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Tokukobelba gen. nov. (Acari: Oribatida: Damaeidae)

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Abstract

Tokukobelba is proposed as a new genus in the oribatid mite family Damaeidae Berlese, 1896. The species *Tokukobelba compta* (Kulczyński, 1902) comb. nov. is redescribed based on specimens collected in Heidelberg in Germany. The distinguishing traits of *Tokukobelba*, which include the presence of prodorsal apophyses Aa and Ap, the occurrence of only 2 setae on femur IV, and a solenidion coupled with the dorsal seta d on the tibiae of legs I-IV are most unusual for a damaeid mite. The taxonomy and evolutionary systematics of the new genus are discussed. Evidence from comparative morphology suggests a basal position of *Tokukobelba* within its family.

Kurzfassung

***Tokukobelba* gen. nov.**
(Acari: Oribatida: Damaeidae)

Tokukobelba wird als neue Gattung der Oribatidenfamilie Damaeidae Berlese, 1896 vorgestellt. Basierend auf Fundmaterial aus Heidelberg wird die Art *Tokukobelba compta* (Kulczyński, 1902) comb. nov. neu beschrieben. Die kennzeichnenden Merkmale von *Tokukobelba* wie die Anwesenheit der prodorsalen Apophysen Aa und Ap, ein Femur IV mit nur 2 Borsten und ein Solenidion gekoppelt mit einer Dorsalborste d auf Tibiae I-IV sind sehr ungewöhnlich für eine damaeide Milbe. Die Taxonomie und evolutionäre Systematik der neuen Gattung werden diskutiert. Die vergleichende Morphologie deutet auf eine basale Stellung von *Tokukobelba* innerhalb der Damaeidae.

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1 Introduction

Belba von Heyden, 1826, is a genus within the mite family Damaeidae Berlese, 1896. The genus is rich in species and shows its greatest diversity in the temperate to boreal regions of the Palaearctic (Kulczyński 1902a, Märkel & Meyer 1960, Bulanova-Zachvatkina 1962, 1967, 1975, Enami 1989, 1994, Tolstikov 1996, Tolstikov & Lyashchev 1996, Wang & Norton 1995, Bayartogtokh 2000a, 2004a) although some *Belba* species have also been recorded from the USA and Canada (Banks 1904, Norton 1977a, 1979b, 1979c, Marshall et al. 1987, Lindo & Winchester 2006), from the volcano Popocatepetl in Mexico (Norton & Palacios-Vargas 1982) and from montane rainforest in Costa Rica and Panama (Schatz 2006). A concise review of the complex systematics of *Belba* is presented by Bayartogtokh (2000), who contributed significantly towards furthering our knowledge of the Damaeidae. More than 100 species have been combined with *Belba* during the previous three centuries. A great number of these presently are synonyms of other species, reside in other genera, like *Damaeus australis* (Banks, 1895) (Norton 1978a) and *Kunstidamaeus lengersdorfi* (Willmann, 1932) (Miko 2006a), or are species inquirenda such as *Belba bulbipedata* Packard, 1887 (Michael 1898), and *Belba longipes* Berlese, 1884 (Mahunka & Mahunka-Papp 1995).

Bayartogtokh (2000, p. 298), building on Bulanova-Zachvatkina (1962, 1967, 1975) and Norton (1979c), diagnosed *Belba* as follows: trochanteral setation 1-1-2-1, rarely 1-1-2-2; genual setation 4-4-3-3, genual associated setal formula 1-1-1-0; tibial associated setal formula 0-1-1-1, one or more rarely two pairs of prodorsal tubercles (Ba, Da) present in the dorsosejugal area or tubercles absent, tubercle Bp mostly absent; propodolateral apophysis P mostly absent; spinae adnatae usually absent, very rarely present. It is apparent that the genus lacks strong, convincing derived features and is primarily defined by traits which have a high likelyhood of being plesiomorph for the Damaeidae (Norton 1977a).

The heterogeneous species composition of *Belba* has been mentioned by several authors (Norton 1979a, Wang & Norton 1995), and the polyphyly of the genus is likely. More than half a century ago Van der Hammen and Strenzke had already noted that *Belba compta* (Kulczyński, 1902) differs from *Belba corynopus* (Hermann, 1804) in epimeral setation and instead shows a close resemblance to representatives of *Metabelba* Grandjean, 1936, in general appearance. They make special mention of the *Metabelba*-like shape of the solenidion φ of tibia IV of this species, and suggest that "a detailed redescription of *B. compta* might prove interesting, as there are also striking differences from *B. corynopus* (Hermann, 1804), the type of the genus *Belba*" (Van der Hammen & Strenzke 1953, p. 152). In the present contribution, a morphologically highly distinct, monophyletic group of species, which includes *Belba compta*, is removed from *Belba* and transferred to a new genus.

2 Material and methods

The specimens of *Tokukobelba compta* (42 adults, 3 tritonymphs, 1 deutonymph, 2 protonymphs, 2 larvae) were collected by the author on 6.9.2010 and 5.7.2012 on the Königstuhl hill near Heidelberg, Germany, from moist moss on rocks. Representatives of *Belba corynopus* (20 adults, 4 tritonymphs, 2 deutonymphs, 1 protonymph) were obtained by the author on 7.5.2009 in the Waldpark forest near Mannheim, Germany, from moss on a decaying tree stump. Ten adults of each species were deposited as voucher specimens in the acarology collection of the Department of Zoology of the State Museum of Natural History Karlsruhe in Germany. Various other oribatids from the author´s own collection and from that of the State Museum of Natural History Karlsruhe were studied for comparative purposes. Mites were fixed in ethanol, macerated with lactic acid and observed under a light microscope. Unmacerated and living specimens were also examined. Descriptions, measurements of structures, and illustrations are based on intact or dissected specimens mounted in temporary cavity slides or on permanent slides. Unless specifically mentioned all descriptions refer to the adult stage.

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 individuals. Adult 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. 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 notogaster is measured from its anterior to its posterior margin. Notogastral thickness is determined in lateral view from the ventral to the dorsal notogastral border. Leg length is measured on whole 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 part 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 of prodorsum and of notogaster are determined between their central insertion points. An explanatory list of the abbreviations used in the text follows the list of references.

Leg setation formulae give 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 give the number of solenidia present on the genu, tibia and tarsus of a 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 show the number of setae present unilaterally on epimeres I-IV.

The general morphological terms used in this paper derive from Behan-Pelletier & Norton (1983, 1985), and Norton & Behan-Pelletier (2009). The nomenclature of the epimeral enantiophyses largely follows Grandjean (1960a) and Norton (1978b), while that of the leg chaetotaxy is based on Norton (1977b). The term centroprodorsal groove is introduced and refers to the furrow situated anteriad the bothridia and posteriad the sigillae of the cheliceral retractor muscles, between the prodorsal apophyses Aa and Ap where these are present.

3 Proposal of a new genus

Tokukobelba gen. nov.

Type species: *Belba mongolica* BAYARTOGTOKH, 2000.
This species is described in: International Journal of Acarology 26(4), pp. 309-312, 316.
The holotype and a paratype of the type species of *Tokukobelba* are located in the Acarology Collection of the Department of Zoology, National University of Mongolia, Ulaanbaatar, Mongolia. Two further paratypes are to be found in the Collection of the National Science Museum, Tokyo, Japan. The type locality is the Khonin Nuga area, District Mandal, Province Selenge, Mongolia, 1.950 m above sea level. Type and paratypes were collected by K. ULYKPAN on 16.5.1998 from litter of coniferous forest of *Larix sibiricus* and *Abies* sp.

Etymology
The genus is named in honour of the Japanese agricultural scientist and acarologist TOKUKO FUJIKAWA. Gender feminine.

Diagnosis
Adults of *Tokukobelba* gen. nov. are unique among the Damaeidae in displaying the following combination of character states: apophyses Aa and Ap of prodorsal enantiophysis present; centroprodorsal groove deep and distinct; apophysis P absent; apophysis Ba present, Bp rarely present; interbothridial protuberance present; spinae adnatae absent; most or all epimeral setae inserted on greatly enlarged tubercles; complete ventrosejugal enantiophysis present with apophysis Va multituberculate, Vp monotuberculate; apophysis E4a mostly present; epimeral groove IV very distinct; epimeral setation 3-1-3-3; acetabular tecta and lateral epimeres with striking verrucose or rarely alveolar sculpturing; trochanteral setation 1-1-2-1; femur I with 7 setae; femur III generally with 3 setae (d, ev´, l´) and femur IV with 2 setae (d, ev´); genual setation 4-4-3-3; genual associated setation 1-1-1-0; tibial associated setal formula mostly 1-1-1-1, rarely 0-1-1-1; setae d of tibiae II-IV regressed, very thin, short, with seta d of tibia IV less than 1/5 the length of its coupled solenidion φ, the latter elongate, tactile, 1,4 to 2 x the length of tibia IV; tarsi of legs I and II with 22 and 18 setae respectively, including famulus, with setae v2´ and v2´´ both present on tarsus I and v2´ on tarsus II; tarsi III and IV each with a single pair of ventral setae and a total 17 and 14 setae each; palptarsus without subultimal seta sul and with ventral seta v2´. Nymphs of *Tokukobelba* differ from those of other damaeids in having: prodorsum with a sclerotized cerotegumental cap anteromediad the bothridia; palptarsus without seta sul and with seta v2´; distance between notogastral setae c1-c2 = 0,3x c2-la; seta c3 elongate, measuring 0,6 x body length.

Differentiation from *Belba*
Tokukobelba adults differ from those of *Belba* in displaying the following traits, most of which are exceptionally rare in damaeid mites: 1) apophyses Aa and Ap of prodorsal enantiophysis present; 2) palptarsus without seta sul and with v2´; 3) verrucose or alveolate sculpturing on acetabular tecta and epimeres; 4) epimeral setation 3-1-3-3; 5) epimeral setae mostly all associated with very large tubercles 6) epimeral groove IV strongly developed; 7) apophysis Va multituberculate; 8) apophysis E4a mostly present; 9) femur III usually with 3 and femur IV with 2 setae respectively; 10) tibial associated setation 1-1-1-1 in some and possibly all species; 11) associated setae d of tibiae II-IV regressed, very thin, short; 12) solenidion φ of tibia IV elongate, tactile; 13) tarsal setation 22-18-17-14 with setae (v2) present on tarsus I and v2´ on tarsus II. *Tokukobelba* nymphs differ from those of *Belba* in: 1) palptarsus without seta sul and with v2´; 2) presence of a prodorsal cerotegumental cap; 3) seta l´ of femora I and II protonymphal in origin 4) presence of very elongate setae c3.
Belba corynopus, the type species and reference point for *Belba* contrasts to *Tokukobelba* in numerous further traits such as: 1) presence of epimeral neotrichy with an epimeral setation 4-4-4-4; 2) elevated femoral setation of 7-7-5-5; 3) tarsal setation 20-17-16-13 with only v1´ found on each of tarsi III and IV and v1´´ absent; 4) sensillus straight rodlike; 5) bothridia located at lateral margin of prodorsum and laterally directed; 6) prodorsal tubercle Ba extremely laterally situated; 7) notogaster asymmetrically dome shaped and very high in lateral perspective with ratio of height to length being about 0,7:1; 8) notogaster carries nymphal exuviae and a compact mass of debris; 9) notogastral setae of c, l- and h-series short, distinctly attenuate and spinelike; 10) insertions of setae ad1-ad3 equidistant from margin of anal plate; 11) presence of nymphal tracheal vestibules; 12) seta h1 of nymphs ex-

tremely short. The North American *Belba* (*Protobelba*) Norton, 1979, besides in the points already mentioned, differs from *Tokukobelba* in: 1) presence of spinae adnatae; 2) epimeral setation of 3-3-3-4; 3) trochanteral setation of 1-1-2-2; 4) presence of 7 setae on femur II; 5) presence of nymphal tracheal vestibules; 6) bothridia located at lateral margin of prodorsum, laterally directed; 7) cerotegument reticulate; 8) notogaster carries large load of compact organic debris.

Description of *Tokukobelba* adult

Dimensions. Small to medium sized species with a body length of 340-620 µm.

Integument. Colour light brown, often with a yellow or red hue. Cuticle finely and regularly microtuberculate throughout. Numerous large cuticular tubercles present on epimeres I-IV. Cerotegument clear, white in colour, thick, granular to tuberculate, not filamentous.

Prodorsum. (Figs 1, 3). Approximately triangular in dorsal view. Apophysis P absent. Bothridium directed posterolaterad, irregularly funnel shaped; Sensillus long to very long, thin, proximally smooth, barbed in middle region, distally smooth and flagellate. Interlamellar setae usually attenuate, barbed, short, measuring about 1/3 of sensillus length. Lamellar setae barbed, inserted mediad to barbed rostral setae and slightly longer than these. Prodorsal apophyses Aa, Ap well developed. Prodorsum raised in the region of the larger muscle attachments with a steep drop-off at the lateral margins of the two anterior sigillary fields and with a deep, conspicuous centroprodorsal groove. In dorsal view this gives the impression of Aa apparently being positioned on each side near the posterior end of a longitudinal arch-shaped ridge, of Ap seemingly situated on a transverse ridge which laterally joins the bothridium, and of there being a ring of dark chitin between the bothridia. Postbothridial apophysis Ba conspicuous, Bp mostly absent or represented by a ridge of thickened integument. Apophyses Da, Dp of dorsosejugal enantiophysis and La, Lp of laterosejugal enantiophysis absent. Laterally between acetabulum I and II a strongly developed enantiophysis with anterior and posterior anterolateral apophyses Ala and Alp in at least one species. Genal notch, pedotectum I, humeral enantiophysis, tutorium and lamellae absent. Tectum of podocephalic fossa not ventrally projecting. Numerous prominent cuticular tubercles present on leg apodemata resulting in an undulate or dentate anterior margin of the pedotectal regions I and II. Prominent fields of muscle sigillae situated between the interlamellar setae and anteromediad of each bothridium. Further sigillae lateral to bothridia and anterior and adaxial to Ba. Dorsosejugal furrow deep, wide, fully convex in dorsal view.

Notogaster (Figs 1, 3). Notogaster slightly ovate, clearly longer than wide when observed from a viewpoint perpendicular to the circumgastric scissure. In lateral perspective notogaster hemispherical, robust, of normal height equalling about 0,5 - 0,6x of its length, with its dorsal margin almost evenly rounded, only anteriorly between setae c2 and lm very slightly flattened. Spinae adnatae absent. Notogaster usually without excuvial scalps or a compact mass of debris; some loosely attached material may be present. Pteromorphae, carina circumpedalis, dorsophragmata and pleurophragmata absent. Dorsosejugal groove anterior to, and distinct from circumgastric scissure. Discidium variously developed, broadly rounded to subtriangular. Notogaster with 11 pairs of setae. Setation quinquedeficient. Setae c2-c3, la-lp, and h1-h3 inserted along two approximately parallel rows relatively close to the mid-sagittal plane; setae c1 more medially placed. Setae of c, l and h-series short to medium in length, slender, directed posteriad, lightly or densely barbed, usually strongly bent near the base and lying close to the notogastral surface. In dorsal view insertion points of setae c1 and c2 almost lie on a straight line and inserted close together. Distance c2-la = 1,5x-2x c1-c2. Setae ps1-ps3 thin, short, positioned lateromarginally. Muscle sigillae along lateral and posterolateral margins of the notogaster form two bands, ending anteriorad just posterior to insertion points of setae c2. Fields of sigillae also exist between setae c1 and c2. Lyrifissures ia, im, ip, ih, ips and opening of latero-opisthosomal gland located on the notogastral margin. Areae porosae absent.

Epimeral region (Figs 2, 3). Parastigmatic apophysis Sa small to medium sized, usually tuberculate, distally rounded, subtriangular or truncate, not elongate, spinelike. Apophysis Sp similar in appearance to Sa. Ventrosejugal enantiophysis mostly present, strongly developed. Apophysis

Va broad, conspicuously multituberculate, Vp monotuberculate. Apophyses of propodoventral enantiophysis present or absent, with E2a multituberculate and E2b monotuberculate. Tubercles comprising Va, Vp, E2a, E2b apically truncate to rounded. Epimeral setation 3-1-3-3. All epimeral setae inserted on conspicuous tubercles, with tubercles on epimeres III and IV usually greatly enlarged. Apophysis E4a mostly present. Numerous large cuticular tubercles not associated with any setae are found on acetabular tecta and laterally on epimeres I-IV. Verrucose sculpturing very distinct on posterior borders of epimeres I and II, giving a dentate appearance to the lateral margin between the discidium and the sejugal groove in ventral perspective. Internal apodemes of epimeres III and especially IV are sclerotized and conspicuous. Ventrosejugal groove and epimeral grooves I, II, IV very distinct.

Ano-genital region (Figs 2, 3). Genital and anal plates large and positioned close together. Genital plates without a transverse scissure. Six pairs of genital, 1 pair of aggenital, 2 pairs of anal and 3 pairs of adanal setae present. Oblique adanal lyrifissures iad antiaxial to anal plates, posteriad their anterior margin. Anal plates with a conspicuously thickened carina. Seta ad3 laterally inserted, its distance from the anal plate is more than twice that of seta ad2. Spermatopositor egg-shaped in ventral view, with 7 pairs of setae. Anterior genital papilla Gp1 only about half the length of Gp2, Gp3 in ventral perspective, with latter two approximately similar in shape and dimensions. Ovipositor short, tubular, longitudinally striated, distally with 3 eugenital lobes. Preanal organ very strongly sclerotized, connected dorsally to rim of circumanal opening.

Gnathosoma (Figs 8, 9). Infracapitulum diarthric with subcapitular setae h, m, a present. Rutella smooth, atelebasic. Each rutellum with a distal hyaline swelling. Adoral sclerite of lateral lips with setae or1 and or2. Chelicera robust, chelate-dentate, moderately elongate with seta cha situated in a dorsal to slightly paraxial position and chb antiaxially situated. Digitus fixus of chelicerae with 4 or 5 and digitus mobilis with 4 well developed teeth, latter triangular in lateral view. Trägårdh´s organ narrow. Pedipalpi slender, pentamerous. Palpal setation 0-2-1-3-9, excluding solenidion ω. The latter baculate, orientated parallel to tarsal surface and not associated with the anteroculminal eupathidium acm. Palptarsus without a eupathidial subultimal seta sul and instead with a supernumerary ventral seta v2´, where known.

Legs (Figs 4-7). Leg segments generally clavate, rarely sub-moniliform. Legs short; leg IV about 1,1 times the ventral body length. Trochanteral setation 1-1-2-1. Femoral setation 7-6-3-2, rarely 7-4-3-2 or 7-6-5-2. Genual setation 4-4-3-3; genual associated setal formula 1-1-1-0. Tibial setation usually 5-5-4-4 or 4-5-4-4; tibial associated setal formula 1-1-1-1 or 0-1-1-1. Seta d of tibia I-IV usually regressed, thin, much shorter than its associated solenidion φ. Seta d of tibia IV measures about 1/5 the length of its associated solenidion φ, the latter being 1,4 to 2,0 times the length of tibia IV. Tarsus of leg I with 22 setae including famulus, with setae v2´ and v2´´ present. Tarsus II with 18 setae with seta v2´ present. Tarsi III and IV generally with 17 and 14 setae respectively, with v1´ and v1´´ both present. Leg solenidial formulae: I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0). Ambulacrum monodactyl. Claws smooth, small, sickle-shaped, of approximately the same length on all tarsi. A conspicuous slit-like lyrifissure ly located dorsoproximally on tarsi I-IV.

Description of larva and nymphs of *Tokukobelba*

Body Dimensions. Body length of larva measures about 0,4x, that of tritonymph 0,8x the adult ventral body length. Ratio of body length to width about 2:1 in larva and in the three nymphal stages.

Integument. Cuticle of body smooth, transparent and white to pale yellow in colour. Gnathosoma, several setal apophyses and sclerites, notogastral cornicle and legs lightly sclerotized, light brown. Degree of sclerotization strongest in the tritonymph and least in the larva. Cerotegument granular, very thick, covers most of body and legs and setal bases. Granules spherical in dorsal view, tuberculate to conical in lateral view. Prodorsum in larva and nymphs with a eye-catching, sclerotized, brown, approximately circular cerotegumental cap anteromediad the bothridia. Cerotegumental granules small, densely packed in central region of cap, but substantially larger at the periphery. Cerotegument generally thicker, with slightly larger granules in tritonymph than in earlier stages.

Prodorsum (Figs 10, 12, 13, 15). Short, about half the length of the notogastral region in lateral perspective, broadly rounded. Prodorsal apophyses absent. Interlamellar seta of moderate length, barbed and attenuate in larva; extremely short and truncate in nymphs. Sensillus very long, about 0,7x body length, barbed in the middle region, distally flagellate and undulating. Bothridia funnel-shaped. Larval setae ro relatively much closer together than those of nymphs. The ratio of the distance of the insertion points ro-ro: la-la is about 1:1 in the larva and 1,6:1 in the nymphs.

Notogaster (Figs 10, 12, 13, 15). Larval setation unideficient with 12 pairs of notogastral setae. Setae c1, c2, da, dm, dp and lp thick, elongate, with flagellate tips. Setae c1, c2 each > 0,8x body length. Setae la, lm, h1, h2 thinner and distinctly shorter with h3 minute measuring 0,05x body length. Larval seta c3 short, straight, orientated perpendicular to the long axis of the body. Nymphal setation quadrideficient with dorsocentral setae absent and pseudanal setae ps1, ps2 and ps3 present instead. Distance c2-la about 3x-4x distance c1-c2 in nymphs. Length of nymphal setae c3 and h1 is roughly 0,6x and 0,75x the body length respectively. Seta c3 is lost in the adult. Notogastral setae insert on sclerites. In nymphs apophyses of setal pairs h1 and ps1 sited on a single common sclerite. Nymphal setal pairs c1 and c2 located on a single fused sclerite. Nymphs eupheredermous with a thin, relatively straight cornicle k present. Latter absent in the larva and adult. Cupules ia, im, ip and ih occur in the larva, with ips added in the protonymph and iad in tritonymph. The latero-ophistonotal gland is found in all stages.

Anogenital region (Figs 11, 14). 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. A genital seta is added on each genital valve in the adult stage. 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, absent in earlier stages.

Epimeral region (Figs 11, 14). 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. In the tritonymph the tubercles associated with setae 3b, 3c, 4a and 4c are slightly broader than those of the remaining epimeral setae and those of the anogenital region. Tracheal vestibules absent.

Gnathosoma. Palp setal formulae: larva 0-1-1-3-9 + 1ω; nymphs 0-2-1-3-9 + 1ω. Seta inf of the palpfemur found in the protonymph. The pedipalps of the immatures show the highly unusual setal arrangement of the tarsus which also characterizes the adult, with the subultimal seta being absent and an additional non-eupathidial ventral seta being found instead. Chelicerae and infracapitulum of larva and nymphs are very similar to those of the adult, barring differences in size and proportion. The number and arrangement of cheliceral teeth is identical. Suture of labio-genal articulation is not visible in immatures, being represented by a integumental fold.

