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Morphological ontogeny of *Eremobelba geographica* (Acaria: Oribatida: Eremobelbidae), with comments on *Eremobelba* Berlese

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Abstract

The morphological ontogeny of *Eremobelba geographica* Berlese, 1908 is described and illustrated. This species was investigated mainly in ecological and biological aspects. It inhabits forest soils and cultivated areas, but is not abundant, and adults dominate in extracted samples. In the juveniles, the prodorsal seta *in* is short, and the bothridial seta is setiform. The nymphs are quadrideficient and eupheredermous, i.e. they carry exuvial scalps of the previous instars, using a cornicle. Paraproctal setae occur in all juvenile instars, which is rare in Brachyppylina, and hypertrichy occurs in the aggenital region of the deutonymph, tritonymph and adult, and adanal region of the adult. In all instars, seta *d* on all genua and tibiae is present, except for tibia I of adult.

Keywords: oribatid mites, juveniles, hypertrichy, leg setation, stage structure

Introduction

Eremobelba Berlese, 1908, with the type species *Eremobelba leporosa* (Haller, 1884, described as *Eremaeus leporosus*), comprises medium sized mites (241–627 µm as adults). Subías (2020) included 45 species in this genus, and four of them he treated as *species inquirendae*, including the type species of *Eremobelba*. The diagnosis of *Eremobelba* is insufficiently known. Balogh (1961) considered the most important characters for this genus filiform bothridial seta, disrupted lamellar ridges, and granular cerotegument, and later (Balogh 1972) insisted the number of pairs of setae on the notogaster (11), genital plates (6), aggenital (8), adanal (3), anal (2) regions and number of claws (1). Weigmann (2002) put main attention to the reticulate cerotegument on the notogaster, presence of branched setae on some parts of body, hypertrichy of adanal and aggenital regions, number of aggenital and adanal setae and the tropic distribution. A diagnosis of *Eremobelba geographica* Berlese, 1908, including the nymphs, gave Weigmann (2002).

According to the catalogue of juvenile oribatid mites by Norton and Ermilov (2014), the morphology of juveniles of *E. geographica*, *E. gracilior* Berlese, 1908 and *E. foliata* Hammer, 1958 is partially known. Weigmann (2002) described the nymphs and illustrated the tritonymph of *E. geographica*, with all exuvial scalps of previous instars, and Hammer (1958) described and illustrated the protonymph of *E. foliata*, with exuvial scalp of the larva. The juveniles of *E. geographica* were also investigated in ecological and biological aspects (Bulanova-Zachvatkina & Shereef 1970; Shereef 1972), as well as those of *E. gracilior* (Hartenstein 1962), but these descriptions are general and insufficient for morphological comparisons.

The aim of this paper is to describe and illustrate the morphological ontogeny of *E. geographica* and compare the morphology of the adult with congeners.

Material and methods

The juveniles and adults of *E. geographica* used in this study were collected on 23 July 2015 by O. Ivan from (1) forest plantation of *Salix alba* L. in Plauru (Danube Delta Biosphere Reserve, Romania), in which all juvenile stages were present. For ecological comparison, we also selected three other habitats from Romania (Table 1): (2) forest plantation of poplar (*Populus x canadensis*) in Stăniște, and two other habitats in Danube Delta Biosphere Reserve—(3) Riparian forest with *Populus alba* L., *Salix alba*, *P. x canadensis* in Plauru and (4) cultivated soil with *Solanum tuberosum* L. in Uzlinia. In all habitats, we investigated the density and stage structure of mites, sex ratio of the adults, number of gravid females and carried eggs, and body length and width. In the most abundant population in Plauru, we investigated 30 randomly selected specimens. We measured the length of mites (from tip of rostrum to posterior edge of notogaster) in lateral aspect, body width (widest part of notogaster) in dorsal aspect, and the length of anal and genital openings and setae perpendicularly to their size in µm. In total 81 adults were examined. In statistic calculations, the basic statistical descriptors included the minimum, maximum, mean and standard deviation values. The values were log-transformed $\ln(x+1)$ (Łomnicki 2010), and normality of the distribution was justified with the Kolmogorov-Smirnov test, while the equality of variance in different samples was verified with the Levene test. The assumption of normality or equality of variance was not met, and the number of replicates in compared groups was different, so the non-parametric ANOVA rang Kruskal-Wallis was used and then, in case of significant differences between averages, the multiple comparison test between average ranks was applied. The level of significance for all statistical tests was accepted at $\alpha=0.05$. Statistical calculations were carried out with STATISTICA 13.1 Software.

TABLE 1. Stage structure and density of *Eremobelba geographica* in different regions of Romania; L—larva, Pn—protonymph, Dn—deutonymph, Tn—tritonymph, Juv—juveniles, Ad—adult.

Place of sampling, date	Plant cover ¹	Coordinates	Juveniles ²						Ad ²	Total	Indiv. /500 cm ³
			L	Pn	Dn	Tn	Juv	%			
1. Plauru 23.07.2015	Willow plantation	45°19'26"N 28°49'48"E 3 m a.s.l.	13	3	10	3	29	44	37	66	13.2
2. Stăniște 08.06.2010	Poplar plantation	46°38'46"N 28°11'23"E 14 m a.s.l.	0	0	0	0	0	0	27	27	5.4
3. Plauru 21.07.2015	Riparian forest	45°17'42"N 28°53'42"E 3 m a.s.l.	0	2	3	0	5	29	12	17	3.4
4. Uzlinia 25.06.1994	Cultivated soil	45°04'24"N 29°13'36"E 4 m a.s.l.	0	0	0	0	0	0	12	12	2.4

¹more details in Material and methods, ²total number from five replicates.

The illustrations of instars of *E. geographica* are limited to the body regions of mites that show substantial differences between instars, including the dorsal and lateral aspect and some leg segments of the larva, tritonymph and adult, ventral regions of all instars, and the palp and chelicera of the adult. Illustrations were prepared from individuals mounted temporarily on slides in lactic acid, using the open-mount technique. In the text and figures, we used the following abbreviations: rostral (*ro*), lamellar (*le*), interlamellar (*in*) and exobothridial (*ex*) setae, bothridium (*bo*), lamellar costula (*Cos*),

bothridial seta (*bs*), notogastral or gastronotal setae (*c*-, *d*-, *l*-, *h*-, *p*-series), cupules or lyrifissures (*ia*, *ip*, *ih*, *ips*, *iad*), exuvial scalps of the larva (L), protonymph (Pn) and deutonymph (Dn), opisthonotal gland opening (*gla*), cornicle (*k*), pedotectum (*Pd*), subcapitular setae (*a*, *m*, *h*), cheliceral setae (*cha*, *chb*), Trägårdh organ (*Tg*), palp setae (*sup*, *inf*, *l*, *d*, *vt*, *ul*, *su*) and solenidion ω , epimeral setae (*1a–c*, *2a*, *3a–c*, *4a–c*), discidium (*Dis*), enantiophyses (*Sa*, *Sp*), adanal and anal setae (*ad*-, *an*-series), aggenital setae (*ag*), leg setae (*bv*, *ev*, *d*, *l*, *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl*, *v*), solenidia (σ , φ , ω) and famulus (ε). Terminology used follows that of Grandjean (1953, 1965) and Norton and Behan-Pelletier (2009). The species nomenclature follows Subías (2004, 2020 updated).

For scanning electron microscopy (SEM), the mites were air-dried and coated with Au/Pd in a Polaron SC502, sputter coated and placed on Al-stubs with double-sticky carbontape. Observations and micrographs were made with a ZEISS Supra 55VP scanning electron microscope.

