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Source: Systematic and Applied Acarology, 26(1) : 240-259

Published By: Systematic and Applied Acarology Society

URL: https://doi.org/10.11158/saa.26.1.13

Systematic & Applied Acarology 26(1): 240–259 (2021) ISSN 1362-1971 (print)
https://doi.org/10.11158/saa.26.1.13 ISSN 2056-6069 (online)

Article http://zoobank.org/urn:lsid:zoobank.org:pub:D81BFCE7-8DC2-4A5E-8E28-BEFDCA4A832B

Morphological ontogeny of *Ctenobelba pilosella* (Acari: Oribatida: Ctenobelbidae), with comments on *Ctenobelba* Balogh

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Abstract

The morphological ontogeny of *Ctenobelba pilosella* Jeleva, 1962 is described and illustrated. This species was investigated from its description mainly in ecological aspect. It was recorded from the forest and meadow soils, with rather low density, and small percent of juveniles.The adult is of medium size and has setiform bothridial seta, with 6–10 anterior spines. Notogaster is covered with asteriform granules and has 10 pairs of medium size, barbed setae. Seta *d* is absent from genua I–III and all tibia. Bothridial seta of juveniles is setiform and barbed, prodorsal and gastronotal setae are short, except of medium size *ro* and long, curved inwards *lp*. Nymphs are quadrideficient and eupheredermous i.e. they carry the exuvial scalps of previous instars. Anal valves of protonymph and deutonymph have two pairs of alveolar setae, which is rare in Brachypylina. The juveniles have seta *d* on all genua and tibiae.

Keywords: oribatid mites, redescription, juveniles, leg setation, stage structure, ecology

Introduction

Ctenobelba Balogh, 1943, with the type species *Ctenobelba pectinigera* (Berlese, 1908) (= *Eremobelba pectinigera* Berlese, 1908), comprises medium sized mites (adults: 340–577 µm). The diagnosis of *Ctenobelba* was given recently by Ahaniazad *et al*. (2017) as follows: prodorsum with one pair of long, parallel costulae, rostrum rounded or dentate, lamellar seta inserted apically on costula, bothridial seta bifurcate or setiform, with cilia or long branches unilaterally, notogaster with one pair of tubercles at anterior margin and 10 pairs of notogastral setae. Pedotecta I and II well developed, three to seven pairs of aggenital and three pairs of adanal setae present, lyrifissure *iad* located posterior to seta ad_3, legs monodactylous. Subías (2004, 2020 update) included 22 species in *Ctenobelba sensu stricto*, and one of them he treated as *species inquirenda*.

According to the catalogue of juvenile oribatid mites by Norton and Ermilov (2014) and further literature, the morphology of juveniles of only *C. pectinigera* (Berlese 1908) is partially known in *Ctenobelba*. Grandjean (1943) investigated the shape of gastronotal setae of the larva and nymphs of *C. pectinigera* (his *Elapheremaeus pectinigera*), and some formulae like anal and gastronotal setae (Grandjean 1949) and leg setae (Grandjean 1951), mainly in a phylogenetic context. He also briefly described the morphology of nymphs and illustrated the bothridium, bothridial seta, anal region, and opisthonotal gland opening (Grandjean 1965).

The aim of this paper is to describe and illustrate the morphological ontogeny of *C. pilosella*, and compare the morphology of the adult with congeners. The original description of the adult by

Csiszár and Jeleva (1962) is brief, incomplete and was based on a single specimen, therefore the redescription is reasonable and important.

Material and methods

The juveniles and adults of *C. pilosella* used in this study were collected on 18 July 2011 by O. Ivan from (1) chestnut-beech forest in Baia Mare, with *Castanea sativa* (Mill.) and *Fagus sylvatica* L., affected by industrial pollution (extraction and processing of non-ferrous metals), with a maximum in the 70s and 80s years (currently, Natura 2000 site). For ecological comparison, we also selected eight other habitats from Romania (Table 1): (2) beech-hornbeam forest in Zlatna, with *Fagus sylvatica* and *Carpinus betulus* L., also affected by industrial pollution (extraction and processing of non-ferrous metals), (3) Ponto-Sarmatic steppe meadow (hayfield) in Ponoare, with *Festuca valesiaca* Schleich. ex Gaudin, *F. rubra* L., *Poa angustifolia* L., *Stipa capillata* L., *Dichanthium ischaemum* (L.) Roberty (Natura 2000), (4) xero-mesophilous meadow (hayfield) in Calafindeşti, with *Agrostis capillaris* L., *Filipendula vulgaris* Moench, *Arrhenatherum elatius* (L.) Beauv. ex J. & C. Presl, *Dactylis glomerata* L., protected area of national interest (IUCN IV), (5) Dacian oak-hornbeam forest in Dobrina with *Quercus petraea* (Matt.) Liebl., *Q. dalechampii* Ten., *Carpinus betulus*, *Tilia tomentosa* Moench (Natura 2000), (6) oak forest in Tismana, with *Quercus robur* L. and *Carpinus betulus*, (7) beech forest in Nămăeşti, with *Fagus sylvatica*, affected by pollution with cement dust, (8) saxicolous vegetation in Horia, with *Festuca valesiaca*, *Asplenium trichomanes* L. and bryophytes on limestone cliffs and (9) Ponto-Sarmatic steppe meadow (hayfield) in Valea lui David, with *Festuca valesiaca, Dichanthium ischaemum, Stipa capillata* and *S. joannis* Čelak (Natura 2000). In all habitats, we investigated the density and stage structure of mites, sex ratio, number of gravid females and eggs, and body length and width. In abundant populations, 30 randomly selected specimens were used. We measured total 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 length in μm. In total 178 adults were examined. In statistic calculations, to differentiate the variables (female length and width, male length and width) among sites, 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 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.

The illustrations of *C. pilosella* are limited to the body regions 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, tables and figures, we used the following abbreviations: rostral (*ro*), lamellar (*le*), interlamellar (*in*) and exobothridial (*ex*) setae, bothridium (*bo*), bothridial seta (*bs*), notogaster (Ng), notogastral or gastronotal setae (*c*-, *d*-, *l*-, *h*-, *p*-series), exuvial scalps of larva (L), protonymph (Pn) and deutonymph (Dn), lamellar costula (La), pedotectum (*Pd*), cupules or lyrifissures (*im*, *ip*, *ih*, *ips*, *iad*), opisthonotal gland opening (*gla*), humeral tubercle (*ht*), discidium (*Dis*), ovipositor setae (*k*, *ψ*, *τ*), subcapitular setae (*a*, *m*, *h*), cheliceral setae (*cha*, *chb*), Trägårdh organ (*Tg*), palp setae (*sup*, *inf*, *l*, *d*, *vt*, *lt*, *ul*, *su*) and solenidion ω, epimeral setae (*1a–c*, *2a*, *3a–c*, *4a–c*), adanal and anal setae (*ad*-, *an*-series), aggenital seta (*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 (1943, 1949, 1951, 1953, 1961, 1965) and Norton and Behan-Pelletier (2009). The species nomenclature follows Subías (2004, 2020 update).

TABLE 1. Stage structure and density of *Ctenobelba pilosella* in different regions of Romania, details on plant cover are given in Material and methods; L—larva, Pn—protonymph, Dn—deutonymph, Tn—tritonymph, Juv—juveniles, Ad—adult.

Place of sampling, date[2]	Coordinates	Habitat	Juveniles[2]						Ad[2]	Total	Indiv. /500 cm³
			L	Pn	Dn	Tn	Juv	%			
1. Baia Mare 18.07.2011	47°41′26″N, 23°33′31″E 469 m a. s. l.	Chestnut-beech forest	1	2	3	10	16	16	82	98	19.6
2. Zlatna 25.05.2011	46°09′32″N, 23°13′16″E 425 m a. s. l.	Beech-hornbeam forest	0	0	0	0	0	0	105	105	21.0
3. Ponoare-Bosanci 13.09.2006	47°34′23″N, 26°15′27″E 345 m a. s. l.	Ponto-Sarmatic steppe meadow	1	3	1	0	5	12	36	41	8.2
4. Calafindeşti 03.07.2007	47°54′35″N, 26°04′04″E 409 m a. s. l.	Xero-mesophilous meadow	0	0	0	0	0	0	31	31	6.2
5. Dobrina 15.05.2019	46°40′27″N, 28°03′35″E 280 m a. s. l.	Dacian oak-hornbeam forest	0	1	1	1	3	14	19	22	4.4
6. Tismana 06.08.2008	45°03′02″N, 22°56′56″E, 350 m a. s. l.	Oak forest	2	1	0	1	4	21	15	19	3.8
7. Nămăeşti 18.06.1998	45°18′17″N, 25°06′48″E 833 m a. s. l.	Beech forest	0	0	0	0	0	0	13	13	2.6
8. Horia 18.04.2008	48º07′19″N, 26º58′27″E 109 m a. s. l.	Saxicolous vegetation	0	0	0	0	0	0	6	6	1.2
9. Valea lui David 09.05.2006	47°12′17″N, 27°27′50″E 107 m a. s. l.	Ponto-Sarmatic steppe meadow	0	0	0	0	0	0	5	5	1.0

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

The transmitted-light photomicrographs of the adult, larva and tritonymph of *C. pilosella* were prepared using a Leica DM3000 microscope and Leica DFC420 camera. 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.