Legs (Figs 16-18). Five free segments present. Legs are not or only slightly sclerotized. Leg IV absent in larva, present in nymphs. Larval seta d of genua minute, with the associated solenidion σ bent very close to the segment, posteriorly directed, baculate. In nymphs the genual seta d and its associated solenidion are both erect, of normal length, being about similar in size. Famulus fully emergent in all juvenile stages, not minute and not sunken in a sclerotized cup. Solenidial formulae are: larva: I (1-1-1), II (1-1-1), III (1-1-0); protonymph I (1-1-2), II (1-1-1), III (1-1-0), IV (0-0-0); deutonymph: I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0); tritonymph I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0). The solenidotaxy of the tritonymph corresponds to that of the adult. The leg setation, where the adult possesses a femoral setation of 7-6-3-2 and a tibial setation of 5-5-4-4 with seta d on tibia I retained, is as follows: larva: I (0-2-3-4-16), II (0-2-3-3-13), III (0-2-2-3-13); protonymph: I (0-3-3-4-16), II (0-3-3-3-13), III (1-2-2-3-13), IV (0-0-0-0-7); deutonymph: I (1-4-4-5-16), II (1-3-4-4-13), III (2-3-3-4-13), IV (1-2-3-3-12); tritonymph: I (1-5-4-5-18), II (1-4-4-5-15), III (2-3-3-4-15), IV (1-2-3-4-12). Seta l´ on femur I and II are protonymphal in origin. Seta d on tibia I is retained in the adult, where reliably known. Setae arising in the adult are: femur I: v1´, v2´´; femur II: v´, v´´; tarsus I: (v1), (v2); tarsus II: (v1), v2´´; tarsus III-IV: (v). In species with 4 setae on femur III, it is very likely that l´ arises in the deutonymph and v´ in the adult on this segment. Where 5 setae occur on femur III, v´ and v´´ are here probably added in the adult stage.

The description of the larva and nymphs is based on *T. compta*, whose adults are similar to those of *T. mongolica*. For the remaining species the ontogenetic stages have not yet been described.

Species composition

The following species belong to the new genus:

Tokukobelba mongolica (Bayartogtokh, 2000) comb. nov. (= *Belba m.*) type species

Tokukobelba barbata (Fujita & Fujikawa, 1986) comb. nov. (= *Belba b.*)

Tokukobelba compta (Kulczyński, 1902) comb. nov. (= *Oribata comptus*, = *Belba c.*)

Tokukobelba farinosa (Trägårdh, 1902) comb. nov. (= *Oribata f.*, = *Damaeus farinosus*)

Tokukobelba japonica (Aoki, 1984) comb. nov. (= *Belba verrucosa j.*)

Tokukobelba itsukiensis (Fujikawa, 2011) comb. nov. (= *Belba i.*)

Tokukobelba sellnicki (Bulanova-Zachvatkina, 1962) comb. nov. (= *Belba s.*)

Tokukobelba verrucosa (Bulanova-Zachvatkina, 1962) comb. nov. (= *Belba v.*)

Species key

1 Femur III with 5 setae; apophyses Ba, Bp present; notogastral setae c1-h3 slender, flagellate, length of seta c1 is 2x distance c1-c1; sensillus smooth in distal half, barbed for 1/5 of its length; setae ex, ro, la, in with dense short barbs; tubercles associated with epimeral setae of about same size on all epimeres; body length 407 µm . . . . *T. itsukiensis*

– Femur III with less than 5 setae 2

2 Femur III with 4 setae; notogastral setae c1-h3 thick, attenuate, very sparsely barbed, elongate, seta c1 > distance c1-c1; sensillus barbed in middle third; setae ex, ro, la, in with short barbs; tubercles associated with setae of epimeres III and IV about 3x the diameter of those of epimeres I and II; body length 350 µm . . . . *T. barbata*

– Femur III with 3 setae 3

3 Exobothridial setae thick, with dense, long barbs; on tibia IV seta d distinctly barbed, similar in length and thickness to l´ and v´; sensillus barbed for most of its length; notogastral setae thick, very short, with conspicuous elongate barbs, seta c1 < distance c1-c1; anterior lateral margin of pedotectum I and II smooth; apophysis Ba present, Bp absent; femur II with 6 setae, tibia III with 5 setae; body length 420-460 µm . . . . *T. sellnicki*

– Exobothridial seta thin, smooth; on tibia IV seta d smooth, thinner and less than 0,5-x the length of l´ and v´ if present; sensillus barbed in middle third, distally flagellate 4

4 Notogastral setae short, attenuate, setae lm, lp shorter than distance lm-lp in dorsal view; body length 350 µm . . . . *T. japonica*

– Notogastral setae elongate, attenuate, setae lm, lp longer than distance lm-lp in dorsal view; anterior margin of pedotectum I and II distinctly dentate; body length > 400 µm . . .5

5 Femur II with 4 setae; tibia III with 3 setae; body length 417-457 µm . . . . . *T. mongolica*

– Femur II with more than 4 setae; tibia III with 4 setae 6

6 Femora I and II with 5 setae each; body length 460-560 µm . . . . *T. verrucosa*

– Femora I and II with 7 and 6 setae respectively; body length 500-620 µm . . . *T. compta*

This key is provisional and, except for *T. compta*, bases on the original descriptions. Almost all included species are only very briefly documented and require extensive redescription.

Geographical distribution

Tokukobelba has a widespread occurrence within the Palaearctic realm, but is unknown from both the Nearctic and Neotropical regions. *Tokukobelba compta* has been collected in Austria (Franz 1943, Schuster 1955, Schatz 1978, 1979, 1983, Schmölzer 1994), the Czech Republic (Willmann 1939, Starý 1994, 2005, Materna 2000, Mourek & Miko 2010), Denmark (Norton 1977a, Warncke et al. 1991), Finland (Nordberg 1936, Strenzke 1952, Karppinen 1956, 1958, 1977, Niemi & Huhta 1981, Niemi et al. 1997, Penttinen et al. 2008, Huhta et al. 2010), Germany (Strenzke 1952, Engelmann 1972, Taylor & Wolters 2005), Great Britain (Luxton 1996), Hungary (Balogh 1943), Iceland (Strenzke 1952, Gjelstrup & Solhøy 1994, Ingimarsdóttir et al. 2012), Italy (Bernini et al. 1995, Schatz 2008, Wilhalm 2009), Latvia (Baranovska 2007, Ito 2011), Norway (Thor 1930, 1937, Cadwalladr 1969, Karppinen 1971, Seniczak et al. 2013) and the arctic volcanic island Jan Mayen belonging to Norway (Gabrielsen et al. 1997). *Tokukobelba compta* has further been noted to occur in Poland (Kulczyński 1902a, Sellnick 1920, Willmann 1931, 1939, 1956, Strenzke 1952, Dziuba & Skubala 1987, Olszanowski et al. 1996), Romania (Vasiliu et al. 1993), Russia (Krivolutsky 1995, Sidorchuk 2009, Zenkova et al. 2011), including the Kaliningrad Oblast (Sellnick 1920), the Czech Republic (Starý 2013), Spain (Subías & Shtanchaeva 2012), Sweden (Trägårdh 1910, Forsslund 1943, Willmann 1943, Dalenius 1960, Lindberg & Persson 2004, Honciuc & Lundqvist 2009, Remén 2010) and Switzerland (Strenzke 1952, Schweizer 1956).

Tokukobelba verrucosa is known from Finland (Niemi 1988, Koponen 1989, Laakso et al. 1995), Norway (Seniczak et al. 2006, Hågvar et al. 2009), the Czech Republic (Starý 1994) and Pakistan (Hammer 1977). The species shows a broad distribution in Russia, ranging from Kandalaksha in the Murmansk Oblast and Arkhangelsk to Moscow, the Ural region, Eastern and Western Siberia and the Russian Far East (Bulanova-Zachvatkina 1962, 1967, 1973, 1975, Krivolutsky 1995, Kolesnikova et al. 2005). It has also been detected in Dagestan (Gazaliev 2011). In China records for *Tokukobelba verrucosa* exist for the provinces Jilin, Heibei and Beijing (Wang & Norton 1995, Wang et al. 2000, Chen et al. 2010). *Tokukobelba farinosa* has only been found in Lapland province in Northern Sweden (Trägårdh 1902, 1910).

Tokukobelba sellnicki occurs in the Ukraine (Karppinen et al. 1992), and is apparently relatively common in Russia with records from for example the Moscow region (Krivolutsky & Lebedeva 2004) and the Russian Far East (Bulanova -Zachvatkina 1962, 1967, 1973, 1975, Krivolutsky 1995). Choi & Namkoong (2002) describe the species from South Korea. In China *T. sellnicki* has so far been only been discovered in the northern Liaoning and Beijing provinces bordering on Mongolia (Wang & Norton 1995, Aoki et al. 1997; Wang et al. 2000, Chen et al. 2010). *Tokukobelba mongolica* has only been recorded from central and northern Mongolia (Bayartogtokh 2000, 2004a), while *Tokukobelba japonica* is known from Japan (Aoki 1984, Kosuge 2005, Ito et al. 2007, Harada et al. 2008, Hasegawa et al. 2013) and Taiwan (Aoki 1995). *Tokukobelba barbata* has been collected in Nayoro on the Japanese island of Hokkaido (Fujita & Fujikawa 1986) and on Honshu (Ito et al. 2007). *Tokukobelba itsukiensis* is only known from its type locality, the Itsuki Village on Kyushu Island, Japan (Fujikawa 2011).

Ecology

Tokukobelba compta has frequently been found in mountainous regions such as the Alps (Schweizer 1956, Schmölzer 1994, Schatz 1978, 2008), the Scandinavian mountains (Heggen 2010), the Carpathians (Kulczyński 1902a, Strenzke 1952), the Köszeg mountains in Hungary (Balogh 1943) and the Krkonoše mountain range in the Czech Republic (Starý 1994, 2005). Several authors such as Franz (1943) and Miko (2006a) have assumed the species to predominantly occur on high mountains. Kulczyński (1902a) himself found the species not only at a subalpine site at an altitude of 2.000 m a.s.l. close to the summit Kozi Wierch, the highest mountain in Poland, but also at a low altitude of about 450 m a.s.l. at Smreczyna in the Tatra region. *T. compta* has subsequently often been encountered in low-lying areas such as the North European Plain (Sellnick 1920, Strenzke 1952, Warncke et al. 1991), and the East European Lowlands (Kagainis 2011).

Tokukobelba verrucosa has been noted to occur on elevated areals in Pakistan at 2.600 m above sea level, but still well below the tree line (Hammer 1977) and on glacier forelands in Fennoscandia (Seniczak et al. 2006, Hågvar et al. 2009) but also is very common in regions of moderate to low elevation such as in the Russian White Sea area and the Moscow region (Bulanova-Zachvatkina 1962, Krivolutsky 1995). Bayartogtokh (2000) initially collected *T. mongolica* from litter of coniferous larch and fir taiga forest at an altitude of 1.950 m a.s.l. but later found the species in a much lower situated grassland habitat (Bayartogtokh 2004a). The type localities of both *T. japonica* and *T. barbata* lie at low elevations, relatively close to sea level (Aoki 1984, Fujita & Fujikawa 1986). The first of these species has subsequently been encountered at altitudes ranging from 300 m to 960 m by Harada et al. (2008) but it has also been recorded from high altitude forest at Nanhu Mountain, one of the highest peaks of Taiwan (Aoki 1995). *Tokukobelba barbata* was found at 1.200 m a.s.l. by Ito et al. (2007).

Tokukobelba therefore often occurs in montane to alpine habitats but is certainly not restricted to these. It is perhaps noteworthy in this context that in Alpine Fennoscandia *T. compta* is found along the entire altitudinal gradient ranging from sub-alpine to high alpine zones without any apparent distributional preferences (Heggen 2010). Schmölzer (1962) and Schatz (2008) view *T. compta* as most likely being a preglacial relict species that survived the Pleistocene ice ages in sheltered ice-free alpine regions in the Southern Limestone Alps. *Tokukobelba compta* was found by me in Southern Germany on elevated sites on the Königstuhl, belonging to the Odenwald mountain range, which similarly were not covered by ice during the last glaciations. During the last glacial maximum almost the entire present-day distribution area of *Tokukobelba* was covered either by a thick ice sheet or by polar or alpine desert, or in the more southern regions by a steppe and tundra vegetation. The presence of *T. compta* on Central and East European lowlands is most likely a case of postglacial range expansion. *Tokukobelba compta* appears to be a cold adapted species and this may also be true of some other representatives of the genus. Sidorchuk (2009) sampled the species in the polar Urals and Ingimarsdóttir et al. (2012) discovered it on recently exposed nunataks in the Vatnajökoll glacier in Iceland. However *T. itsukiensis* occurs in the subtropical climate zone of southern Japan (Fujikawa 2011).

Species of *Tokukobelba* have most often been found in forests, not only predominantly coniferous ones of the taiga biome (Bulanova-Zachvatkina 1962, Bayartogtokh 2000), but also including mixed and broadleaf forests (Hammer 1977, Fujita & Fujikawa 1986). *Tokukobelba compta*, the best studied species, may also occur in moors and bogs (Starý 2005) and habitats devoid of trees such as alpine heath (Heggen 2010) or arctic tundra (Thor 1930, 1937). It is clearly tolerant of acidic conditions (Strenzke 1952). Representatives of *Tokukobelba* typically inhabit the litter or upper soil layer, and are also frequently seen on mosses, like most Damaeidae (Kulczyński 1902a, Bulanova-Zachvatkina 1962, Fujita & Fujikawa 1986, Bayartogtokh 2000, 2004a). Although they may occasionally be associated with lichens as was noted for *T. verrucosa* by Bulanova-Zachvatkina (1962) who sampled the species from reindeer lichen, they appear to show no preference for these.

Strenzke (1952), Miko (2006a), Schatz (2008) and also others such as Honciuc & Lundqvist (2009) perceive *T. compta* as being hygrophilic and the same appears to apply to *T. verrucosa*, which has been found beneath flora with a high humidity requirement such as fern (Hammer 1977). The Heidelberg specimens of *T. compta* were found in dripping wet humus in little gullies between rocks on a mountain slope, which to some extent channel the water streaming downhill, while others occurred in wet moss, but were not detected in directly adjacent dry microhabitats such as on or in lichen. For the remaining species of *Tokukobelba* the data are not yet conclusive, but *T. mongolica* has been collected on the banks of a stream under willow by Bayartogtokh (2004a), while *T. barbata* has been sampled at its type locality under bamboo grass (*Sasa senanensis*) and the fern *Dryopteris monticola* (Fujita & Fujikawa 1986), both with a high soil moisture requirement, which suggests these *Tokukobelba* species may similarly be hygrophilic.

Nordberg (1936) detected *Tokukobelba compta* in the nests of various bird species. Krivolutsky & Lebedeva (2004) record the presence of numerous mite species which included *T. verrucosa* and *T. sellnicki* in nests of the magpie (*Pica pica*) and the hooded crow (*Corvus corone*), respectively. The authors suggest that birds may play a significant role in the dispersal of mites. This appears to be the case in *Tokukobelba*.

Available data indicate that *Tokukobelba* species reproduce sexually and have a 1:1 sex ratio. A population sample of 20 adult *T. compta* collected in Heidelberg comprised 11 males and 9 females. The members of *Tokukobelba*, like other Damaeidae (Schuster 1956, Luxton 1972, Norton 1977a, Siepel & De Ruiter-Dijkman 1993) appear to be microphytophagous where known (Schatz 1983, Honciuc & Lundqvist 2009), feeding predominantly on saprotrophic fungi and sometimes algae. The gut contents of *T. compta* examined by me contained fungal hyphae. Already Forsslund (1938) noted that *Tokukobelba compta* feeds primarily on fungi. Similarly, Schuster (1956) studying the gut content of a specimen of *T. compta* found a single food bolus of parenchymous material, but all others were of the remains of fungi.

4 Description of *Tokukobelba compta* specimens from Heidelberg

Adult

With the general characteristics of its genus.

Body dimensions. Total body length 539 (493-569) µm. Ventral body length 508 (477-527) µm. Body width 326 (305-347) µm. Body height 301 µm. Length of proterosoma 204 µm. Length of hysterosoma 304 µm. Ratio of ventral body length to body width 1,56:1.

Integument. Colour light to medium chestnut-brown. Cuticle finely microtuberculate. Besides the microtubercles and the strongly sclerotized apophyses numerous large cuticular tubercles with a diameter of mostly 4-6 µm present on epimeres I-IV. Cerotegument clear, white in colour; covers most of external body surface. Cerotegument very thick on prodorsum, sejugal region, epimeral region and proximal leg segments; absent on chelicerae and pedipalps. Distal part of tarsi usually cerotegument-free. Cerotegument granular to tuberculate. Cerotegumental granules on prodorsum, epimeres and notogaster evenly spaced with a diameter of 1-2 µm.

Prodorsum (Figs 1, 3)**.** Tip of rostral tectum rounded in dorsal view, not incised. Rostrum distinctly projecting anteroventrally in lateral view. Measured from the rostral tip to the dorsosejugal groove in lateral perspective, the length of the prodorsum (204 µm) approximately equals its width (198 µm). The rostral and lamellar setae initially are curved laterad and then strongly inwards towards the sagittal plane. The latter are strongly barbed while the former display only a few minute barbs. Seta la (85 µm) > ro (73 µm). Mutual distance between insertion points of setae la: 40 µm < ro: 64 µm. Exobothridial setae thin, attenuate, short (35 µm). Sensillus extremely long (226 µm), initially smooth, isodiametric and bilaterally barbed in the middle region, becoming smooth, flagellate and undulating in the distal third. Bothridium directed dorsally and slightly posterolaterad, irregularly funnel shaped with a fairly large opening, and proximally with indistinct internal ring-like ridges. Interlamellar setae short (69 µm), straight and rod-like, thin, bilaterally barbed, attenuate. Apophyses Aa, Ap, centroprodorsal groove and associated ridges strongly developed. Prodorsum with a central elevation between bothridia, distinctly higher than these in lateral view. Postbothridial apophysis Ba conspicuous, Bp represented by a ridge of thickened integument. Apophyses Da, Dp, La, Lp, P absent. Anterior apophysis Ala of anterolateral enantiophysis present. Posterior anterolateral apophysis Alp represented by a large tubercle.

Notogaster (Figs 1, 3). Notogastral length 377 (360-397) µm, width 328 (305-347) µm. Notogaster slightly ovate, observed from a viewpoint perpendicular to the circumgastric scissure about 1,15 times as long as wide. In lateral perspective hemispherical and robust, maximum thickness about 190 µm; dorsal margin almost evenly rounded, only anteriorly between setae c2 and lm slightly flattened. Dorsoventral thickness of hysterosoma, measured perpendicular to the imaginary line connecting the tip of the rostrum and the posterior margin of the ventral plate is about 300 µm. Spinae adnatae absent. 11 pairs of notogastral setae present. Setae of c-, l- and h-series short to medium in length, slender, tapering, lightly barbed, strongly bent near the base, and lying close to the notogastral surface. In dorsal view setal pair c1 directed posteriad; remaining setae of c-, l- and h-series directed posteriad and slightly laterad. Their length ranges from 63-96 µm, with the posteriormost setae being the shortest. Distance between insertion points of setae c1-c2 (35 µm) much less than that between setae c2-la (70 µm). Setae ps1 (50 µm), ps2 (28 µm), ps3 (23 µm) thin, short. Opening of latero-opisthonotal gland gla and lyrifissures ia, im, ip, ih and ips well developed, the latter two only visible in lateral view. Distance ia-im = 2x im-ip.

Gnathosoma (Figs 8, 9). Mentum slightly wider than long, medio-posteriad with two slightly irregular clusters of sigillae of pharyngeal muscles. Genae anteriorly with pedipalps and a very short supracoxal seta e. Mentum forms a process which extends anteriad under the genuae at their basal meeting point, giving the impression of a spine in ventral view. Labrum elongate, arrow-like, with an acute tip anteriorly. Subcapitular setae h, m, a bilaterally barbed, tapering, medioventrally curved and of medium length; relative lengths: h ≥ m > a. Ventral surfaces of mentum and genuae distinctly microtuberculate. Rutella with three rounded weakly sclerotized teeth and a larger, more strongly sclerotized central tooth; rutellar brush situated on paraxial surface. Lateral lip anteriomediad with a long weakly sclerotized, membranous triangular tip, distally with slender, smooth, needle-like adoral setae or1 and or2. Dorsal manubrial area porosa forms border between rutella and gena. Area porosae also situated on antiaxial side of genae and in the cheliceral groove.

Chelicera moderately elongate with a length of 117 µm and a height of 46 µm. Digitus fixus and digitus mobilis both robust, the former with 5, the latter with 4 large, triangular teeth. Ratio of length (37 µm) to height (17 µm) of digitus mobilus is 2,2:1. Point of articulation of cheliceral digits approximately ventrad insertion point of seta chb.

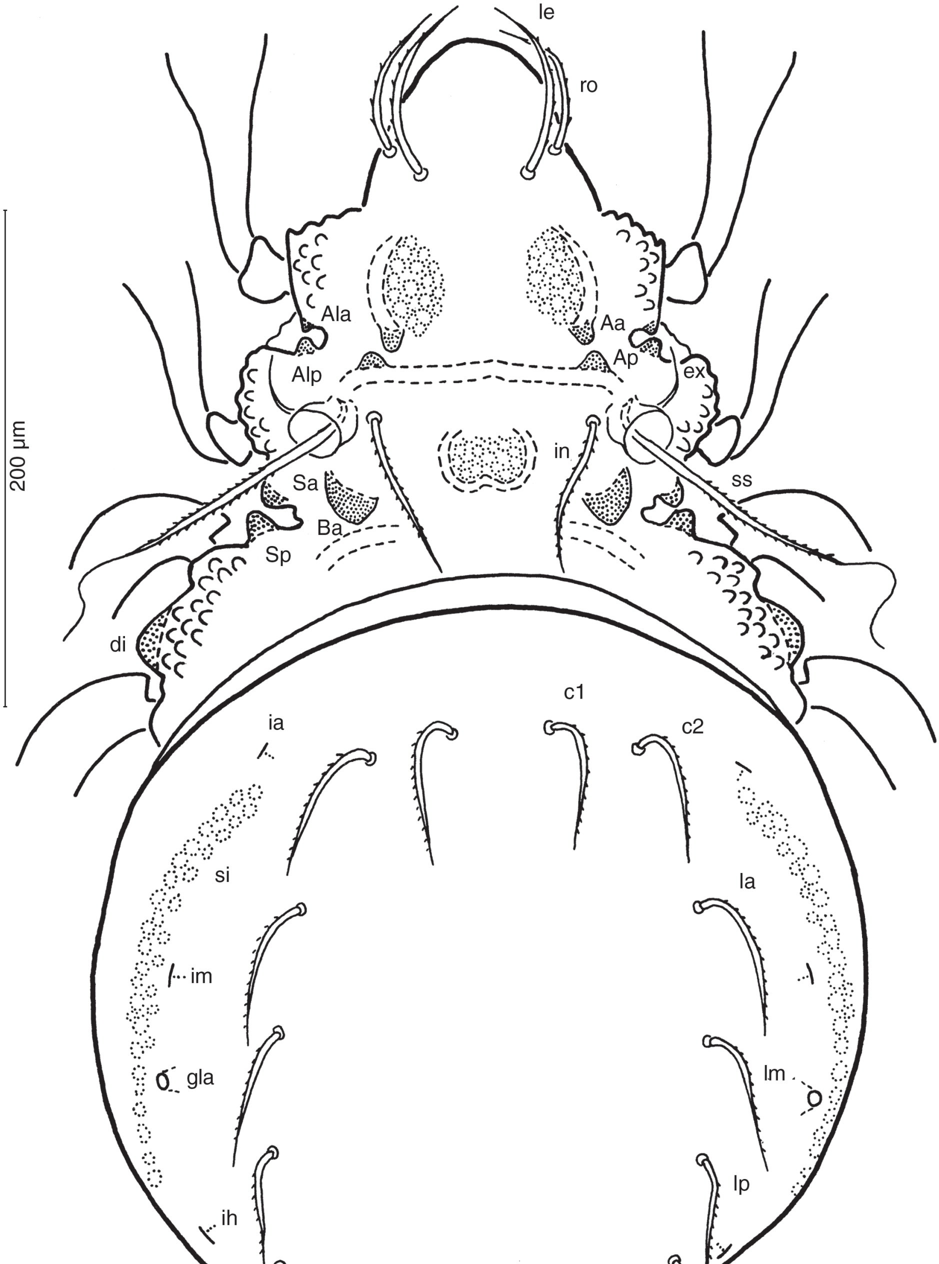

Figure 1. *Tokukobelba compta* adult, dorsal aspect.

