh, more closely set pair is observed in the illustration of the posterior view. The seta which is not figured appears to be seta c1. With reference to the original publications, *Belba bartosi* differs from *B. pseudocorynopus* in the shape of its bothridium and in having much shorter interlamellar setae (BECK et al. 2018). Evidently the probably still existing holotype and three paratypes of *B. bartosi* in Prague need to be inspected and redescribed before any definite conclusions about synonymies involving this species may be drawn.

The species *Belba (B.) daghestanica* was not included in the species key because the original description is too brief and misses significant detail in several places. For example, no information is supplied on the presence or absence of prodorsal apophyses Ba, Bp or the ventral apophyses, E2a, E2p, Va, Vp, and the interlamellar setae are not mentioned or depicted. A major diagnostic feature according to its author is the quadrate apophysis Sp. Only two species in the *Belba* keys of BULANOVA-ZACHVATKINA (1962, 1967, 1975) possess this trait, the other one being *Belba tenuisetosa*. However, TOLSTIKOV & LYASHCHEV (1996) who redescribed *B. tenuisetosa*, illustrate and comment on a tuberculate apophysis Sp with a broad base and a rounded tip in this species instead. The shape of Sp is likely to be subject to both ambiguities of interpretation and to intraspecific variation, and in the case of *B. daghestanica* too, may possibly not be a very reliable species diagnostic trait.

Nevertheless, it is possible to distinguish the taxon from other species. Based on BULANOVA-ZACHVATKINA (1962, 1967, 1975), *Belba daghestanica* differs from all members of *Belba* except *B. bulanovae*, *B. meridionalis* and *B. sculpta* in the combined possession of the traits: femur II with a thick spinelike seta; propodolateral apo-

physis absent. It differs from these three species in its shorter setae d and l' on genu IV. The longest of the three setae of this segment of *B. daghestanica* illustrated by BULANOVA-ZACHVATKINA (1962, p. 207, fig. 2, 1) measures only about 1.4x the segment length. It is not quite clear in this drawing which seta is d and which is l', though. *Belba daghestanica* requires redescription.

WALTER et al. (2014) describe two formally unnamed Canadian damaeid species, which they classify under *Belba*. Their "*Belba* species A DEW", informally named DAVE'S Hobbit Mite, is readily identifiable by the combination of traits: sensillus clubbed, distally with dense, elongate barbs, plumose; interlamellar setae and leg setae strongly plumose; spinae adnatae absent; ventral body length 440 µm (WALTER et al. 2014: p.164, 166). Their second species, "*Belba* species B DEW", called DAVE'S Hairy Hobbit Mite is characterized by: interlamellar setae, pseudanal setae and leg setae coarsely plumose; spinae adnatae present; propodolateral apophysis absent; notogastral setae long (80 µm), smooth with black sheaths; prodorsal tubercles Ba absent, based on WALTER et al. (2014: p.167, 168). This species is classified in the present publication under *Belbodamaeus* and differs in the combination of the characters here mentioned from all members of this genus listed in the recent key presented by ERMILOV et al. (2013).

### 3.6 Ecology of *Belba sculpta*

The site where *Belba sculpta* was encountered in Germany is situated in the Upper Rhine Rift Valley, a narrow strip of land, averaging about 40 km in width and being 300 km in length which stretches from Basel in Switzerland in the South to Frankfurt in the North. This low-lying region is the warmest in Germany, with the hottest summers, mildest winters and low to moderate amounts of rainfall (HOLZHAUER 2013). Mannheim itself is situated at an altitude of merely 95-110 m above sea level and is to a considerable extent shielded from cold weather and rain approaching from the East by the Odenwald Mountains. The Palatinate Forest similarly partially blocks off the effect of the vagaries of weather advancing towards the city from the West. Both mountain ranges formed as horsts during the rifting process which was initiated by subsidence in the Eocene about 50 million years ago, with the Dossenwald site being located in the graben itself. Accordingly, Mannheim is ranked as having a temperate oceanic climate (type Cfb) in the Köppen climate classification.

The daily mean temperature in Mannheim is 11,3 °C, while the average annual high temperature is 16,1 °C. Summers in Mannheim are hot, with an average of 87,6 days per year with temperatures above 25 °C, of which 20 days are classified as tropical with a maximum temperature of 30 °C or more. Winters in Mannheim are very mild with only about 8 frost days annually. Mannheim experiences 1722 hours of sunshine per year and the rainfall in the city and its surroundings is very sparse even for the Oberrhein-graben, with an average yearly precipitation of merely 650 mm. The climate statistics presented here derive from the annual values recorded by the Deutscher Wetterdienst during the past 25 years for the measuring station Mannheim Vogelstang (DWD 2019).

The *Belba sculpta* specimens from Mannheim were only found in sandy soil with a sparse vegetation cover of predominantly drought-tolerant moss and lichen. The sand in the Dossenwald is associated with dry grassland habitats and with continental dunes. Twenty large dune fields exist in the area, several of which have been overgrown with forest (FISCHER et al. 2009).

The continental dunes of the Dossenwald arose during the Younger Dryas stage (LÖSCHER 1994) at the end of the Würm glaciation about 11700-12900 years ago. During this comparatively short timespan of deglaciation a general period of deglaciation, the Rhine river carried only very little water, and therefore sediments which had been deposited earlier on the floodplain lay exposed. A tundra flora and fauna and steppe elements had invaded the Dossenwald region during the cold periglacial conditions of the Younger Dryas. This made it possible for the wind to pick up sand particles on a large scale and to deposit them on the lower fluvial terrace of the Rhine at distances up to 3 km away (FISCHER et al. 2009). The formation of aeolian dune deposits mostly stopped with a return to warmer conditions in the Holocene when the Rhine water flow returned to a normal level and reforestation commenced.

Sand possesses a negligible water retention capacity and a high evaporation rate. It is also poorly equipped with nutrients since significant organic remains and humus are absent as a rule. The plant growth on sand is therefore generally severely restricted and frequently patchy. The lack of a closed plant cover then exposes the sandy surface even more to climatic extremes. The surface temperatures of the sandy soil of the Dossenwald may exceed 70 °C in the summer



(FISCHER et al. 2009) as is the case in similar continental dune habitats in Sandhausen near Heidelberg (RUSSELL & ALBERTI 2010).

The preliminary results, based on a very small sample size, suggest that the *Belba sculpta* from the Dossenwald prefer a relatively warm and perhaps also a dry habitat. This agrees well with the geographical distribution of *Belba sculpta* in Western Europe, where the species is so far known only from warm semi-arid locations in peninsular Spain (SUBÍAS et al. 2017) and the Canary Islands (MORAZA & PEÑA 2005). However, MURVANIDZE & MUMLADZE (2016) mention *Belba sculpta* occurring at humid subtropical locations in Georgia, including the rainy Mtirala National Park. Nevertheless, the temperatures of the locations where *B. sculpta* has so far been collected in Georgia, including Anaklia and Tbilisi itself, are mostly warm and distinctly higher than those of Mannheim, especially in winter.

Although *Belba sculpta* may conceivably have been introduced to the Dossenwald area by human activity, it is more likely that the species is in fact a steppe relict or a Mediterranean faunal element which first colonized suitable habitat patches in Southern Germany already during the late Pleistocene or earlier. It would be interesting to find out whether *B. sculpta* is also found in other inland aeolian sand or dune sites, such as the one nearby Sandhausen, where a not further identified "Belboidae sp." was discovered by RUSSELL et al. (1994, p. 337), and whether in Southern Germany the species is endemic to such habitats.

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