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Morphological ontogeny of *Lopheremaeus mirabilis* (Acari: Oribatida: Plateremaeidae), and comments on *Lopheremaeus* Paschoal

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Abstract

The morphological ontogeny of *Lopheremaeus mirabilis* (Csiszár 1962), the type species of *Lopheremaeus* Paschoal, 1988 (Plateremaeidae**)** is described and illustrated. The adult of this species has six pairs of notogastral setae (*lp*, h_1, h_2 and *p*-series), epimeral and anogenital hypertrichy, and 4–5 pairs of anal setae. The cuticle of juveniles is plicate, the larva lacks the gastronotal setae c_3, *la*, *lm* and h_3, the nymphs are multideficient (they lack also setae of *d*-series) and eupheredermous, i.e. they carry the exuvial scalps of previous instars on the gastronotum. In the adult, dorsal and ventral crests are present on all femora and trochanter III, and dorsal crest is present on trochanter IV, the nymphs have also dorsal and ventral crests on genua, whereas the larva has no crests. In all instars, seta *d* on all genua and tibiae is present, and all tarsi have basal bulb (containing muscles) and uniformly narrow distal stalk (with only tendons) at about mid-length. This species was reported only from Bulgaria, Bosnia-Herzegovina and North Macedonia, Romania and Georgia.

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

Introduction

Lopheremaeus mirabilis (Csiszár 1962) was originally proposed as *Plateremaeus mirabilis* Csiszár, 1962 based on specimens from Bulgaria (Csiszár & Jeleva 1962), but now this species is known also from Bosnia-Herzegovina, North Macedonia, Romania and Georgia (Tarman 1983; Ivan & Vasiliu 2000; Murvanidze & Mumladze 2016). Paschoal (1988) revised the Plateremaeidae, and appointed it the type species of *Lopheremaeus* Paschoal, 1988. He presented the main diagnostic characters of the genus as: apodemes poorly sclerotized or absent; bothridial seta long, setiform, with very short spines at distal part, notogaster rounded, seta h_1 well developed, epimeral formula 8-7-12-4, genital and anal openings separated, with seven and four pairs of setae, respectively. However, adults of *L. mirabilis* from Romania studied herein have also three pairs of *p*-series setae on the notogaster and some individuals have more anal setae, which were not mentioned in Csiszár and Jeleva (1962) paper, modifying the diagnosis of *Lopheremaeus* given by Paschoal (1988). Subías (2020) included three species in *Lopheremaeus*, and one of which he considered *species inquirenda*. According to the catalogue of juvenile oribatid mites by Norton and Ermilov (2014) and further literature, the juveniles of *Lopheremaeus* are not described and any other member of the family.

The aim of this paper is to describe and illustrate the morphological ontogeny of *L. mirabilis*.

Material and methods

Sampling

The juveniles and adults of *L. mirabilis* used in this study were collected on 7 July 2019 by O. Ivan from a Dacian oak-hornbeam forest, located in Eastern Romania (46°40′27″N, 28°03′35″E, 280 m a. s. l.), near the southern limit of the continental bioregion where it contacts the steppe. This forest is about 100 years old (Natura 2000 site), and is composed mainly of *Quercus petraea* (Matt.) Liebl., *Q. dalechampii* Ten., *Carpinus betulus* L. and *Tilia tomentosa* Moench. We investigated population parameters of L. mirabilis, including density and developmental stage structure. The gender of adults is not visible through the thick, reticulate integument, and therefore metric data (in μm) were based on 15 randomly selected adults, which were dissected in order to determine the gender, number of gravid females and carried eggs, and included: total length (tip of rostrum to posterior edge of notogaster, measured in lateral aspect); maximum width (widest part of notogaster, measured in dorsal aspect); length of anal and genital openings; and length of setae (measured from the appropriate plane).

Studies of type material

We studied the morphology of a specimen of *L. mirabilis* from the Csiszár collection stored at the Hungarian Natural History Museum (HNHM). This individual is in a good condition, except for legs, which are broken. It is labelled as follows: *Plateremaeus mirabilis* Csisz., 1962; Bulgaria, Karlovo–Kalofer; 1956 June 9–11, Balogh–Csiszár. Measurements: length—512, width—301.

Illustrations and photographs

The illustrations of *L. mirabilis* 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 (Grandjean 1949). In the text and figures, we used the following abbreviations: rostral (*ro*), lamellar (*le*), interlamellar (*in*) and exobothridial (*ex*) setae, bothridium (*bo*), bothridial seta (*bs*), notogastral or gastronotal setae (*c*-, *d*-, *l*-, *h*-, *p*-series), cupules or lyrifissures (*ia*, *ih*, *ips*, *iad*), scalps of larva (L), protonymph (Pn) and deutonymph (Dn), subcapitular setae (*a*, *m*, *h*), cheliceral setae (*cha*, *chb*), palp setae (*inf*, *l*, *d*, *lt*, *vt*, *ul*, *su*) and solenidion ω, Trägårdh's organ (*Tg*), Claparède's organ (*Cl*), epimeral setae (*1a–c*, *2a*, *3a–c*, *4a–c*), 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 (1951, 1953) and Norton and Behan-Pelletier (2009). The species nomenclature follows Subías (2004).

For scanning electron microscopy (SEM), the mites were air-dried and coated with Au/Pd in a Polaron SC502 sputter coater and placed on Al-stubs with double-sticky carbontape. Observations and micrographs were made with a ZEISS Supra 55VP scanning electron microscope. Light photographs were prepared from individuals mounted temporarily on slides in lactic acid, using a Leica DM3000 microscope and Leica DFC420 camera.

Lopheremaeus mirabilis **(Csiszár, 1962)**

(Figs. 1–20)

Plateremaeus mirabilis Csiszár, 1962: Tarman 1983.
Lopheremaeus mirabilis: Paschoal 1988; Subías 2004; Murvanidze and Mumladze 2016.