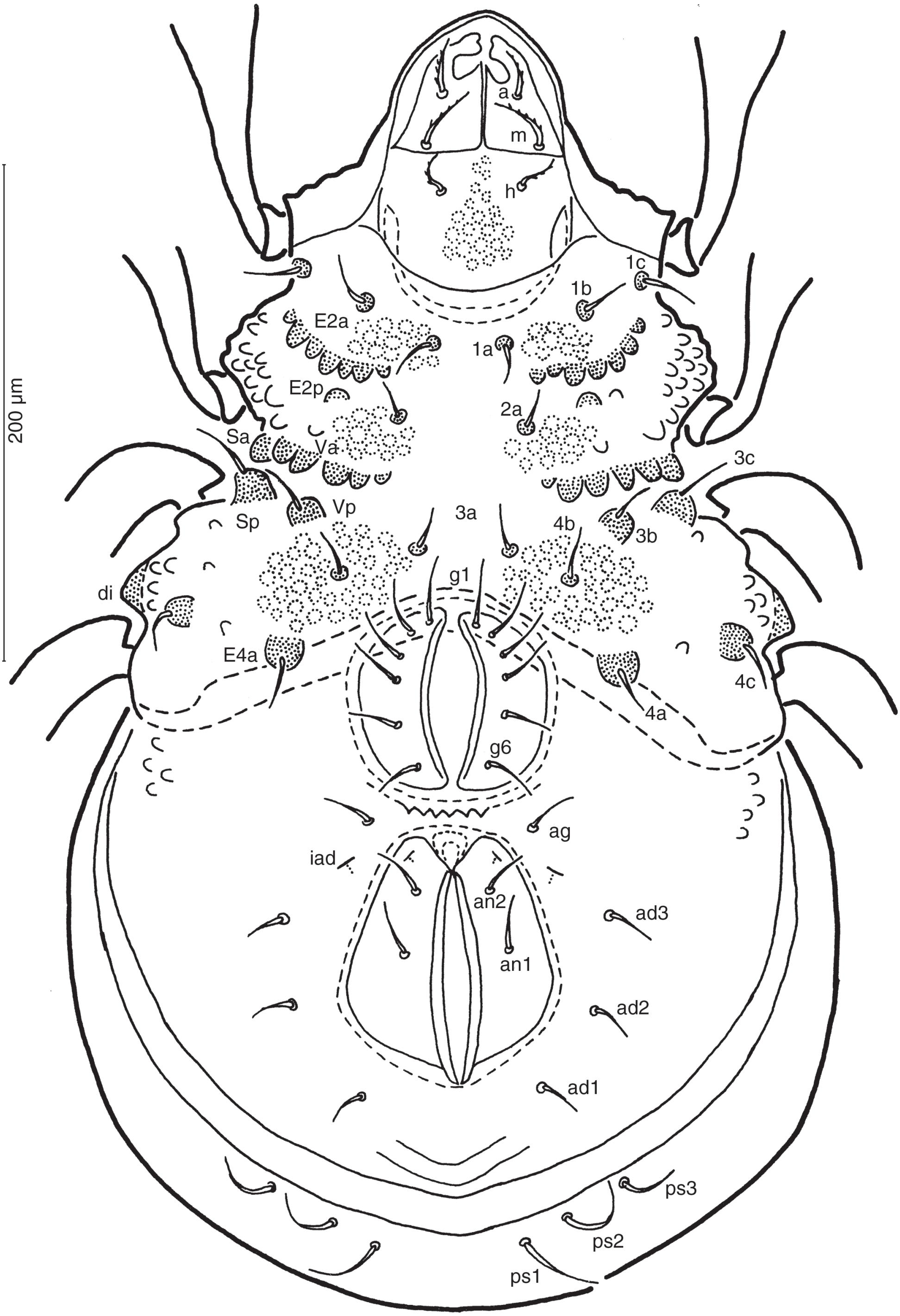

Figure 2. *Tokukobelba compta* adult, ventral aspect.

Seta cha situated in a dorsal to slightly paraxial position, directed anteriad, long (44 µm), evenly barbed with dense small barbs, with a ventral bend in the distal half and gently tapering at the tip. Seta chb slightly shorter (33 µm), antiaxially situated, barbed with the longest barbs near the midpoint. Paraxial surface with three minute chitinous spines sp posteriad cha. Body wall obliquely attached to roughly the proximal third of the chelicerae. A conspicuous very large area porosa present antiaxially, distal to line of attachment of cheliceral sheath. A second small area porosa situated in ventral part of digitus mobilis. A striated fossa fc situated on the antiaxial side and two unstriated fossae on the paraxial side. Trägardh´s organ Trg long, fingerlike, tapering, on paraxial side. Coxal opx, ventral opv and paraxial oncophyses op´ present.

Pedipalpi slender, with a length measured from femur to tarsus of 108 µm. Setal formula: 0-2-1-3-9 + ω. Femur antiaxially with a large oval dorsolateral porose area. Femoral setae inf, sup, genual setae d, l´´, and tibial setae l´, l´´ acuminate with distinct rows of small barbs; inf (50 µm) and d (46 µm) longest and thickest. Solenidion ω (15 µm) prone, baculate. Eupathidia acm, ul´, ul´´ distally on tarsus, baculate and short, with a length of approximately 6 µm. Subultimal eupathidium sul absent. Tarsal setae cm, it´, it´´, vt´, vt´´ smooth, slender; cm (28 µm) longest with the remainder measuring about 22 µm. An unusual third ventral seta vt2´ occurs axially. Three-dimensional arrangement of tarsal setae with respect to the tarsal axis is constant and highly specific, as shown (Fig. 8b).

Epimeral region (Figs 2, 3). Parastigmatic apophysis Sa small, tuberculate, Apophysis Sp similar in appearance to Sa. Discidium subtriangular. Well developed ventrosejugal enantiophysis spans the ventrosejugal groove. Apophysis Va multituberculate, Vp monotuberculate. Apophyses E2a of propodoventral enantiophyses multituberculate, E2b monotuberculate, indistinct. Very large apophysis E4a present. Epimeral setation 3-1-3-3. All epimeral setae short, roughly 23 µm in length, smooth or with rare minute barbs, inserted on conspicuous tubercles, with those on

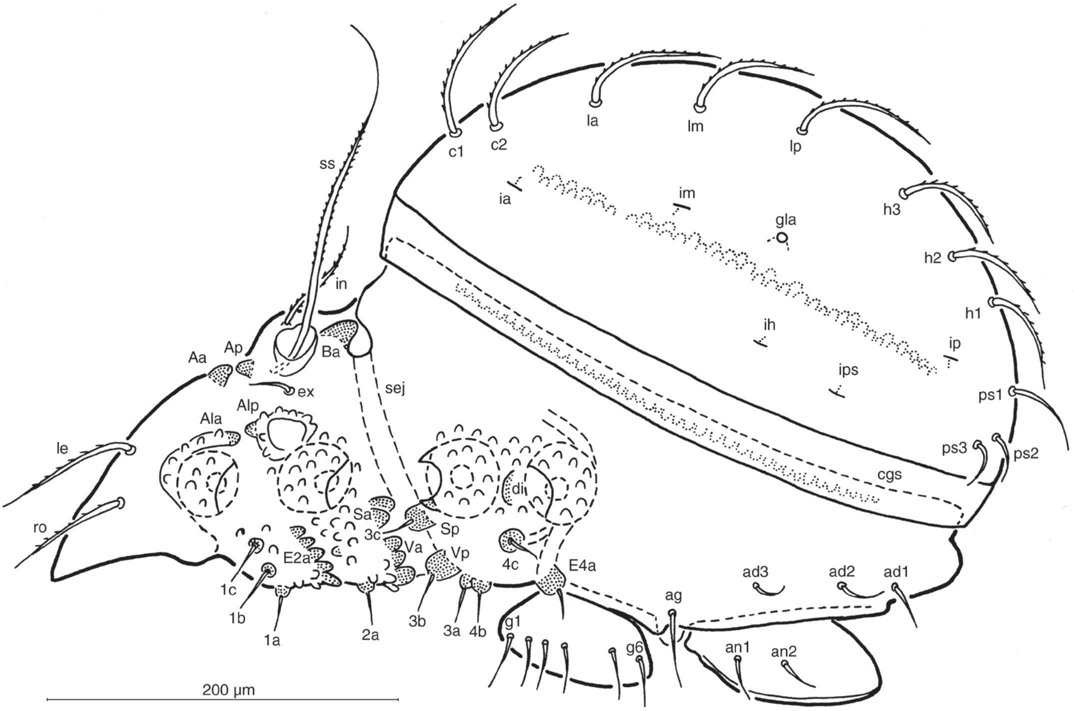

Figure 3. *Tokukobelba compta* adult, lateral aspect.

epimeres III and IV greatly enlarged. Numerous smaller cuticular tubercles not associated with any setae are present on the acetabular tecta and laterally on epimeres I-IV, giving these a dentate margin in ventral perspective. Internal apodemes of epimeres III and IV strongly sclerotized and very conspicuous. Epimeral groove IV deep and very distinct.

Anogenital region (Figs 2, 3). Six pairs of genital, 1 pair of aggenital, 2 pairs of anal and 3 pairs of adanal setae present. Anal plates with a conspicuous thickened reflexed rim. Genital and anal plates situated close together. Setae ad3 laterally inserted, their distance from the anal plate is more than twice that of seta ad2. Anal and adanal setae short (25 µm) and smooth. Lyrifissure ian a small slit in

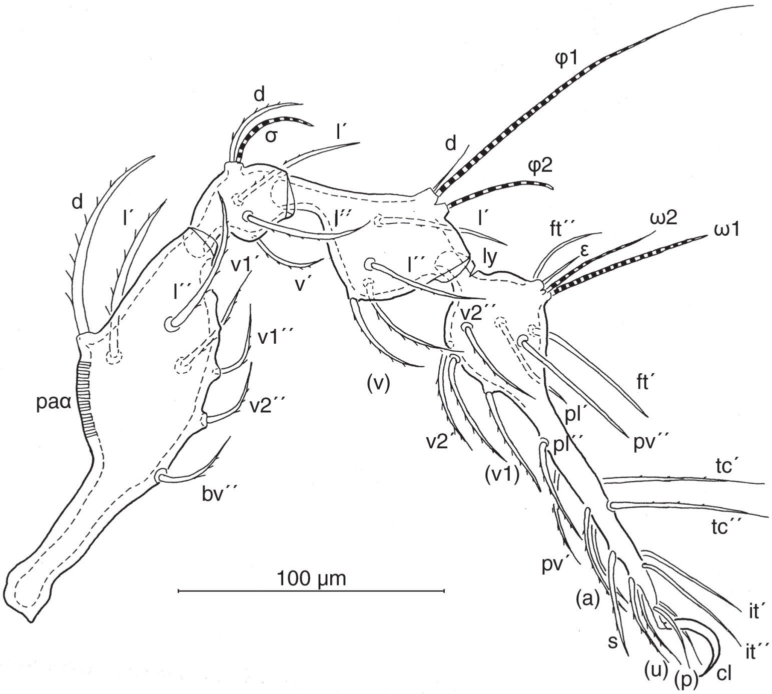

Figure 4. *Tokukobelba compta* adult, femur to tarsus of leg I, antiaxial aspect.

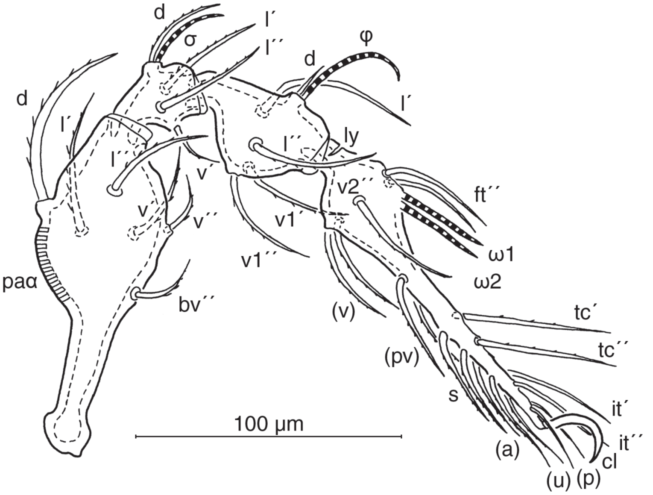

Figure 5. *Tokukobelba compta* adult, femur to tarsus of leg II, antiaxial aspect.

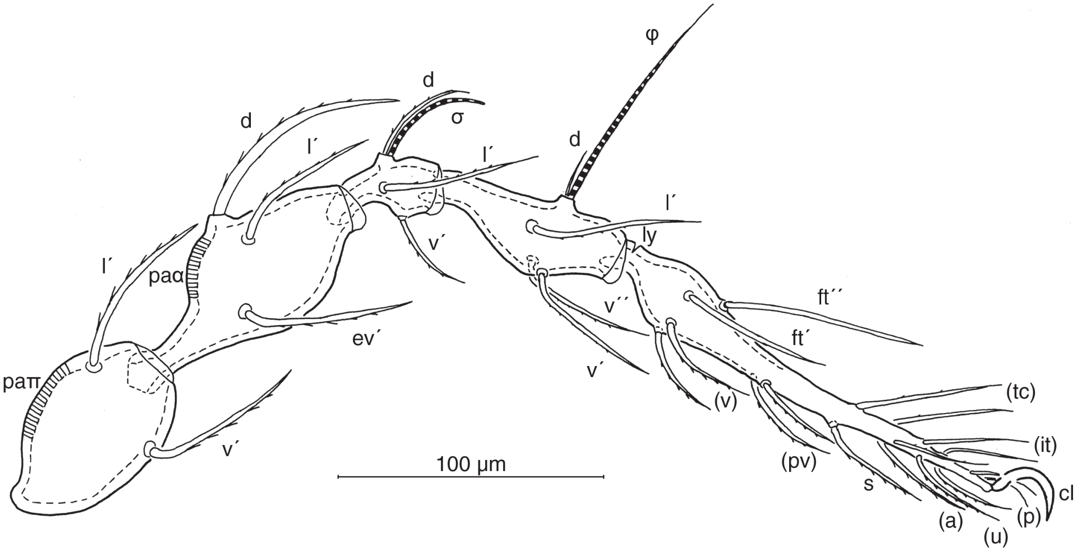

Figure 6. *Tokukobelba compta* adult, leg III, antiaxial aspect.

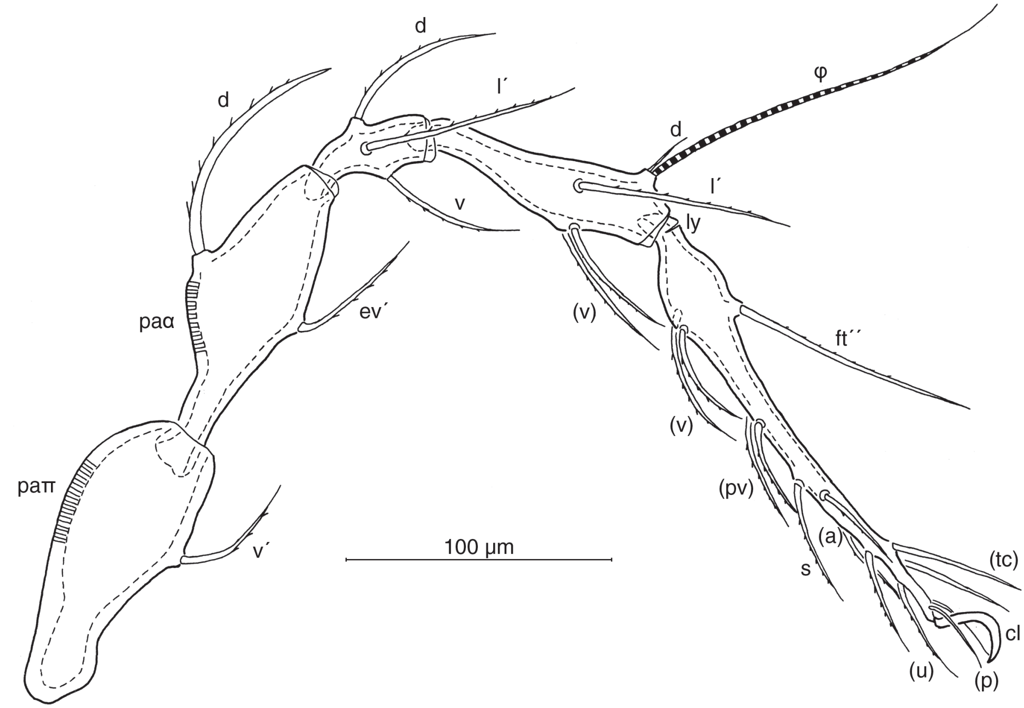

Figure 7. *Tokukobelba compta* adult, leg IV, antiaxial aspect.

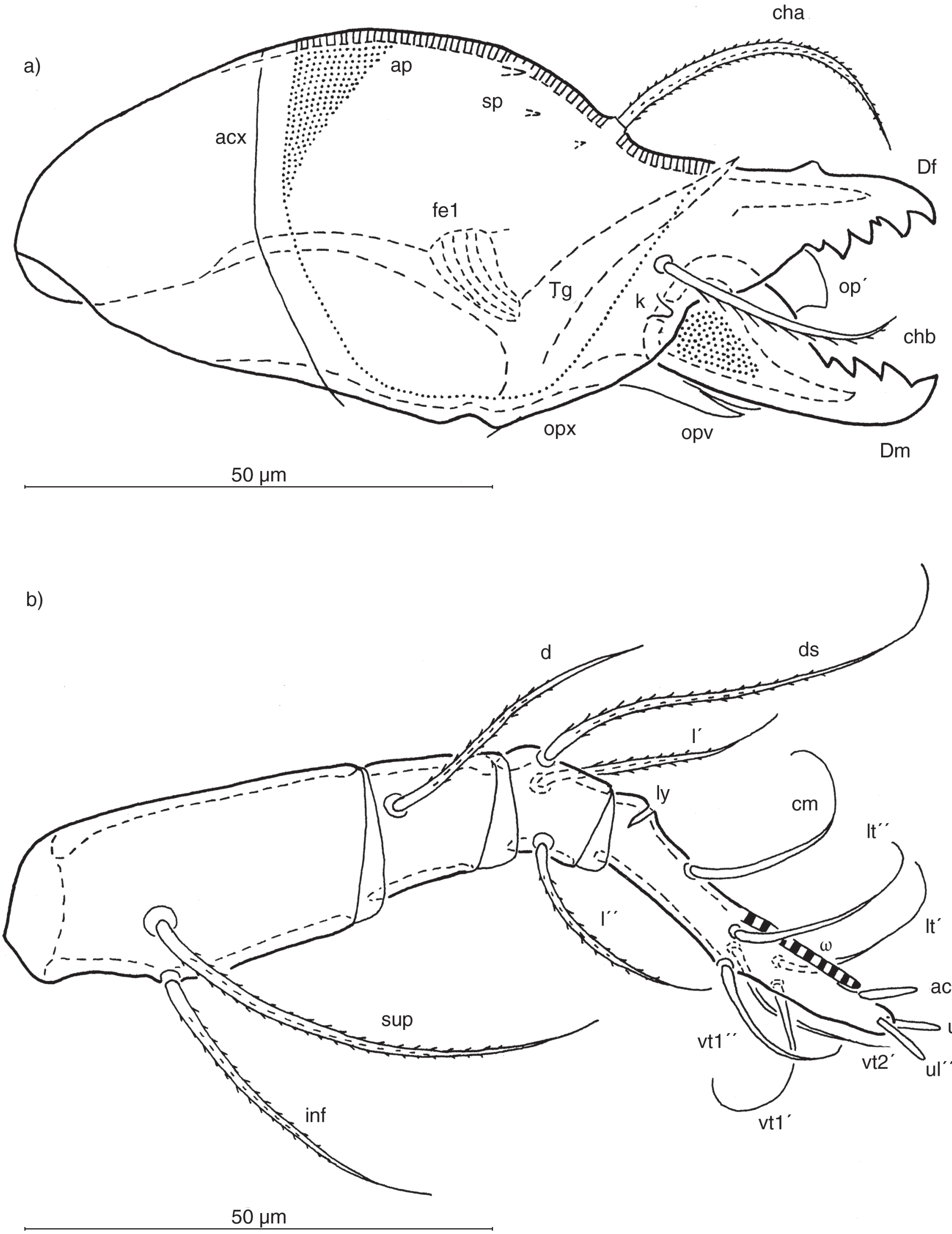

Figure 8. *Tokukobelba compta* adult. a) chelicera, antiaxial view. b) femur to tarsus of palp, antiaxial view.

the anterolateral corner of the anal valve, anteriad seta an2. Aggenital setae ag (49 µm) lateroventrad genital plates, slightly longer but otherwise similar in appearance to genital setae (28 µm).

Legs (Figs 4-7). Leg segments clavate to submoniliform except for tarsi; often with slightly wrinkled integument on bulbs, particularly the femora. In specimens well cleared in lactic acid internal muscle scars visible on femora, tibiae and to a lesser extent the tarsi. Trochanters I and II much shorter than trochanters III and IV. An area porosa positioned dorsally to mediodorsally on the proximal region of the bulbs of femur I-IV and on trochanter III and IV. Trochanters III and IV with a ventro-distal protectum. Tectum and area porosa absent on trochanter I and II. Legs short. Lengths of legs I-IV are: 453 µm, 366 µm, 446 µm, 544 µm. Relative lengths of legs I-IV are 1: 0,81: 0,98: 1,20. Leg IV short, measuring about 1,07 times the ventral body length. Lengths of the individual leg segments from trochanter to tarsus are: leg I: 31 µm, 156 µm, 49 µm, 80 µm, 165 µm; leg II: 26 µm, 128 µm, 37 µm, 59 µm, 139 µm; leg III: 78 µm, 111 µm, 46 µm, 82 µm, 171 µm; leg IV: 116 µm, 125 µm, 53 µm, 98 µm, 190 µm. Trochanteral setation 1-1-2-1. Femoral setation 7-6-3-2. Genual setation 4-4-3-3; genual associated setal formula 1-1-1-0. Tibial setation 5-5-4-4; tibial associated setal formula 1-1-1-1. Tarsal setation 22-18-17-14, including famulus. Leg solenidial formula: I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0). Adult chaetotaxy with number of solenidia in brackets:

I	1-7-4(1)-5(2)-22(2)
II	1-6-4(1)-5(1)-18(2)
III	2-3-3(1)-4(1)-17
IV	1-2-3-4(1)-14

Most setae inserted on conspicuous tubercles. Setae d on femora I-IV darkly pigmented, thick, conspicuously barbed, strongly developed; remaining setae, except for some lateral setae, generally much thinner, of lighter colour and with finer barbs. Only setae d, ev´, l´´ found on femur III, and d, ev´ found on femur IV. Setae v2´ and v2´´ present on tarsus I, and v2´ on tarsus II. Setae d of genua I-III barbed, almost as long as their short coupled solenidia σI (39 µm), σII (34 µm), σIII (42 µm). Seta d of tibia I very slender, smooth, diminutive (22 µm) much shorter

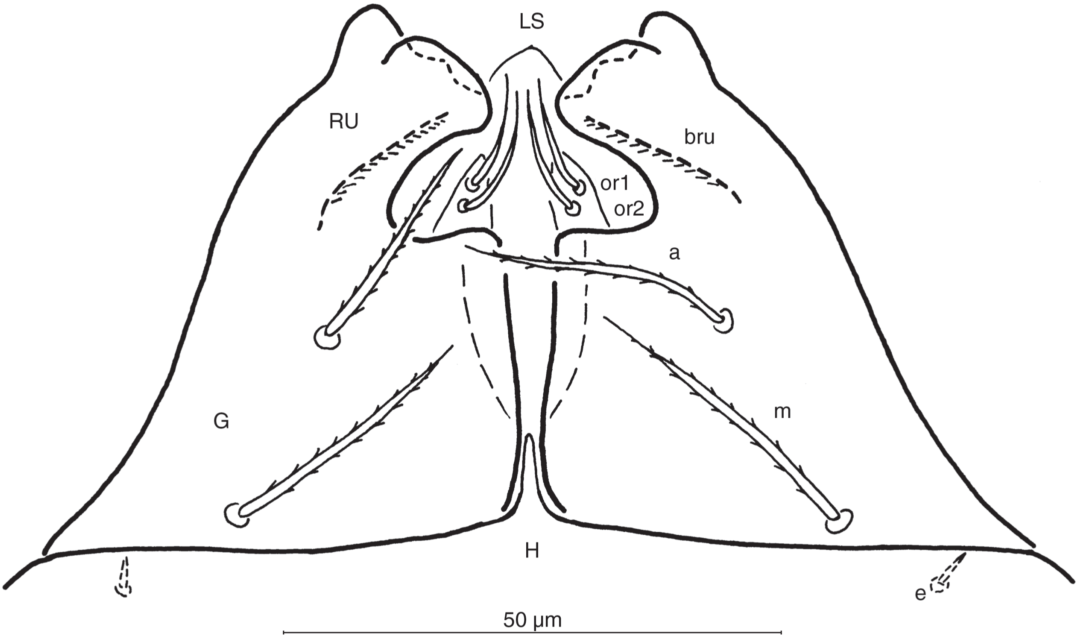

Figure 9. *Tokukobelba compta* adult, infracapitulum, ventral aspect.