Ctenobelba pilosella **Jeleva, 1962**
(Figs. 1–17)

Diagnosis

Adults of medium size (440–566), prodorsum elongated, with rounded rostrum and two long lamellar costulae, and barbed setae *le* and *in* on their basal and apical parts. Bothridial seta setiform, with 6–10 anterior spines. Anterior border of notogaster straight to concave, with humeral tubercle, and other tubercle positioned opposite to basal part of bothridium. Notogaster with asteriform granules and 10 pairs of thickened, barbed setae, *gla* opening close to lyrifissure *im*. Seta *d* absent from genua I–III and all tibia.

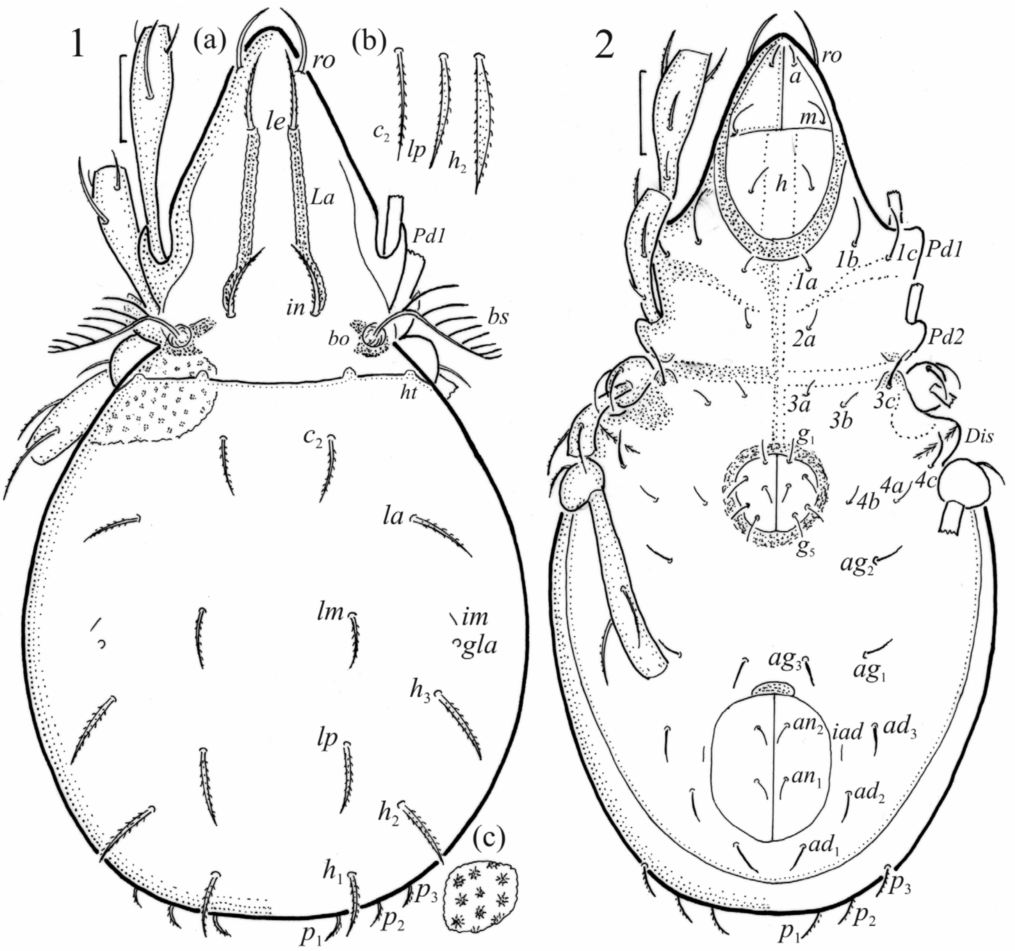
Juveniles unpigmented, cuticle with tubercles. Bothridial seta setiform, barbed, prodorsal and gastronotal setae short, except for medium sized *ro* and long, curving inwards *lp*. Nymphs quadrideficient and eupheredermous i.e. they carry exuvial scalps of previous instars, with reticulate pattern. Anal valves of protonymph and deutonymph with two pairs of alveolar setae, which is rare in Brachypylina. Seta *d* on all genua and tibia present.

Redescription of morphology of adult

Measurements. Mean length (range) of females—503.5±26.0 (458–566, N= 124) and males—475.2±21.9 (440–518, N= 54), and mean width (range) of females 281.4±13.2 (253–313) and males—260.7±11.8 (241–283).

Integument. Dark-brown, with asteriform granules, in alcohol samples granular cerotegument in some parts of body absent (Figs. 1c, 3a, 4, 5, 6a–d, 7a).

Prodorsum. Subtriangular, longer (187–191) than wide (129–133). Rostrum rounded, with pair of medium sized (45–47) and smooth seta *ro* (Figs. 1a, 2, 3a, 4a, 4b, 5d). Two long (85–88) prodorsal lamellar costulae present, separated from bothridium, with medium sized, barbed setae *le* (44–47) and *in* (48–51) on their basal and apical parts (Figs. 1a, 3a, 4a, 4b, 6a, 6b). Bothridium rounded, bothridial seta setiform (107–111), with 7–8 anterior spines, basal spine of medium size (35), length decreasing to apical part (Figs. 1a, 3a, 4a–c, 5a, 6c). Seta *ex* short (12) and smooth, located lateroventral to bothridium (Fig. 3a).



FIGURES 1–2. *Ctenobelba pilosella*, female, legs partially drawn, scale bar 50 µm. 1. (a) Dorsal aspect, (b) shape of some notogastral setae, (c) shape of granular cerotegument (b, c—enlarged). 2. Ventral aspect.

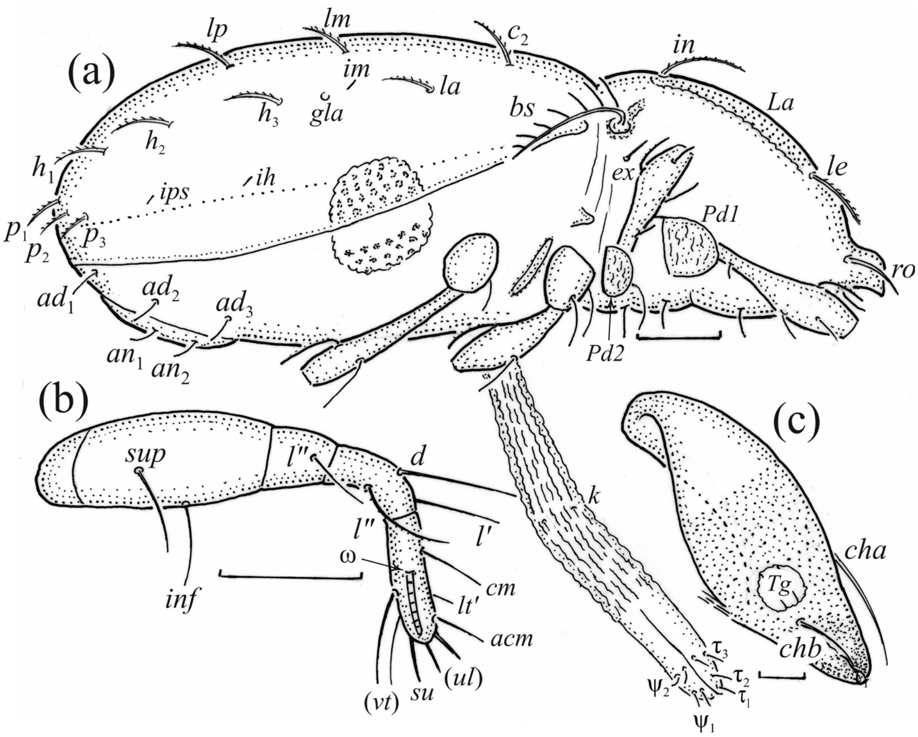


FIGURE 3. *Ctenobelba pilosella*, female. (a) Lateral aspect, including ovipositor, legs partially drawn, scale bar 50 µm; mouthparts, right side, scale bars 20 µm; (b) palp, (c) chelicera.