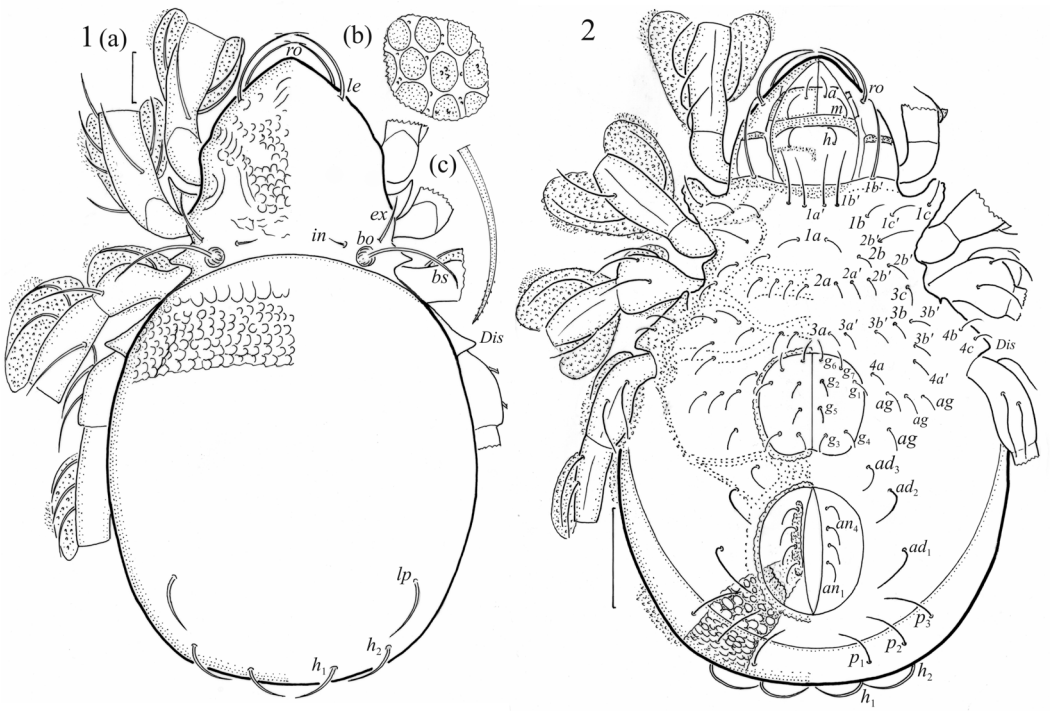
Diagnosis

Adults of medium size (592–656), oval, with rounded rostrum, and polygonal pattern on prodorsum and notogaster. Bothridial seta setiform, with very short spines near distal end. Notogaster elliptical in dorsal aspect, with six pairs of notogastral setae (*lp*, h_1, h_2 and *p*-series). Formula of epimeral setae 8-7-12-4 (hypertichy occurs), genital setae (seven pairs) in two rows (4 pairs in inner rows, 3 pairs in lateral rows), four pairs of aggenital setae and 4–5 pairs of anal setae; all short and smooth. Adanal seta ad_3 inserted roughly in alignment with lateral margin of genital and anal plate, at level about midway between them, other two pairs in lateral position to anal plates. All femora and trochanter III with dorsal and ventral crests, trochanter IV with dorsal crest. Solenidion φ_1 on tibia I on large apophysis, covering basal dorsal part of tarsus I, famulus ε on tarsus I short, semispherical. Seta *d* present on all genua and tibiae, slightly removed from respective solenidion. All tarsi with basal bulb and uniformly narrow distal stalk about mid-length, with three claws and short setae *p*.

Prodorsum in juveniles reticulate, prodorsal setae *ro* and *le* of medium size, setae *in* and *ex* short. Bothridial seta clavate in larva, setiform in nymphs. Larva with eight pairs of gastronotal setae (c_3, *la*, *lm* and h_3 absent), nymphs with same number (*d*-series lost, *p*-series appears). In larva, crests on legs not evident, nymphs with dorsal and ventral crests on all femora, genua and trochanter III, and dorsal crest on trochanter IV. On all genua and tibiae seta *d* present, slightly removed from respective solenidion. All tarsi with basal bulb and uniformly narrow distal stalk at about mid-length, with one claw and short setae *p*.

Morphology of adult

Adult (Figs. 1–8) similar to that described by Csiszár and Jeleva (1962), but see Remarks. Mean length (range) of females 633.3±13.5 (606–656, N=9) and mean width (range) 374.6±13.5 (352–400), and mean length (range) of males 611.0±11.9 (592–624, N=6) and mean width (range) 384.7±42.1 (352–468). Setae *ro* and *le* (Figs. 1a, 2, 3a, 5a–c, 6a, 6d, Table 1), and bothridial seta (Figs. 1c, 5a–c, 6a–c) as in Csiszár and Jeleva (1962). Notogaster reticulate (Figs.1a, 1b, 3a, 5, 6a–c, 7a, 8a), setae (6 pairs, *lp*, h_1, h_2 and *p*-series) strongly curved inwards, smooth and long (Table 1), *p*-series slightly thinner than others (Figs. 1a, 2, 3a, 5d, 7a, 8a). Subcapitular setae *h*, and *m* slightly longer than *a*, all smooth. Formula of epimeral setae 8-7-12-4 (I–III hypertrichous, variation not observed); setae in first row of epimere I clearly longer than others, all smooth (Fig. 2). Genital setae (7 pairs) in two rows, inner setae (4 pairs) and lateral setae (3 pairs) of similar length, all smooth. Aggenital setae (4 pair) similar to genital setae. Adanal seta ad_3 inserted roughly in alignment with lateral margin of genital and anal plate, at level about midway between them; all strongly curved and smooth. Anal setae (4–5 pairs) similar to genital setae. Chelicera relatively slim, seta *cha* longer than *chb*, both barbed, in some individuals second seta *chb* present (Figs. 3b, 3c). Palp relatively short and thin, solenidion ω separated from seta *acm* (Fig. 3d). Formula of palp setae (and solenidion): 0-2-1-3-9(1). Setae *sup*, *inf*, *l″* and *d* finely barbed, other setae and eupathidia shorter, smooth. Leg segments protected by retrotecta. All femora and trochanter III with dorsal and ventral crests, trochanter IV with dorsal crest (Figs. 1a, 2, 3a, 4, 5b, 5d, 7a–c, 8b–d). Most leg setae relatively long, strongly curved and smooth, most distal setae on tarsi slightly curved or almost straight and finely barbed. Solenidion φ_1 on tibia I long, on large apophysis, covering large dorsal part of tarsus I; tarsal solenidia ω_1 and ω_2 clearly shorter, other solenidia short. Famulus ε semispherical (Figs. 4a, 7d, 8b). Seta *d* present on all genua and tibiae, removed from the respective solenidion (Fig. 4). All tarsi with basal bulb (containing muscles) and uniformly narrow distal stalk (with only tendons) at about mid-length, with three claws and short setae *p* (Figs. 4, 7d, 8b). Some parts of leg segments and leg setae covered with granular cerotegument. Formulae of leg setae (and solenidia, from trochanter to tarsus): I–1-6-4(1)-5(2)-20(2); II–1-5-4(1)-5(1)-15(2); III–3-5-3(1)-4(1)-15; IV–3-5-3-4(1)-12.



FIGURES 1–2. *Lopheremaeus mirabilis*, adult, legs partially drawn, scale bars 50 μm. 1. (a) Dorsal aspect, (b) central part of notogaster, (c) bothridial seta (b, c, enlarged). 2. Ventral aspect.

Remarks

Females and males investigated herein are slightly larger than those studied by Csiszár and Jeleva (1962) — holotype length 530, width 312, sex not investigated – and have three pairs of setae of *p*-series, which were overlooked by these authors. The topotype specimen from HNHM is smaller (512 x 301) than holotype, has the notogastral setae of *p*-series (strongly curved, visible in ventral and posterior aspects) and dorsal crest on trochanter III. The adults from Romania have more crests on the legs, 4–5 pairs of anal setae (versus four pairs in Csiszár and Jeleva 1962), but not observed by Csiszár and Jeleva (1962). These authors mentioned in *Plateremaeus* Berlese, 1908 crispins (or retrotecta) on legs and 4–5 pairs of anal setae, but this genus was further divided in *Plateremaeus* and *Lopheremaeus* (Paschoal 1988). In our individuals, the shape of leg setae, solenidion φ_1 on tibia I and famulus ε on tarsus I are similar as in Csiszár and Jeleva (1962). All these characters widen the diagnosis of *Lopheremaeus* given by Csiszár and Jeleva (1962).

Description of juvenile stages

Larva oval in dorsal aspect (Figs. 9a, 10a) and unpigmented. Prodorsum subtriangular, prodorsal setae *ro* and *le* of medium size (Table 1), *in* and *ex* short. Mutual distance between setal pairs *le* and *in* about two times longer than between pair *ro*. Seta *le* inserted closer to *ro* than to *in*. Bothridium large, rounded, bothridial seta long, clavate and barbed. Central part of prodorsum reticulate, posterior part punctate, and ridge present between bothridium and central part of prodorsum (Figs. 9b, 10a). Some parts of body and most setae covered with granular cerotegument.

Gastronotum of larva plicate, relatively flat, with horizontal edge and eight pairs of setae, including h_2 inserted lateral to medial part of paraproctal valves (Figs. 10a, 11a, 12a), setae c_3, *la*, *lm* and h_3 not observed. Setae c_1 and of c_2 short (Table 1), other setae of medium size, all curved, inserted on small apophyses and covered with granular cerotegument, but setae of *d*-series with thicker

granular cerotegument than other setae, and appearing barbed. Cupule *ih* lateral to anterior part of anal valves, other cupules and gland opening not observed in plicate integument. Paraproctal valves (segment PS) glabrous.