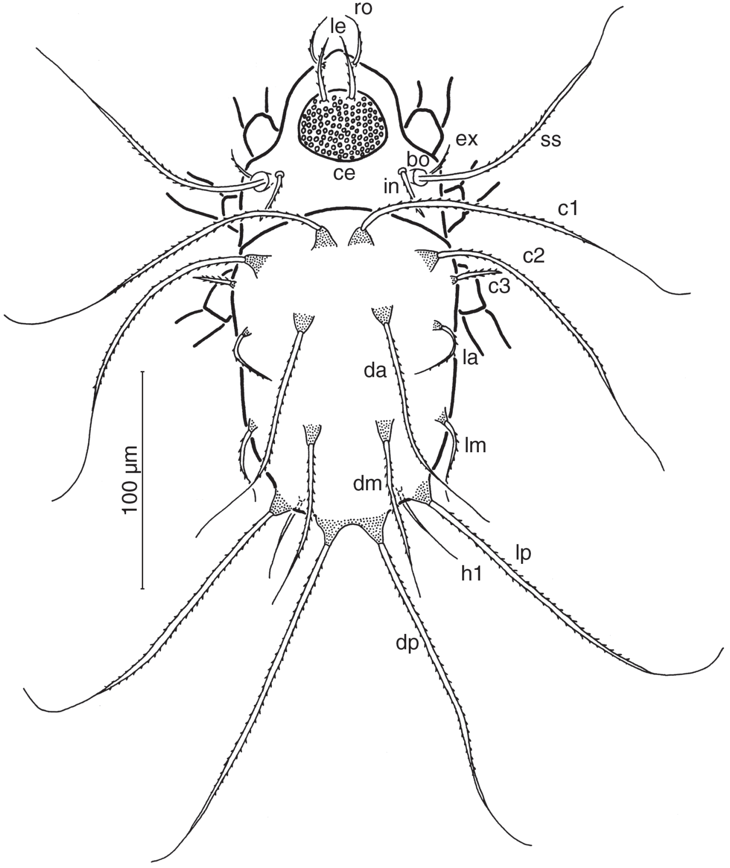

Figure 10. *Tokukobelba compta* larva, dorsal view.

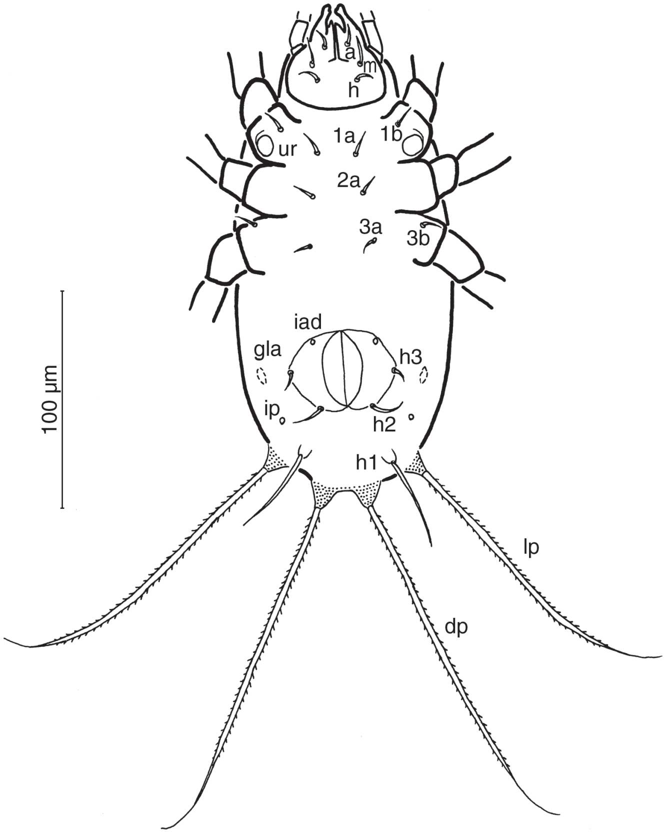

Figure 11. *Tokukobelba compta* larva, ventral view.

than its coupled solenidion φ1 (158 µm). Setae d of tibia II-IV are short (15-23 µm), thin, but not as slim as seta d of leg I, and without barbs. They measure about 0,27, 0,19 and 0,11 of the lengths of their associated solenidia φII (51 µm), φIII (98 µm) and φIV (155 µm), respectively. Tibial solenidia φ1 on leg I and φ on leg IV very elongate, flagellate and tactile. Solenidia σI, σII, σIII, φ2I (44 µm) and φI short and approximately ceratiform, curved towards the ambulacrum. Tarsal solenidia ω1I, ω2I, ω1II and ω2II short, rod-like. Solenidion ω1I about 1,3 times the length of ω2I; ω1II and ω2II roughly similar in length. Famulus ε short, (17 µm), smooth, strongly tapering.

Larva and nymphs

With the general characteristics of their genus.

Eggs. Length 232 µm, width 102 µm, elongate, ovoid in shape. Egg shells lightly sclerotized, amber brown in colour after immersion in lactic acid, and with a distinct porose surface pattern. The pore density is roughly 64 per 1.000 square µm. Females may carry up to 5 large eggs at a time in the oviducts or vagina.

Body Dimensions. Larva: length 220 µm, width 110 µm. Protonymph: length 280 µm, width 146 µm. Deutonymph: length 322 µm, width 152 µm. Tritonymph: length 412 µm, width 216 µm. Length and especially width vary somewhat depending on the degree of body distension.

Integument. Cuticle of body smooth, transparent and white to pale yellow in colour. Gnathosoma, some setal apophyses and sclerites, notogastral cornicle and legs lightly sclerotized, light brown. The extent of sclerotization is most pronounced in the tritonymph and least in the larva. Cerotegument granular, very thick, covers most of body and legs and setal bases. Granules spherical in dorsal view, tuberculate to conical or bottle-shaped in lateral view, mostly with a diameter of 1-2 µm or less. Prodorsum in larva and nymphs with a conspicuous brown cerotegumental cap anteromediad the bothridia (Figs 9-10). Cerotegumental granules small (diameter 1 µm in tritonymph) densely packed in central region of cap; but appearing substantially larger and puffy in the periphery, due to the cerotegumental granules there being irregularly fused at their bases and forming discrete clusters. Cerotegument thicker, with slightly larger granules in tritonymph than in earlier stages. Setae of prodorsum, notogaster and legs light to very dark brown, with a hyaline base. Degree of pigmentation much less in ventral setae. Notogaster of at least larva and

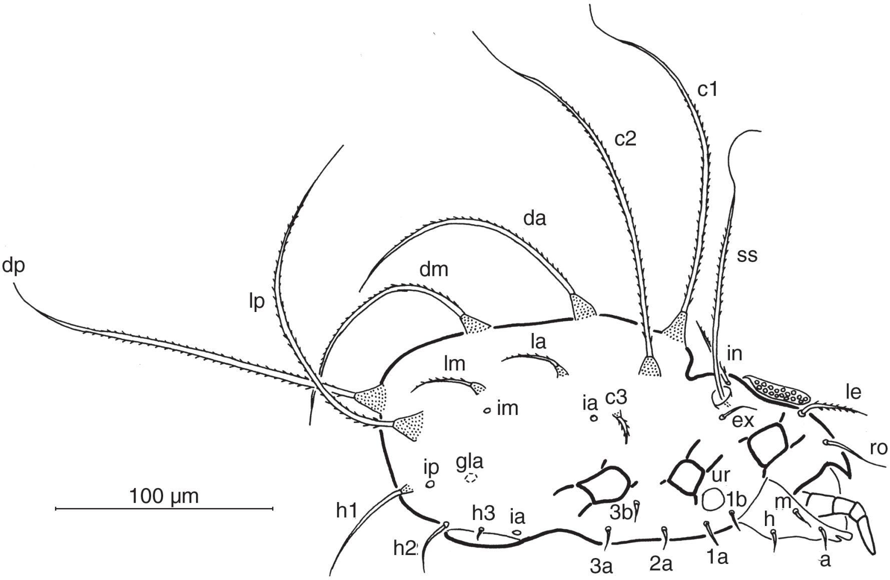

Figure 12. *Tokukobelba compta* larva, lateral view.

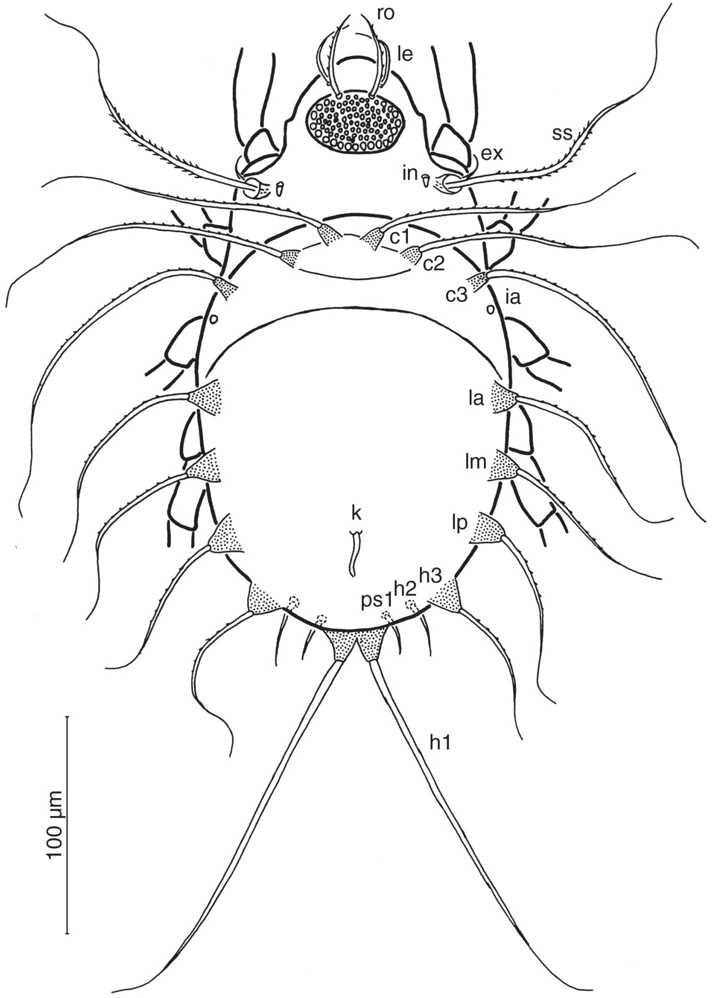

Figure 13. *Tokukobelba compta* protonymph, dorsal view.

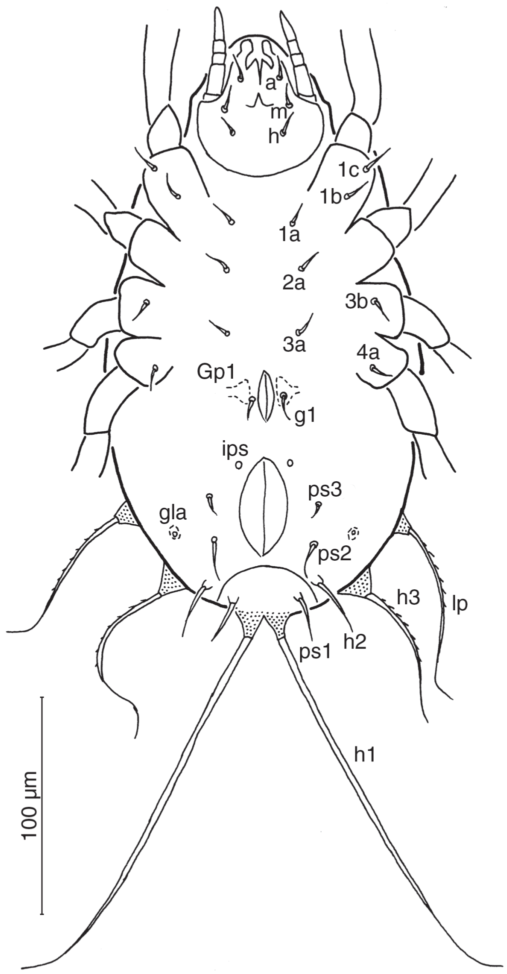

Figure 14. *Tokukobelba compta* protonymph, ventral view.

protonymph with a regular reticulate pattern between approximately the insertion points of setae lp, h1, h2 and the opisthonotal gland opening.

Prodorsum (Figs 10, 12, 13, 15). Short, about half the length of the notogastral region in lateral perspective. Rostrum broadly rounded. Interlamellar seta of moderate length (30 µm), barbed and attenuate in larva; very short (5 µm) and truncate in nymphs. Sensillus very long, (larva 175 µm; protonymph 190 µm; tritonymph 275 µm) barbed in the middle region, distally flagellate and undulating. Exobothridial seta straight, short, unilaterally barbed in larva, smooth or with sparse minute barbs in nymphs. Rostral setae of larva barbed, about similar in length (37 µm) to the smooth lamellar setae. Rostral setae in nymphs barbed, slightly shorter (tritonymph 72 µm) than the smooth lamellar setae (tritonymph 86 µm).

Notogaster (Figs 10-15). The 12 pairs of notogastral setae of the larva display a substantial range of size and form. Setae c1 (188 µm), c2 (182 µm), da (130 µm), dm (112 µm), dp (208 µm) and lp (203 µm) are thick, elongate, dark coloured, bilaterally barbed and with flagellate tips which are very frequently broken off. Setae c3 (27 µm), la (47 µm) and lm (52 µm) differ from these in being thinner, shorter, not possessing pronounced flagellate tips and in that they insert on much smaller apophyses. They resemble the former in being densely barbed and in their dark brown colour. Larval seta c3 is unusual in being straight, orientated approximately perpendicular to the long axis of the body in dorsal aspect. Setae h1 (80 µm), h2 (30 µm) are smooth and thin with h3 (9 µm) being minute and exceptionally slender. Setae h1 and h3 insert on tubercles.

The nymphal setation differs from that of the larva in that dorsocentral setae are absent and pseudanal setae ps1, ps2 and ps3 are present instead. Furthermore setae c3, la, lp, are all much longer in the nymphal stages relative to the body length. The setae of the c-, l- and h-series are thick, elongate, dark coloured, conspicuously bilaterally barbed (except h1) and with flagellate tips, Their dark brown strongly sclerotized basal apophyses are situated on relatively large sclerites of a lighter colour. Setal pairs c1 and c2 located on a single fused sclerite in nymphs. Setal pair h1 similarly placed on a single common sclerite. Setal measurements for the protonymph are as follows. The longest are pair h1 (210 µm) which are smooth and characteristically

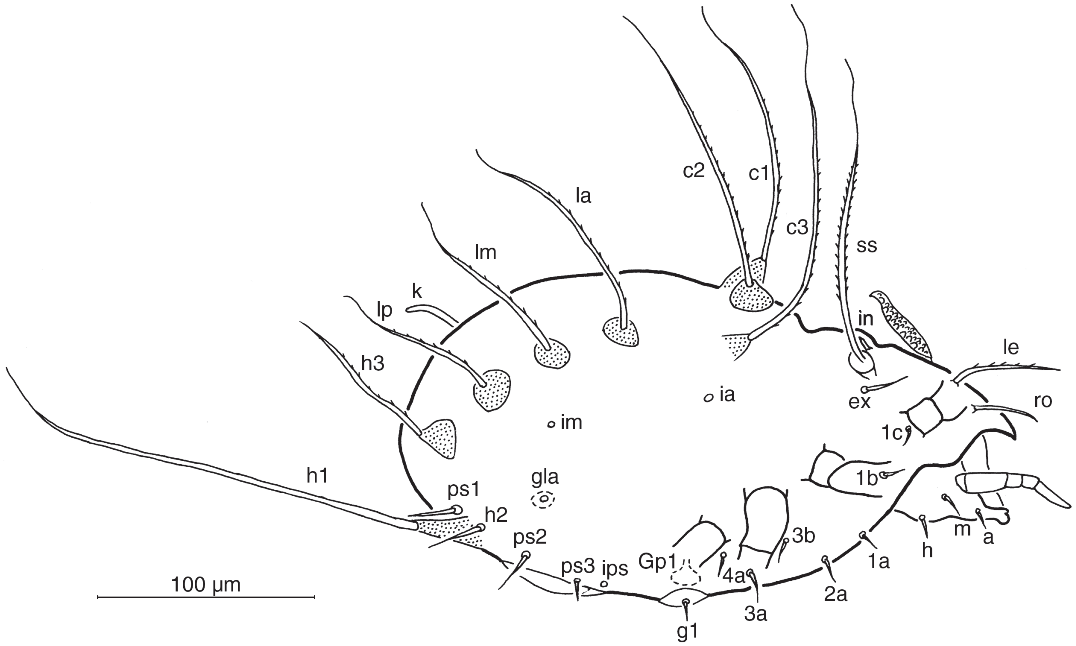

Figure 15. *Tokukobelba compta* protonymph, lateral view.

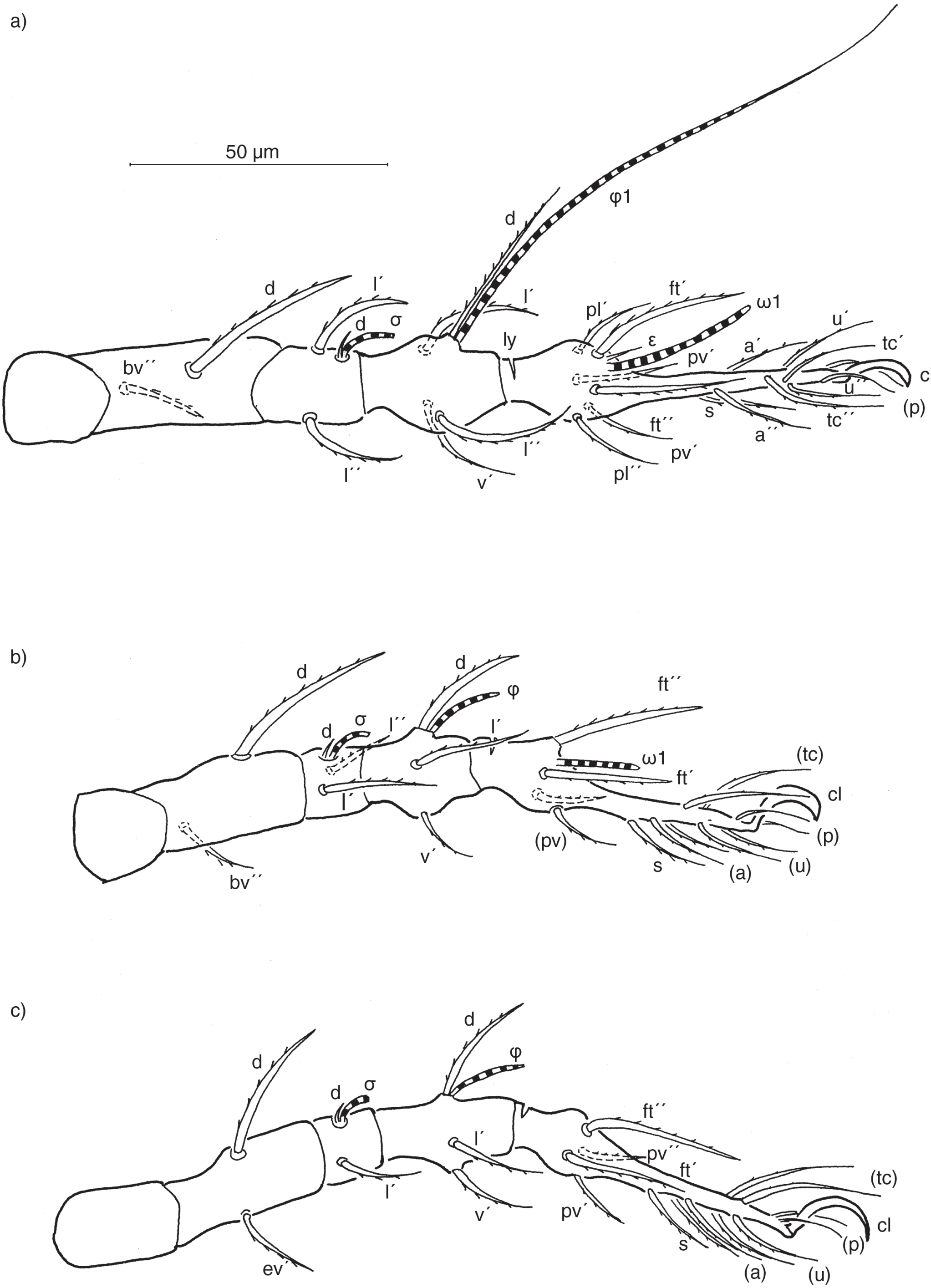

Figure 16. *Tokukobelba compta* larva. a) leg I, antiaxial view. b) leg II, paraxial view. c) leg III, antiaxial view.