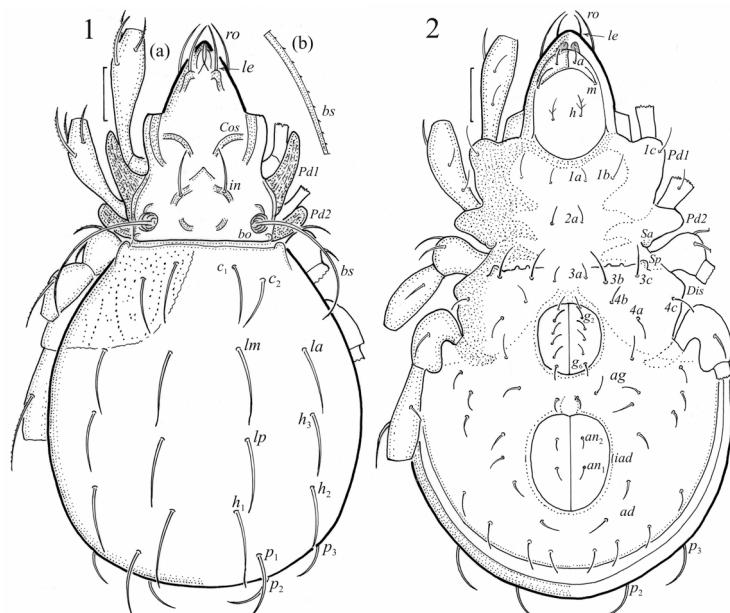
Eremobelba geographica Berlese, 1908

(Figs. 1–15)

Diagnosis

Adults of medium size (364–542), prodorsal setae of medium size, except for long, curved and smooth bothridial seta. Dorsosejugal furrow straight, with shoulder crests. Eleven pairs of notogastral setae, all slightly curved and smooth, granules of cerotegument formed in polygonal pattern. Genital setae (6 pairs) in one row, hypertrichy of aggenital and adanal setae present (13–15 pairs). On genu I and genua and tibiae II–IV seta *d* present, slightly separated from proper solenidia.

Prodorsal setae of juveniles short and bothridial seta setiform, most gastronotal setae long in larva and short in nymphs. Nymphs quadrideficient and eupheredermous, i.e. they carry the exuvial scalps of previous instars, using cornicle. Larva with two pairs of paraproctal setae (including alveolar pair), protonymph with three pairs, and deutonymph and tritonymph with two pairs each. In deutonymph and tritonymph, hypertrichy present in aggenital region. In all instars, seta *d* on all genua and tibiae present.



FIGURES 1–2. *Eremobelba geographica*, adult, legs partially drawn, scale bars 50 μm . 1. (a) Dorsal aspect, (b) shape of bothridial seta (enlarged). 2. Ventral aspect.

Morphology of adult

Adult (Figs. 1–8) similar to that investigated by Weigmann (2002), but see Remarks. Mean length (range) of females— 492.2 ± 13.6 (464–542, N= 63) and males— 459.7 ± 7.9 (446–470, N= 18), mean width (range) of females 294.1 ± 10.3 (277–325) and males— 267.7 ± 6.9 (259–283). Some parts of body and some setae covered with thin layer or single granules of cerotegument, larger granules form on notogaster polygonal pattern (Figs. 5–8). Notogastral setae (11 pairs, including c_1 and c_2) of medium size (Figs. 1, 2, 3a, 5, 6a–c, Table 2) and smooth. Subcapitular setae h and m slightly longer than a , h with 2–3 cilia, other setae smooth. Epimeral setae $1a$, $2a$, $3a$ and $4b$ short, other setae longer, all smooth (Fig. 2), formula of epimeral setae 3-1-3-3. Genital setae (6 pairs), aggenital and adanal setae (13–15 pairs), and anal setae (2 pairs) short and smooth, some aggenital and adanal setae thickened. Chelicera chelate, cha longer than chb , both barbed (Fig. 3b). Palp relatively small and thin, setae sup and inf on femur and l'' on tibia barbed, other setae smooth (Fig. 3c). Formula of palp setae (and solenidion ω): 0-2-1-3-9(1). Most leg setae barbed, all tibiae slim, on genu I and genua and tibiae II–IV seta d present, separated from proper solenidia (Fig. 4). Solenidia ω_1 and ω_2 on tarsus I relatively short, famulus ϵ relatively long. Some parts of leg segments and some setae covered with thin layer or single granules of cerotegument. Formulae of leg setae (and solenidia, from trochanter to tarsus): I—1-5-4(1)-4(2)-20(2); II—1-5-4(1)-5(1)-15(2); III—2-3-2(1)-4(1)-15; IV—1-3-2-4(1)-12. Legs monodactylous (Figs. 4, 5, 8c, d).

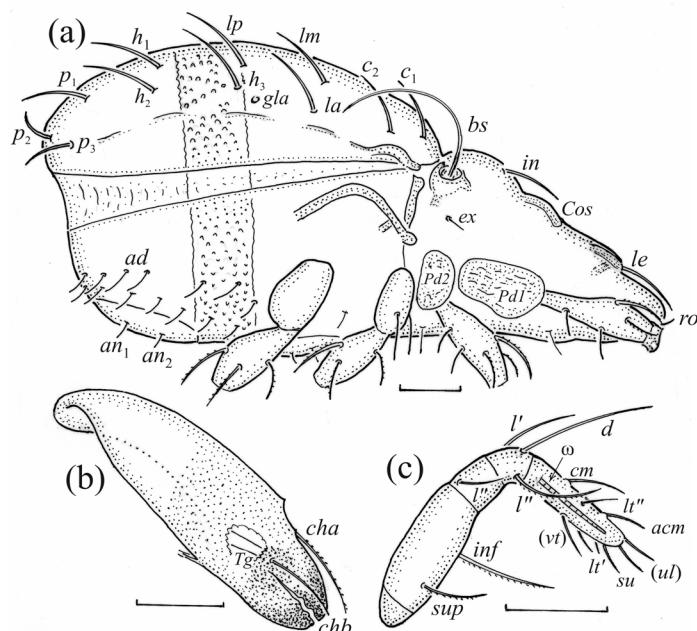


FIGURE 3. *Eremobelba geographica*, adult. (a) Lateral aspect, legs partially drawn, scale bar 50 μ m; mouthparts, right side, scale bars 10 μ m; (b) chelicera, (c) palp.

Remarks. Females of *E. geographica* investigated herein are slightly smaller than those studied by Weigmann (2002, length 475–550), but males are of similar size. In our adults, subcapitular seta h has 2–3 long cilia (versus barbed in adult by Weigmann 2002) and aggenital and adanal setae are thinner. Our adults and those investigated by Weigmann (2002) are clearly larger than those investigated by Toluk *et al.* (2015, length 364, sex not investigated), and in the SEM micrographs they have thinner layer of cerotegument than in the latter individuals.