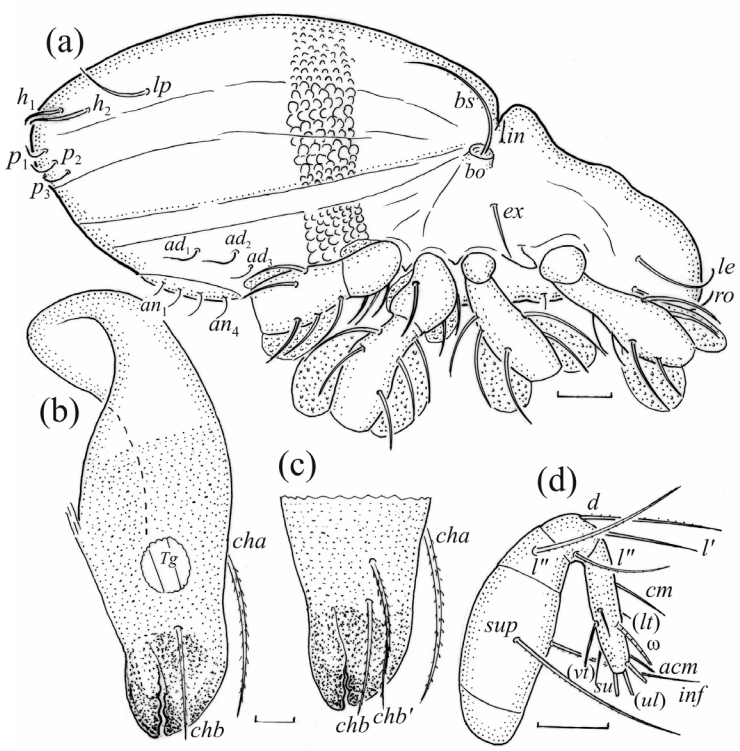


FIGURE 3. *Lopheremaeus mirabilis*, adult. (a) Lateral aspect, legs partially drawn, scale bar 50 μm; mouthparts, right side, scale bars 10 μm; (b) chelicera, (c) part of chelicera of another individual, (d) palp.

All tarsi with thick basal bulb and uniformly narrow distal stalk at about mid-length, with one claw and short setae *p* (Figs. 9a, 13). Crests on legs not evident. Solenidion φ_1 on tibia I on large apophysis, covering large dorsal part of tarsus I, other solenidia short or of medium size, famulus ε on tarsus I relatively long, with apical globule. Most distal setae on tarsi long, slightly curved or nearly straight, other setae long or of medium size and curved; all smooth. Seta *d* present on all genua and tibiae, removed from the respective solenidion. Some parts of leg segments and setae covered with granular cerotegument.

Shape and colour of nymphs (Figs. 9c, 9d) as in larva, but prodorsal seta *ro* and *le* relatively longer (Table 1), strongly curved inwards, and *le* inserted closer to *ro* than in larva, setae *in* and *ex* short. Bothridium rounded, with posterolateral edge, bothridial seta setiform, covered with granular cerotegument. In protonymph, anterior and medial part prodorsum reticulate, and lateral and posterior parts punctate. Gastronotum with eight pairs of setae: *p*-series appears in protonymph (Fig. 11b) and remains in deutonymph and tritonymph (Figs. 14a, 14b), and *d*-series lost and remains absent through rest of ontogeny. In all nymphs, setae c_1 and c_2 short, h_1 long, and other setae of medium size (Table 1). Dorsal part of gastronotum flat, with exuvial scalps of previous instars, other gastronotal setae in marginal position on gastronotum (Figs. 15b, 18, 19b). Seta h_1 curved upwards and can be helpful in carrying exuvial scalps. Genital valves of protonymph with one pair of setae, three pairs added in deutonymph (one pair in inner row and two pairs in outer row), and one pair added in tritonymph in inner row (Figs. 1b, 14a, 14b); all short and usually covered with granular

cerotegument. In deutonymph, one pair of aggenital setae appearing and remaining through ontogeny. Paraproctal valves of protonymph (segment AD) and deutonymph (segment AN) glabrous, but in tritonymph 4–5 pairs of anal setae present, all short and smooth. In protonymph, cupule *ips* lateral to anal valves, other cupules and gland opening not observed, possibly obscured by granular cerotegument in this and other nymphs (Figs. 11b, 14a, 14b).

In all nymphs, hypertrichy present in epimeral region, variation not observed. In protonymph, one pair of setae added on epimere II, and one pair on epimere III, compared to larva (Figs. 16a, 16b), in deutonymph three pairs of setae added on epimere III, and one pair added on epimere IV (Figs. 17b, 17a), compared to protonymph. In tritonymph, four pairs of setae added on epimere I, three pairs added on epimere II, one pair added on epimere III, and two pairs added on epimere IV, compared to deutonymph (Figs. 17a, 17b).

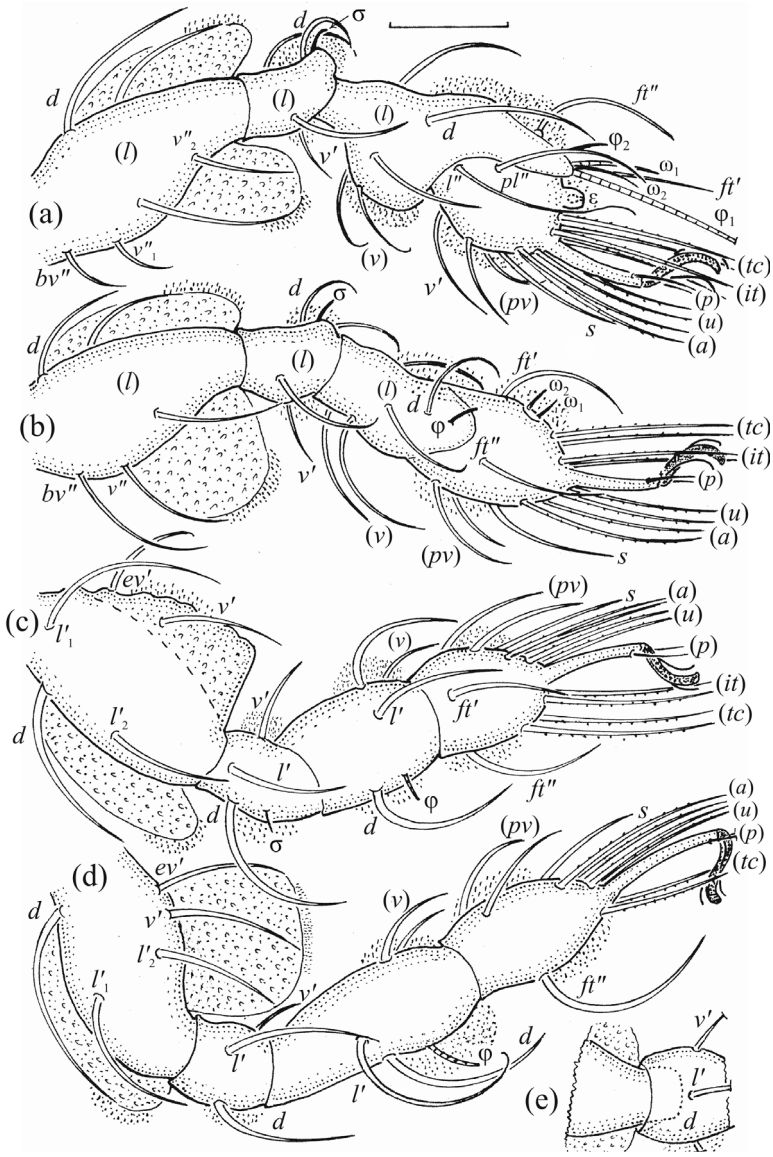


FIGURE 4. *Lopheremaeus mirabilis*, leg segments of adult (part of femur to tarsus), right side, seta on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, tarsus (*pl′*); (b) leg II; (c) leg III; (d) leg IV; (e) part of femur and genu IV (slightly enlarged).