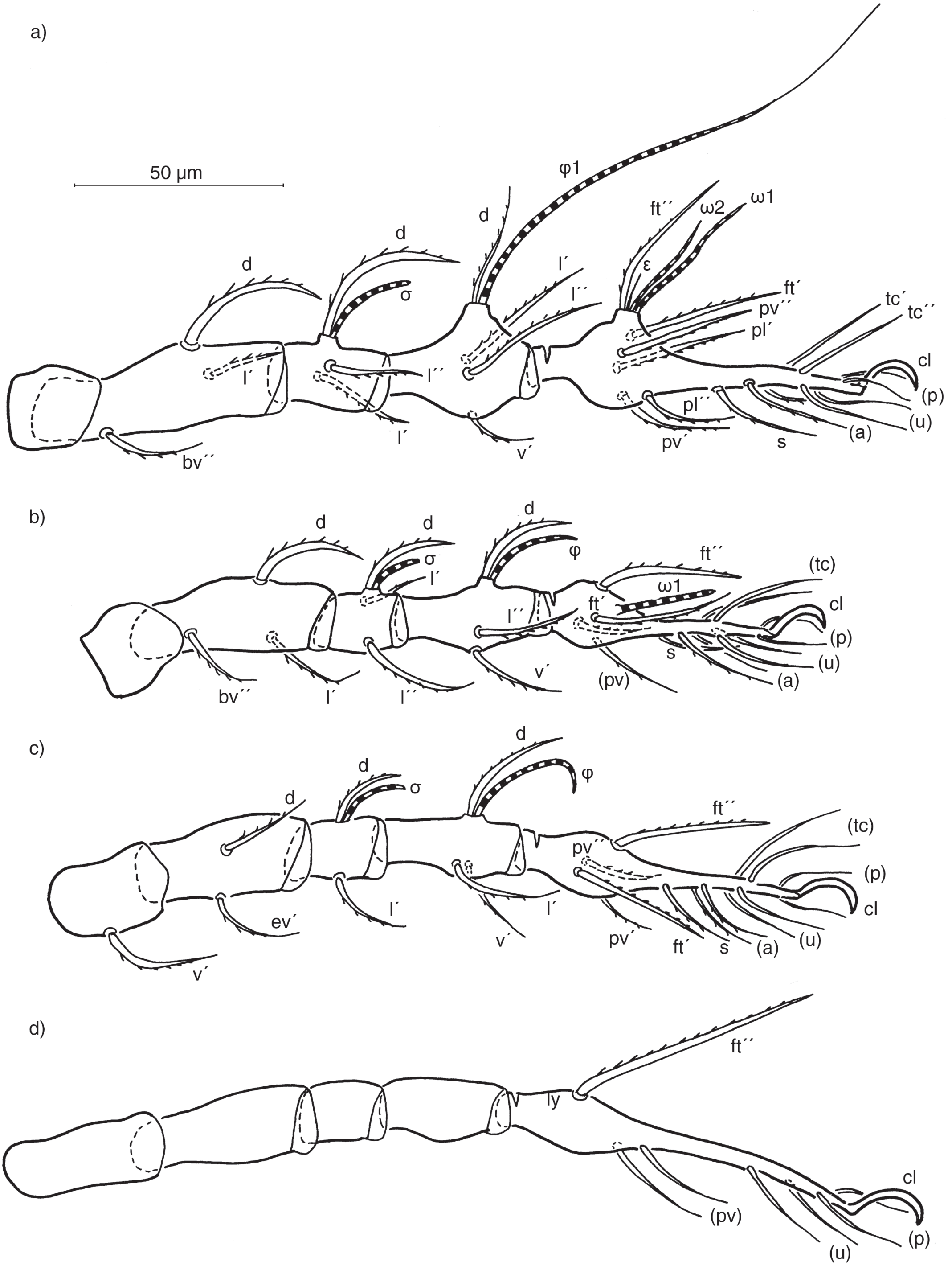

Figure 17. *Tokukobelba compta* protonymph. a) leg I. b) leg II. c) leg III. d) leg IV. All in antiaxial view.

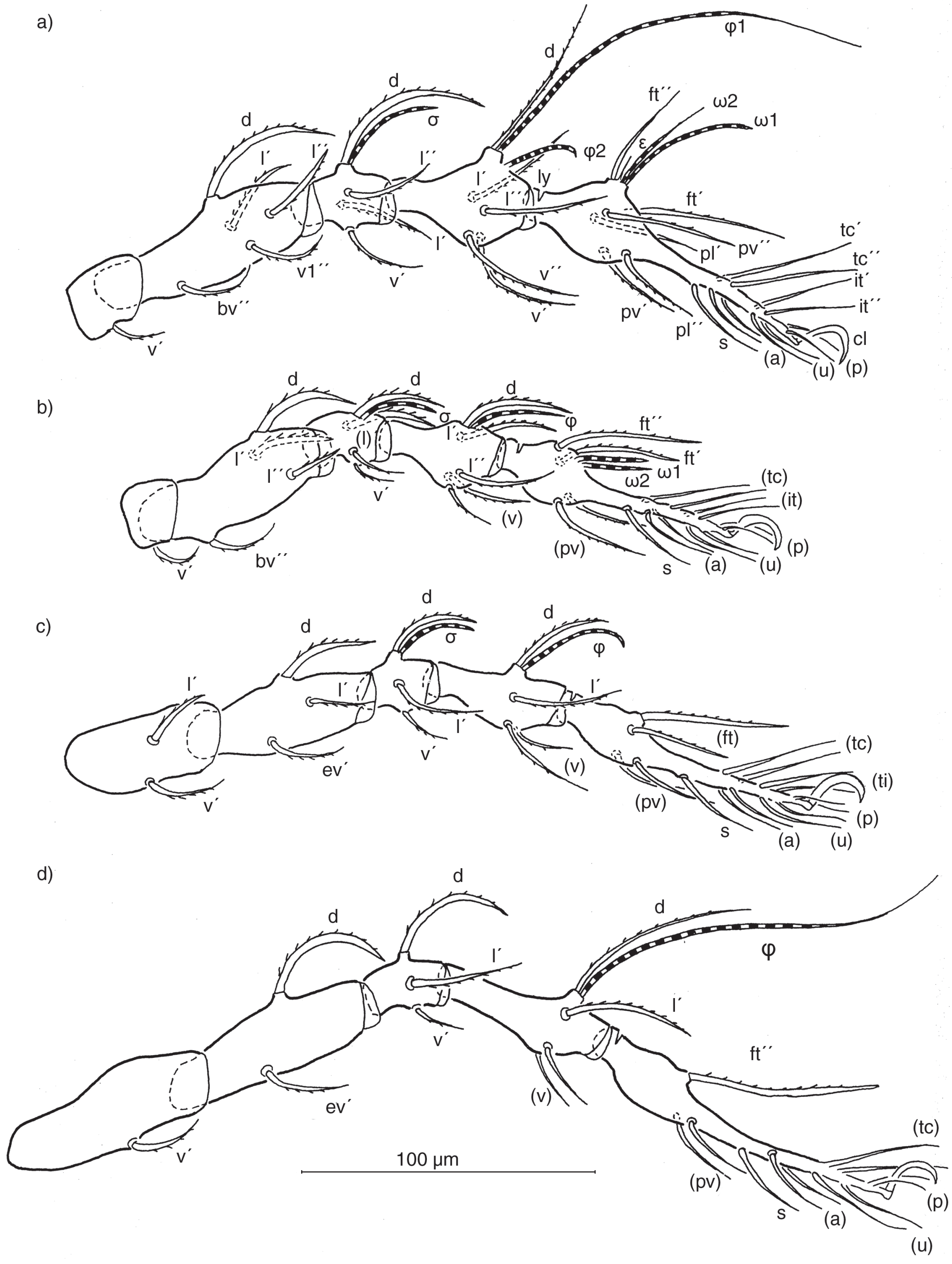

Figure 18. *Tokukobelba compta* tritonymph. a) leg I. b) leg II. c) leg III. d) leg IV. All in antiaxial view.

straight along most of their length. Very elongate setae are also c3 (171 µm), c1 (140 µm) and c2 (133 µm). The setae of the l- series, la (108 µm), lm (100 µm), lp (91 µm) and also h3 (88 µm) are somewhat shorter. Shortest are the smooth h2 (34 µm) and the unbarbed, thin pseudanal setae ps1-ps3 which range in length between 20 and 30 µm. The relative setal lengths in the tritonymph are very similar to those in the protonymph, being only somewhat longer.

Legs (Figs 16-18). Solenidion σ on genu I-III, φ on tibia II-III and its homologue φ1 on tibia I, as well as ω1 on tarsus I-II are larval in origin. Solenidion ω2 on tarsus I first arises in the protonymph. Solenidia φ2 on tibia I, φ on tibia IV, and ω2 on tarsus II, are deutonymphal in appearance as in the vast majority of Brachypylina. The solenidotaxy of the tritonymph corresponds to that of the adult.

Solenidial formulae are:

larva:	I (1-1-1)	II (1-1-1)	III (1-1-0)	
protonymph:	I (1-1-2)	II (1-1-1)	III (1-1-0)	IV (0-0-0)
deutonymph:	I (1-2-2)	II (1-1-2)	III (1-1-0)	IV (0-1-0)
tritonymph:	I (1-2-2)	II (1-1-2)	III (1-1-0)	IV (0-1-0)

Leg setation formulae including famulus:

larva:	I (0-2-3-4-16)	II (0-2-3-3-13)	III (0-2-2-3-13)	
protonymph:	I (0-3-3-4-16)	II (0-3-3-3-13)	III (1-2-2-3-13)	IV (0-0-0-0-7)
deutonymph:	I (1-4-4-5-16)	II (1-3-4-4-13)	III (2-3-3-4-13)	IV (1-2-4-3-12)
tritonymph:	I (1-5-4-5-18)	II (1-4-4-5-15)	III (2-3-3-4-15)	IV (1-2-3-4-12)
adult:	I (1-7-4-5-22)	II (1-6-4-5-18)	III (2-3-3-4-17)	IV (1-2-3-4-14)

Fundamental setae present in the larva are: femur I-II: d, bv´´; femur III: d, ev´; genu I-II: d, (l); genu III: d, l´; tibia I: d, (l), v´; tibia II-III: d, l´, v´; tarsus I: (ft), (tc), (p), (u), (a), s, (pv), (pl), e; tarsus II-III: (ft), (tc), (p), (u), (a), s, (pv). This conforms to the standard damaeid pattern. Setae of protonymphal origin are: trochanter III: v´; femur I-II: l´; tarsus IV: ft´´, (p), (u), (pv). Setae of deutonymphal origin are: trochanter I-II: v´; trochanter III: l´; femur I-II: l´´; femur III: l´: femur IV: d, ev´; genu I-III: v´; genu IV: d, l´, v´; tibia I, III: v´´; tibia II: l´´; tibia IV: d, l´, v´; tarsus IV: (tc), (a), s. Setae of tritonymphal origin are: trochanter IV: v´; femur I: v1´´; tibia II, IV: v´´; tarsus I-III: (it). Setae arising in the adult are: femur I: v1´, v2´´; femur II: v´, v´´; tarsus I: (v1), (v2); tarsus II: (v1), v2´´; tarsus III-IV: (v). The adult retains an associated seta d on tibia I-IV. Solenidia of genu I-III and of tibiae of all legs each coupled with a companion seta d in larva, nymphs and adult.

5 Taxonomy of *Tokukobelba*

The excellently documented *Tokukobelba mongolica* was chosen as type species of *Tokukobelba*. The most ancient member of the new genus is *T. compta*. The original description of this species in the classic work of Kulczyński (1902a), outstanding for its time, suffices to clearly locate the species in *Tokukobelba*. Nevertheless, it is very short, and only the dorsal perspective of the whole mite and lateral views of legs I and IV are illustrated. During the past 114 years numerous authors have briefly described *T. compta* in determination keys or faunal lists (Sellnick 1929, 1960, Willmann 1931, Strenzke 1952, Schweizer 1956, Bulanova-Zachvatkina 1962, Miko 2006a) or commented on aspects of its morphology such as Norton (1977a, b), who remarks on the setation of femora III and IV, or Mourek & Miko (2011), who investigated the ontogeny of the famulus. Nevertheless, a substantial amount of unclarity and lack of knowledge about the identity and morphology of *T. compta* has remained.

Identity of *Tokukobelba compta*. Seniczak et al. (2013) recently described *T. compta* from specimens found in a bog close to Bergen in southern Norway. They describe adults of *T. compta* as displaying: trochanteral setation 1-1-2-2; femoral setation 7-6-4-4; tibial setation 4-5-4-4 with tibia of leg I without an associated seta d; tarsal setation 20-17-17-14 with setae (v2) absent on leg I and v2´ absent on leg II; apophysis Da present, apophyses Ala, Alp absent; epimeral region without large tubercles on which the epimeral setae insert and without conspicuous apophysis E4a. In every one of these traits their species deviates greatly from the *Tokukobelba* collected in Heidelberg.

Seniczak & Seniczak (2013) describe the larva, tritonymph and adult of *Belba corynopus* from southern Poland. For this species they give: trochanteral setation 1-1-2-2; femoral setation 7-6-4-4; tarsal setation 20-17-17-14, epimeral setation 3-1-3-3. The leg setal scores in my specimens of *B. corynopus* from Mannheim were instead: trochanter 1-1-2-1; femur 7-7-5-5; tarsus 20-17-16-13, corresponding to those given for the species by Grandjean (1936, p. 65). Here seta v1´ is found on each of tarsi III and IV with v1´´ being absent on these segments. The insertion point of seta pv´ on tarsus IV in this species experiences a significant distal shift during ontogeny, while pv´´ remains inserted on the tarsal bulb in the adult, mimicking seta v´´. Like the specimens found by Grandjean (1936), the ones discovered by me in Mannheim had an epimeral setation of 4-4-4-4.

The *T. compta* specimen illustrated by Seniczak et al. (2013, p. 295, Figs 1-3) exhibits a typical *Tokukobelba* habitus, however, with the body dimensions, notogastral setation, sensillus, interlamellar setae and several other features being very similar to the specimens collected by me. Their specimens also show: 1) apophyses Aa, Ap, Ba present with Bp absent; 2) verrucose sculpturing; 3) epimeral groove IV distinct. The larva and tritonymphs partially described by Seniczak et al. (2013) show a good fit to the *T. compta* from Heidelberg. Most notably their tritonymphs also show the highly elongate notogastral seta c3. They differ in that they apparently lack the distinct prodorsal cerotegumental cap and instead are described as possessing large granules of cerotegument in the medial part of the prodorsum (Seniczak et al. 2013, p. 296). Except for a detailed drawing of the tibia and tarsus of a leg I of the tritonymph, the leg setation of the larva and tritonymphs is not sufficiently well documented by these authors. The illustration (Seniczak et al. 2013, p. 295, Fig. 3) shows their tritonymph to differ from the species studied by me in displaying a smooth seta d on tibia I and in missing a seta on the tarsal bulb. The seta lacking is probably pl´, with the more distal of the primiventral setal pair in the illustration labelled (pv) presumably being seta pl´´.

Based on the description of Seniczak et al. (2013) their species is clearly not conspecific to the *Tokukobelba* I found in Heidelberg. Nevertheless, although it seems to miss several of the major diagnostic character states shown by the other members of *Tokukobelba* it still appears to belong to the genus. Its morphology conflicts, however, with the original description of *T. compta*.

Kulczyński (1902a, p. 43) presented the following species diagnosis of *T. compta*: “cephalothoracis lateribus inter pedes I et II rotundatis, eminentia pseudostigmata gerenti in latere postico tuberculis duobus ornata, organis pseudostigmaticis flagelliformibus, notogastere modice et subaequabiliter convexa, spinis adnatis carenti, eius pilis dorsalibus parum elevatis, anticis duobus retro directis, pedibus moniliformibus, eorum pilis modice longis, unguibus monodactylus, coxa IV longitudine femur aequanti saltem. Long. 0.55 mm”. Based on this as well as on the more comprehensive species description, written in Latin, and the three illustrations presented by Kulczyński (1902a), the species may be characterized as follows:

Body length 550 µm; body width 360 µm. Prodorsum broad, in dorsal perspective with a rounded lobe laterally between legs I and II. Rostral setae and lamellar setae inserted close to rostral margin in dorsal view. Lamellar setae inserted slightly medial and posterior to the rostral setae, longer than the latter. Bulge of the acetabula of leg I moderately convex. Propodolateral apophysis absent. Laterally situated tubercles Ba present. Tubercles Bp, Da, Dp absent. Laterally between legs II and III with a short, subacute, outwardly directed apophysis Sa. Dorsosejugal groove and centroprodorsal groove distinct. Apophyses Aa and Ap of prodorsal enantiophysis present, former apophysis acute-tipped and associated with a short carina. Bothridium situated on a prominence and directed dorsally and slightly laterally and posteriorly. Sensillus long (240 µm), flagelliform; in proximal straight part with very fine barbs. Interlamellar seta short, directed mediad and posteriad. Exobothridial seta oriented dorsally and somewhat laterally, very little to the posterior.

Notogaster in dorsal view somewhat longer (390 µm) than wide (340 µm), elliptical. In lateral view of only moderate height and almost symmetrically convex. Spinae adnatae absent. Anterior notogastral margin without a sulcus and without tubercles. Discidium at the base of coxa IV acute or obtuse, not recurved. Dorsal notogastral setae all of medium length, moderately curved, lying close to the notogastral surface, but distally not touching the latter. Setae c2-h3 on both sides arranged in a slightly curved line, directed posteriad and slightly laterad. Setae c1 more medially inserted, directed posteriad. Anteriormost two setal pairs c1 and c2 arched, slightly recurved; distance between adjacent setae subequal.

Legs I and II strongly moniliform; legs III and IV moderately moniliform. Leg setae mostly of moderate length. Ungues monodactyle. Segment lengths of leg I: femur 160 µm, genu 49 µm, tibia

80 µm, tarsus 160 µm. Tibia of leg I with 5 setae (v´, v´´, l´, l´´, d) and solenidia φ1 and φ2. Seta d of the tibia of leg I coupled with solenidion φ1, with seta d very thin and short, measuring less than a tenth of the length of its associated solenidion. Famulus on tarsus I emergent.

Segment lengths of leg IV: trochanter 130 µm, femur 120 µm, genu 53 µm, tibia 11 µm, tarsus 200 µm. Leg IV setal formula: 1-2-3-5-4(1)-11. Trochanter IV with only a single seta (v´). Trochanter IV elongate, about similar in length to femur. Femur IV with only 2 setae: d and ev´. Solenidion of tibia IV extremely long and coupled with a minute seta d, latter measuring less than an eighth of the length of solenidion φ.

This description by KULCZYŃSKI (1902a) fits the specimens collected by me in Heidelberg almost perfectly. It conflicts with the portrayal of *T. compta* by SENICZAK et al. (2013) in several major points. KULCZYŃSKI (1902a) does not describe or depict any prodorsal apophyses Da. His illustration of leg I of *T. compta* (KULCZYŃSKI 1902a, pl. 4, Fig. 65) shows 7 setae on the dorsal region of the tibia with the solenidia φ1 and φ2, the lateral setae l´ and l´´ as well as the ventral setae v´and v´´ accurately depicted. Additionally, he clearly shows a seta d associated with the solenidion φ1. Furthermore, he (1902a, pl. 4, Fig. 64) portrays the tibia of leg IV of *T. compta* with 5 setae. Two dorsal setae are here inserted very close to each other. The much longer one clearly represents the solenidion φ, while the tiny seta adjacent to it is the seta d. KULCZYŃSKI (1902a pl. 4, Fig. 64) also depicts the trochanter of leg IV with 1 seta and the femur of leg IV with only 2 setae which clearly can be seen to be d and ev´. The depiction of the setation of leg IV by KULCZYŃSKI is identical to that shown in Fig. 7 of the present publication except that KULCZYŃSKI draws his species with only 1 primiventral seta and 1 antilateral seta instead of two of each. These tarsal setae are among the most difficult to detect on leg IV, because one of each pair is typically hidden behind the tarsus in lateral view. The species portrayed in the present paper therefore shows a much better match to the account of KULCZYŃSKI (1902a) than the one in SENICZAK et al. (2013).

MIKO (2006a, p. 198-200) provides a brief portrayal of *T. compta* in a determination key to Central European species of *Belba*. He does not comment on the leg setation of the species in any detail but (MIKO 2006a, p. 198, Fig. 106f-g) shows it without an apophysis Da, with numerous prominent lateral tubercles, and strongly developed apophysis E4a. The very incomplete account of the species by MIKO (2006a) agrees well with the specimens from Heidelberg, except that in his Fig. 106g the species is shown to possess 4 setae on epimere II, all similar in length to those on epimere I. In contrast to this all species of *Tokukobelba* for which the epimeral setation is known have been described as possessing only 1 seta on epimere II (BULANOVA-ZACHVATKINA 1962, 1975, AOKI 1984, FUJITA & FUJIKAWA 1986, BAYARTOGTOKH 2000, FUJIKAWA 2011). The specimens of *Tokukobelba* from Heidelberg similarly also display only a single seta on epimere II. At 400x magnification I several times observed structures on epimere II that seemed to be additional setae. Yet all turned out to be artifacts caused by the interplay of the numerous tubercles and the dense cerotegument. In those Damaeidae which display 3 or more setae on each epimere II such as *Belba corynopus*, the tritonymph similarly possesses supernumerary setae on epimere II. In the tritonymph of *T. compta* from Heidelberg however, only 1 seta is found on each epimere II. MIKO (2006a) bases his description on representatives of the species collected at various sites in Central Europe. The collection sites of MIKO and me are both much closer to Smreczyna and the other sites in southwestern Poland where KULCZYŃSKI (1902a) collected his *T. compta* than Bergen is. If they should turn out to possess the same epimeral setation formula, it is very likely that the specimens from Heidelberg and the ones studied by MIKO (2006a) are conspecific and do belong to *T. compta* but this requires verification from topotypic material.

Synonyms of *Tokukobelba compta*. MIKO (2006a) has suggested that *T. verrucosa* is a junior synonym of *T. compta*, arguing that oribatids of these species from various collection sites in Central Europe show a close similarity to each other, but not elaborating on this and not mentioning the Asian species of *Tokukobelba*. With apparently no type material of *T. compta* existing, the foremost source of information about the species is the original description. In the Latin text of KULCZYŃSKI (1902a, p. 43-44) the author does not mention any barbs on the notogastral setae, and these also appear smooth in the illustration of the dorsal view of the species (pl. III, Fig. 22), whereas *T. verrucosa* possesses distinctly barbed notogastral setae of the c-, l-, and h-series. The prodorsal lateral margin in KULCZYŃSKI´s Fig. 22 is smooth and does not indicate the presence of the tubercles which are characteristic of *T. verrucosa*. He also does not mention these in his text. These are two of the traits distinguishing the species which are employed by Bulanova-Zachvatkina (1962, p. 209-210, 1975, p. 134) in her species keys of *Belba*. She also states (1962, p. 209-210) that *T. compta* further differs from *T. verrucosa* in the absence of sclerotized prodorsal ridges and in the relatively longer interlamellar setae.

However, Kulczyński (1902a, p. 43) comments in considerable detail on the ridges and sulci of the prodorsum of *T. compta* in his text, and the differences in the lengths of the interlamellar setae between the two species may be considered to be minor. The notogastral setae of the *T. compta* specimens examined by me were very lightly barbed, but this is only visible at high magnification. Assuming that barbs were present, it would be readily understandable that these were not seen or not shown by Kulczyński (1902a). Similarly, not too much significance should be attached to the absence of a dentate prodorsal margin in the very brief account of Kulczyński (1902a). The Latin word “compta” means ‘decorated’ or ‘ornamented’ and may be a reference to the eye-catching tubercles of the species

The synonymy of *T. compta* and *T. verrucosa* sensu Bulanova-Zachvatkina (1962) is possible but not yet proven. Bulanova-Zachvatkina (1962) depicts the latter in her very concise description as possessing only a single median seta on each epimere II instead of the 4 portrayed by Miko (2006a). No type appears to have been designated for *T. verrucosa*, but the first specimens collected and on which the description was based do not originate from Central Europe (Bulanova-Zachvatkina 1962). Based on the shaky evidence at our disposal *T. verrucosa* is therefore not a synonym of *T. compta* sensu Miko (2006a). The identification of a specimen as being either *T. compta* or *T. verrucosa* during the past 50 years has up to now primarily depended on the author of the identification key employed. *Tokukobelba verrucosa* needs to be redescribed from topotypic material to determine whether or not the species is a synonym of the *Tokukobelba* species from Heidelberg.