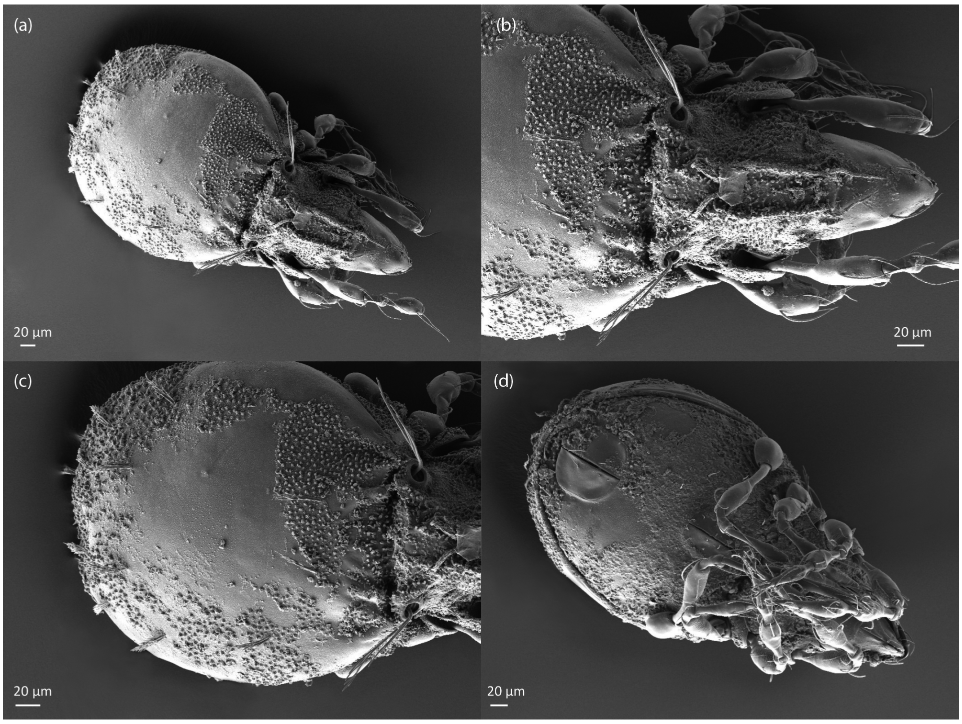


FIGURE 4. *Ctenobelba pilosella*, adult, SEM micrographs. (a) Dorsal view, (b) anterior part, dorsal view, (c) notogaster with granular cerotegument, (d) ventral view.

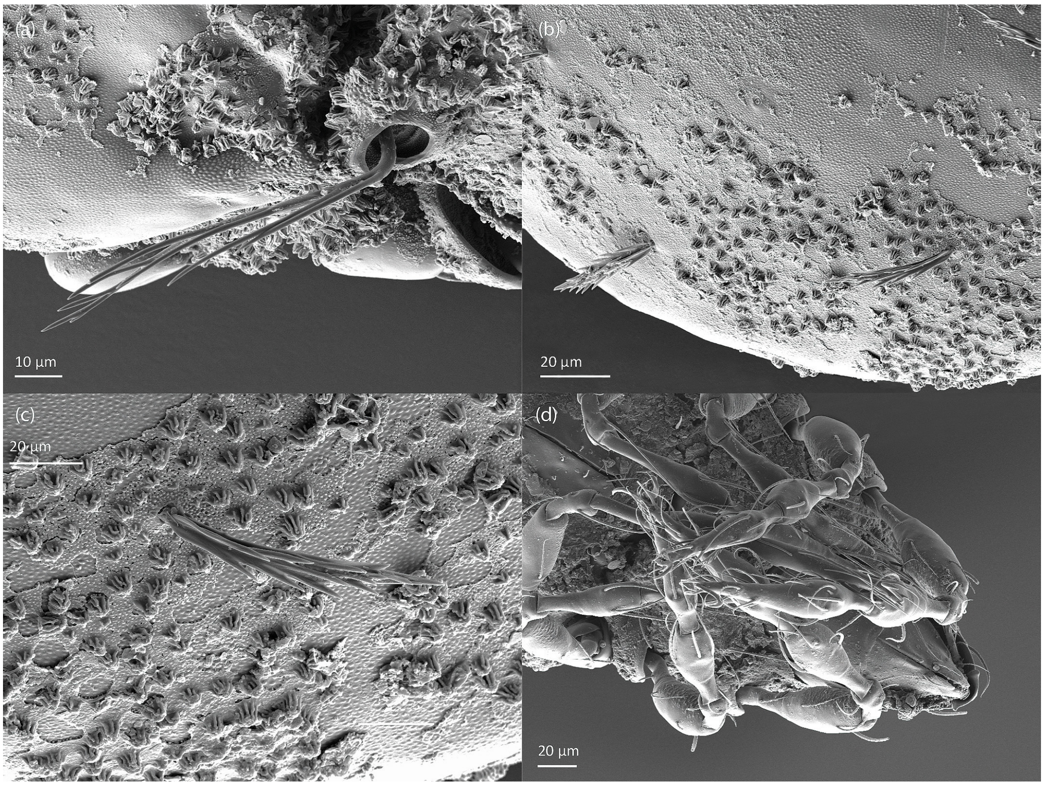


FIGURE 5. *Ctenobelba pilosella*, adult, SEM micrographs. (a) Bothridium and bothridial seta, (b), (c) posterior part of notogaster, dorsal view, (d) anterior part of body, ventral view.

Notogaster. Longer (311–315) than wide (295–299). Anterior border of notogaster straight to concave, humeral tubercle present, other tubercle opposite to basal part of bothridium (Figs. 1a, 4a–c). Notogastral setae (10 pairs, including c_2) of medium size (Table 2), barbed and of different shapes (Figs. 1a, 1b, 3a, 4, 5b, 5c). Lyrifissures *ia* and *ip* not observed, *im* close to opisthonotal gland opening, *ih* and *ips* in normal positions (Figs. 1a, 3a).

Gnathosoma. Subcapitular setae *h* and *m* slightly longer (24–26) than *a* (16), all smooth (Figs. 2, 5d). Palp relatively short (98), most palp setae smooth, except barbed seta *l″* on tibia (Fig. 3b), solenidion ω separated from seta *acm*, seta *lt″* on tarsus absent. Formula of palp setae (and solenidion): 0-2-1-3-8(1). Chelicera elongated (154 x 62), chelate (Fig. 3c), *chb* shorter than *cha*, both smooth. Axillary saccule of subcapitulum long (24).

Ventral and lateral regions. Epimeral seta *1b*, *1c*, longer (30) than other setae (15–21, Fig. 2). Genital setae (5 pairs) short (15–17) and smooth, g_1 and g_3 in inner row, other setae in lateral row. All setae on ovipositor short and smooth (Fig. 3a). Aggenital setae (3 pairs), adanal setae (3 pairs) and anal setae (2 pairs) short (17–23) and smooth. Lyrifissure *iad* short, located lateral to medial part of anal plates. Pedotectum I large, oval (48 x 32), Pedotectum II smaller (36 x 19), discidium well-formed, distally rounded (Figs. 3a, 4).

Legs. Leg femora relatively slim, most leg setae finely barbed, seta *d* from genua I–III and all tibiae absent (Figs. 7a, 8). Most leg solenidia of medium size, except long φ_1 on tibia I and φ on tibia III and IV. Formulae of leg setae (and solenidia, from trochanter to tarsus): I – 1-5-3(1)-4(2)-20(2); II – 1-5-3(1)-4(1)-15(2); III – 2-3-1(1)-3(1)-15; IV – 1-2-2-3(1)-12. Legs monodactylous.

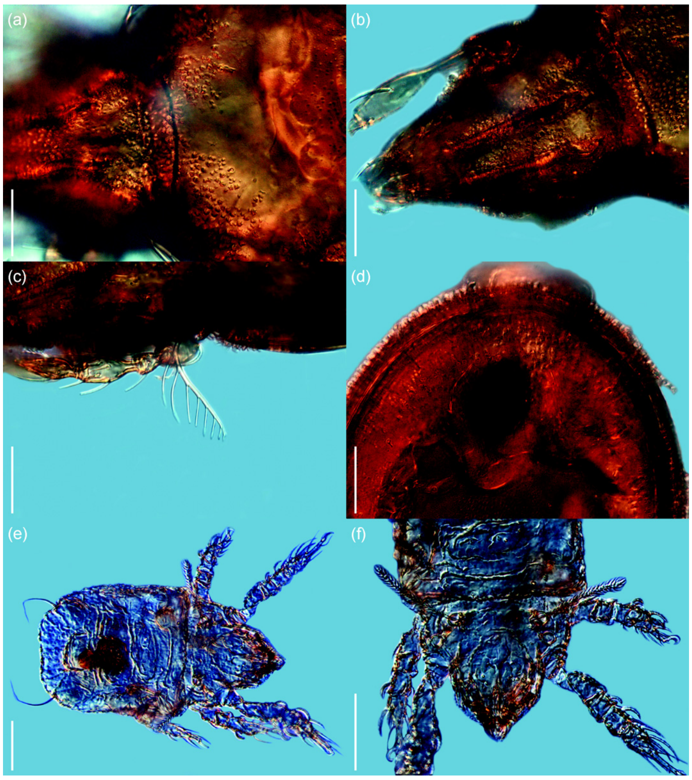


FIGURE 6. *Ctenobelba pilosella*, transmitted-light photomicrographs. Adult, (a) distribution of granular cerotegument, dorsal view, (b) shape of lamellar costulae, (c) bothridium and bothridial seta, (d) posterior part of body; larva, (e) whole body, (f) anterior part of body. Scale bars 50 µm.