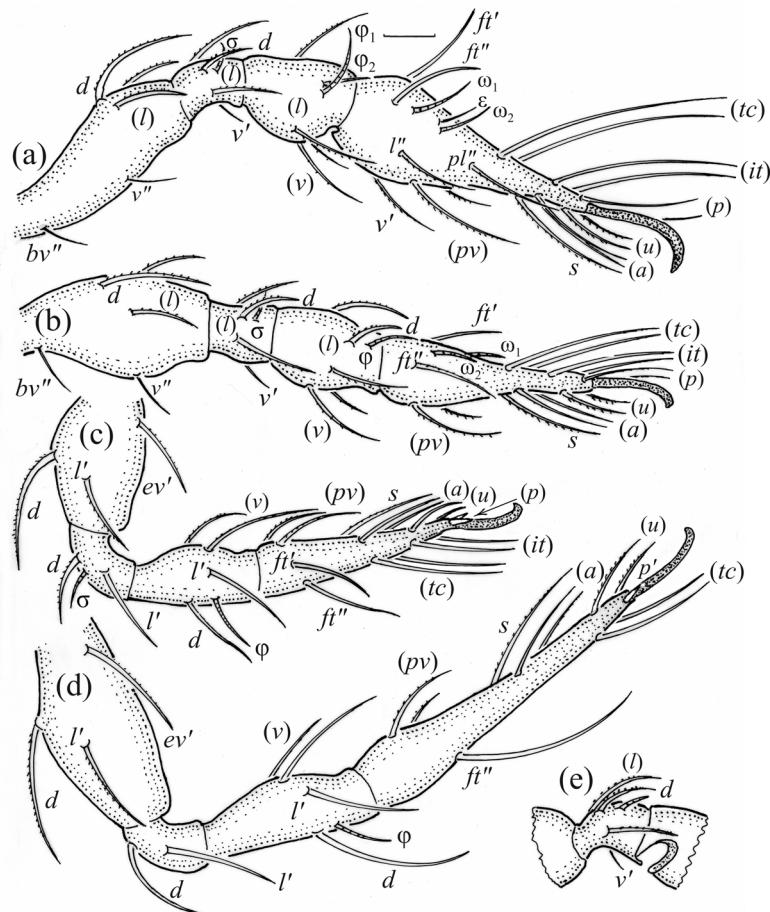


FIGURE 4. *Eremobelba geographica*, leg segments of adult (part of femur to tarsus), right side, setae on the opposite side not illustrated are indicated in the legend, scale bar 20 µm. (a) Leg I, tarsus (*p*''); (b) leg II; (c) leg III; (d) leg IV, tarsus (*p*''); (e) genu II and part of femur and tibia II of other individual, lateral aspect.

Description of juvenile stages

Larva oval in dorsal aspect and unpigmented. Prodorsum subtriangular, prodorsal seta *ro* inserted on lateral part of rostrum. Setae *ro* and *le* of medium size and barbed, other setae short and smooth (Figs. 9, 11a, Table 2). Mutual distance between setal pairs *ro* and *in* about two and nearly four times longer than between pair *le*, respectively. Seta *le* inserted closer to *ro* than to *in*. Bothridium oval, bothridial seta setiform, barbed.

Gastronotum of larva with 12 pairs of setae, including h_3 inserted laterally to medial part of anal valves (Figs. 9a, 10a, 11a). Setae c_2 and h_3 short and smooth, c_1 , lm and h_2 of medium size, other setae long; all barbed, setae da , dm and lp clearly shorter than c_3 , la , dp and h_1 . Most setae inserted on small apophyses, d -series inserted on large apophyses. Anal valves (segment P) with pair of short setae and pair of alveolar setae. Cupule ih lateral to anterior part of anal valves, cupules ia and im not observed in granular cerotegument, cupule ip between setae h_1 and h_2 , gland opening anteroventral to seta lp . Most leg setae barbed. All tarsi with basal bulb (containing muscles) and uniformly narrow distal stalk (only with tendons) at about mid-length (Fig. 12). Seta d present on all genua and tibiae, separated from proper solenidia, solenidion ω_1 on tarsus I and ϕ_1 on tibia I longer than other solenidia. Some parts of body, legs and some setae covered with thin layer or single granules of cerotegument.

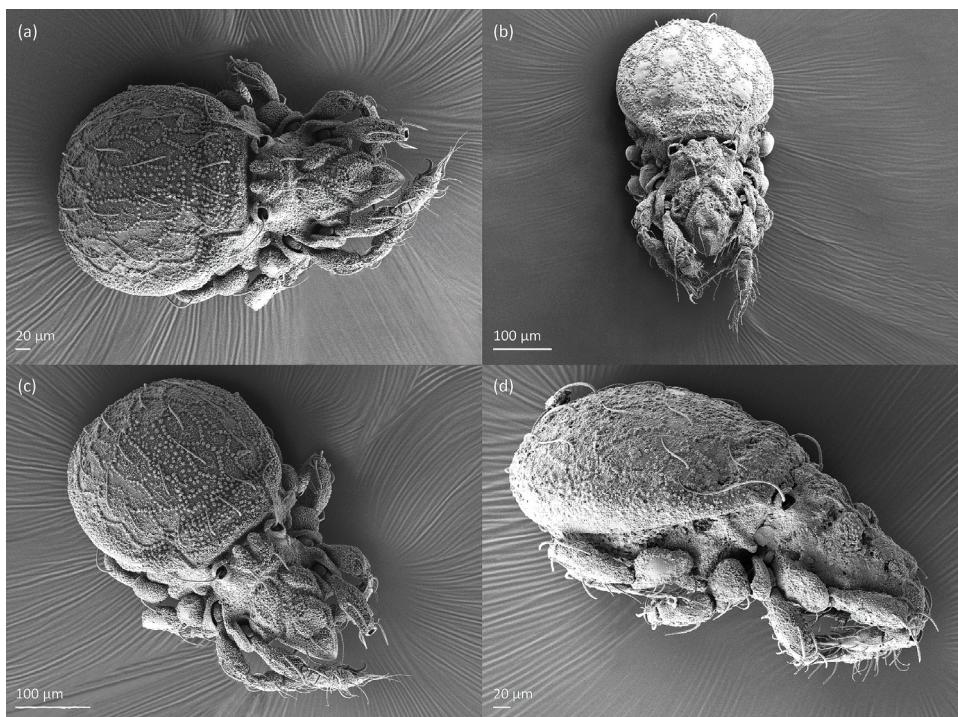


FIGURE 5. *Eremobelba geographica*, adult, SEM micrographs. (a) Dorsal view, (b), (c) frontal view, (d) lateral view.

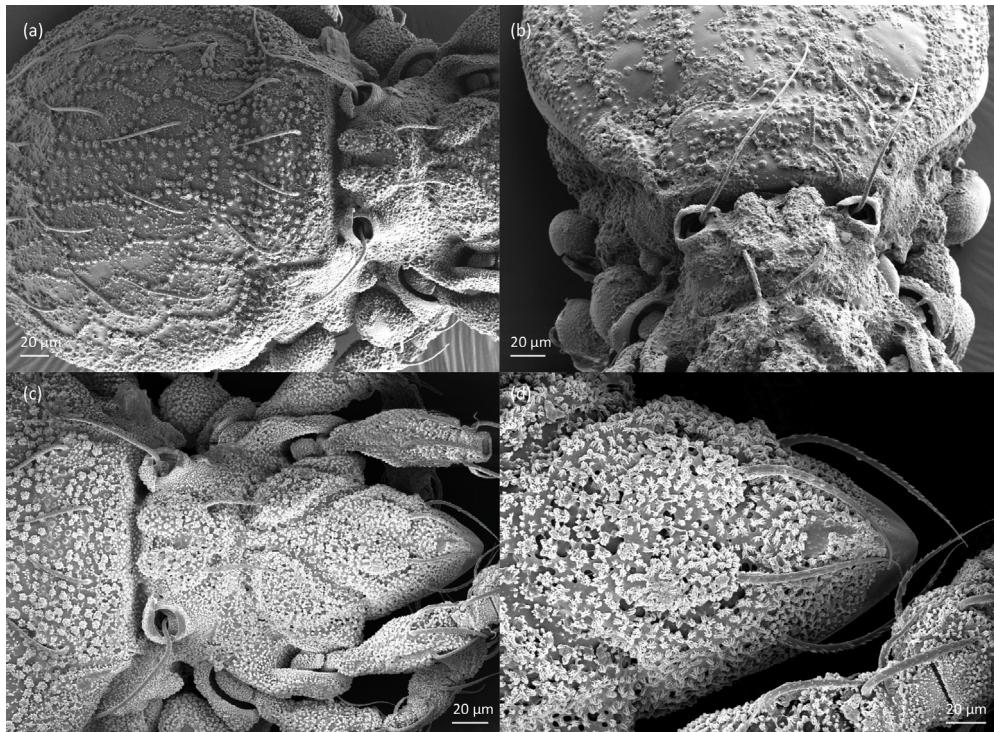


FIGURE 6. *Eremobelba geographica*, adult, SEM micrographs. Central part of body, (a) dorsal view, (b) frontal view; (c), (d) anterior part of body, dorsal view.