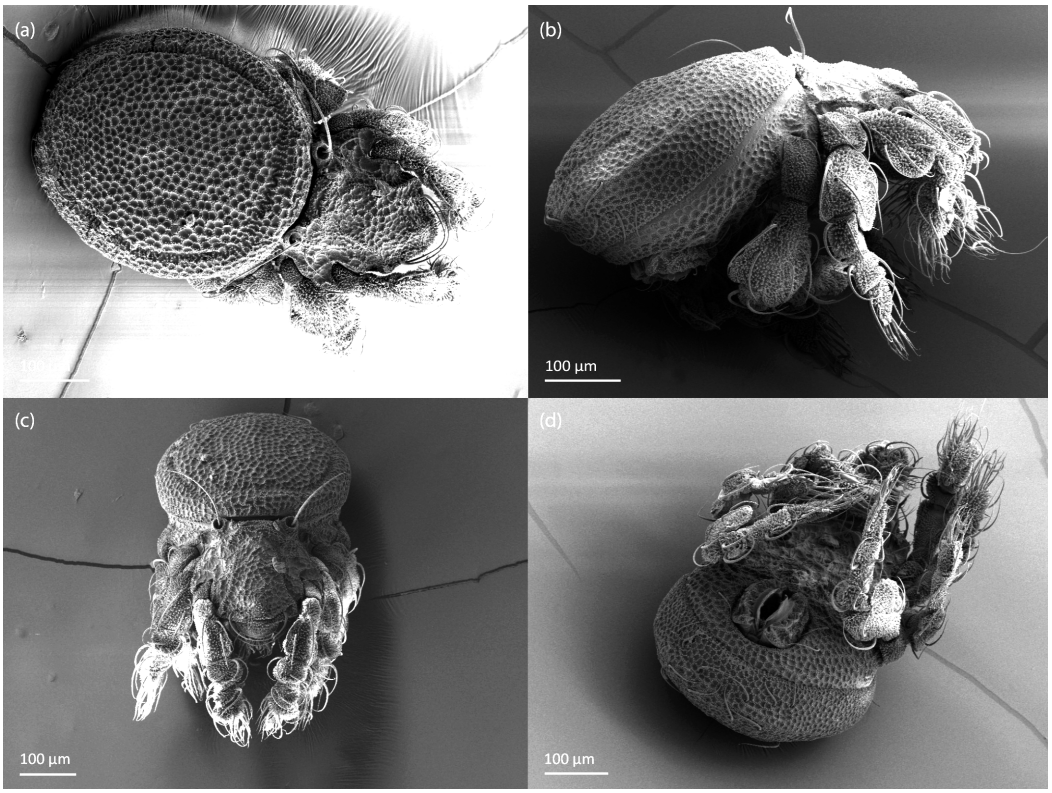


FIGURE 5. *Lopheremaeus mirabilis*, adult, SEM micrographs. (a) Dorsal view, (b), lateral view, (c) frontal view, (d) posteroventral view.

In nymphs, dorsal and ventral crests present on trochanter III, all femora and genua, and dorsal crest present on trochanter IV (Figs. 12b, 18, 19, 20). Solenidion φ_1 on tibia I on large apophysis, covering large dorsal part of tarsus I, other solenidia short or of medium size, famulus ε on tarsus I semispherical. On all genua and tibiae, seta *d* present, removed from respective solenidion (Fig. 20). All tarsi with basal bulb and uniformly narrow distal stalk at about mid-length, with one claw and short setae *d*. Most distal setae on tarsi long, slightly curved or nearly straight and finely barbed, other setae long or of medium size, curved and smooth. Some parts of leg segments and leg setae covered with granular cerotegument.

Summary of ontogenetic transformations

In all juveniles of *L. mirabilis*, the prodorsal setae *ro* and *le* are of medium size, while *in* and *ex* are short; by contrast, in the adult seta *ex* is of medium size, but shorter than *ro* and *le*. In all instars, the opening of the bothridium is rounded, but the bothridial seta is clavate in the larva, and setiform in other instars. The larva has eight pairs of gastronotal setae (*c*-, *d*-series, *lp*, h_1, h_2), and the nymphs have also eight pairs (*p*-series appears, *d*-series is lost in protonymph), but the notogaster of the adult loses the *c*-series, such that six pairs of notogastral setae remain. The formula of gastronotal setae of *L. mirabilis* is therefore 8-8-8-8-6 (from larva to adult). Formulae of epimeral setae are: 3-1-2 (larva, including scaliform *1c*), 3-2-3-1 (protonymph), 3-2-6-2 (deutonymph), 7-5-7-4 (tritonymph) and 8-7-12-4 (adult). Formula of genital setae is 1-4-5-7 (protonymph to adult), aggenital setae is 1-1-4 (deutonymph to adult), and segments PS–AN is 03333-0333-0(4-5)(4-5). Seta *d* is present on genua and tibiae of all instars. The ontogeny of leg setae and solenidia is given in Table 2.

TABLE 1. Measurements of some morphological characters of juvenile stages and adult of *Lopheremaeus mirabilis* (mean measurements of 3–7 juveniles and 10 adults in μm); Nd—not developed.

Morphological characters	Larva	Protonymph	Deutonymph	Tritonymph	Adult
Body length	281	371	468	579	631
Body width	150	208	281	310	337
Length of prodorsum	104	142	159	215	208
Length of: seta *ro*	25	38	54	64	79
seta *le*	14	34	52	59	85
seta *in*	2	2	3	4	8
seta *ex*	3	3	4	5	53
seta *bs*	80	89	104	116	149
seta *c*1	4	7	11	17	Lost
seta *c*2	4	6	10	16	Lost
seta *da*	27	Lost	Lost	Lost	Lost
seta *dp*	28	Lost	Lost	Lost	Lost
seta *lp*	32	20	21	22	83
seta *h*1	27	88	102	117	61
seta *h*2	15	34	44	56	63
seta *p*1	Nd	19	25	32	65
seta *p*3	Nd	16	23	30	63
genital opening	Nd	32	49	72	88
anal opening	28	61	84	117	120

Distribution, *ecology and biology*

According to Subías (2004, 2020), *L. mirabilis* has an eastern Mediterranean distribution, and this species was reported only from Bulgaria, Bosnia-Herzegovina and North Macedonia, Romania and Georgia (Csiszár & Jeleva 1962, Tarman 1983, Ivan & Vasiliu 2000, Murvanidze & Mumladze 2016). This species inhabits alpine meadows, forests and urban soils (Murvanidze & Mumladze 2016). It was collected in Romania for the first time in 1992 in a small number (Ivan & Vasiliu 2000), but was misidentified as *Lopheremaeus laminipes* (Berlese 1916). Our additional collection and the comparison with a specimen from the Csiszár collection allowed us to identify these individuals as *L. mirabilis*. Thus, this is the first record of *L. mirabilis* in Romania, and represents the most northern record of the species.

In our study, the density of *L. mirabilis* in the soil of Dobrina forest (Romania) varied between May and July, being highest in June 2014 (6.4 individuals per 500 cm^3), and lowest in May 1992 (0.4 individuals per 500 cm^3, Table 3). In most samples, adults dominated the juveniles, comprising 41–64% of individuals. In the sample with the most abundant juveniles (July 2019), the juveniles dominated (64% of individuals) the adults, and the stage structure of *L. mirabilis* was the following: seven larvae, four protonymphs, four deutonymphs, three tritonymphs and 10 adults. Among 15 dissected adults, nine were females and six males, but we rather not like to give the sex ratio of this species because these mites were collected in different dates. Most females (78%) were gravid, carrying 1–3 (mostly two) relatively large eggs, each 247–271 x 181–199, and one of which constitutes about 40% of the total body length of females.