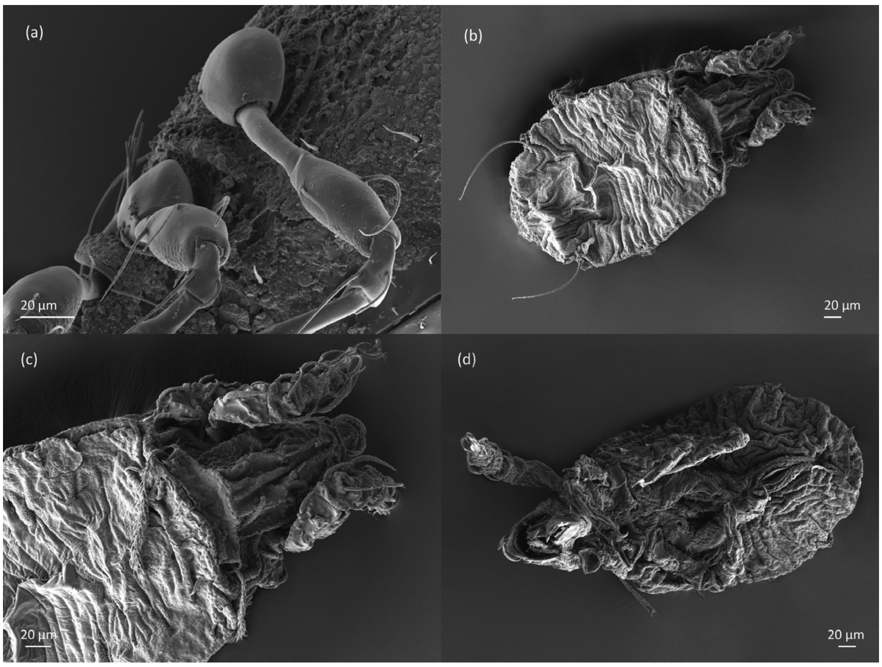


FIGURE 7. *Ctenobelba pilosella*, SEM micrographs. (a) Part of legs III and IV of adult, ventral view; tritonymph, (b) dorsal view, (c) anterior part of body, dorsal view, (d) ventral view.

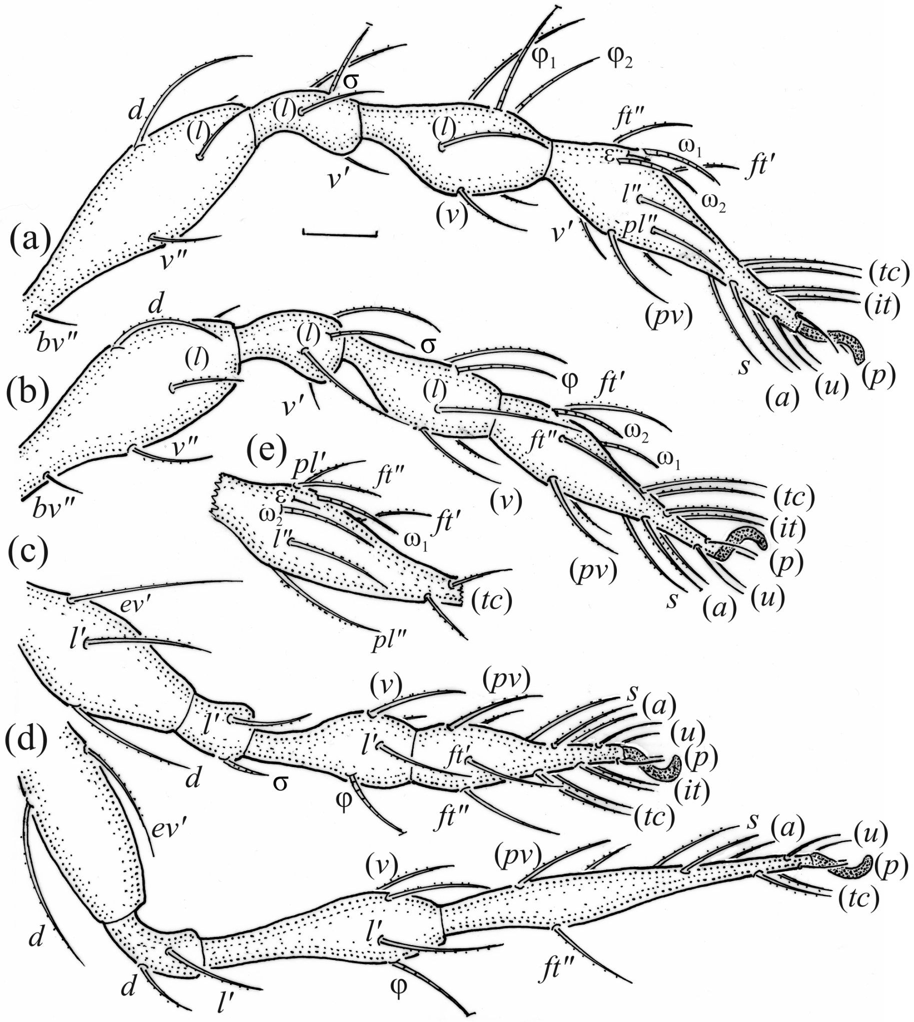
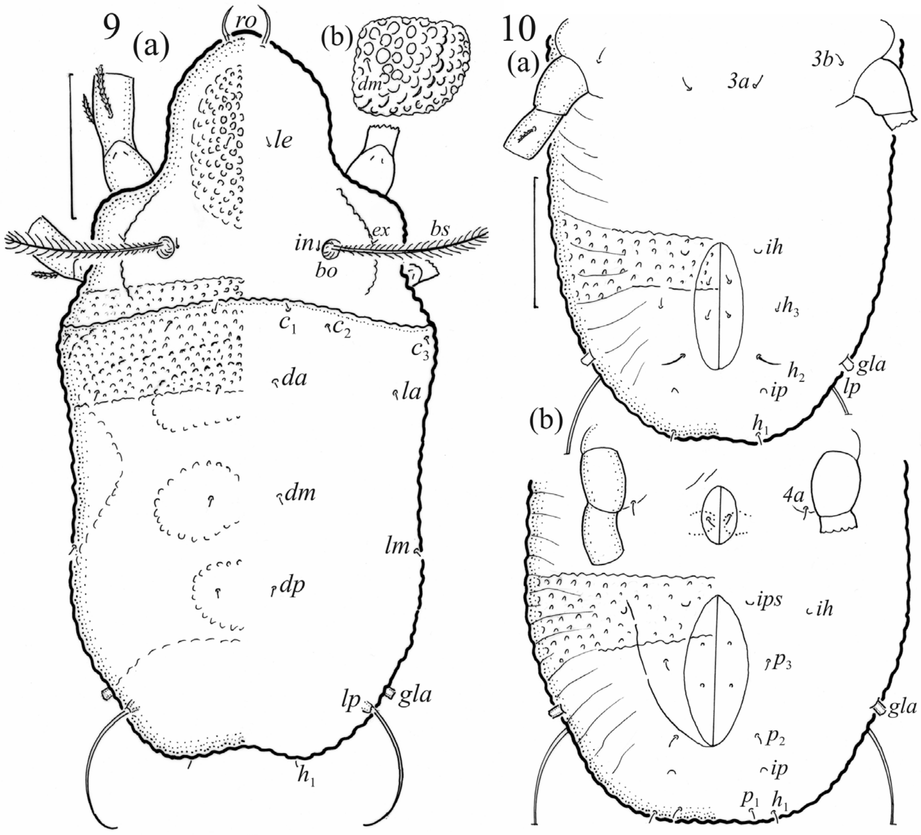


FIGURE 8. *Ctenobelba pilosella*, leg segments of adult (part of femur to tarsus), right side, antiaxial aspect, seta on the opposite side not illustrated is indicated in the legend, scale bar 20 µm. (a) Leg I, tarsus (*pl′*); (b) leg II; (c) leg III; (d) leg IV; (e) region of solenidia ω_1 and ω_2 on tarsus I, dorsal aspect.

Description of juvenile stages

Larva oval in dorsal aspect, unpigmented, cuticle with tubercles (Figs. 6e, 6f, 9, 10a,12a). Prodorsum subtriangular, prodorsal seta *ro* of medium size, setae *le*, *in* and *ex* short, all smooth (Table 2). Mutual distance between setal pair *le* as between setal pair *ro*, and between setal pair *in* nearly four times longer than between pair *ro*. Pair *le* inserted approximately midway between pairs *ro* and *in*. Seta *in* inserted close to bothridium. Bothridium rounded, bothridial seta setiform, barbed.