Wang & Norton (1995) describe *T. verrucosa* from China, but do not mention *T. compta*. The leg chaetotaxy of their specimens is identical to that of *T. compta* from southern Germany, but apparently different to that of *T. verrucosa* from Russia in that these possess 5 setae each on femora I-II (Bulanova-Zachvatkina 1962, p. 264). The illustration that Kulczyński (1902a) gives of the legs I and IV (tab. IV, Figs 64, 65) of *T. compta* in many aspects agrees with the specimens from China and also with those from Germany. Although the numbers of setae in Kulczyński (1902a) differ from those in Wang & Norton (1995), the size and shape of the individual segments and the lengths and positions of major setae indicate a very close overall correspondence.

Oribata farinosa Trägårdh, 1902, a species name very rarely encountered in the damaeid literature, is recombined as *Damaeus* (*Epidamaeus*) *farinosus* by Subías (2004, p. 79). An inspection of the brief original description by Trägårdh (1902) shows that the leg setation of this species is not sufficiently well described to reliably ascertain the tibial associated setation. Furthermore, spinae adnatae are not described for this species and the illustrations of the dorsal and lateral views of *Oribata farinosa* by Trägårdh (1902, Fig. 1, 5-6) show these to be definitely absent. The sensillus of *O. farinosa* is identical in appearance to the highly distinctive sensillus of *T. compta*. The length, shape and insertions of the notogastral setae agree well with those of *T. compta* as depicted by Kulczyński (1902a) as does the overall body shape and the short legs, with leg IV only very slightly longer than the body. Kulczyński (1902a, p. 43) and Trägårdh (1902, p. 16) give identical body lengths of 0,55 mm for *O. comptus* and *O. farinosa*, respectively, and both depict the femur IV as possessing only two setae (Kulczyński 1902a, pl. 4, Fig. 64, Trägårdh 1902, Fig. 1, 9), which can be seen to be d and ev´.

Some years later Trägårdh (1910) redescribed *O. farinosa* in more detail from additional specimens which, like the ones he collected earlier, originate from sites in Lapland Province in Northern Sweden. He recombines *O. farinosa* to *Damaeus farinosus* (Trägårdh 1910). Here he illustrates the prodorsal apophyses Aa and Ap (Trägårdh 1910, p. 521, Fig. 294) as well as the large tubercles on which the epimeral setae insert. It can be seen that the structure which appears to be an apophysis P in the earlier publication (Trägårdh 1902, Fig. 1.5.) is just the large acetabulum II. (Trägårdh 1910, Fig. 294). A prominent apophysis E4a is found in this species (Trägårdh 1910, p. 522, Fig. 297). *Oribata farinosa* therefore clearly belongs to *Tokukobelba* and is a potential synonym of *T. compta*.

Since *T. farinosa* and *T. compta* were both published in the same year, this raises the question of priority. The publication of Trägårdh (1902) was printed on 7th May of that year. Kulczyński introduced his new species in not one, but two separate papers published shortly after each other. One of these (Kulczyński 1902a) is written only in the Latin language, while in the other (Kulczyński 1902b) the text is partially in Latin and partially in German. I have not been able to determine the exact date of publication of the former, but a copy of the latter (Kulczyński 1902b) residing in the library of the Museum of Comparative Zoology at Harvard University bears a library stamp of 28 April 1902. Hence *T. farinosa* is very likely a junior synonym of *T. compta* and not the other way round.

In the present publication only *T. farinosa* and *T. verrucosa verrucosa* are accepted as potential synonyms of *T. compta*. The subspecies *T. verrucosa japonica* from Japan, introduced by Aoki (1984), differs considerably from *T. verrucosa* and is here treated as a full species. Based on the paper of Aoki (1984), *T. japonica* differs from *T. compta* in: 1) smaller body size with a body length of 342-360 µm instead of 460-560 µm for European and Russian specimens of *T. compta*; 2) distinctly longer sensillus; 3) rostrum broadly rounded in dorsal perspective instead of narrow, pointed; 4) femora I and II with 5 and 4 setae, respectively; 5) associated seta d absent on tibia IV. There are several discrepancies between the written description and the illustrations of the species supplied. For example, Aoki (1984, p. 111) states that the femur and tibia of leg I both possess 4 setae, whereas he (p. 113, Fig. 6c) depicts 5 setae on both of these segments. Aoki (1984) describes his species as having only 9 pairs of notogastral setae. However, the pseudanal setae ps2 and ps3 are somewhat cryptic in *Tokukobelba* species since they are short and lie close to the notogastral surface and are hence easy to miss. The associated seta d of tibia IV is very short and regressed in other *Tokukobelba* species. Possibly the protecting seta d was overlooked, but it may also have been strongly reduced or even lost in this species as was noted by Bayartogtokh (2000). *Tokukobelba japonica* needs to be thoroughly redescribed. At present there is no solid basis for establishing a synonymy between this species and *T. compta*.

Species which may belong to or show affinities to *Tokukobelba*. There appear to be several as yet undescribed species within the new genus. For example, the leg setation of *T. sellnicki* from Russia (Bulanova-Zachvatkina 1962) differs significantly from those of China as noted by Wang & Norton (1995), with the Chinese specimens being incompletely described. In a similar fashion, representatives of this species from Korea (Choi & Namkoong 2002), for which the leg setation and ventral features are unknown, differ from the Russian ones in their much shorter notogastral setae and a non flagellate sensillus. It is very likely that a detailed revision also incorporating molecular data will increase the species count of the genus.

A new species of *Parabelbella* Bulanova-Zachvatkina, 1975, was recently reported from China: *Parabelbella dimidiaspina* Xie, Yan & Yang, 2013. Based on its original description this shares with *Tokukobelba*: notogastral setae c1 and c2 inserted very close together and directed posteriad; sensillus barbed in the middle region, distally flagellate; bothridia oriented distinctly posteriolaterad; apophysis Ba present with Bp, Da, Dp absent; centrodorsal apophyses Aa and Ap present; presence of numerous small tubercles on epimeral regions; solenidion of tibia III-IV elongate tactile. Xie et al. (2013, p. 280, Figs 6, 11-12) depict the tarsus of leg I with setae (v1) and (v2) both present, and with a pair of ventral setae located on each of tarsi III and IV. Tarsus I therefore very likely possesses 22 setae instead of the 20 given by these authors, and accordingly, the proral setae are not depicted in the illustration of leg IV (Xie et al. 2013, p. 280, Fig. 6). The authors state that the species displays an associated seta d on tibia II but do not illustrate this, while an associated seta d is instead depicted on tibia III (Fig. 10). The seta d here is not shown as sharing an alveolus with its solenidion φ, but neither is any of the genual setae d shown as inserting in the same alveolus as their associated solenidia σ. *Parabelbella dimidiaspina* seems to be no *Parabelbella* but instead is an unusual *Dyobelba* Norton, 1979, with possibly very close affinities to *Tokukobelba*. This interesting species deserves detailed re-examination.

The enigmatic, incompletely described species *Costeremus yezoensis* Fujikawa & Fujita, 1985, and *C. barbatus* Choi, 1997, both displaying a distinct damaeid habitus and located in the Hungarobelbidae Miko & Travé, 1996, by Subías (2004) and Bayartogtokh & Ermilov (2015), but in the Damaeolidae Grandjean, 1965, by Fujikawa & Fujita (1985), Choi (1997a) and Chen et al. (2010) instead, share several character states with *Tokukobelba*, including the presence of prodorsal apophyses Aa and Ap, absence of spinae adnatae, femora III and IV with 3 and 2 setae, respectively, and an epimeral setation of 3-1-3-3. *Costeremus barbatus* is mentioned as possessing 10 notogastral setae (Choi 1997a). Based on the text of the original description (Fujikawa & Fujita 1985), *C. yezoensis* similarly seems to differ from *Tokukobelba* in the presence of only 10 notogastral setae. The illustrations in Choi (1997a) and Fujikawa & Fujita (1985), however, distinctly show the presence of 11 notogastral setae in both of these species. The leg chaetotaxy of *C. barbatus* is not known, while *C. yezoensis* is characterized by a tibial associated setal formula of 1-1-1-1.

Tokukobelba differs from *Costeremus ornatus* Aoki, 1970, the type of its genus and from *C. cornutus* Wang & Cui, 1996, in: 1) ratio of distance between insertion points of prodorsal setal pairs ro-ro to la-la ranges from 1:1 to 1,3:1 instead of 4:1; 2) notogastral setae setae c2, la, lm, lp insert more or less in a line along the notogastral margin instead of presence of a conspicuous centrodorsal setal pair, inserted very close together; the ratio of distance between the insertion points of the setal pairs la-la or lm-lm to that between those of the centrodorsal setal pair, termed dp by Wang & Cui (1996), is between 3:1 to 4:1; 3) anterior prodorsal ridges do not extend to insertion points of rostral setae; 4) notogastral and adanal setae not short, with long barbs and a stellate appearance; 5) anteriormost genital seta not hypertrophied and not 3x length of setae g3, g4; 6) substantially longer legs; 7) notogaster posteriorly without a distinct protuberance; 8) bothridium without spinelike processus; 9) humeral processes or spinae adnatae absent; 10) absence of two pairs of ridges on the anterior of the notogaster, posterior to the structures called first notogastral ridges by both Aoki (1970) and Wang & Cui (1996), but which I interpret as being humeral processes or spinae adnatae instead.

Neither *C. yezoensis* nor *C. barbatus* or the recently discovered *C. stebaevae* Bayartogtokh & Ermilov, 2015, display any of these ten attributes in which the type species of *Costeremus* Aoki, 1970, differs from *Tokukobelba*, and I consider their inclusion in *Costeremus* most uncertain. I agree with Bayartogtokh & Ermilov (2015) in locating these 3 species in the Hungarobelbidae, however, based on our current knowledge about them. Like *Hungarobelba* Balogh, 1943 they may be considered proto-damaeids, and their phylogenetic relationship to *Tokukobelba* requires investigation.

6 Comparative morphology and evolutionary systematics of *Tokukobelba*

In this section I will comment in depth on several of the extraordinary traits characterizing the new genus and also on those characters which it shares with *Belba*. This is followed by an attempt to shed some light on the position of *Tokukobelba* within the Damaeoidea.

Trochanteral setation

Tokukobelba shares a leg trochanteral setation formula of 1-1-2-1 with the great majority of Damaeidae, including all representatives of *Belba* except *B. californica* (Banks, 1904), *B. rossica* Bulanova-Zachvatkina, 1962, and *B. crassisetosa* Bayartogtokh, 2000, in which the setation is 1-1-2-2 based on the original descriptions and the redescription of *B. californica* by Norton (1979c). A trochanteral setation of 1-1-2-1 characterizes numerous basal Brachypylina (Woas 2002) and appears to represent the ancestral state for the Damaeidae and also for the Brachypylina as a whole. Higher setal counts appear to have evolved independently within many families of higher Oribatida.

Femoral setation

Tokukobelba is characterized by a strongly reduced femoral setation with 3 setae usually found on femur III and 2 on femur IV (Figs 6-7). Here setae d, ev´ and l´ are developed on femur III, while on femur IV only setae d and ev´ occur. Compared to *Belba corynopus*, ventral setae v´ and v´´ are both absent on femora III and IV, with seta l´ additionally missing on the femur of leg IV. In the Damaeidae setae d and ev´ are found on femur III in the larval stage, while l´ is deutonymphal in appearance on this segment, whereas in sharp contrast setae d and ev´ are deutonymphal in appearance on femur IV (Norton 1977b). Ventral setae in the Damaeidae are added in the tritonymph or more often in the adult, as in *B. corynopus* and *B. sculpta* (pers. obs.).

In the ontogeny of *Tokukobelba* no regression or loss of femoral setae occurs. Instead the ventral setae on femora III and IV, and seta l´ on femur IV are simply never formed. Such a low femoral setal count is unique in Damaeidae where reliably known, although *Dasybelba perona* Wool-

LEY & HIGGINS, 1979, *D. aphelesa* WOOLLEY & HIGGINS, 1979, and *Tectodamaeus cordatus* XIE & YANG, 2010, have been described with a femoral setation formula of 5-5-3-3, based on the original descriptions. That the femoral setation of *Tokukobelba* is clearly more primitive than in all other Damaeidae was already noted many years ago by NORTON (1977b). Indeed, it is reminiscent of numerous other basal brachypyline groups (WOAS 2002).

Genual setation

The genua I-III of *Tokukobelba* show a solenidion and a companion seta d originating from a shared alveolus with the solenidion being distal to the seta. A solenidion is absent on genu IV but seta d is present. *Tokukobelba* shares a genual associated setal formula of 1-1-1-0 with all damaeids except three species of *Damaeus* KOCH, 1835, in which more than one seta d is absent on genu I-IV (NORTON 1977b, PÉREZ-ÍÑIGO 1987, MIKO 2006a). Among the Damaeidae with companion setae d on genua I-III the great majority share a genual setation of 4-4-3-3. NORTON (1977a) in his PhD considered a genual associated setation of 1-1-1-0 to be plesiomorph for the Damaeidae. This is indeed very probable. The genual setation of 4-4-3-3, shown by both *Belba* and *Tokukobelba* is likely to represent the ancestral character state.

The larval seta d on genua I-III of *Tokukobelba* is extremely small, smooth and very difficult to perceive (Fig. 16). *Tokukobelba* shares this character state, which is probably derived within the Eupheredermata (NORTON 1977a) with all members of its family except *Quatrobelba* NORTON, 1980, where the seta is almost as long as the solenidion and barbed (NORTON 1980).

Tibial setation

Tokukobelba barbata is described as possessing an associated seta d on tibia I by FUJITA & FUJIKAWA (1986), and the authors clearly illustrate this (p. 8, Fig. 2b). AOKI (1984) mentions the presence of 4 setae and 2 solenidia on the tibia of leg I of *T. japonica* but his illustration of leg I (p. 113, Fig. 6c) shows the presence of 5 setae and the solenidia φ1 and φ2. In addition to setae v´, v´´, l´ and l´´ a short seta is depicted which in its proximal half appears to lie directly proximal to solenidion φ1 in the antiaxial perspective shown. Although the insertion point of this seta is not visible, its size and location match that of the associated seta d of *T. barbata*. KULCZYŃSKI (1902a, tab. IV, Fig. 65) similarly portrays a seta d associated with the solenidion φ1 on the tibia of leg I. In all specimens of *T. compta*, in which the tibial leg setation was examined in detail by me (n = 12), a short, very thin seta d was seen to be present on the tibia of leg I (Fig. 4). This was coupled to solenidion φ1. The thickness and relative size of the seta d shows a very close correspondence to that drawn by KULCZYŃSKI (1902a), AOKI (1984) and FUJITA & FUJIKAWA (1986). An associated seta d on tibia I has not been discovered for Russian or Chinese specimens of *T. verrucosa* and *T. sellnicki* (BULANOVA-ZACHVATKINA 1962, 1967, 1975, WANG & NORTON 1995), for *T. mongolica* (BAYARTOGTOKH 2000) or for *T. itsukiensis* (FUJIKAWA 2011). Possibly it is also present in these species as the very thin seta is extremely easy to overlook.

A tibial associated setation of 1-1-1-1 is already found in basal Oribatida such as the Brachythonioidea THOR, 1934, (MORITZ 1976), the Pthiracaroidea PERTY, 1841, (NIEDBALA 1992) and Crotonioidea THORELL, 1876, such as *Nothrus* KOCH, 1836, (OLSZANOWSKI 1996) and *Camisia* VON HEYDEN, 1826, (COLLOFF 1993, OLSZANOWSKI 1996). Within the Brachypylina this pattern occurs in, for example, *Tricheremaeus* BERLESE, 1908, (WOAS 2002), as well as in basal Circumdehiscentiae such as the Neoliodidae SELLNICK, 1928, Plasmobatidae GRANDJEAN, 1961, and the Hermanniellidae GRANDJEAN, 1934, if the tibial solenidia are present (WOAS 2002, NORTON & BEHAN-PELLETIER 2009, ERMILOV et al. 2010b). Within the Ameroidea BULANOVA-ZACHVATKINA, 1957, a tibial associated setal formula of 1-1-1-1 is so far apparently only documented for two species of *Hungarobelba* (MIKO & TRAVÉ 1996) and for *Costeremus yezoensis* (FUJIKAWA & FUJITA 1985).

The presence of an associated seta on tibia I is exceptionally rare in Damaeidae besides *Tokukobelba*, having only once been noted by GRANDJEAN (1954) for some specimens of a single population of *Porobelba spinosa* (SELLNICK, 1920) from Italy. NORTON (1979a) considered a tibial associated setal formula of 0-1-1-1 to be plesiomorph for the Damaeidae. The tibial associated setation of 1-1-1-1 of *Tokukobelba* is evidently even more primitive than that, and the genus therefore lacks a major derived character state of the Damaeidae.

Tokukobelba usually possesses setae d on tibiae II-IV which are quite short and thin; and at the same time displays a very elongate solenidion φ of tibia IV, about 5 times the length of its associated seta d (Figs 6-7). This is unique in Damaeidae and differs greatly from *Belba* in which there is no such extreme reduction in the length and diameter of seta d of tibia IV when compared to the remaining setae and in which the solenidion φ of tibia IV is relatively short, not elongate and tactile, based on the descriptions in Grandjean (1936), Märkel & Meyer (1960), Bulanova-Zachvatkina (1962), Norton (1979c), Enami (1989, 1994), Wang & Norton (1995), Tolstikov (1996), and Bayartogtokh (2000).

Tarsal setation

Tokukobelba is characterized by the presence of 22 and 18 setae on the tarsi of legs I and II, respectively (Figs 4-5), while 17 setae are usually found on tarsus III, and 14 on tarsus IV (Figs 6-7). Here ventral setae v1´, v1´´, v2´and v2´´ are found on tarsus I, setae v1´, v1´´ and v2´ on tarsus II, and setae v1´, v1´´ on both tarsus III and IV. This setation pattern is unique within Damaeidae. Only in *Epidamaeus folium* Fujikawa & Fujita, 1985, based on the original description, and in *Epidamaeus tenuissimus* Hammer, 1967, (Behan-Pelletier & Norton 1985) has the presence of 22 setae on tarsus I so far been detected. However, in both of these species 19 setae are found on tarsus II instead (Behan-Pelletier & Norton 1985, Fujikawa & Fujita 1985).

In the vast majority of Damaeidae, including the genera *Belba*, *Metabelba* and *Dyobelba* only 20 setae occur on tarsus I. Solely in a small number of species of the huge genus *Epidamaeus* Bulanova-Zachvatkina, 1957, (Behan-Pelletier & Norton 1983, Fujikawa & Fujita 1985, Bayartogtokh 2004b), in *Spatiodamaeus* Bulanova-Zachvatkina, 1957, (Norton 1977b, Miko 2006a), and in the majority of the representatives of *Damaeus* (Grandjean 1960a, Norton 1977b, 1978a), including the subgenus *Tectodamaeus* Aoki, 1984, (Wang & Cui 1994, Enami & Aoki 1998, Xie & Yang 2009) are 21 setae present on tarsus I. Where 21 setae are found on tarsus I in these species, with setae v1´, v1´´and v2´ present, and seta v2´´ absent, the seta v2´ is generally present on the tarsi of legs II-IV as well, resulting in a tarsal setation formula of 21-18-18-15 (Norton 1977b), very different from that of *Tokukobelba*.

In *Tokukobelba* the setae v1´, v1´´, v2´ and v2´´ of tarsus I arise in the adult stage, being absent in the tritonymph (Fig. 18). In those damaeids with 21 setae on tarsus I, such as *Damaeus* and *Spatiodamaeus* seta v1´ is tritonymphal in origin instead with v1´´ and v2´ added in the adult (Norton 1977b). An ontogeny of setae v1 and v2 on tarsus I identical to *Tokukobelba* is extremely rare in the Brachypylina, but is known from *Nothrina* van der Hammen, 1982, such as *Novonothrus* Hammer, 1986, (Casanueva & Norton 1997). The occurrence of a supernumerary tarsal setation in *Damaeus*, *Spatiodamaeus* and some *Epidamaeus* frequently is correlated with the evolution of very elongate legs, including long tarsi (Behan-Pelletier & Norton 1985). The short stubby legs typical of *Tokukobelba* however contrast greatly with those of species like *Epidamaeus tenuissimus*, where the length of leg IV equals between 2 and 3 times the body length (Behan-Pelletier & Norton 1985).

In almost all species of *Belba* for which a description of the leg chaetotaxy is reliably known, with the exception of *B. rossica* (Wang & Norton 1995), *B. crassisetosa* (Bayartogtokh 2000) and *B. californica* (Norton 1979c), 16 setae are found on tarsus III and 13 on tarsus IV (Grandjean 1936, Bulanova-Zachvatkina 1962, Enami 1994, Tolstikov 1996, Tolstikov & Lyashchev 1996, Bayartogtokh 2000, 2004a). In this case only a single ventral seta, namely v1´, occurs on each of tarsi III and IV. *Tokukobelba* does not share this possibly derived trait. The tarsal setal count of legs III and IV of *Tokukobelba* is instead identical to genera such as *Dyobelba* (Norton 1979c, 1979d, Bayartogtokh et al. 2001, Enami & Aoki 2001, Bayartogtokh & Norton 2007) and *Metabelba* (Grandjean 1954, Mourek et al. 2011a). The tarsal setal formula of *Tokukobelba* appears to be highly derived and an autapomorphy of the genus.

Aoki (1984: p. 113) states that there are 21 setae on the tarsus of leg I of *Tokukobelba japonica* and he includes the famulus in the setal count. Bayartogtokh (2000, p. 313) similarly counts 21 setae on tarsus I of *T. mongolica*. These setal scores differ from those given by Wang & Norton (1995) for Chinese specimens of *T. verrucosa* and *T. sellnicki* and also from those obtained by Fujita & Fujikawa (1986) for *T. barbata*. These authors discovered 22 setae on tarsus I, which agrees with results obtained for specimens of *T. compta* collected by me in southern Germany. In *T. itsukiensis* setae v1´, v1´´, v2´ and v2´´ are similarly found on tarsus I based on Fujikawa (2011, Fig. 3a). The illustration of leg I presented by Aoki (1984, p. 113, Fig. 6c) shows the tarsus with the two solenidia ω1 and ω2, and 19 setae, including the famulus. Only 6 setae are shown situated on the tarsal bulb, instead of the 9 present in, for example, *T. barbata* and the 8 that would be expected, if the total setal count were 21. Since it is often very difficult to accurately determine the tarsal chaetotaxy with a light microscope, the tarsi here require re-examination. The illustration of leg I given by Bayartogtokh (2000, p. 311, Fig. 28) does show 21 setae and two solenidia. However, the famulus is apparently not depicted. *T. mongolica* therefore very likely possesses 22 setae on the tarsus of leg I. Bayartogtokh (2000) accordingly clearly pictures, but does not name, the ventral setae v1´, v1´´, v2´ and v2´´.

The famulus on tarsus I is fully emergent in the larva and nymphs of *Tokukobelba compta* (Figs 16-18), (Mourek & Miko 2010, Seniczak et al. 2013, pers. obs.) as in the ontogenetic stages of genera such as *Belba* (Grandjean 1954, Norton 1977b, 1979c, Norton & Palacios-Vargas 1982, Seniczak & Seniczak 2013), *Porobelba* Grandjean, 1936, (Grandjean 1954, Ermilov & Lochynska 2009), *Quatrobelba* (Norton, 1980), *Metabelba* (Grandjean 1954, Ermilov 2010b, Ermilov et al. 2010a) and *Metabelbella* Bulanova-Zachvatkina, 1957, (Ermilov & Khaustov 2011) while a sunken famulus, reduced in size and submerged in a sclerotized cup, occurs in the larva and the nymphs of, for example, *Damaeus* (Grandjean 1935, 1954, 1960a, Norton 1977b, 1978a, Ermilov et al. 2010a), most *Epidamaeus* (Norton 1977b, 1979c, Enami & Fujikawa 1989, Ermilov & Lochynska 2009) and *Weigmannia* Miko & Norton, 2010, (Norton 1977b, p. 46). An emergent famulus appears to have been ancestral within the eupherederm mites and occurs in the large majority of Brachypylina (Grandjean, 1935) although some groups such as the Gymnodamaeidae Grandjean, 1954, (Paschoal 1987) and Zetorchestidae Michael, 1898, (Grandjean 1951) display a sunken famulus in all stases. The emergent famulus of *Tokukobelba* appears to represent a phylogenetically very ancient character.