TABLE 2. Measurements of some morphological characters of juvenile stages and adult of *Eremobelba geographica* (mean measurements of 3–10 individuals in µm); Nd—not developed.

Morphological characters	Larva	Protonymph	Deutonymph	Tritonymph	Adult
Body length	257	274	320	403	520
Body width	139	174	185	211	304
Length of prodorsum	94	96	104	148	190
Length of: seta <i>ro</i>	29	31	33	35	43
seta <i>le</i>	34	36	38	40	35
seta <i>in</i>	4	3	3	4	7
seta <i>bs</i>	115	126	149	191	139
seta <i>c1</i>	24	26	43	64	39
seta <i>c2</i>	10	12	15	22	48
seta <i>c3</i>	88	109	115	145	lost
seta <i>da</i>	50	lost	lost	lost	lost
seta <i>dp</i>	158	lost	lost	lost	lost
seta <i>la</i>	155	5	6	7	51
seta <i>lp</i>	57	5	6	7	53
seta <i>h1</i>	126	165	185	194	70
seta <i>h2</i>	17	45	49	67	69
seta <i>h3</i>	6	149	245	303	70
seta <i>p1</i>	Nd	23	29	35	35
seta <i>p2</i>	Nd	15	22	301	33
seta <i>p3</i>	Nd	6	11	19	32
genital opening	Nd	24	26	47	56
anal opening	31	61	69	89	88

Nymphs stockier than larva, but setal pair *le* inserted between pair *ro*, and seta *ex* of medium size. Gastronotum of protonymph with 12 pairs of setae because setae of *p*-series appearing (Fig. 10b), and remaining in deutonymph and tritonymph (Figs. 13a, 13b), and setae of *d*-series lost and remaining absent in all nymphs. Length of setae of *p*-series decreasing from *p*₁ to *p*₃. Setae *c*₂, *p*₂, *p*₃ and *l*-series short and smooth, *c*₁ and *p*₁ longer and barbed, other setae long and barbed, *h*₂ shorter than other setae of *h*-series. In all nymphs, dorsal part of gastronotum relatively flat, and carrying exuvial scalps of previous instars using cornicle (Figs. 11b, 14), easily lost in samples stored in alcohol. In protonymph, one pair of setae appearing on genital valves, and two pairs added in deutonymph and tritonymph each (Figs. 10b, 13a, 13b); all short and smooth. In deutonymph, two pairs of aggenital setae and three pairs of adanal setae appearing, and three pairs of aggenital setae added in tritonymph; all short and smooth. Anal valves of protonymph (segment AD) with three pairs of setae, those of deutonymph (segment AN) and tritonymph with two pairs each (Figs. 10b, 13a, 13b), all short and smooth. In all nymphs, cupules *ia* and *im* not observed in granular cerotegument, cupule *ip* between *h*₂ and *p*₁. In tritonymph, cupule *iad* lateral to anterior part of anal valves, and cupules *ips* and *ih* displaced posterolateral to *iad*. Opisthonotal gland opening lateral to seta *p*₃ (Figs. 10b, 13). In tritonymph, most leg setae barbed, all tarsi with basal bulb (containing muscles) and uniformly narrow distal stalk (only with tendons) at about mid-length (Fig. 15). Seta *d* present on all genua and tibiae, separated from proper solenidia, solenidion φ_1 on tibia I longer than other solenidia. Some parts of body, legs and setae covered with thin layer or single granules of cerotegument.

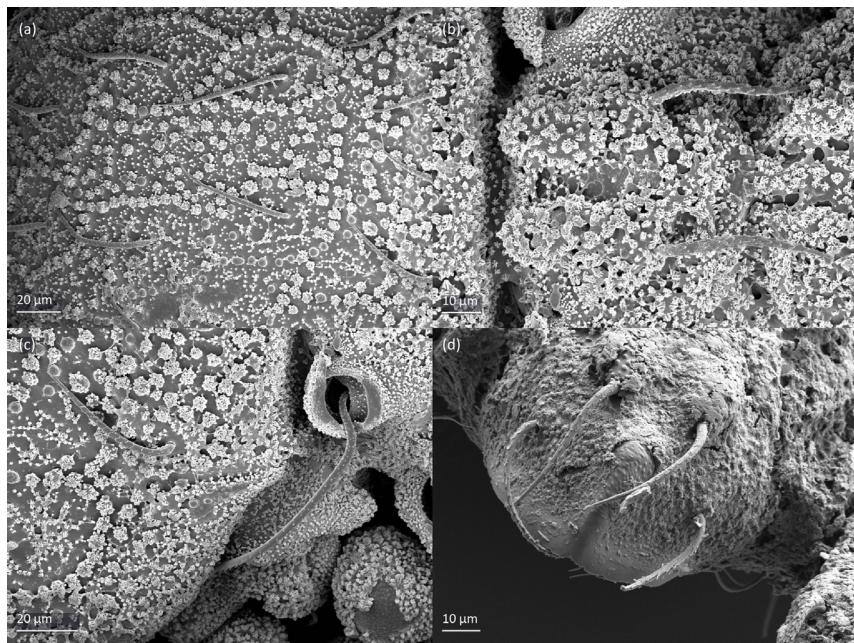


FIGURE 7. *Eremobelba geographica*, adult, SEM micrographs. (a), (b) Central part of body, dorsal view, (c) bothridial seta, dorsal view, (d) anterior part of body, frontal view.