Gastronotum of larva with 12 pairs of setae, including h_3 inserted laterally to medial part of anal valves (Figs. 10a, 11a). All gastronotal setae short, except slightly longer h_2 and long *lp* (Figs. 9a, 10a, 11a), all smooth. Setae *da*, *dm* and *dp* on large apophyses. Anal valves (segment P) with two pairs of small setae. Cupules *ia* and *im* not observed in plicate cuticle, cupule *ip* between setae h_1 and h_2, cupule *ih* lateral to anterior part of anal valves. Tube-like opisthonotal gland opening anterior to seta *lp*. Most leg setae barbed, seta *d* coupled to proper solenidia present (Fig. 13), most of medium size, except longer *d* on tibia I. Distal part of tarsus I relatively thin and long, with setae *u* and *p*.



FIGURES 9–10. *Ctenobelba pilosella*, legs partially drawn, scale bars 50 μm. 9. (a) Larva, dorsal aspect, (b) pattern of gastronotum (enlarged). 10. Ventral part of hysterosoma, (a) larva, (b) protonymph.

Nymphs slimmer and with relatively shorter prodorsum than in larva, but shape of prodorsal setae as in larva. Prodorsum with longitudinal ridges between bothridia and setae *le*, posterior part porose. Gastronotum of protonymph with 11 pairs of setae due to appearance of *p*-series setae (Fig. 10b), and loss of setae c_3 and *d*-series, remaining absent in deutonymph and tritonymph (Figs. 11b, 14a, 14b). All nymphs unpigmented, cuticle with tubercles, gastronotum relatively flat, and setae of *l*- and *h*-series on marginal part of gastronotum, all short except long and inward curving *lp*, positioned anteroventral to tube-like *gla* opening (Figs. 7b, 10b, 12d, 14a, 14b, 16a–c, Table 2). All nymphs carry exuvial scalps of previous instars (Fig. 15), easily lost in alcohol samples (Figs. 7b, 7c, 11b, 12b–d). In protonymph, one pair of setae appearing on genital valves, and two pairs added in deutonymph and tritonymph each (Figs. 10b, 14a, 14b), all short and smooth. In deutonymph, one pair of aggenital setae and three pairs of adanal setae appearing; next pair of aggenital setae added in tritonymph; all short and smooth. Anal valves of protonymph (segment AD) and deutonymph (segment AN) with two pairs of alveolar setae, in tritonymph two pairs of anal setae present (Figs. 10b, 11b, 14a, 14b); all short and smooth. In all nymphs, cupules *ia* and *im* not observed in plicate cuticle, cupule *ip* observed in ventral aspect posterolateral to seta p_2, cupules *ih*, *ips* and *iad* in normal positions. Most setae on legs barbed, tarsi I and II with uniformly narrow distal stalk of medium length, with one claw and short setae *u* and *p*, whereas in other tarsi distal part relatively shorter (Fig. 17). Seta *d* on all genua and tibiae of medium size, barbed and coupled with proper solenidia, except longer and smooth *d* on tibia I. Solenidion φ_1 on tibia I longest, solenidia ω_1 and ω_2 on tarsi I and II shorter, other solenidia short.

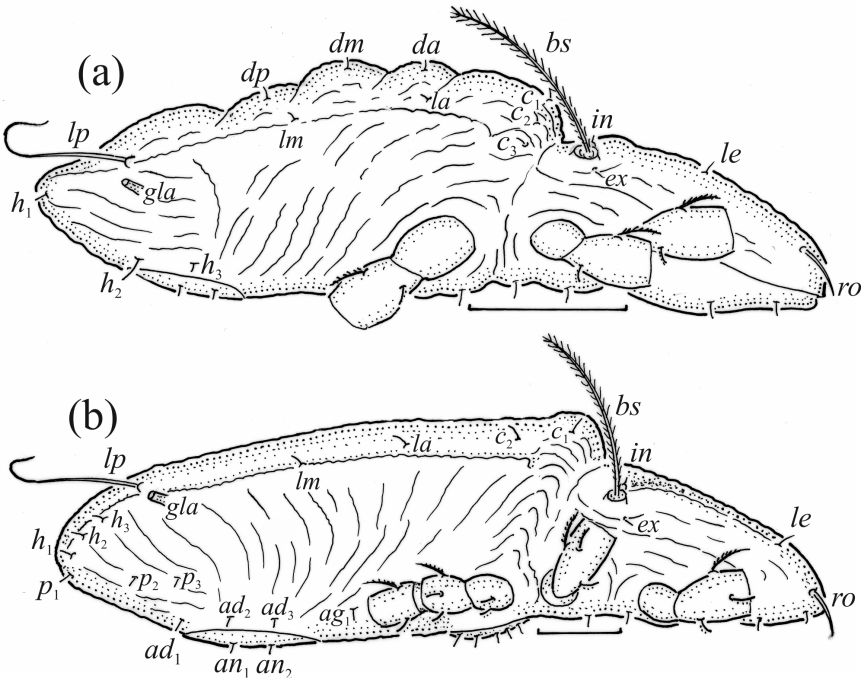


FIGURE 11. *Ctenobelba pilosella*, lateral aspect, legs partially drawn, scale bars 50 µm. (a) Larva, (b) tritonymph without exuvial scalps.

TABLE 2. Measurements of some morphological characters of juvenile stages and adult of *Ctenobelba pilosella* (mean measurements of 1–10 individuals in µm); Nd — not developed.

Morphological characters	Larva	Protonymph	Deutonymph	Tritonymph	Adult
Body length	251	320	392	481	520
Body width	132	182	205	271	297
Length of prodorsum	93	98	120	139	198
Length of: seta *ro*	12	16	19	22	46
seta *le*	2	2	2	3	46
seta *in*	2	2	2	3	50
seta *bs*	69	77	99	106	109
seta *c*1	2	2	2	11	Lost
seta *c*2	2	2	2	14	44
seta *c*3	2	Lost	Lost	Lost	Lost
seta *da*	2	Lost	Lost	Lost	Lost
seta *dp*	2	Lost	Lost	Lost	Lost
seta *la*	2	2	2	12	39
seta *lp*	55	102	145	159	49
seta *h*1	2	2	2	3	45
seta *h*2	2	2	2	3	47
seta *h*3	Nd	2	2	3	48
seta *p*1	Nd	2	2	3	27
seta *p*3	Nd	2	2	3	26
genital opening	Nd	26	34	44	55
anal opening	57	62	88	93	78

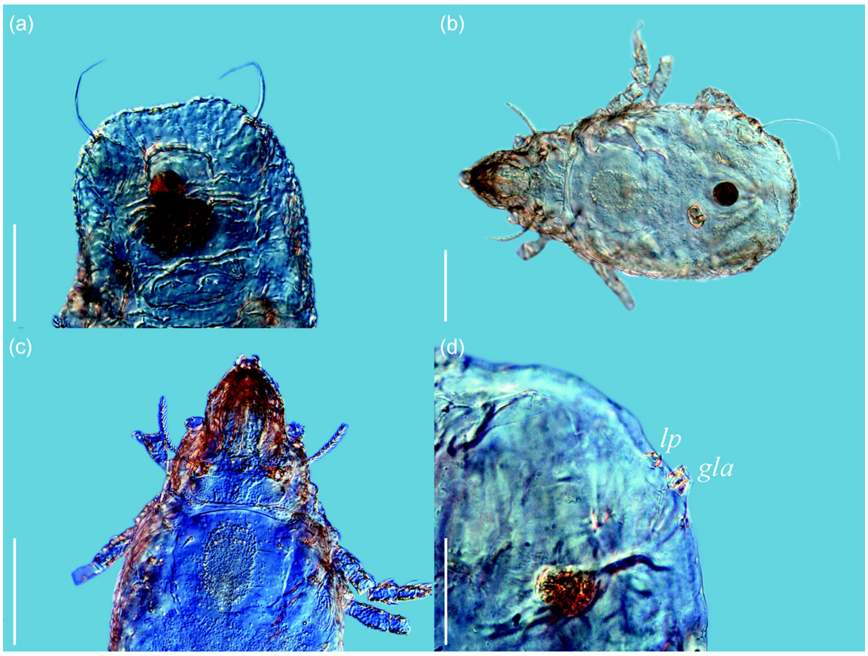


FIGURE 12. *Ctenobelba pilosella*, transmitted-light photomicrographs, dorsal view. (a) Larva, posterior part of body; tritonymph, (b) whole body, (c) anterior part of body, (d) posterior part of body. Scale bars: a, d—50 µm, b, c—100 µm.