On the tarsus of leg I of adult *Tokukobelba* the primilateral pl´´ and primiventral seta pv´ do not insert on the tarsal bulb but in the middle region of the tarsus instead, whereas setae pl´ and pv´´ do insert on the bulb based on my own observations, on Wang & Norton (1995) and on the illustrations in Aoki (1984), Fujita & Fujikawa (1986), Bayartogtokh (2000) and Fujikawa (2011), although in the last four papers these setae are not identified by name by the authors. In the larva of *Tokukobelba compta* all of these setae insert on the bulb, but seta pv´ and pl´´ are distally displaced in later ontogenetic stages (Figs 10-13). This ontogenetic pattern differs strongly from genera such as *Damaeus* (Norton 1977a, 1978a, Bernini & Arcidiano 1979, Enami & Aoki 1988, Xie & Yang 2009), almost all *Epidamaeus* (Miko et al. 2011), *Kunstidamaeus* Miko, 2006, (Miko 2006b, Miko & Mourek 2008) and *Dyobelba* (Norton 1979b, Norton 1979c, Norton & Ryabinin 1994, Enami & Aoki 2001, Bayartogtokh & Norton, 2007) in which seta pv´´ additionally shifts anteriad in the adult stage. An ontogenetic setal shift of the primiventral setae corresponding to *Tokukobelba* occurs in *Belba* (*Protobelba*) (Norton, 1979c), *Weigmannia* (Miko & Norton, 2010) and also *Lanibelba* Norton, 1980, based on its original description.

Setal ontogenies in *Belba* (*Belba*) (Grandjean 1936, Norton & Palacios-Vargas 1982, Enami 1994, Wang & Norton 1995, Tolstikov 1996, Tolstikov & Lyashchev 1996, Bayartogtokh 2000, 2004a), *Metabelba* (Mourek et al. 2011a), *Porobelba* (Miko 2008) and *Acanthobelba* Enami & Aoki, 1993, based on its initial description and on Choi 1997b) contrast with *Tokukobelba* in that on the tarsus I of leg I of these, with very rare exceptions, pl´´, and particularly pv´ and pv´´, experience only a minimal distal migration and all are inserted on the bulb in the adult. This pattern is also known from many other Brachypylina, including species within the Autognetidae Grandjean, 1960, (Grandjean 1960b, 1960c, Bayartogtokh 2012), Staurobatidae Grandjean, 1966, (Grandjean 1966), Damaeolidae (Grandjean, 1965a) and *Hungarobelba* (Miko & Travé, 1996). Compared to this ancestral state the one in *Tokukobelba* is moderately derived and that of *Damaeus* highly derived.

Spinae adnatae

Spinae adnatae are found in approximately two thirds of the presently known species of Damaeidae. Other than in *Tokukobelba* and *Belba* (*Belba*) (Bayartogtokh 2000), the structures are absent in *Dameobelba* Sellnick, 1929, (Grandjean 1955, Norton 1977a, pers. obs.), *Caenobelba* (Norton, 1979c), *Subbelba* Bulanova-Zachvatkina, 1967, (Skubala 1992), *Neobelba* Bulanova-Zachvatkina, 1967, (Bulanova-Zachvatkina 1975, p. 121, 131), *Metabelba* (Bulanova-Zachvatkina 1965, Mourek et al. 2011a), *Mirobelba* Pérez-Íñigo & Peña, 1994, and *Parabelbella* (Bulanova-Zachvatkina 1975, Miko et al. 2011). *Belba* (*Protobelba*) possesses spinae adnatae (Norton 1979c). Spinae adnatae are variably present or absent within *Dyobelba* (Norton 1979b, Norton & Ryabinin 1994, Bayartogtokh & Norton 2007), *Epidamaeus* (Norton

1979b, Lyashchew & Tolstikov 1993, Miko et al. 2011), *Porobelba* (Subías 1977, Miko 2008), *Damaeus* (*Tectodamaeus)* (Aoki 1984, Wang & Cui 1994, Lu & Wang 1995, Xie & Yang 2009), and *Metabelbella* (Bulanova-Zachvatkina 1967, 1975, Arillo & Subías 2006, Ermilov & Khaustov 2011, Ermilov, Shtanchaeva & Subías 2012).

Only exceptionally rarely are spinae adnatae present in Brachypylina other than the Damaeidae. They are seen, however, in a few isolated members of the Ameroidea such as *Hungarobelba* (Norton 1977a, Miko & Travé 1996), *Costeremus ornatus* (Aoki 1970) and *C. cornutus* (Wang & Cui 1996) within the Damaeolidae, and also *Roynortonia* Ermilov, 2011, in the Amerobelbidae Grandjean, 1961, (Ermilov 2011). In the overwhelming majority of Ameroidea spinae adnatae are absent, but in many, including the Ameridae Bulanova-Zachvatkina, 1957, (Chen et al. 2004), Heterobelbidae Balogh, 1961, (Beck 1962), Eremulidae Grandjean, 1965, (Pérez-Íñigo 1997), Amerobelbidae (Grandjean 1961), Staurobatidae (Grandjean 1966), Ctenobelbidae Grandjean, 1965, (Mahunka 1974, 1977, Woas 1986, Baran 2012) and Rhynchoribatidae Balogh, 1961, (Balogh 1970, Mahunka 1985, Woas 1986), humeral condyles are often visible in an analogous position.

Norton (1977a) sees the spinelike spinae adnatae as derived from such humeral tubercles and (1977a, 1979a) assumes their presence to be plesiomorph for the Damaeidae. However, it is quite possible that spinae adnatae arose one or more times within the Damaeidae and that the character state of *Tokukobelba* may represent the ancestral one. Spinae adnatae appear to have been gained or lost independently or in parallel in several lineages or clades of Damaeidae. Nevertheless their presence is a very strong indicator that a mite does belong to the Damaeidae. *Tokukobelba* misses this major family character.

Propodolateral apophyses

An apophysis P is generally absent in *Tokukobelba* (Fig. 1), although Choi & Namkoong (2002, p. 27, Fig. 4) depict what appears to be a minute tip-like apophysis P for *T. sellnicki*, and is also not detected in any species of *Belba* except *B. cornuta* Wang & Norton, 1995, *B. sarvari* Tolstikov, 1996, and *B. flammeisetosa* Tolstikov, 1996, based on their original descriptions. The apophysis P is missing in *Quatrobelba* (Norton 1980), *Dameobelba* (Norton 1977a), *Porobelba* (Miko 2008), *Caenobelba* (Norton 1979c), *Subbelba* (Skubala 1992), *Acanthobelba* (Enami & Aoki 1993, Choi 1997b), *Mirobelba* (Pérez-Íñigo & Peña 1994), *Dasybelba* (Woolley & Higgins 1979) and *Lanibelba* (Norton 1980). The structure is variably present or absent within *Epidamaeus* (Norton 1979c, 1979d, Lyashchew & Tolstikov 1993), *Metabelba* (Mourek et al. 2011a), *Belbodamaeus* (Bayartogtokh 2004a) and *Dyobelba* (Norton 1979c, 1979d, Wang & Norton 1993, Enami & Aoki 2001).

Within the latter genus it is not even a constant feature of the otherwise morphologically very homogeneous and clearly monophyletic *Dyobelba tectopediosa* species group (Bayartogtokh & Norton 2007). An apophysis P is seldomly encountered outside of the Damaeidae, but is known, for example from Pheroliodidae Paschoal, 1987, (Grandjean 1964) and the genera *Veloppia* Hammer, 1955, (Norton 1978b, Chen & Wang 2002), *Hungarobelba* (Norton 1977a; Miko & Travé 1996) and *Costeremus* (Aoki 1970, Fujikawa & Fujita 1985, Wang & Cui 1996, Choi 1997a).

Norton (1979a), following Grandjean (1960a), argues that the apophysis P is derived from the pedotectum I. The latter is commonly found in pycnonotic Oribatida (Woas 2002). Pedotecta I are auriculate or scale-like structures projecting from the body wall immediately posterior to acetabulum I, whereas the apophyses P are toothlike or ceratiform projections between legs I and II which are not directly adjacent to an acetabulum (Grandjean 1960a, Norton & Behan-Pelletier 2009). Norton (1977a, 1979a) assumes the presence of an apophysis P to be the ancestral state for the Damaeidae. If so, the character state of absence of apophysis P appears to have been subject to considerable convergent or more likely parallel evolution within the Damaeidae.

Anterolateral apophyses

Both anterior Ala and posterior anterolateral apophyses Alp are present in *Tokukobelba compta* (Figs 1, 3). The simultaneous occurrence of both of these structures, which may be attributes of other species in the genus, as they are very easy to overlook, has amongst Damaeidae so far only been noted for *Metabelba denscanis* by Mourek et al. (2011a). Due to the strongly laterally displaced bothridia and apophyses Ba of this species, the homology of its anterolateral apophyses with those in *Tokukobelba* is somewhat unclear, but very likely. A clear homologue of the apophysis Ala of *T. compta* is found in four species of the *Dyobelba tectopediosa* species group, based on Bayartogtokh & Norton (2007), who view the structure as belonging to acetabular tectum I.

In an illustration of the prodorsum of *T. sellnicki*, a structure resembling a minute apophysis P is depicted unilaterally by Bulanova-Zachvatkina (1962, p. 209, Fig. 4.3). In a later illustration of the prodorsum of this species by Bulanova-Zachvatkina (1975, p. 133, Fig. 255) this apophysis is not shown, and the author does not describe the species as possessing an apophysis P. The structure appears to correspond to the posterior anterolateral apophysis Alp of the specimens of *T. compta*. The hypothesis that apophysis Alp of *Tokukobelba* is homologous to apophysis P seems unlikely since these structures differ considerably in several details regarding their location on the prodorsum. In lateral view, apophysis P is usually on the same plane as insertions of legs, whereas Alp is situated much higher up, and mediad to the propodolateral apophysis. Structurally Alp is derived from acetabular tectum II.

In *Hungarobelba*, which displays an apophysis P, a sclerotized ridge is described in the area between the bothridium and acetabulum II, ventral to the insertion point of the exobothridial seta by Miko & Travé (1996). A clearly identical structure occurs in *T. compta* and apparently also in *T. itsukiensis* (Fujikawa 2011, p. 2, Fig. 1). In *Hungarobelba* the ridge terminates rostrally without an apophysis (Miko & Travé 1996), while in *T. compta* its rostral tip is formed by apophysis Alp. The phylogenetic significance of the anterolateral apophyses is unclear. They seem to be rare in Oribatida.

Prodorsal apophyses Aa and Ap

Apophyses Aa and Ap are exceptionally rare within the more than 270 described species of Damaeidae. Other than in *Tokukobelba* (Figs 1, 3), apophyses Aa are only found in *Dyobelba dindali* Bayartogtokh & Norton, 2007, and *D. granulata* Bayartogtokh & Norton, 2007, based on the original descriptions as well as in *Caenobelba alleganiensis* (Norton 1979c) and *Parabelbella dimidiaspina* (Xie et al. 2013). Among the Damaeidae presently known only the latter species shares the presence of apophysis Ap with *Tokukobelba* and may possibly even belong to the new genus.

Prodorsal enantiophyses Aa and Ap are quite uncommon within the Oribatida as a whole and generally absent in both the Lower Oribatida and the Poronota (Woas 2002). Within the Brachypylina, they can be found within the Autognetidae such as in *Autogneta* Hull, 1916, (Grandjean 1960b), *Conchogneta* Grandjean, 1936, (Bayartogtokh 2012) and *Cosmogneta* Grandjean, 1960, (Grandjean 1960c), and also the species *Licnobelba latiflabellata* (Paoli, 1908) and *Flabellobelba almeriensis* (Ruiz, Kahwash & Subías, 1990) in the Licnobelbidae Grandjean, 1965, (Pérez-Íñigo 1993, 1997). They also occur in some representatives of the gymnodamaeid Eupheredermata such as the genera *Lopholiodes* Paschoal, 1987, and *Pheroliodes* Grandjean, 1931, in the Pheroliodidae (Balogh 1962, Grandjean 1964, Paschoal 1987) and similarly *Plateremaeus* Berlese, 1908, and *Calipteremaeus* Paschoal, 1987, in the Plateremaeidae Trägårdh, 1926, (Grandjean 1964, Paschoal 1987, Woas 2002).

In the Ameroidea, prodorsal enantiophyses A are very rare. Apophyses Aa and Ap are present in *Rhynchoribates robinsoni* Balogh, 1962, based on its original description and also in *Caleremaeus monilipes* Michael, 1882, (Miko & Travé 1996). In *Staurobates schusteri* Grandjean, 1966, a conspicuous enantiophysis is sited laterally on the prodorsum anterior to acetabulum I. This was called an “énantiophysis collaire” by Grandjean (1966, p. 702) who did not identify it as a prodorsal enantiophysis, although he had already used that name previously (Grandjean 1960b, p. 366). Woas (2002) perceives the “énantiophysis collaire” as being a homologue of the prodorsal enantiophysis. The species *Veloppia kananaskis* Norton, 1980, located in the family Caleremaeidae Grandjean, 1965, by its author, but sharing significant character states with the Hungarobelbidae (Woas 2002), displays a complete prodorsal enantiophysis, but the structure is absent in the remaining two *Veloppia* species (Norton 1978b, Chen & Wang 2002).

Hungarobelba visnyai Balogh, 1938, displays distinct apophyses Aa and also anterior ridges, ridges associated with the bothridia, and a central prodorsal elevation between the bothridia (Miko & Travé 1996) as is typical of *Tokukobelba*. In *H. pyrenaica* Miko & Travé, 1996, apophysis Aa is absent, but the other structures are still present. The posterior apophysis Ap is absent in these species (Miko & Travé 1996). *Costeremus ornatus* displays a system of prodorsal ridges and apophyses very similar to *Tokukobelba*. Here a posterior apophysis Ap is clearly present while the presence of Aa is probable, although the description by Aoki (1970) is somewhat unclear about this. *Costeremus cornutus* possesses similar ridges to the latter and a complete prodorsal enantiophysis also appears to exist (Wang & Cui 1996). In *Costeremus yezoensis* and *C. barbatus* the apophyses Aa and Ap are both present (Fujikawa & Fujita 1985, Choi 1997a).

The phylogenetic distribution of the prodorsal enantiophysis suggests that in possessing this, *Tokukobelba* retains a highly primitive character state, linking it to *Hungarobelba*, *Costeremus* and also several basal Eupheredermata, that has become lost in virtually all other Damaeidae. The combined presence of Aa and Ap may however also be interpreted as an autapomorphy of *Tokukobelba*.

Interbothridial protuberance

An interbothridial protuberance forming a circular structure when viewed from above (Figs 1, 3) -appears to be characteristic of *Tokukobelba*, based on the contributions of Bulanova-Zachvatkina (1962, 1967, 1975), Bayartogtokh (2000), Fujikawa (2011), Choi & Namkoong (2012) and my own observations, although the character is not mentioned or clearly depicted in the brief descriptions of *T. japonica* or *T. barbata* (Aoki 1984, Fujita & Fujikawa 1986). Such a prodorsal protuberance is apparently absent in all Damaeidae besides *Tokukobelba*. Clearly homologous prodorsal elevations exist in *Hungarobelba* (Miko & Travé 1996) and in at least three species of *Costeremus* (Aoki 1970, Wang & Cui 1996; Bayartogtokh & Ermilov 2015) but are otherwise very seldomly encountered in brachypyline oribatid mites.

Epimeral setation

A setal formula of 3-1-3-3 for epimeres I-IV (Figs 2, 3) is shown by all members of *Tokukobelba* (Bulanova-Zachvatkina 1962, Aoki 1984, Fujita & Fujikawa 1986, Bayartogtokh 2000, Fujikawa 2011) where reliably known. Such a pattern is so far unknown for *Belba*.

In *Belba* (*Protobelba*), 3 setae are found on epimere II (Norton 1979c). Similarly 3 or 4 setae are present on epimere II in the *Belba corynopus* group (Grandjean 1936, Märkel & Meyer 1960, Enami 1994). In *Belba* (*Protobelba*) (Norton, 1979c) and within the *Belba corynopus* species group, 4 or more setae are inserted on epimere IV, where dependably known (Grandjean 1936, Enami 1994, Pérez-Íñigo 1997). All members of *Belba* without epimere II neotrichy and for which the epimeral setation is known, such as *B. cornuta* Wang & Norton, 1995, *B. flammeisetosa* Tolstikov, 1995, *B. heterosetosa* Bayartogtokh, 2000, and *B. prasadi* Bayartogtokh, 2000, possess an epimeral setation of 3-1-3-4 as evidenced by the original descriptions.

Within the Damaeidae, an epimeral setation of 3-1-3-3 is quite rare and has so far been noted for *Metabelba platynotus* Grandjean, 1954, *Metabelba glabriseta* Mahunka, 1981, (Ermilov et al. 2010a), *Porobelba weigmanni* Miko, 2008, *Nododamaeus monticola* Hammer, 1977, as well as for some *Epidamaeus* such as *E. tenuissimus* Hammer, 1967, (Behan-Pelletier & Norton 1985) and *E. berlesei* Michael, 1898, (Bernini 1970). Like numerous other features of significance in damaeid systematics, the epimeral setation formula may be subject to variability within some species. In *Damaeus flagellifer* Michael, 1890, for example, epimeral setations of 3-1-3-3 coexist with those of 3-1-3-4, with the latter formula being the most common (Bernini & Arcidiano 1979).

Tokukobelba shares an epimeral setation of 3-1-3-3 with all five species of *Costeremus* (Aoki 1970, Fujikawa & Fujita 1985, Wang & Cui 1996, Choi 1997a, Bayartogtokh & Ermilov 2015) and *Veloppia* (Norton 1978b, Chen & Wang 2002). This characteristic is also found in virtually all Ameroidea (Grandjean 1959b, 1961, 1965a, 1965b, 1966, Beck 1962, Woas 1986, 2002, Aoki & Yamamoto 2000, Chen et al. 2004, Mahunka 2009, 2010, Ermilov et al. 2011, 2012, Ermilov & Coetzee 2012) except apparently only the Rhynchoribatidae with a setation formula of 3-1-2-5 or 3-1-3-5 (Mahunka 1985, 1986, Woas 1986) and *Hungarobelba* which features 3 or 4 setae on epimere II (Norton 1977a, Miko & Travé 1996).

The possession of 2 or 3 setae on epimere IV is typical of the great majority of basal Brachypylina (Grandjean 1934, Woas 2002) such as most Neoliodidae (Woas 2000), Gymnodamaeidae (Paschoal 1987, Woas 1992, Bayartogtokh 2001, Hugo 2010) and Plateremaeidae (Paschoal 1987, Woas 1992, Hunt 1996), as well as the Licnodamaeidae Grandjean, 1954, (Pérez-Íñigo 1997), Pheroliodidae (Pérez-Íñigo 1997), Licnobelbidae (Grandjean 1965, Pérez-Íñigo 1993), Cymbaeremaeidae Sellnick, 1928, (Woas 2000) and Eremaeidae Oudemans, 1910, (Behan-Pelletier 1993). Norton (1979a) suggests that an epimeral setation of 3-1-3-4 is plesiomorph for the Damaeidae. I agree with this conclusion insofar that I regard the rich epimeral setations of the *Belba corynopus* group as being derived. I believe, however, that the epimeral setation of 3-1-

3-3 shown by *Tokukobelba* reflects the anchestral character state for the family instead.

Epimeral apophyses

In *Tokukobelba* the epimeral setae, particularly those of epimeres III and IV, insert on or directly adjacent to greatly enlarged tubercles or apophyses (Figs 2, 3) except apparently in *T. itsukiensis* (Fujikawa 2008). Although epimeral setae are sited on tubercles in several damaeid species including *Dyobelba carolinensis* (Norton 1979c), *D. paucituberculata* (Bayartogtokh et al. 2001) and *Epidamaeus gilyarovi* (Behan-Pelletier & Norton 1985), these are generally small, relatively inconspicuous and not associated with setae 4a, 4b, 4c. The only other Damaeidae besides *Tokukobelba* in which all epimeral setae insert on enlarged tubercles are *Dyobelba crossleyi*, *D. dindali*, *D. granulata* and *D. tectopediosa* based on Bayartogtokh & Norton (2007). However, in these as in all Damaeidae besides *Tokukobelba*, epimeral grooves III and IV and their apodemes are inconspicuous.

Furthermore, in *Tokukobelba* the tubercles associated with setae 3a, 3c, 4a, 4b and especially 4c are massive, relatively very much larger than in any other damaeid mite. In *Costeremus yezoensis* and *C. barbatus*, all of the epimeral setae insert on sizeable tubercles (Fujikawa & Fujita 1985, Choi 1997a). The tubercles of *Hungarobelba* (Miko & Travé 1996) are somewhat smaller than those of *Tokukobelba*. In other Ameroidea such tubercles are generally absent, and they only rarely occur within the Brachypylina (Woas 2002). The enlarged epimeral apophyses of *Tokukobelba* associated with the epimeral setae appear to be a derived feature of the genus and is suggestive of affinities to *Dyobelba* and possibly to some species of *Costeremus*.

Complete enantiophyses E2 and V are found in *Tokukobelba compta*. Apophyses E2p and Vp are monotuberculate. The posterior borders of epimeres I and II of *T. compta* are exceptional, very different from all other Damaeidae, where typically either one or both of the apophyses E2a and Va are present and monotuberculate or both are absent, and the region shows no apophyses. In *T. compta* there is a row of closely spaced sizeable tubercles or a tuberculate ridge at the posterior margins of epimeres I and II (Figs 2, 3). Apophyses E2a and Va are conspicuously multituberculate. A complete ventrosejugal enantiophysis with Va multituberculate also occurs in *Tokukobelba mongolica* (Bayartogtokh 2000), *T. barbata* (Fujita & Fujikawa 1986) and *T. japonica* (Aoki 1984). The latter two contributions also depict a multituberculate apophysis E2a. Enantiophyses E2 and V are only known to be absent in *T. itsukiensis* (Fujikawa 2011).

The tubercles comprising the epimeral ridges in *Tokukobelba* are frequently fused at the base, and the ridges are elongate, with the one of epimere II in *T. compta*, for example, opposing a region on epimere III ranging from a point situated well mediad apophysis Vp to the lateral margin of the posterior parastigmatic apophysis Sp, when observed in ventral perspective. One of the large tubercles of the epimeral ridge, the one with the greatest lateral extension, appears to correspond to the anterior parastigmatic apophysis Sa. A posterior epimeral margin II with a tuberculate ridge, reminiscent of *Tokukobelba* is found in some Eremaeidae such as *Eremaeus gracilis* Behan-Pelletier, 1993, *E. nortoni* Behan-Pelletier, 1993, and *Eueremaeus nemoralis* Behan-Pelletier, 1993, based on their excellent descriptions and illustrations in Behan-Pelletier (1993) and also in *Costeremus yezoensis*, based on the depiction in Fujikawa & Fujita (1985, Fig. 1c), being otherwise highly uncommon within the Brachypylina.