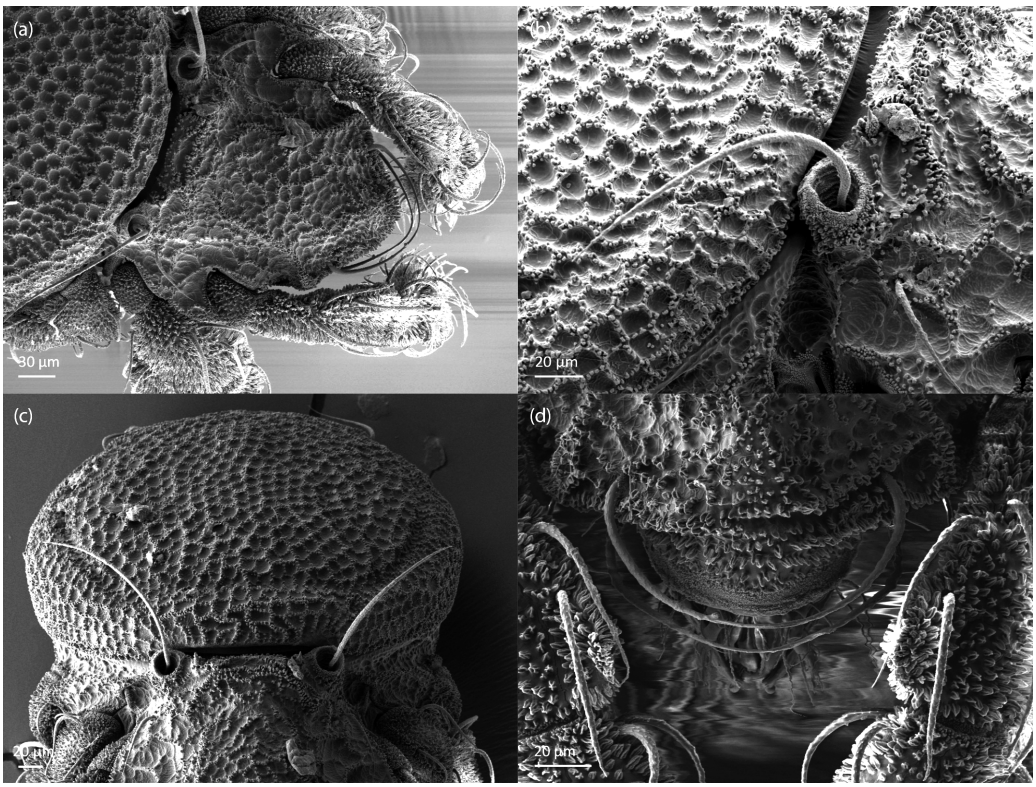


FIGURE 6. *Lopheremaeus mirabilis*, adult, SEM micrographs. (a) Anterior part, dorsal view, (b) bothridium and bothridial seta, (c) bothridial setae and notogaster, frontal view, (d) rostrum, frontal view.

Comparison of morphology of *Lopheremaeus mirabilis* with congener and remarks

The adult of *L. mirabilis* is morphologically similar to that of *L. laminipes*, but Csiszár and Jeleva (1962) recognized the latter species as distinct mainly by the lighter cerotegument and notogastral sculpture, without dense black punctation, and more posterior location of all notogastral setae in the latter species. However, in the figure of *L. laminipes* drawn by Mahunka and Mahunka-Papp (1995) the location of posterior setae on the notogaster is similar to that of *L. mirabilis* as shown by Csiszár and Jeleva (1962) and specimens studied herein, which suggests that the distinction of these species needs more investigation.

The homologies of notogastral setae in the adult of *L. mirabilis* are inconsistently reported in the literature. Csiszár and Jeleva (1962) observed only three pairs of notogastral setae, and labeled none of them. Paschoal (1988) revised the Plateremaeidae and used the old Grandjean's (1951) "*Dometorina* nomenclature" of notogastral setae, but he treated the notogastral setae r_2 and r_3 as homologes of *lp* and *lm*, respectively, which is inconsistent with Grandjean's (1951) unideficient nomenclature. In our opinion, setae r_2 and r_3 are located posterior to porose areas *A1* and *A2*, respectively, and should be labeled as h_3 and h_2, respectively. In the case of *L. mirabilis*, the adult has no porose areas, seta h_3 is absent in the larva, and it is difficult to judge if this seta appears in the protonymph because normally this seta occupies the lateral position, as seta *lp*, which is present in the larva. There is no trace that h_3 appears in the protonymph and *lp* is lost, and therefore we consider seta *lp* in all nymphs and adult of *L. mirabilis*.

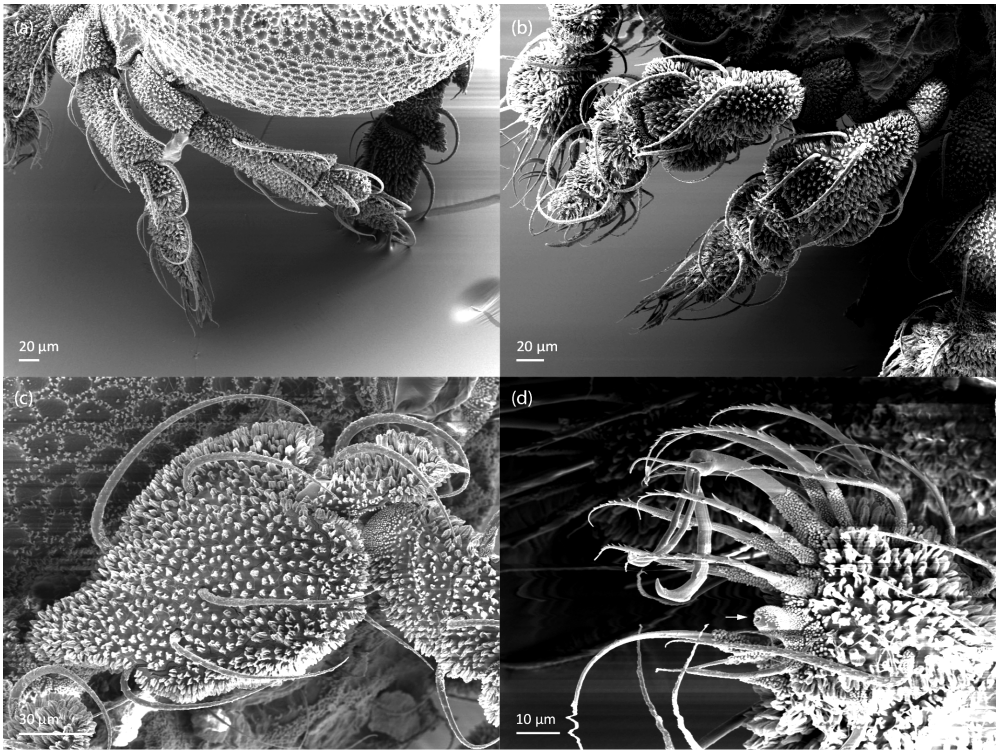


FIGURE 7. *Lopheremaeus mirabilis*, adult, SEM micrographs. (a) Legs III and IV, dorsal view, (b) legs I and II, dorsal view, (c) femur and part of genu III, lateral view, (d) tarsus I, lateral view (arrow points famulus ε).