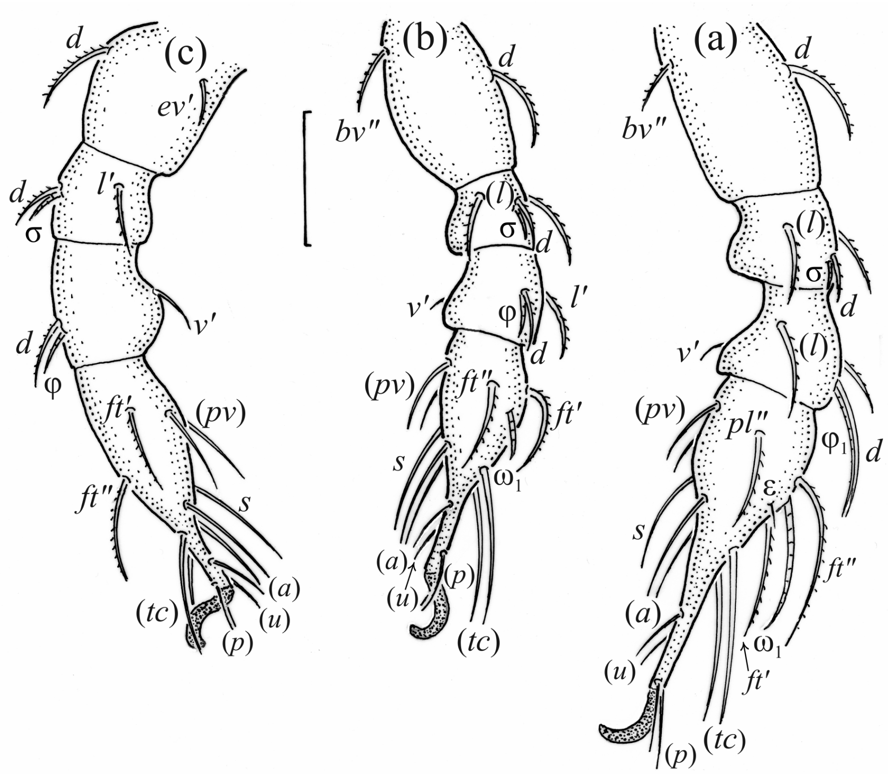
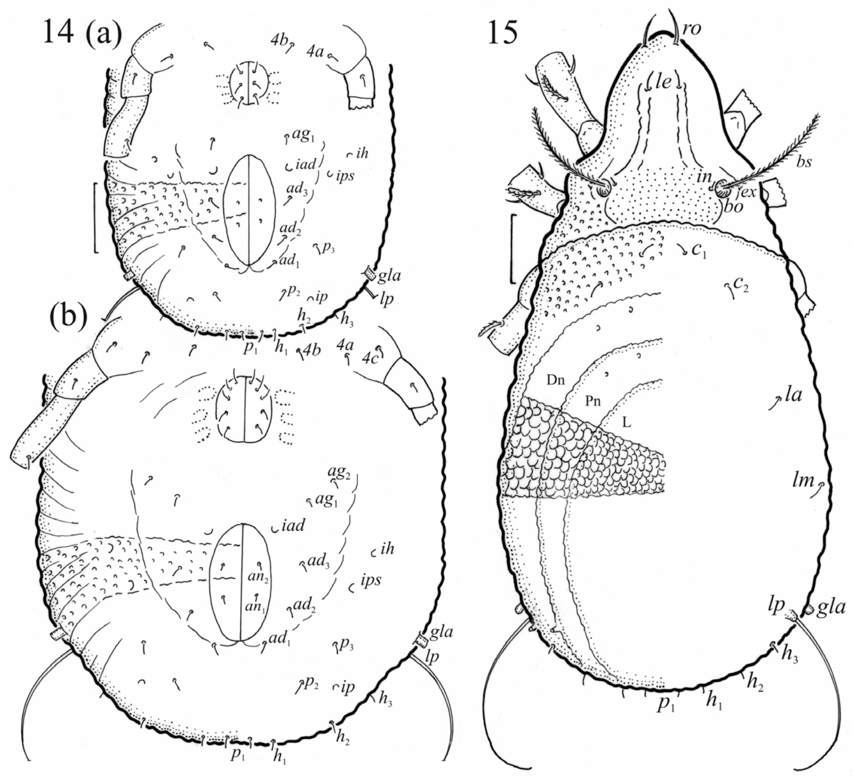


FIGURE 13. *Ctenobelba pilosella*, leg segments of larva (part of femur to tarsus), right side, antiaxial aspect, seta on the opposite side not illustrated is indicated in the legend, scale bar 20 µm. (a) Leg I, tarsus (*pl′*); (b) leg II; (c) leg III.



FIGURES 14–15. *Ctenobelba pilosella*, legs partially drawn, scale bars 50 μm. 14. Ventral part of hysterosoma, (a) deutonymph, (b) tritonymph. 15. Tritonymph, dorsal aspect.

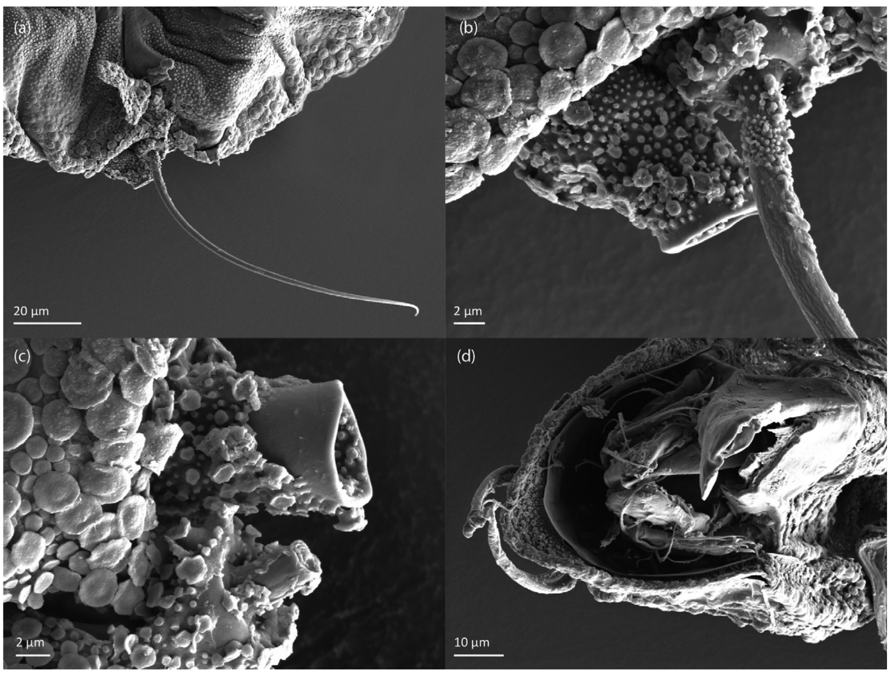


FIGURE 16. *Ctenobelba pilosella*, tritonymph, SEM micrographs. (a) Seta *lp* and *gla* opening, dorsal view; (b), seta *lp* and *gla* opening, dorsal view (enlarged); (c) *gla* opening near broken seta *lp*, dorsal view; (d) mouthparts, ventral view.

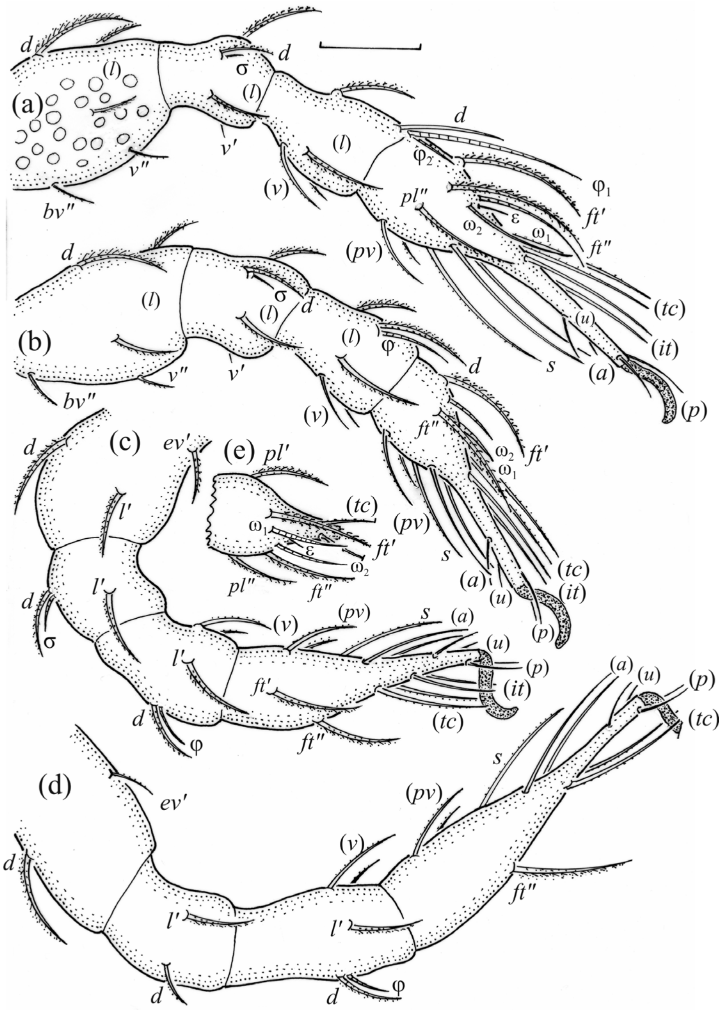


FIGURE 17. *Ctenobelba pilosella*, leg segments of tritonymph (part of femur to tarsus), right side, antiaxial aspect, seta on the opposite side not illustrated is indicated in the legend, scale bar 20 µm. (a) Leg I, tarsus (*pl′*); (b) leg II; (c) leg III; (d) leg IV; (e) region of solenidia ω_1 and ω_2 on tarsus I, dorsal aspect.