The homology of the tuberculate posterior ridges of epimeres I and II with apophyses E2a, Va and Sa respectively, is probable, but not absolutely certain. The possibility exists that they are, for example, enlarged microtubercles and/or that the genetic factor resulting in the general verrucose ornamentation of the epimeres is simply acting more strongly in the posteriormost region of epimeres I and II. In the tritonymph of *T. compta*, enlarged tubercles representing the future apophyses E2p and especially Vp are distinct, but there is no trace of tuberculate structures on the posterior borders of epimeres I and II.

Enantiophyses E3 and E4 have up to now been assumed to be absent in the Damaeidae, although Norton & Behan-Pelletier (2009, p. 498, Fig. 15.6 F) illustrate an exemplary damaeid mite based on *Damaeus arvernensis* Grandjean, 1960, with a pronounced epimeral enantiophysis IV. In *Tobukobelba compta*, *T. verrucosa* (Bulanova-Zachvatkina 1962) and *T. barbata* (Fujita & Fujikawa 1986), the tubercles associated with seta 4a are of the same size as apophysis Vp (Figs 2, 3), with the ratio of their surface area relative to body length considerably exceeding that of any other damaeid mite. Their size and position strongly suggest that they represent apophyses

E4a, with E4b being absent. In *T. mongolica* and *T. japonica* the tubercles of seta 4a are somewhat smaller (Aoki 1984, Fujita & Fujikawa 1986), while they are seemingly missing in *T. itsukiensis* (Fujikawa 2011).

Enantiophysis E4 is very seldomly found in the Oribatida, although its presence has been noted in, for example, the genus *Epieremulus* Berlese, 1916, (Norton & Behan-Pelletier 2009), within the Anderemaeidae as well as in the genera *Caleremaeus* Berlese, 1910, (Norton & Behan-Pelletier 2009, pers. obs.), and *Veloppia* (Norton 1978b, Chen & Wang 2002) within the closely related Caleremaeidae. All of these differ from *Tokukobelba* in displaying apophysis E4p, but in each case a seta homologous to seta 4a of *Tokukobelba* inserts on apophysis E4a.

Verrucose ornamentation

In contrast to all other damaeid mites, *Tokukobelba*, where reliably known, possesses numerous striking moderately sized tubercles situated on the acetabular tecta and the lateral epimeral regions other than the larger apophyses associated with the epimeral setae or the posterior epimeral margins I and II (Figs 2, 3). Such extreme tuberculate cuticular ornamentation is unknown in other Damaeidae, where any significant prodorsal or epimeral sculpturing is exceptionally rare. Based on the original description *Epidamaeus verrucatus* Enami & Fujikawa, 1989, and *E. fragilis* Enami & Fujikawa, 1989, both display a prodorsum which has an alveolar to corrugate appearance, very different from the tubercles of *Tokukobelba* and the epimeral region is not sculptured. The *Dyobelba tectopediosa* species-group is similarly characterized by a highly distinctive alveolate, but not tuberculate prodorsal sculpturing (Bayartogtokh & Norton 2007). Extensive tuberculate ornamentation of the epimeres is found in Ameroidea within the Rhynchoribatidae (Mahunka 1985, Woas 1986) and Heterobelbidae (Beck 1962, Ermilov et al. 2011), being apparently absent in the other families, and also appears in several other Brachypylina such as the Autognetidae (Grandjean 1960b, 1960c, 1963, Bayartogtokh 2012).

Palptarsus

In the Damaeidae, there usually are 9 setae and additionally a prone, distally directed solenidion ω situated on the palpal tarsus. Four setae, the anteroculminal, the subultimal and the paired ultimal setae are short, conical and hollow and insert distally. These are the eupathidia, which are transformed homologues of setae (Grandjean 1946). The remaining 5 normal setae insert considerably more proximally on the tarsus, are elongate, of setiform shape and not hollow. Of these, the single culminal seta inserts dorsoproximally, roughly midway between lyrifissure ly and the insertion point of solenidion ω. Distally to this, the paired lateral setae lt´ and lt´´, and also the ventral setae vt´and vt´´ are found (Norton 1977a).

The specimens of *Tokukobelba compta* examined by me display the typical recumbent damaeid solenidion ω, usually only clearly discernible in squash preparations, and a total of 9 setae on the palpal tarsus. Setae cm, lt´, lt´´, vt´and vt´´ are present. However, only three distal eupathidial setae are found: acm, ul´ and ul´´. The subultimal seta is absent or vestigial. An additional elongate normal seta is found ventrally on the tarsus, inserted much closer to seta lt´ than to setae acm, ul´and ul´´ (Fig. 8). This highly unusual setation pattern, which I also observed in the larva and nymphs of *T. compta*, and which is similar to that depicted for *T. itsukiensis* by Fujikawa (2011, Fig. 2b), differs from that of all other Damaeidae for which the palptarsal setation is known.

The standard tarsal chaetotaxy of the Damaeidae with 9 setae, of which the four distal ones are eupathidial, occurs in *Belba corynopus* (Grandjean 1936), *B. sculpta* (pers. obs.), *B. minuta* (Tolstikov & Lyashchev 1996) and *B. clavasensilla* (Norton & Palacios-Vargas 1982). It is also known for several species of *Damaeus* (Grandjean 1936, Norton 1978a) and for *Metabelba platynotus* (Grandjean 1954), *Metabelbella tichonravovi* (Ermilov & Khaustov 2011), as well as for *Nortonbelba italica* **(**Bernini 1980) and *Porobelba weigmanni* (Miko 2008). *Parabelbella elisabethae* Bulanova-Zachvatkina, 1967, in which 4 palptarsal setae are eupathidial is described as having 8 setae on this segment by Miko et al. (2011). Based on the illustration supplied by these authors (p. 43, Fig. 5), the solenidion ω of this species is apparently similar in appearance to a normal seta and not recumbent. The adult of *Weigmannia parki* shows only 3 eupathidia on the tarsal tip and 8 setae in total (Miko & Norton 2010). The species of the *Dyobelba tectopediosa* species group are mentioned as possessing only 8 setae on the tarsus of the palp, but more detail is not provided, and the palps are not illustrated (Bayartogtokh & Norton 2007).

Tokukobelba mongolica is characterized by BAYARTOGTOKH (2000) as possessing only 7 setae on the palptarsus. On the illustration provided for this species, 8 setae are visible on the palptarsus, but the recumbent solenidion is not depicted. *T. mongolica* shows only 3 distal eupathidial setae (BAYARTOGTOKH 2000), similar to *T. compta*. The seta sul appears to be absent. TRÄGÅRDH (1910, p. 521, Fig. 296) depicts the palptarsus of *T. farinosa* with 7 setae, not showing the solenidion or seta cm. Again only 3 distal eupathidial setae are seen.

Two main hypotheses may account for the highly unusual palptarsal setation of *Tokukobelba*. The first is that the seta sul is absent and instead an additional ventral or lateral seta is present, while the second posits that seta sul exists but does not become eupathidic in ontogeny and is strongly proximally displaced on the tarsus when compared to other Damaeidae.

In the legs the ontogeny of the eupathidia is always progressive in that no eupathidium transforms back to a normal seta (NORTON 1977b) and the same appears to be the case in the palptarsus. In *Tokukobelba compta* the subunguinal seta s of the tarsus of leg I, which may be a homologue of the tarsal subultimal seta is not eupathidic in the nymphs but becomes so in the adult. During ontogeny the insertion point of this seta migrates in a distal direction on the tarsus. In the larva and nymphs it is inserted proximally to setae (a) (Figs 16, 17, 18), whereas in the adult (Fig. 4) it is distal to them. It is conceivable that the subultimal setae share the same genetic program here acting on the subunguinal setae and that this, usually already active in the palptarsus prior to the larva stage, is here repressed, preventing the normal development and migration or distal insertion of the seta sul. If the seta here tentatively identified as vt2´ is instead a subultimal seta, the factors leading to the inhibition of the eupathidial nature and also the peculiar proximal insertion of this seta must have acted prior to the larval stage.

Where it exists, seta sul is closely associated with the ultimal setae and located on the tarsal tip in all Oribatida and in primitive representatives such as *Hypochthonius* KOCH, 1835, and *Collohmannia* SELLNICK, 1928, and may even be partially fused with these (WOAS 2002). If the seta sul is present in adult Brachypylina, it virtually always is eupathidic, not elongate and seta-like with a curled tip such as the ventral and lateral setae, and not with a completely different appearance to the short and stubby ultimal setae. I am not aware of any instance in Brachypylina where seta sul shows a significant proximal insertion on the palptarsus. Although it is not possible to state with absolute certainty whether the development of seta sul has been strongly retarded, effectively being suspended at the prelarval state or earlier with the normal number of ventral setae being present, or whether seta sul is just absent, I tend to favour the latter hypothesis. What is apparent is that the subultimal seta of *Tokukobelba* either experiences a highly unusual, early, drastic developmental slow-down, or has been completely lost.

Based on GRANDJEAN (1946), the setal priorities for the eupathidia of the palptarsus are as follows: ul´, ul´´, acm, sul, with the latter being the one most likely to experience retardation in development or regressive loss. The loss of seta sul is most unusual in brachypyline mites, but has been noted for a few taxa such as *Fosseremus quadripertitus* GRANDJEAN, 1965, based on the detailed documentation of the species by its author, and *Veloppia* (NORTON 1978b, CHEN & WANG 2002).

The apparent loss of the palptarsal seta sul and the presence of an extra ventral seta in *Tokukobelba* are both highly derived states. The same would apply to a developmentally retarded seta sul. Plesiomorph for the Damaeidae and also for the Brachypylina as a whole is the presence of 9 palptarsal setae, including a eupathidic distally inserted seta sul. Since the 5-segmented damaeid palps are homologous to the legs, it is noteworthy that *Tokukobelba* is characterized not only by supernumerary ventral setae on the tarsus of legs I and II, but also on the palptarsus, which is highly suggestive of a shared underlying developmental program.

Nymphal seta c3

In all Damaeidae, the notogastral seta c3 is found in the larva and all nymphal stages but gets lost in the adult (NORTON 1977b). The ontogeny of *Tokukobelba compta* conforms to this pattern. Seta c3 of the larva of this species is very short and thin compared to the thick, elongate setae c1, c2, da, dm, dp and lp, being approximately similar in length to the short lateral setae la and lm (Fig. 9). A similarly short larval seta c3, whose length approximately equals that of the rostral setae, is typical of all damaeid larvae.

In the nymphs of *Tokukobelba compta* the seta c3 in contrast is extremely elongate (Fig. 10), with a length exceeding the width of the notogaster, and very roughly of the same length as the long setae c1, c2, la and lp. This character state is unknown in other Damaeidae, where the seta c3 of the nymphs is always regressed and very much shorter than c1, c2, la and lp. A short nymphal seta c3 appears to be a highly conserved derived character state of the Damaeidae when compared to various brachypyline outgroups.

A reduced tiny seta c3 in nymphs is characteristic of *Belba* species such as *B. corynopus* (Seniczak & Seniczak 2013, pers. obs.), *B. sculpta* (pers. obs.), *B.* (*Protobelba*) *californica* (Norton 1979c), and *B. clavasensilla* (Norton & Palacios-Vargas 1982). A very short thin seta c3 in the nymphs has, for example, also been described for *Caenobelba alleganiensis* (Norton 1980), *Quatrobelba montana* (Norton 1980), *Lanibelba pini* (Norton 1980), *Dyobelba carolinensis* (Norton 1979c), *Dyobelba reevesi* (Norton & Ryabinin 1994), *Porobelba spinosa* (Grandjean 1954, Ermilov & Lochynska 2009), *Spatiodamaeus verticillipes* (Seniczak et al. 2013), *Weigmannia parki* (Miko & Norton 2010) as well as in several species of each of the genera *Metabelba* (Ermilov 2010b, Ermilov et al. 2010a, Seniczak & Seniczak 2013), *Metabelballa* (Ermilov & Khaustov 2011, Seniczak & Seniczak 2013), *Damaeus* (Norton 1978a, Seniczak & Seniczak 2011), *Kunstidamaeus* (Miko & Mourek 2008) and *Epidamaeus* (Bulanova-Zachvatkina 1957, Norton 1979c, Enami 1992, Ermilov & Lochynska 2009, Seniczak et al. 2013).

In nymphs of most other Eupheredermata such as in *Fosseremus quadripertitus* (Grandjean 1965a) and *Amerus troisi* (pers. obs.), there are no pronounced length differences between setae c1, c2, c3 and la. However, seta c3 may be minute and the neighbouring setae normal sized as in *Polypterozetes cherubin* Berlese, 1916, (Grandjean 1959a), or seta c2 instead of c3 may be very strongly reduced in size, as in two species of *Gustavia* Kramer, 1879, (Ermilov 2010a, Ermilov et al. 2013). The strongly developed and elongate seta c3 of nymphs of *Tokukobelba* may be perceived of as being an autapomorphy of the genus that evolved within the Damaeidae but more likely may be interpreted as *Tokukobelba* retaining a more ancestral brachypyline character state, compared to which the minute seta c3 of other Damaeidae is derived, suggesting an outgroup relationship of *Tokukobelba* to these.

Position of *Tokukobelba*

An attempt to unravel the detailed phylogeny of *Tokukobelba* is a challenging endeavour and is limited by our presently very incomplete knowledge of the evolution of the Damaeidae and of the Higher Oribatida in general (Norton & Behan-Pelletier 2009), by the substantial limitations imposed by the methodology of phylogenetic analysis and also by the scarce fossil record. The only pre-Pleistocene damaeids known so far have been collected in Baltic amber from the Middle Eocene (Sellnick 1931, Perkovsky et al. 2007) while the oldest specimen of *Tokukobelba* known dates to the Quaternary (Dunlop et al. 2016).

It is a thorny issue to suggest a sister taxon for *Tokukobelba* within the Damaeidae. The morphological gap between *Tokukobelba* and other representatives of its family is substantial, much more so than that between any other damaeid genus and its morphologically most similar neighbour.

Tokukobelba differs greatly from other damaeid genera in the presence of the exceptionally rare character states: femur III mostly with 3, and femur IV with 2 setae; tibial associated setation mostly 1-1-1-1; tarsal setation 22-18-17-14; tarsus IV with a regressed seta d and elongate tactile solenidion; prodorsal tubercles Aa and Ap both present; palptarsus without seta sul and with a supernumerary ventral seta; interbothridial protuberance present; epimeral setation 3-1-3-3; all epimeral seta usually associated with greatly enlarged tubercles and huge apophysis E4a present; ventral apophyses Va and E2a conspicuously multituberculate; epimeral grooves III and especially IV, as well as their apodemes strongly developed; epimeres and lateral prodorsum with verrucose sculpturing; nymphal seta c3 elongate. These traits together with those shared with *Belba* result in a combination of generic defining characters for *Tokukobelba* with a very high degree of uniqueness, which not only very strongly argues in favour of the monophyly of the group, but also justifies giving this a name.

The above unusual character states of *Tokukobelba* may conceivably all have arisen within the Damaeidae, with the genus not being basal to the other damaeid genera. In this case, all of these traits would most parsimoniously have to be interpreted as being autapomorphies of the genus. However, the tibial associated setation of 1-1-1-1, the epimeral setation of 3-1-3-3, the reduced setal count on femur IV and the non regressed nymphal seta c3 of *Tokukobelba* are all very likely plesiomorph for the Brachypylina. Here *Tokukobelba* does not share the derived states that characterize almost all other Damaeidae. Furthermore, several other features such as the apophyses Aa, Ap, the unusually developed ventral apophyses, the conspicuous epimeral groove IV, and the verrucose integumental sculpturing echo traits found in genera such as *Costeremus*, *Hungarobelba* and *Veloppia* which appear to be closely related to the Damaeidae.

Most of these apparently more primitive traits of *Tokukobelba* such as the verrucose sculpturing, the presence of Aa and Ap, the presence of only 2 setae of femur IV and the tibal associated setation of 1-1-1-1 may nevertheless be seen as being synapomorphies of the genus. Some traits may be parallelisms or reversals at the level of the phenotype, but derived features of *Tokukobelba* at the level of the genotype, Parallelisms are of course more likely in closely related taxa, and are indicative of genealogical and phylogenetic relationship.

Tokukobelba shares a trochanteral setation of 1-1-2-1, a genual setation of 4-4-3-3, a genual associated setation of 1-1-1-0 and an emergent famulus with *Belba*. However, these are primitive brachypyline traits which have been retained by most damaeids. The character state of absence of spinae adnatae which these two genera display similarly may be plesiomorph for the Damaeidae and is not a strong phylogenetic character. *Tokukobelba* does not possess those traits of *Belba* which may be interpreted as having been derived within the Damaeidae such as presence of 16 and 13 setae on tarsus III and IV respectively with v1´´ being absent. It also does not share any of the highly derived features of the *Belba corynopus* species group such as an elevated dome-like notogaster, a femoral setation of 7-7-5-5 or epimeral neotrichy. *Tokukobelba* similarly does not share the probably derived elevated trochanteral, femoral and genual setations or the similarly derived tibial associated setal formula of 0-1-1-0 of *Metabelba*, *Mirobelba* and *Metabelbella* or the derived tibial associated setation of 0-0-0-0, sunken nymphal famulus and presence of spinae adnatae of the group of genera centered on *Damaeus* and *Epidamaeus*.

Tokukobelba stands relatively isolated within the Damaeidae, although it shares several unusual traits with members of *Dyobelba tectopediosa* species group, and seems to have had a prolonged independent evolutionary trajectory. This is also suggested by the unusual palptarsal and tarsal setation of the genus which both appear to be highly derived. *Tokukobelba* appears to occupy a relatively basal position within its family. A detailed redescription of *Costeremus yezoensis* and *C. barbatus* may help to give us more clarity on the character polarities involved.

While *Tokukobelba* is undoubtedly a damaeid mite, the morphology of the genus with its mix of ancestral and derived characters, appears to demonstrate well the mosaic evolution characteristic of ancient taxa such as *Archaeopteryx* MEYER, 1861, basally situated within their clades. One reason for the considerable number of characters distributed in a mosaic pattern, not only in the Damaeidae but also in other oribatids (WOAS 1990, 1991, 1998, 2002), appears to lie in the great phylogenetic age of these mites with the oldest oribatids known dating to the Devonian (NORTON et al. 1988), although molecular studies suggest a Precambrian origin of the order (SCHAEFER et al. 2010).

Based on the fossil record of the oribatid infraorder Desmonomata (ARILLO et al. 2009, DUNLOP et al. 2016) we may reasonably assume that mites of the family Damaeidae, with an appearance similar to that of extant members of the taxon, were present on this planet at least since the early to middle Jurassic and are possibly much more ancient than that. *Tokukobelba* appears to be a living fossil and may perhaps even prove to be the sister group to all other Damaeidae. At any event, it is a morphologically very extraordinary genus.

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Abbreviations

The abbreviations are grouped according to the major body subdivisions and are arranged alphabetically within each section. The body of a damaeid mite consists of two main regions, an anterior propodosoma, which contains the head structures, and a posterior hysterosoma or abdomen. These are separated by the sejugal groove. The dorsal part of the propodosoma, which includes all structures located dorsally to the leg insertions, is called the prodorsum. The anterior part of the prodorsum, the rostrum, surrounds a cavity, the camerostome, in which a pair of chelicerae and a pair of pedipalps are located. The ventral border of this cavity is formed by the postero-laterally hinged infracapitulum. Together these five structures form the mite mouthparts or gnathosoma. Epimeres I and II are the lateral and ventral part of the propodosoma located between and below the leg insertions. Each epimere is associated with a 5-segmented leg consisting of trochanter, femur, genu, tibia and a distal tarsus with single claw. The notogaster is the dome-like shield which in the adult dorsally covers most of the hysterosoma. It is separated from the ventral part of the hysterosoma by a groove, the circumgastric scissure. Ventrally to this one finds the epimeres of legs III and IV, and posterior to these the genital and anal regions.

Prodorsum

Aa	anterior apophysis of prodorsal enantiophysis
Ala, Alp	anterior and posterior apophysis of anterolateral enantiophysis
Ap	posterior apophysis of prodorsal enantiophysis
Ba, Bp	anterior and posterior apophysis of postbothridial enantiophysis
bo	bothridium
dsg	dorsosejugal groove
ex	exobothridial seta
in	interlamellar seta
le	lamellar seta
ro	rostral seta
sej	sejugal groove
si	muscle sigillae
ss	sensillus

Notogaster

c1-c3	anterior series of notogastral setae
cgs	circumgastric scissure
da, dm, dp	anterior, median and posterior dorsocentral setae
gla	opening of opisthonotal gland
h1-h3	notogastral setae of h-series
ia, ih, im, ip, ips	notogastral lyrifissures
la, lm, lp	dorsolateral notogastral setae
ps1-ps3	pseudanal setae

Ventral and lateral region

1a-1c	setae of epimere I
2a	seta of epimere II
3a-3c	setae of epimere III
4a-4d	setae of epimere IV
ad1-ad3	adanal setae
ag	aggenital seta
an1, an2	anal setae
di	discidium
E2a, E2p	anterior and posterior apophysis of propodoventral enantiophysis
E4a	anterior apophysis of epimeral enantiophysis IV
g1-g6	genital setae
Gp1-Gp3	genital papillae
iad	adanal lyrifissure
Sa, Sp	anterior and posterior apophysis of parastigmatic enantiophysis
ur	urstigma
Va, Vp	anterior and posterior apophysis of ventrosejugal enantiophysis

Chelicerae, pedipalps and infracapitulum

a	anterior genal seta
acm	anteroculminal seta of palptarsus
ap	porose area
acx	attachment of cheliceral sheath
bru	rutellar brush
cha	posterior cheliceral seta
chb	anterior cheliceral seta
cm	culminal seta of palptarsus
Df	fixed cheliceral digit
Dm	mobile cheliceral digit

ds	dorsal seta of palptibia
e	supracoxal spine
fe1	fenestrate area of chelicera
G	gena
h	seta of mentum
H	mentum
inf	inferior femoral seta of palp
k	articulation condyle
lt	lateral seta of palptarsus
LS	labrum
LL	lateral lip
m	posterior genal seta
op	paraxial oncophysis
opv	ventral oncophysis
opx	coxal oncophysis
or1, or2	adoral setae
RU	rutellum
sul	subultimal seta of palptarsus
sup	superior femoral seta of palp
Tg	Trägårdh´s organ
ul	ultimal seta of palptarsus
vt1	seta of first pair of ventral setae of palptarsus
vt2	seta of second pair of ventral seta of palptarsus

Legs

a	antilateral seta of tarsus
bv	basiventral seta of femora I, II
cl	claw
d	dorsal seta
ev	basiventral seta of femora III, IV
ft	fastigial seta of tarsus
it	iteral seta of tarsus
l	lateral seta
ly	lyrifissure of tarsus
p	proral seta of tarsus
paα	porose area of femur
paπ	porose area of trochanter
pl	primilateral seta of tarsus
pv	primiventral seta of tarsus
s	subunguinal seta of tarsus
tc	tectal seta of tarsus
u	unguinal seta of tarsus
v	ventral seta
v1	seta of first pair of ventral setae of tarsus I or II
v2	seta of second pair of ventral setae of tarsus I or II
ε	famulus of tarsus I
σ	genual solenidion
φ, φ1, φ2	tibial solenidia
ω1, ω2	tarsal solenidia

A setal name abbreviation followed by the symbol ´ as in v´ signifies that the seta is inserted on the anterior leg surface if one imagines the mite with the legs perpendicular to the long axis of the body. Analogously v´´ means that the seta in the same leg position is here inserted on the posterior surface. In damaeids the natural position is for the first two pairs of legs to be directed anteriorly and the last two pairs posteriorly. The term paraxial refers to structures closer to the sagittal plane. Antiaxial structures are those that are more distant from this plane. If a setal notation is placed in parentheses as in (v) this refers to a setal pair and in this case would be the equivalent of writing v´and v´´.

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