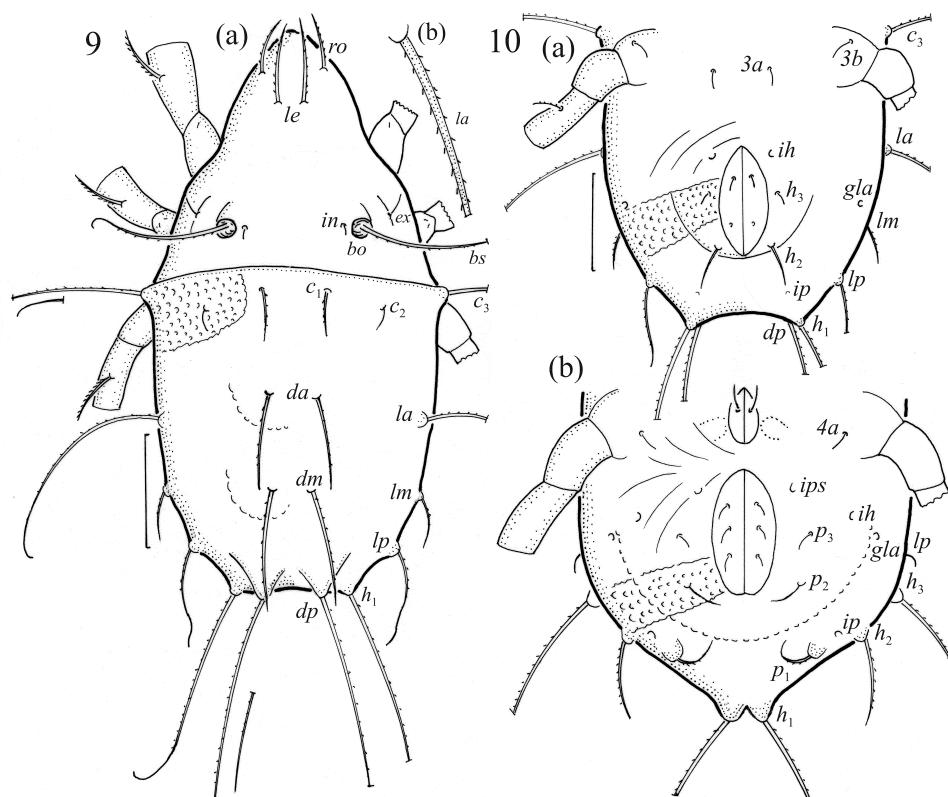


FIGURE 8. *Eremobelba geographica*, adult with thick cerotegument, SEM micrographs. (a) Central part of body, dorsal view, (b) region of bothridium, dorsal view, (c) anterior part of body, dorsal view (d) anterior part of legs I and II, dorsal view.

Summary of ontogenetic transformations

In all juveniles of *E. geographica*, the prodorsal seta *in* is short, and setae *ro* and *le* are of medium size, whereas seta *ex* is short in the larva, and of medium size in the nymphs. In the adult, setae *ro*, *le* and *in* are of medium size, and seta *ex* is short. In all instars, the bothridium is rounded,

and the bothridial seta is setiform and finely barbed. The larva has 12 pairs of gastronotal setae, including h_3 , and the nymphs have also 12 pairs (p -series appear, d -series lost), whereas the notogaster of adult loses setae c_3 such that 11 pairs of notogastral setae remain. The formula of gastronotal setae of *E. geographica* is 12-12-12-12-11 (from larva to adult). Formulae of epimeral setae are 3-1-2 (larva, including scaliform $1c$), 3-1-3-1 (protonymph), 3-1-3-2 (deutonymph) and 3-1-3-3 (tritonymph and adult). Formula of genital setae is 1-3-5-6 (protonymph to adult), paraproctal setae (including alveolar setae, from larva to tritonymph) is 2-3-2-2 and segments PS-AN (including alveolar setae) is 23333-3333-222. In deutonymph, two pairs of aggenital setae appear, and three pairs are added in the tritonymph, whereas in the adult the hypertrichy occurs in the aggenital and adanal regions and total number of setae is 13–15 pairs. Ontogeny of leg setae and solenidia of *E. geographica* is given in Table 3.



FIGURES 9–10. *Eremobelba geographica*, larva, legs partially drawn, scale bars 20 µm. 1. (a) Dorsal aspect, (b) basal part of seta *la* (enlarged). 2. Ventral part of hysterosoma, (a) larva, (b) protonymph.

Distribution, ecology and biology

Eremobelba geographica has a Holarctic or Southern Holarctic distribution (Murvanidze & Mumladze 2016; Subías 2020), respectively, and was included in the meso-hygrophilous group (Ivan & Vasiliu, 2006). This species was recorded from South and Central Europe (Bernini *et al.* 1995; Weigmann 2002, Mahunka & Mahunka-Papp 2004, Niedbała & Olszanowski 2008), the Balkan Peninsula (Tarman 1983), Romania (Vasiliu & Ivan 1995), Caucasus (Shtanchaeva & Subías 2010; Murvanidze & Mumladze 2016) and Iran (Akrami 2015).

Eremobelba geographica was reported from wet habitats, exposed or not to periodical floods (Weigmann 2002; Mahunka & Mahunka-Papp 2004), while Murvanidze & Mumladze (2016) found it in forest soils. This species was also recorded from forest plantations and riparian forests (Ivan *et*

al. 2006), cultivated soils (Vasiliu & Ivan 1995; Ľuptáčik & Miklisová 2005) and rhododendron litter (Murvanidze & Arabuli 2015), which illustrate ecological plasticity of this species. *Eremobelba geographica* was also found on feather of hoazel grouse (*Tetrao tetrix* L.) and red-necked grebe (*Colymbus grisegena* Boddaert) (Krivolutsky & Lebedeva 2004; Lebedeva & Poltavskaya 2013).

TABLE 3. Ontogeny of leg setae (Roman letters) and solenidia (Greek letters) of *Eremobelba geographica*.

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	—	<i>d, bv''</i>	<i>(l), d, σ</i>	<i>(l), v', d, φ1</i>	<i>(ft), (tc), (p), (u), (a), s, (pv), (pl) ε, ω1</i>
Protonymph	—	—	—	—	ω2
Deutonymph	<i>v'</i>	<i>(l)</i>	—	φ2	—
Tritonymph	—	—	—	<i>v''</i>	<i>(it)</i>
Adult	—	<i>v'</i>	<i>v'</i>	<i>d lost</i>	<i>l'', v'</i>
Leg II					
Larva	—	<i>d, bv''</i>	<i>(l), d, σ</i>	<i>l', v', d, φ</i>	<i>(ft), (tc), (p), (u), (a), s, (pv), ω1</i>
Protonymph	—	—	—	—	—
Deutonymph	<i>v'</i>	<i>(l)</i>	—	<i>l''</i>	ω2
Tritonymph	—	—	—	<i>v''</i>	<i>(it)</i>
Adult	—	<i>v'</i>	<i>v'</i>	—	—
Leg III					
Larva	—	<i>d, ev'</i>	<i>l', d, σ</i>	<i>v', d, φ</i>	<i>(ft), (tc), (p), (u), (a), s, (pv)</i>
Protonymph	<i>v'</i>	—	—	—	—
Deutonymph	<i>l'</i>	—	—	<i>l'</i>	—
Tritonymph	—	<i>l'</i>	—	<i>v''</i>	<i>(it)</i>
Adult	—	—	—	—	—
Leg IV					
Protonymph	—	—	—	—	<i>ft'', (p), (u), (pv)</i>
Deutonymph	<i>v'</i>	<i>d, ev'</i>	<i>d, l'</i>	<i>v', d, φ</i>	<i>(a), s</i>
Tritonymph	—	<i>l'</i>	—	<i>l', v''</i>	<i>(tc)</i>
Adult	—	—	—	—	—

Note: structures are indicated where they are first added and are present through the rest of ontogeny; pairs of setae in parentheses, dash indicates no additions.

In this study, *E. geographica* was more abundant in forested areas (3.4–13.2 individuals per 100 cm²) than in cultivated soil (2.4 individuals per 100 cm², Table 1). In willow plantation, this species was clearly more abundant than in poplar plantation and riparian forest. The juveniles were present only in willow plantation and riparian forest, constituting 44% and 29% of all individuals, respectively. In the former habitat, the stage structure of *E. geographica* was the following: 13 larvae, 3 protonymphs, 10 deutonymphs, 3 tritonymphs and 66 adults. In all habitats, females were clearly more abundant than males, and the sex ratio (females: males) was 1:0.2–1:0.5 (Table 4). In most habitats, females were gravid, carrying 2–5 large eggs, each about 184 x 116, which constitutes about 37% of the total body length of females.

The largest females of *E. geographica* lived in cultivated soil, whereas in the other habitats they were significantly smaller (Table 4). In these habitats, the body length and width of males were insignificantly different from females, but males were significantly smaller than females.