Summary of ontogenetic transformations

In all juvenile instars of *C. pilosella*, the prodorsal seta *ro* is of medium size, and setae *in*, *le* and *ex* are short, whereas in the adult all setae are of medium size. In all instars, the opening of bothridium is rounded and the bothridial seta is setiform; in the juveniles it is barbed, whereas in the adult it has 7–8 long anterior cilia. The larva has 12 pairs of gastronotal setae, the nymphs have 11 pairs (*p*-series appear, c_3 and *d*-series lost), whereas the notogaster of adult loses seta c_1 such that 10 pairs of notogastral setae remain. The formula of gastronotal setae in *C. pilosella* is 12-11-11-11-10 (from larva to adult). In deutonymph, one pair of aggenital setae appears, and one pair is added in the tritonymph and adult each. Formulae of epimeral setae is 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), aggenital setae is 1-2-3 (deutonymph to adult), and segments PS−AN is 23333-2333-222 (including alveolar setae). Ontogeny of leg setae and solenidia is shown in Table 3.

TABLE 3. Ontogeny of leg setae (Roman letters) and solenidia and famulus (Greek letters) of *Ctenobelba pilosella*.

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	–	*d*, *bv″*	(*l*), *d*, σ	(*l*), *v′*, *d*, φ_1	(*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*), (*pl*) ε, ω_1
Protonymph	–	–	–	–	ω_2
Deutonymph	*v′*	(*l*)	–	*v″*, φ_2	–
Tritonymph	–	*v″*	*v′*	–	(*it*)
Adult	–	–	*d* lost	*d* lost	*l″*, *v′*
Leg II					
Larva	–	*d*, *bv″*	(*l*), *d*, σ	*l′*, *v′*, *d*, φ	(*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*), ω_1
Protonymph	–	–	–	–	–
Deutonymph	*v′*	(*l*)	–	*l″*	ω_2
Tritonymph	–	*v″*	*v′*	*v″*	(*it*)
Adult	–	–	*d* lost	*d* lost	–
Leg III					
Larva	–	*d*, *ev′*	*l′*, *d*, σ	*v′*, *d*, φ	(*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*)
Protonymph	*v′*	–	–	–	–
Deutonymph	*l′*	*l′*	–	*l′*	–
Tritonymph	–	–	–	*v″*	(*it*)
Adult	–	–	*d* lost	*d* lost	–
Leg IV					
Protonymph	–	–	–	–	*ft″*, (*p*), (*u*), (*pv*)
Deutonymph	*v′*	*d*, *ev′*	*d*, *l′*	*v′*, *d*, φ	(*a*), *s*
Tritonymph	–	–	–	*l′*, *v″*	(*tc*)
Adult	–	–	–	*d* lost	–

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.

Distribution, ecology and biology

According to Subías (2004, 2020) and Mahunka and Mahunka-Papp (2004), *C. pilosella* has Mediterranean and Ponto-Mediterranean distribution, respectively, but Shtanchaeva and Subías (2010) extended this distribution to South Europe. This species was recorded from Bulgaria (Csiszár & Jeleva 1962), Slovenia and Croatia (Tarman 1983), Slovakia (Miko 1990), Romania (Vasiliu *et al.* 1993), Hungary (Mahunka & Mahunka-Papp 2004) and Caucasus (Shtanchaeva & Subías 2010; Murvanidze & Mumladze 2016).

Mahunka and Mahunka-Papp (2004) and Murvanidze and Mumladze (2016) recorded *C. pilosella* from forest soils. In Romania *C. pilosella* was recorded both from forests (Ivan & Vasiliu 2000) and open habitats, such as meso-xerophilous meadows (Ivan 2007) and saxicolous habitats (Ivan & Călugăr 2004), which indicates its ecological plasticity. Moreover, *C. pilosella* is tolerant to the presence of heavy metals (Vasiliu & Vasiliu 1989) and cement dust (Ivan & Vasiliu 2012) in soil.

In this study, *C. pilosella* was most abundant in soils of beech-hornbeam forest (density 21 individuals per 500 cm^3), and also abundant in chestnut-beech forest (19.6 individuals per 500 cm^3), where the juveniles were most abundant (Table 1). This species was relatively abundant in Ponto-Sarmatic steppe meadow and xero-mesophilous meadow, whereas in other habitats it had low densities, illustrating its ecological plasticity.

In all habitats, adults dominated, and only in four juveniles were present, comprising 12–16% of all individuals. In the chestnut-beech forest, where the juveniles were most abundant, the stage structure of *C. pilosella* was the following: one larva, two protonymphs, three deutonymphs, 10 tritonymphs and 82 adults. In all habitats, females were more abundant than males, the sex ratio (females: males) varied slightly (1:0.36–1:0.50) and 0–60% of females (mean 24%) were gravid. The gravid females carried 1–2 relatively large eggs, each 229 x 145, which constituted about 46% of the total body length of females.

Females with the longest body size occurred in the soil in Baia Mare (chestnut-beech forest) (see Table 4 for details). The widest females of *C. pilosella* occurred in Baia Mare and Dobrina (Dacian oak-hornbeam forest), while they were significantly narrower in the other habitats. The longest and widest males were found in Baia Mare and Dobrina, while they were significantly shorter in the other habitats. In most habitats, females were significantly larger than males (Table 4).

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

Place/ month of sampling[1]	Females	Gravid (%)	Males	Sex ratio	Females		Males	
					Length	Width	Length	Width
1. Baia Mare/ July	20	0(0)	10	1:0.50	535.7±23.8*^{a} (494-566)	291.4±6.9*^{a} (283-313)	507.8±9*^{a} (494-518)	274.6±10.3*^{a} (253-283)
2. Zlatna/ May	22	7(32)	8	1:0.36	524.3±14.4*^{ab} (494-554)	282.5±9.2*^{b} (271-301)	478.3±15*^{bc} (452-494)	257.5±7.7*^{bc} (247-271)
3. Ponoare-Bosanci/ September	18	0(0)	12	1:0.67	474.7±8.1*^{c} (464-494)	265.0±7.7*^{c} (253-289)	450.5±9.6*^{d} (440-464)	250.5±6.5*^{b} (241-259)
4. Calafindeşti/ July	23	10(43)	7	1:0.30	489.6±8.3*^{de} (476-506)	279.9±8.7*^{b} (265-289)	464±6.9*^{bde} (452-470)	253.9±4.1*^{b} (247-259)
5. Dobrina/ May	13	5(38)	6	1:0.46	510.2±14.6*^{abf} (488-542)	292.7±9.0*^{a} (283-313)	486.0±6.2*^{ac} (476-494)	270.0±5.9*^{ad} (265-277)
6. Tismana/ August	10	0(0)	5	1:0.50	498.8±9.3*^{df} (488-518)	286.6±7.6*^{ab} (277-301)	478.4±3.3*^{bce} (476-482)	269.8±5.0*^{acd} (265-277)
7. Nămăeşti/ June	9	5(56)	4	1:0.44	504.7±9.4*^{bdf} (488-518)	292.3±7.4*^{a} (277-301)	476.0±8.5*^{bce} (470-488)	257.5±5.7*^{bcd} (253-265)
8. Horia/ April	4	0(0)	2	1:0.50	464.0±4.9ns^{ce} (458-470)	259.0±4.9ns^{c} (253-265)	446.0±8.5ns^{de} (440-452)	244.0±4.2ns^{b} (241-247)
9. Valea lui David/ May	5	3(60)	0	-	473.8±6.9 nc^{ce} (464-482)	261.4±6.8nc^{c} (253-271)	-	-

[1]coordinates as in Table 1; ^{a,b,c,d,e,f}different letters in superscript means significantly different between plots;*significantly different between females and males at α= 0.05, ns — not significant, nc — not calculated.