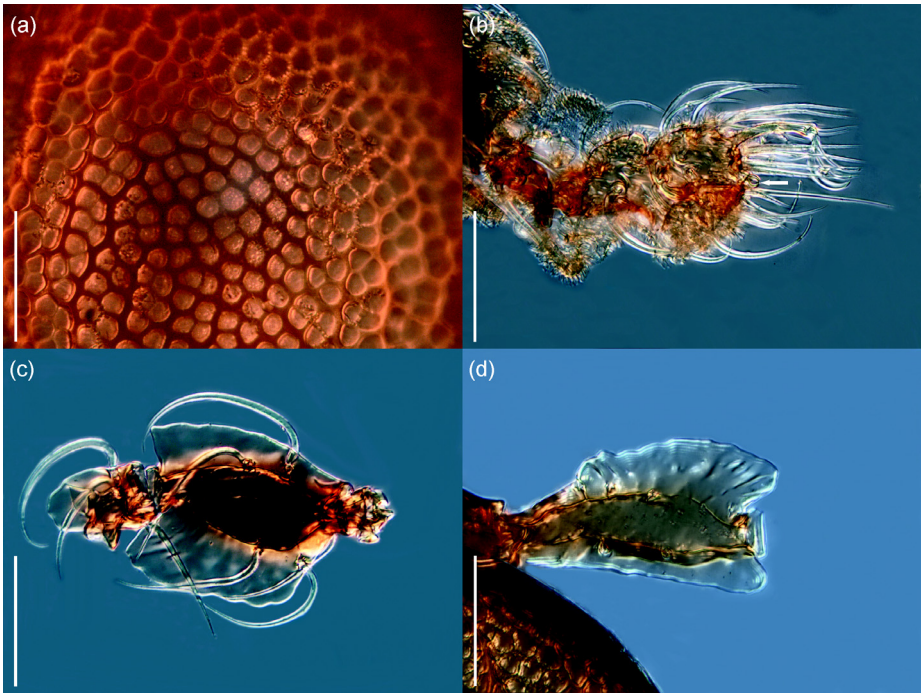


FIGURE 8. *Lopheremaeus mirabilis*, adult, photo, scale bars 50 µm. (a) Notogaster, dorsal view, (b) part of leg I, lateral view (arrow points famulus ε), (c) femur and genu III, lateral view, (d) femur IV, dorsal view (setae broken).

TABLE 2. Ontogeny of leg setae (Roman letters) and solenidia (Greek letters) of *Lopheremaeus mirabilis*.

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	–	(*l*)	–	–	ω_2
Deutonymph	*v*′	–	*v*′	*v*″, φ_2	–
Tritonymph	–	v''_1	–	–	(*it*)
Adult	–	v''_2	–	–	*l*″, *v*′
Leg II					
Larva	–	*d*, *bv*″	(*l*), *d*, σ	*l*′, *v*′, *d*, φ	(*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*), ω_1
Protonymph	–	(*l*)	–	*l*″	–
Deutonymph	*v*′	–	*v*′	*v*″	ω_2
Tritonymph	–	*v*″	–	–	(*it*)
Adult	–	–	–	–	–
Leg III					
Larva	–	*d*, *ev*′	*l*′, *d*, σ	*v*′, *d*, φ	(*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*)
Protonymph	v'_1	–	–	–	–
Deutonymph	*l*′	l'_1	*v*′	*l*′, *v*″	–
Tritonymph	–	–	–	–	(*it*)
Adult	v'_2	l'_2, *v*′	–	–	–
Leg IV					
Protonymph	–	–	–	–	*ft*″, (*p*), (*u*), (*pv*)
Deutonymph	v'_1	*d*, *ev*′	*d*, *l*′	*v*′, *d*, φ	(*a*), *s*
Tritonymph	v'_2	l'_1	*v*′	*l*′, *v*″	(*tc*)
Adult	v'_3	l'_2, *v*′	–	–	–

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.

The presence of epimeral hypertrichy and crests on some leg segments support the membership of *L. mirabilis* in Plateremaeidae. Epimeral hypertrichy also occurs in *Plateremaeus*, *Allodamaeus* Banks, 1947, *Paralopheremaeus* Paschoal, 1988 and *Calipteremaeus* Paschoal, 1988; and in *Paralopheremaeus* small crests also are present on some leg segments (Paschoal 1988). Epimeral hypertrichy also occurs in *Hermannia reticulata* Thorell, 1871 and *H. scabra* (Koch 1879), but in *L. mirabilis* and *H. reticulata* hypertrichous are epimeres I–III, whereas in *H. scabra* epimeres III and IV (Seniczak *et al*. 2017a, b).

Seniczak and Seniczak (2011) and Seniczak *et al*. (2012, 2016) compared the morphological ontogeny of some species of Plateremaeoidea, and the juveniles of *L. mirabilis* are most similar to those of *Gymnodamaeus bicostatus* (Koch 1836), which have plicate cuticle. However, the larva of *G. bicostatus* has 11 pairs of gastronotal setae (h_3 absent), whereas that of *L. mirabilis* has eight pairs (c_3, *la*, *lm* and h_3 absent). The nymphs of the former species have 10 pairs of gastronotal setae (*lp*, *c*-, *h*- and *p*-series), whereas those of the latter species have eight pairs (c_1, c_2, *lp*-series, h_1, h_2 and *p*-series). The adult of *G. bicostatus* retains five pairs of notogastral setae (h_1, h_2 and *p*-series), whereas that of *L. mirabilis* retains six pairs (*lp*, h_1, h_2 and *p*-series). The nymphs of both species carry the exuvial scalps, but *L. mirabilis* has long, curved upwards seta h_1, which can be helpful in carrying the scalps, whereas in *G. bicostatus* this seta is short (Seniczak & Seniczak 2011). *Aleurodamaeus*

setosus (Berlese 1883), *Arthrodamaeus italicus* (Berlese 1916), *A. mongolicus* Bayartogtokh & Weigmann, 2005 and *Licnobelba latiflabellata* (Paoli 1908) have also long, curved upwards seta h_1, which can be helpful in carrying the exuvial scalps (Seniczak *et al*. 2012, 2016).

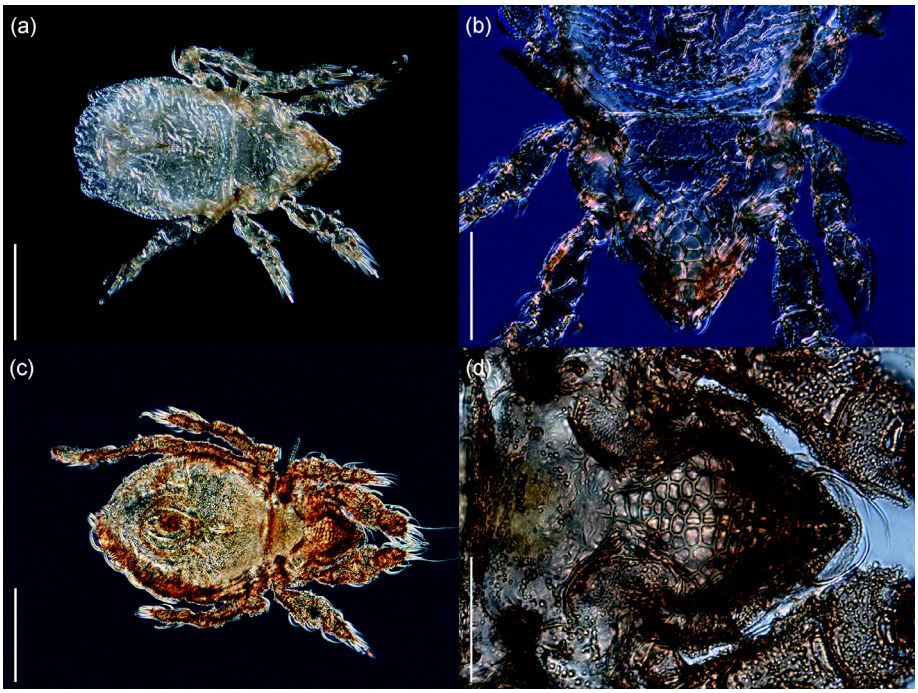


FIGURE 9. *Lopheremaeus mirabilis*, photo, dorsal view. (a) Larva, (b) anterior part of body of larva, (c) tritonymph without exuvial scalps, (d) prodorsum of tritonymph. Scale bars (um): a —100; b, d —50 um; c —200.