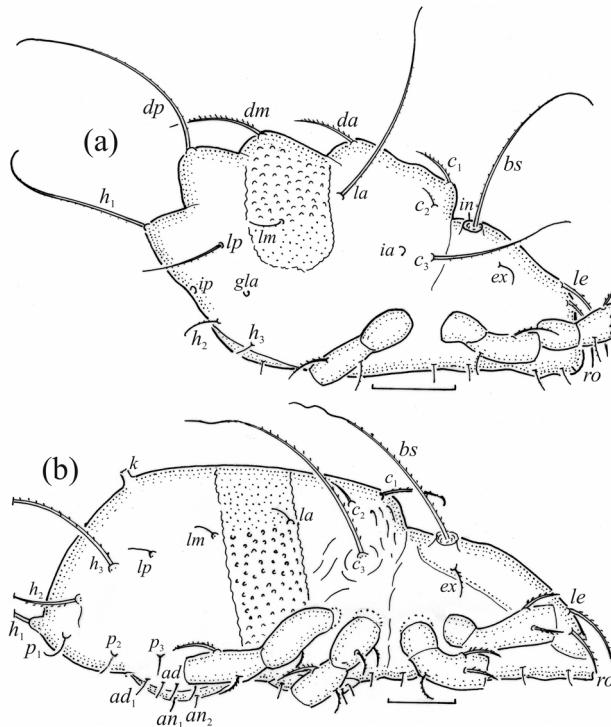


FIGURE 11. *Eremobelba geographica*, lateral aspect, legs partially drawn, scale bars 50 µm. (a) Larva, (b) tritonymph.

TABLE 4. Sex ratio, number of gravid females and mean body length and width (and range) of *Eremobelba geographica* in µm in different regions of Romania.

Place/month of sampling ¹	females	gravid (%)	males	females		males	
				sex ratio	length (range)	width (range)	length (range)
1. Plauru/07	25	4(16)	5	1:0.2	490.2±7.7 ^a (476–506)	292.1±8.8 ^a (277–319)	464.0±6.0 ^a (458–470)
2. Stăniște/06	20	11(55)	7	1:0.35	492.5±18.8 ^a (464–542)	295.9±12.6 ^{ab} (277–325)	457.1±9.4 ^a (446–470)
3. Plauru/07	8	0(0)	4	1:0.5	485.0±10.6 ^a (470–500)	289.8±7.5 ^a (283–301)	461.0±7.8 ^a (452–470)
4. Uzlina/06	10	7(70)	2	1:0.2	502.4±10.7 ^b (482–518)	299.2±9.4 ^b (283–313)	455.0±4.2 ^a (452–458)
Total	63	22(35)	18	1:0.29	492.2±13.6 [*] (464–542)	294.1±10.4 [*] (277–325)	459.7±7.9 [*] (446–470)

¹Plant cover as in Table 1; different letters in the superscript indicate significant differences between studied regions at $\alpha=0.05$; *significantly different between females and males at $\alpha=0.05$.

Comparison of morphology of *Eremobelba geographica* with congeners and remarks

Among *Eremobelba* species, the largest is *E. bellicosa* Balogh & Mahunka, 1967, and smallest is *E. porcella* Mahunka, 2001, and the body length of most species overlaps (Table 5). In most species, the prodorsal seta *in* is either long or of medium size, but in few species it is short. In all species, the bothridial seta is setiform, in most species it is barbed, and in others is smooth. Most species have 11

pairs of notogastral setae, but some species have 10 pairs (*E. hamata* Hammer, 1961, *E. okinawa* Aoki, 1987, *E. piffla* Mahunka, 1985). In most species, the notogastral setae are long or of medium size, but seta c_1 can be long, of medium size or short (Table 5). In most species, the shoulder crest on the anterior edge of notogaster is absent, but in other species it is present. In most species, the prodorsal pattern of ridges is similar to that of *E. geographica* (setae *le* and *in* are positioned on sclerotized ridges, the lamellar costula is short and curved, sclerotized ridges are present between bothridia), but in several species these ridges are indistinct or absent, which lowers their taxonomic value. These species differ also from one another by the shape of prodorsal seta *in* and pattern of notogastral sculpture (Table 5). The adult of *E. gracilior* Berlese, 1908 (length 440) is poorly described in two short sentences, and therefore is omitted in this table.

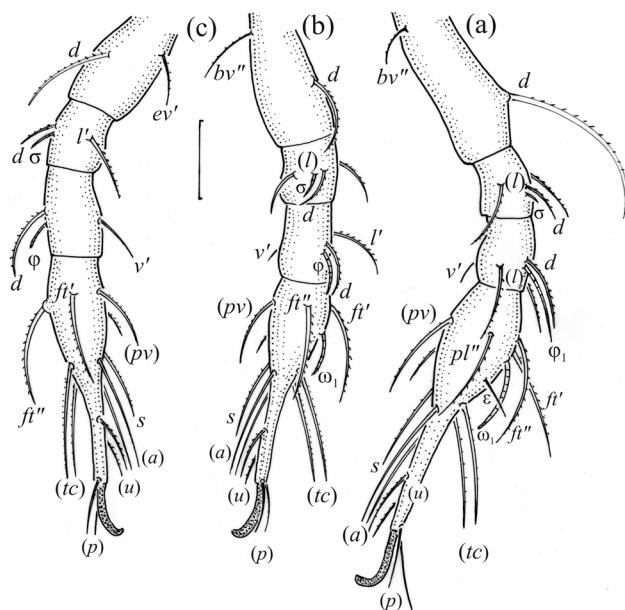


FIGURE 12. *Eremobelba geographica*, leg segments of larva (part of femur to tarsus), right side, seta on the opposite side not illustrated is indicated in the legend, scale bar 10 μm . (a) Leg I, tarsus (pl'); (b) leg II; (c) leg III, (d) part of tarsus, dorsal aspect.

In the adult *Eremobelba*, the leg setation was investigated in *E. jenoi* Ermilov & Khaustov, 2018 and *E. asagiriensis* Fujikawa & Tominaga, 2014, whereas in *E. cellulosa* it was investigated on legs I and IV (Mahunka 1997). In *E. geographica*, the number of leg setae and solenidia is similar as in *E. jenoi*, except for seta *l''* on tarsus II and seta *l'* on femora III and IV, which are present in the latter species (Ermilov & Khaustov 2018), but absent in *E. geographica* (Table 6). The number of leg setae of *E. geographica* differs also from that of *E. asagiriensis* and *E. cellulosa* (Table 6), but Mahunka (1997) and Fujikawa & Tominaga (2014) gave only numeric data, and therefore it is impossible to analyse which setae are lacking or present in these species, in comparison to *E. geographica*.

The larva of *E. geographica* has most of gastronotal setae long and inserted on apophyses, and it is similar to those of Damaeidae (Norton 1978, 1980; Seniczak & Seniczak 2011, 2013; Seniczak *et al.* 2013, 2016). It has 12 pairs of notogastral setae, including h_3 , and two pairs of paraproctal setae, including alveolar pair, whereas in the larvae of Damaeidae seta h_3 can be present, alveolar or absent and two pairs of alveolar setae can be present or absent on anal valves. The protonymph and deutonymph of *E. geographica* have three and two pairs of paraproctal setae, respectively, whereas the paraproctal setae are absent in these stages of Damaeidae. In the tritonymph of *E. geographica*,

setae c_1 , c_2 and of l -series are short or of medium size (versus they are long in Damaeidae), and long seta c_3 , which in Damaeidae is usually clear shorter than c_1 and c_2 . The tritonymph of *E. geographica* is similar to that described by Weigmann (2002), except for seta ex , which is barbed, but in the figure by this author it is smooth. Moreover, Weigmann (2002) labelled probably by mistake a long posterior seta h_1 as p_1 , the latter is short and inserted between setae h_2 and h_1 .