Comparison of morphology of *Ctenobelba pilosella* with congeners and remarks

Among *Ctenobelba* species, *C. mikaeeli* Ahaniazad *et al*. 2017 is the largest while *C. csiszarae* Mahunka, 1977 is the smallest (Table 5). The notogastral setae of most species are setiform, but they are flagelliform in *C. pseudomahnerti* Subías & Shtanchaeva, 2013 and leaf-like in *C. foliata* Hammer, 1961, *C. heterosetosa* Murvanidze & Weigmann, 2007, *C. martyanensis* Ermilov *et al*., 2012, *C. mikaeeli*, *C. parafoliata* Pérez-Íñigo, 1991, *C. parapulchellula* Subías & Shtanchaeva, 2013 and *C. pulchellula* Gil-Martín & Subías, 1997. *Ctenobelba brevipilosa* Mahunka, 1964 and *C. ayyildizi* Baran, 2012 have the largest number of cilia on the bothridial seta (13–15 cilia) while *C. martyanensis* and *C. perezinigoi* Moraza, 1985 have the lowest number (4–5 cilia). Most species have three pairs of aggenital setae, *C. apatomorpha* Iturrondobeitia *et al*., 1998 has two pairs, *C. marcuzzii* Mahunka, 1974 has 5–6 pairs and *C. mahnerti* Mahunka, 1974 – seven pairs (unknown in *C. foliata* and *C. serrata* Mahunka, 1964). These species differ also from one another by other morphological characters given in Table 5 (also see Ahaniazad *et al*. 2017 for comparison of *Ctenobelba* species). Ahaniazad *et al*. (2017) stated that *C. mikaeeli* is most similar to *C. pilosella*, differing mainly in having more branches on the bothridial setae, serrated prodorsal seta *le* (versus barbed in *C. pilosella*), most gastronotal setae leaf-like, including p_1 (versus setiform in *C. pilosella*) and shape of epimeral setae. Here we also add a difference in the shape of the lamellar costulae, where it extends up to the bothridium in *C. mikaeeli*, whereas in *C. pilosella* they most often do not extend up to the bothridia.

TABLE 5. Selected morphological characters of the adults of *Ctenobelba* species, abbreviations explained in Material and methods.

Species	Body length	Shape of most Ng setae	Number of cilia on *bs*	*La* connects with *bo*	Setae *ag*	
					Pairs	Length
C. apatomorpha Iturrondobeitia *et al*., 1998	440–480	Setiform, smooth	8–13	Yes	2	As short as ad_2
C. ayyildizi Baran, 2012	340–369	Setiform, smooth	13–15	No	3	As short as ad_2
C. brevipilosa Mahunka, 1964	461–490	Setiform, smooth	12-17	No	?	?
C. csiszarae Mahunka, 1977	320–354	Setiform, smooth	9	No	3	Shorter than ad_2
C. foliata Hammer, 1961[1]	420	Leaf-like	5–6	Yes	?	?
C. foveolata Subías & Shtanchaeva, 2013	395-435	Setiform, smooth	7–11	Yes	3	?
C. grancanariae Pérez-Íñigo & Peña, 1997	454-489	Setiform, smooth	4–5	No	3	?
C. heterosetosa Murvanidze & Weigmann, 2007	375–410	Leaf-shaped	9–11	Yes	3	?
C. mahnerti Mahunka, 1974	430–445	Setiform, barbed	7	No	7	Shorter than ad_2
C. marcuzzii Mahunka, 1974	430–445	Setiform, barbed	7	No	5–6	Shorter than ad_2
C. martyanensis Ermilov *et al*., 2012	498–564	Leaf-shaped	4–5	No	3	As short as ad_2
C. mikaeeli Ahaniazad *et al*., 2017	544–577	Leaf-shaped	12–13	Yes	3	As short as ad_2
C. parafoliata Pérez-Íñigo jr., 1991	462–516	Leaf-shaped	7–8	Yes	3	As short as ad_2
C. parapulchellula Subías & Shtanchaeva, 2013	400–450	Leaf-shaped	5–6	No	3	?
C. pectinigera (Berlese, 1908)[1]	450	Setiform, smooth	6	No	?	?
C. perezinigoi Moraza, 1985	526	Setiform, barbed	5	No	3	As short as ad_2
C. pilosella Jeleva, 1962[2]	516	Setiform, barbed	7	Yes/No	3	As short as ad_2
C. pseudomahnerti Subías & Shtanchaeva, 2013	475-525	Setiform, smooth	4–7	No	3	Shorter than ad_2
C. pulchellula Gil-Martín & Subías, 1997	456	Leaf-shaped	6	No	3	Shorter than ad_2
C. serrata Mahunka, 1964	416-431	Setiform, barbed	6	No	?	?
C. translamellata Iordansky, 1990	516-521	Setiform, smooth	13	Yes	3	As short as ad_2

[1]also with data of Mahunka (1964), [2]according to Csiszár and Jeleva (1962).

The adults investigated herein are of similar length as in Csiszár and Jeleva (1962, length 516, width 287, sex not investigated) and Miko (1990, length 505–560, width 275–290, sex not investigated). In our adults, the lamellar costula has setae *in* and *le* on its basal and apical parts, respectively and is separated from the bothridium (versus it is connected with bothridium in figure 36 by Csiszár & Jeleva 1962), as in Miko (1990). Setae *le* and *in* are of medium size and barbed (versus *le* is smooth and *in* is broken in Csiszár & Jeleva 1962), and the tubercle is present on the anterior margin of the notogaster, opposite to basal part of bothridium (versus it is absent in Csiszár & Jeleva 1962), as in Miko (1990). In our individuals, the notogastral setae are barbed and barbs are of different shape (versus they are only barbed in figure by Csiszár & Jeleva 1962). The drawing of *C. pilosella* by Mahunka (1964) is similar to our specimen, except we observed thinner gastronotal setae. In the adult of *C. pilosella* drew by Csiszár and Jeleva (1962), the bothridial seta has seven cilia, in our individuals and those studies by Mahunka (1964) it has 7–8 cilia, whereas in those investigated by Miko (1990), this seta has 6–10 cilia.

The juvenile stages of *C. pilosella* are similar to those of *C. pectinigera* investigated by Grandjean (1965) in having the bothridial seta setiform and barbed, tube-like opisthonotal gland opening, long gastronotal seta *lp* and other setae short. In both species, two pairs of alveolar setae are present on the anal valves of protonymph and deutonymph, which are rare in Brachypylina. The juveniles of *C. pectinigera* were only partially described by Grandjean (1965), which limits more detailed comparison of morphology of juveniles the two species.

The nymphs of *C. pilosella* carry the exuvial scalps of previous instars on the gastronotum, which are easily lost in alcohol samples. Most gastronotal setae of nymphs are short, except for long and inward curving *lp*, which does not protect the exuvial scalps against loss, so the question appears how the exuvial scalps are fasten to the gastronotum of living nymphs. The nymphs of other species of the superfamily Ameroidea, to which *Ctenobelba* and Ctenobelbidae belong, use different methods of protection against loss of exuvial scalps. For example, the nymphs of *Gymnodampia setata* (Berlese 1916) from Ameridae retain setae of *d*-series on the gastronotum and are apheredermous, with a circular line of dehiscence (Chen *et al*. 2004), whereas the nymphs of *Amerus polonicus* Kulczynski, 1902 lost setae of *d*-series and are eupheredermous (Seniczak *et al*. 2020c), but the peripheral setae on the gastronotum are long and protect the exuvial scalps against lost. The nymphs of *Hungarobelba pyrenaica* Miko & Travé, 1996 (Hungarobelbidae) also have long dorsal peripheral setae on the gastronotum (Miko & Travé 1996), but *Mongaillardia granjeani* Călugăr & Vasiliu, 1984 (Amerobelbidae) and *Damaeolus ornatissimus* Csiszár, 1962 (Damaeolidae) have short marginal gastronotal setae, which do protect exuvial scalps against loss (Călugăr & Vasiliu 1984; Seniczak *et al*. 2020a), as in *C. pilosella*. By contrast, *Basilobelba parmata* Okayama, 1980 (Basilobelbidae) and *Caleremaeus arboricolus* Norton & Behan-Pelletier, 2020, *C. monilipes* (Michael 1882) and *C. retractus* (Banks 1947) (Caleremaeidae) use a cornicle (Seniczak *et al*. 2019, Norton & Behan-Pelletier 2020), typical for Damaeidae (Norton 1978, 1980; Seniczak & Seniczak 2011, 2013; Seniczak *et al*. 2013, 2016).

The percentage of juvenile *C. pilosella* was rather low or juveniles were absent in the soil samples of investigated habitats. For example, the highest abundance was found in the beech-hornbeam forest in Zlatna, but no juveniles were found. The absence of juveniles cannot be explained by the season (May) because in other samples from different localities, taken during this time, juveniles were present. The absence of juveniles in the Zlatna samples is probably a result of the small number of replicates (5) and the aggregated occurrence of *C. pilosella* in soil. Similar ecology was observed with *Damaeolus ornatissimus* Csiszár, 1962, *Oribatella hungarica* Balogh, 1943 and *Tectoribates ornatus* (Schuster 1958) (Seniczak *et al*. 2019, 2020a, b).

Acknowledgements

We thank two anonymous reviewers for helpful suggestions that improved the scientific value of this paper. This study was done under the program of the Polish Minister of Science and Higher Education "Regional Initiative of Excellence" in 2019–2022 (Grant No. 008/RID/2018/19). The ecological investigation was supported by a grant of Romanian Ministry of Education and Research through the Core Program, Contract no. 25N/2019, project 19-270301.

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Submitted: 7 Oct. 2020; accepted by Maka Murvanidze: 11 Nov. 2020; published: 15 Jan. 2021