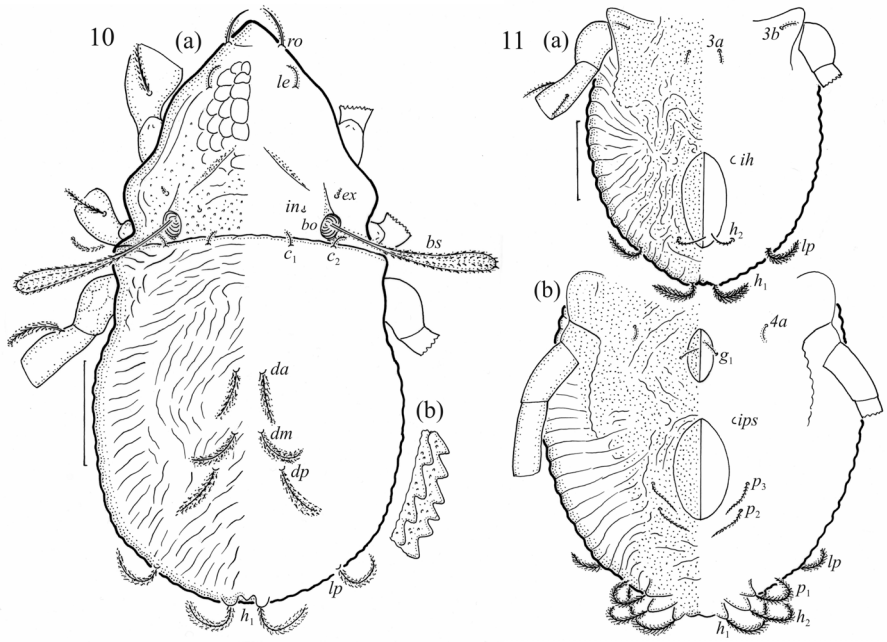


FIGURE 10–11. *Lopheremaeus mirabilis*, legs partially drawn, scale bars 20 μm. 10. (a) Larva, dorsal aspect, (b) edge of gastronotum (enlarged). 11. Ventral part of hysterosoma, (a) larva, (b) protonymph.

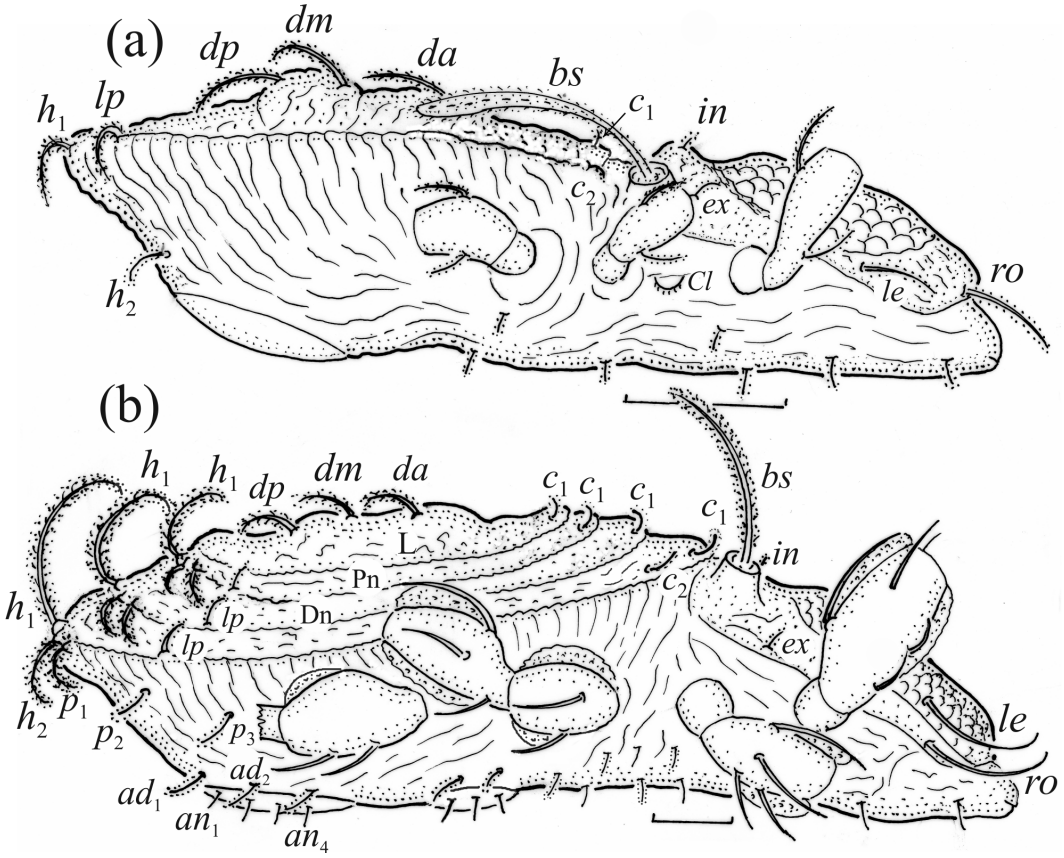


FIGURE 12. *Lopheremaeus mirabilis*, lateral aspect, legs partially drawn, scale bar 50 μm. (a) Larva, (b) tritonymph.

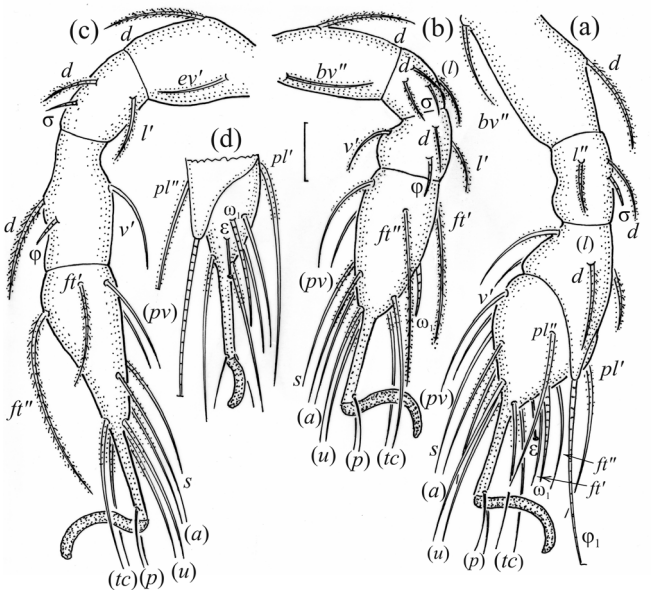
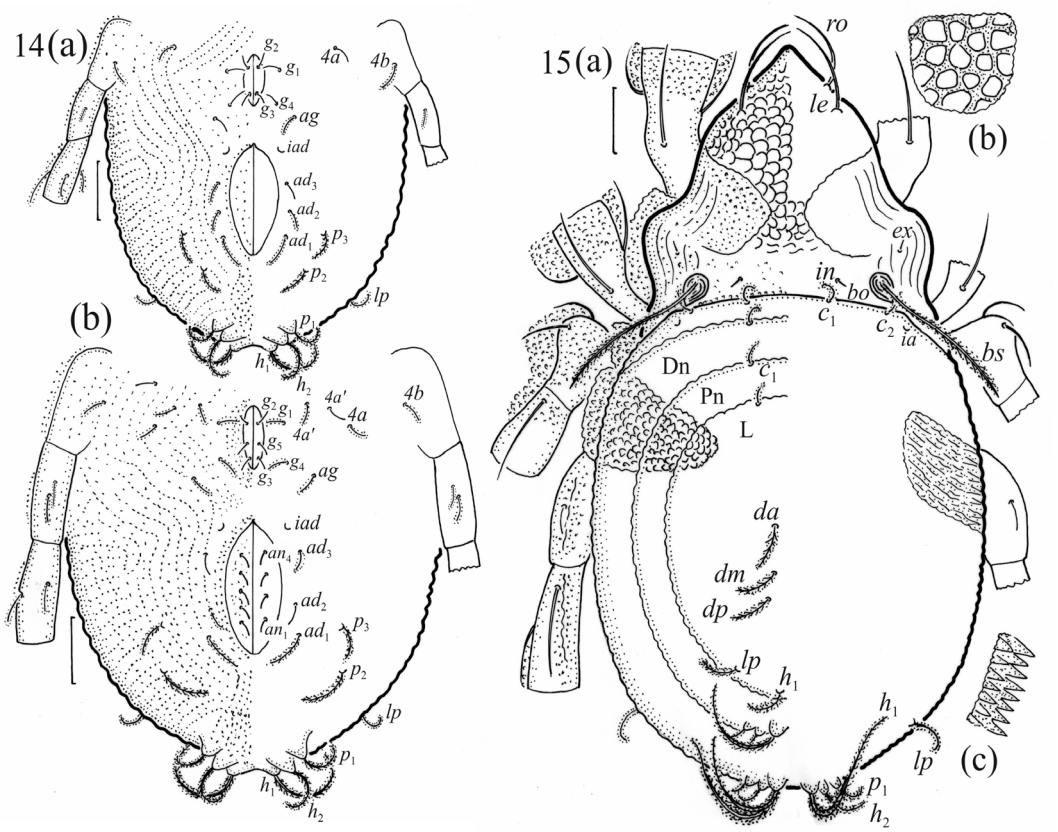


FIGURE 13. *Lopheremaeus mirabilis*, leg segments of larva (part of femur to tarsus), right side, seta on the opposite side not illustrated, but indicated in the legend, scale bar 10 μm. (a) Leg I, genu (*l′*); (b) leg II; (c) leg III, (d) part of tarsus, dorsal aspect.