TABLE 5. Selected morphological characters of *Eremobelba* species (abbreviations as in Material and methods).

Species	body length	polygonal pattern of Ng	Ng shoulder crest	shape of setae					
				bs	in	ex	c_1	most Ng	most ag
<i>E. asagiriensis</i> Fujikawa & Tominaga, 2014	464–536	No	Absent	Setiform	Long	Long	Long	Flagellate	Setiform
<i>E. balazzi</i> Mahunka, 1983	451–492	Yes	Present	Barbed	Medium sized ¹	Short	Medium sized ²	Phylliform	Setiform
<i>E. bella</i> Hammer, 1982	410	Yes	Absent	Barbed	Short	Short	Long	Flagellate	Setiform
<i>E. bellicosa</i> Balogh & Mahunka, 1967	627	No	Present	Smooth	Long	Medium sized ¹	Long	Phylliform	Setiform
<i>E. breviseta</i> Balogh, 1968	325–363	Yes	Present	Smooth	Short	Short	Medium sized	Phylliform	Setiform
<i>E. brevispathulata</i> Balogh & Mahunka, 1969a	387–421	Yes	Absent	Smooth	Medium sized	Medium sized	Medium sized	Phylliform	Setiform
<i>E. capitata</i> Berlese, 1913 ³	505	Yes	Present	Smooth	Medium sized	Short	Medium sized	Flagellate	Setiform
<i>E. cellulosa</i> Mahunka, 1997	386–463	Yes	Absent	Barbed	Long	Medium sized	Long	Flagellate	Setiform
<i>E. comteae</i> Mahunka, 1988	353–374	Yes	Absent	Smooth	Long	Long	Long	Flagellate	Setiform
<i>E. coronata</i> Pérez-Íñigo & Baggio, 1989	360–396	No	Absent	Barbed	Short	?	Long	Flagellate	Setiform
<i>E. curtipedata</i> Wen, 1996	312–360	Yes	Absent	Smooth	Short	Medium sized	Long	Flagellate	Setiform
<i>E. editae</i> Mahunka, 2008	335	Yes	Absent	Barbed	Short	?	Long	Flagellate	Setiform
<i>E. espositi</i> Balogh & Mahunka, 1969b	697–736	Yes	Absent	Barbed	Medium sized	Medium sized	Medium sized	Phylliform	?
<i>E. flexuosa</i> Hammer, 1979	560	Yes	Present	Smooth	Medium sized	Medium sized	Long	Flagellate	Setiform
<i>E. foliata</i> Hammer, 1958	500	Yes	Absent	Smooth	Medium sized	?	Medium sized	Phylliform	?
<i>E. geographica</i> Berlese, 1908	364–542	Yes	Present	Barbed	Medium sized	Short	Medium sized	Flagellate	Setiform
<i>E. graciosa</i> Mahunka, 1984	318–360	No	Absent	Barbed	Medium sized	?	Medium sized	Phylliform	Setiform
<i>E. hamata</i> Hammer, 1961	575	No	Present	Smooth	Medium sized	Medium sized	Long	Flagellate	?
<i>E. heterotricha</i> Mahunka, 1977	502–526	Yes	Absent	Barbed	Short	Medium sized	Medium sized	Flagellate	Phylliform
<i>E. himalayensis</i> Mondal & Kundu, 1984	530–53	No	Present	Barbed	Long	Long	Long	Flagellate	Setiform
<i>E. indica</i> Ghosh & Bhaduri, 1979	455	No	Absent	Barbed	Long	?	Long	Flagellate	Setiform

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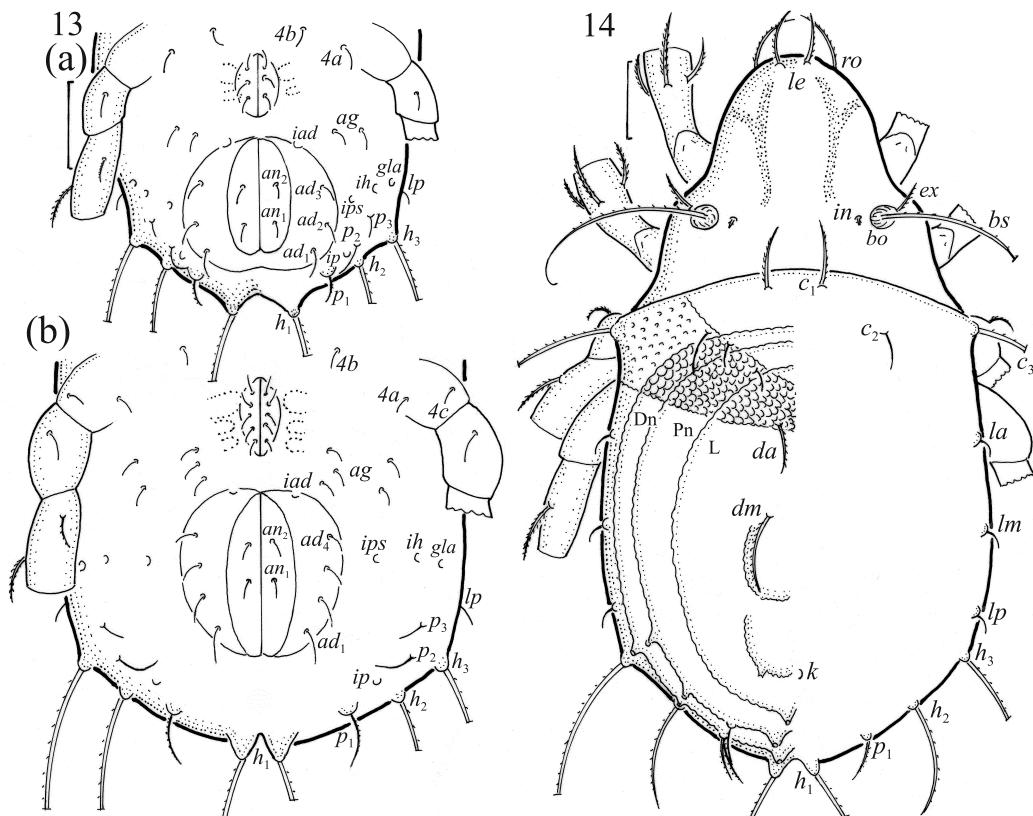
TABLE 5. (Continued)

Species	body length	polygonal pattern of Ng	Ng shoulder crest	shape of setae					
				bs	in	ex	c_1	most Ng	most ag
<i>E. japonica</i> Aoki, 1959	680–690	No	Absent	Setiform	Medium sized	?	Long	Flagellate	?
<i>E. jenoi</i> Ermilov & Khaustov, 2018	448–481	Yes	Absent	Barbed	Long	Long	Medium sized	Flagellate	Phylliform
<i>E. longisetosa</i> Subías <i>et al.</i> , 1990	437	No	Absent	Smooth	Long	Medium sized	Long	Flagellate	Setiform
<i>E. mahunkai</i> Balogh, 1968	591	Yes	Absent	Smooth	Long	?	Long	Flagellate	Setiform
<i>E. miliae</i> Sanyal, 1992	440	No	Present	Smooth	Medium sized	Medium sized	Medium sized	Flagellate	Setiform
<i>E. minuta</i> Aoki & Wen, 1983	330–370	Yes	Present	Setiform	Medium sized	Medium sized	Medium sized	Flagellate	Setiform
<i>E. nagaroorica</i> Haq, 1978	468–561	No	Absent	Barbed	Long	?	Long	Flagellate	Setiform
<i>E. okinawa</i> Aoki, 1987	462–515	No	Absent	Barbed	Long	Long	Long	Flagellate	Setiform
<i>E. ornata</i> Balogh & Mahunka, 1969a	411–456	Yes	Absent	Barbed	Medium sized	Medium sized	Medium sized	Phylliform	Phylliform
<i>E. perrugosa</i> Balogh & Mahunka, 1968	554–617	No	Present	Smooth	Medium sized	Short	Medium sized	Flagellate	Setiform
<i>E. piffli</i> Mahunka, 1985	408–425	Yes	Present	Barbed	Medium sized	Medium sized	Long	Flagellate	Setiform
<i>E. porcella</i> Mahunka, 2001	262–283	Yes	Absent	Barbed	Short	Medium sized	Short	Phylliform	Phylliform
<i>E. pulchella</i> Balogh & Mahunka, 1969a	416–431	Yes	Absent	Barbed	Medium sized	Long	Medium sized	Phylliform	?
<i>E. shillongensis</i> Sanyal, 1988	563	No	Absent	Smooth	Long	?	Long	Phylliform	Setiform
<i>E. truncata</i> Wen, 1996	508–560	No	Present	Smooth	Long	Long	Long	Flagellate	Setiform
<i>E. tuberculata</i> Mahunka, 1982	473–482	No	Present	Barbed	Long	Medium sized	Medium sized	Flagellate	Setiform
<i>E. wittmeri</i> Bayoumi & Mahunka, 1979	470–486	No	Present	Smooth	Long	Long	Long	Flagellate	Phylliform

¹slightly shorter than the distance between insertions of setae in and ex,²slightly shorter than the distance between insertions of setae c_1 ,³according to Balogh (1968).

The nymphs of *E. geographica* carry the exuvial scalps of previous instars, using a cornicle that fastens the exuvial scalps to the gastronotum of mites, as in the nymphs of *Caleremaeus* Berlese, 1910 (Seniczak & Seniczak 2019; Norton & Behan-Pelletier 2020). The cornicle plays the same role in the nymphs of Damaeidae (Norton 1978, 1980; Seniczak & Seniczak 2011, 2013; Seniczak *et al.* 2013, 2016), but in *E. geographica* and *Caleremaeus*, the cornicle is positioned in the posterior or medial part of gastronotum, respectively, whereas in Damaeidae it is present in the posterior, medial or anterior part of gastronotum, depending on species, suggesting that in Damaeidae the position of cornicle on the gastronotum has taxonomic value. The nymphs of other eupheredermous species of Ameroidea have either long gastronotal setae, which protect the exuvial scalps against loss (Miko & Travé 1996; Seniczak *et al.* 2020b, c) or short setae (Călugăr & Vasiliu 1984; Seniczak *et al.* 2020a 2021). By contrast, the nymphs of *Gymnodampia setata* (Berlese, 1916) retain setae of *d*-series on the gastronotum and are apheredermous (Chen *et al.* 2004). The anal valves of protonymph and deutonymph of *E. geographica* have three and two pairs of setae, respectively, whereas those of

Ctenobelba pilosella and *Ct. pectinigera* have two pairs of alveolar setae (Grandjean 1965; Seniczak *et al.* 2021), and these setae are rare in Brachypylina.



FIGURES 13–14. *Eremobelba geographica*, legs partially drawn, scale bars 50 µm. 13. Ventral part of hysterosoma, (a) deutonymph, (b) tritonymph. 14. Tritonymph, dorsal aspect.

In *Eremobelba*, the mouthparts were investigated in *E. jenoi* (Ermilov & Khaustov 2018) and *E. asagiriensis* (Fujikawa & Tominaga 2014). The chelicera of *E. geographica* studied herein is chelate, with barbed setae and small articulation posterior to seta *cha*, as in *E. jenoi*, whereas in *E. asagiriensis* cheliceral setae are smooth, and articulation is absent. The palp of *E. geographica* is more slender than that of *E. jenoi*, but in both species solenidion ω is of similar shape and the number of setae and eupathidia are the same.

Diagnostic characters of *Eremobelba* given by Balogh (1961, 1972) and Weigmann (2002, 2006) seem to be insufficient. For example, the shape of lamellar ridges insisted by Balogh (1961) varies between species, and in some species the ridges are absent. The number of notogastral, genital, adanal and anal setae considered by Balogh (1972) as diagnosis does not characterise *Eremobelba*, and the diagnostic characters given by Weigmann (2002, 2006) are true only for some species of *Eremobelba*. Considering the most important morphological characters of *Eremobelba*, we can give the following diagnosis of *Eremobelba*: adults of medium size (262–627), rostrum rounded, bothridial seta setiform, barbed or smooth, notogastral setae (10–11 pairs) flagellate or phylliform, hypertrichy of aggenital and adanal setae present. Nymphs quadrideficient and euphoredermous, carrying the exuvial scalps of previous instars using cornicle, in all juveniles paraproctal setae present, in deutonymph and tritonymph hypertrichy present in aggenital region. In all juveniles, seta *d* on all genua and tibiae present.

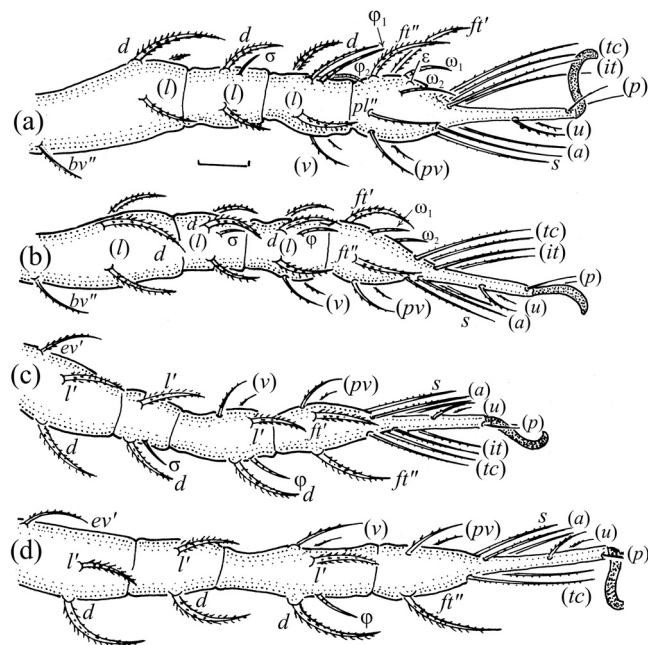


FIGURE 15. *Eremobelba geographica*, leg segments of tritonymph (part of femur to tarsus), right side, seta on the opposite side not illustrated is indicated in the legend, scale bar 20 μm . (a) Leg I, tarsus (pl'); (b) leg II; (c) leg III; (d) leg IV.

TABLE 6. Comparison of number of leg setae in *Eremobelba geographica*, *E. jenoi*, *E. asagiriensis* and *E. cellulosa*.

Species	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
<i>E. geographica</i>	1	5	4	4	20
<i>E. jenoi</i>	1	5	4	4	20
<i>E. asagiriensis</i>	1	5	3	4	19
<i>E. cellulosa</i>	1	5	3	4	20
Leg II					
<i>E. geographica</i>	1	5	4	5	15
<i>E. jenoi</i>	1	5	4	5	16
<i>E. asagiriensis</i>	1	5	3	4	17
Leg III					
<i>E. geographica</i>	2	3	2	4	15
<i>E. jenoi</i>	2	3/4	2	4	15
<i>E. asagiriensis</i>	2	3	1	2	15
Leg IV					
<i>E. geographica</i>	1	3	2	4	12
<i>E. jenoi</i>	1	3/4	2	4	12
<i>E. asagiriensis</i>	1	3	2	3	11
<i>E. cellulosa</i>	1	3	2	4	13

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