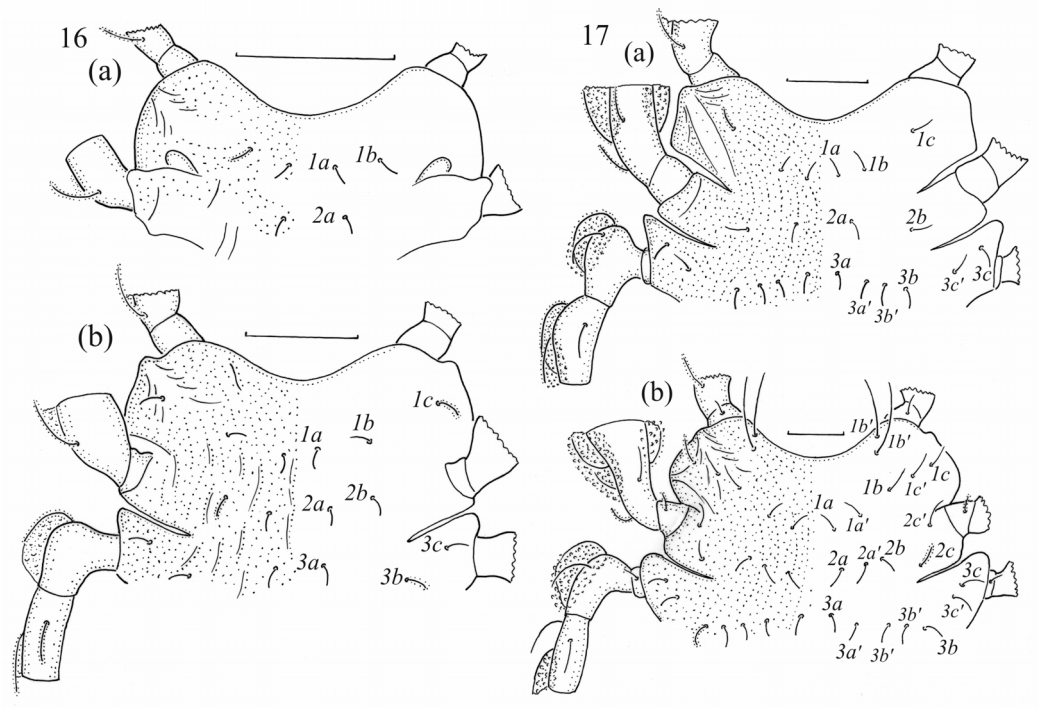
TABLE 3. Density (individuals/500cm^3), stage structure and vertical distribution of *Lopheremaeus mirabilis* in the soil of Dobrina forest (Romania); L—larva, Pn—protonymph, Dn—deutonymph, Tn—tritonymph, Juv—juveniles, Ad—adult, Olf—litter and fermentation layer, Ah—humus layer, C—constancy in five samples (in%).

Date of sampling	Juveniles						Adult	Total	Indiv/500cm^3	Presence in Olf/Ah	C
	L	Pn	Dn	Tn	Juv	%					
May 1992	0	0	0	0	0	0	2	2	0.4	1/1	20
July 1992	0	0	0	0	0	0	4	4	0.8	2/2	40
June 2014	0	5	4	4	13	41	19	32	6.4	29/3	40
May 2019	0	1	2	2	5	45	6	11	2.2	11/0	20
July 2019	7	4	4	3	18	64	10	28	5.6	25/3	40
Total	7	10	10	9	36	47	41	77	3.1[1]	16.6/1.8[1]	32[1]

[1]Mean value.



FIGURES 14–15. *Lopheremaeus mirabilis*, legs partially drawn, scale bars 50 μm. 14. Ventral part of hysterosoma, (a) deutonymph, (b) tritonymph. 15.Tritonymph, (a) dorsal aspect, (b) reticulation of prodorsum, (c) edge of gastronotum (b, c, enlarged).



FIGURES 16–17. *Lopheremaeus mirabilis*, epimeral regions, partially drawn, scale bars 50 μm. 16. (a) Larva, (b) protonymph. 17. (a) Deutonymph, (b) tritonymph.

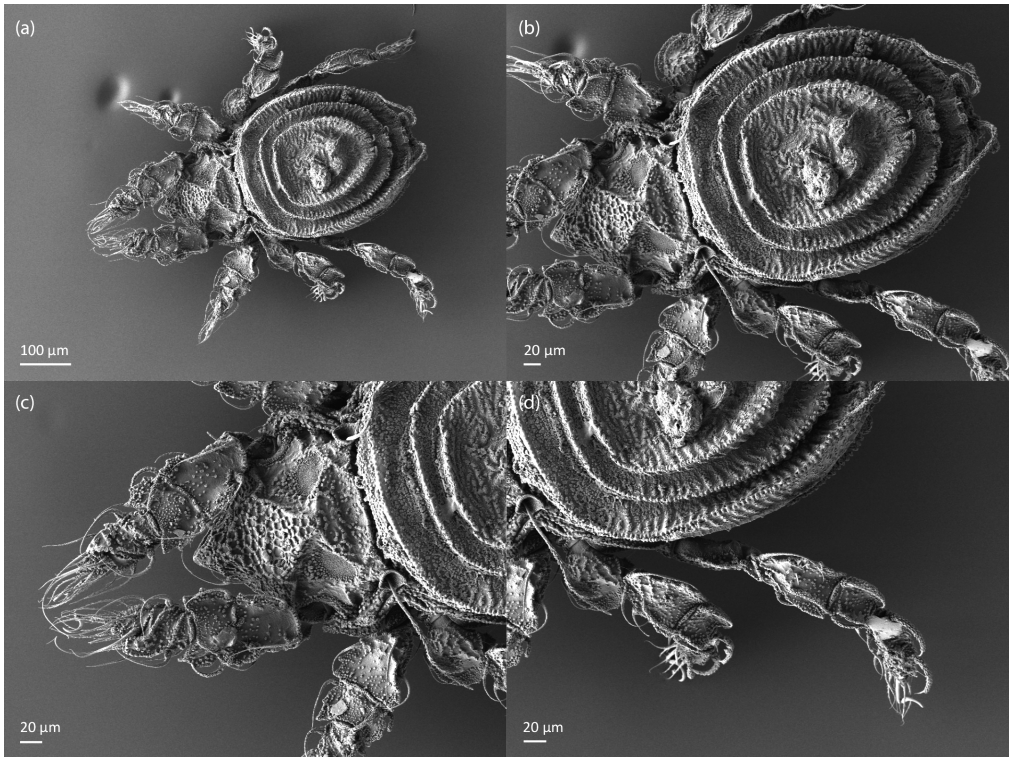


FIGURE 18. *Lopheremaeus mirabilis*, tritonymph with exuvial scalps, dorsal view. (a) Whole body, (b) prodorsum and gastronotum, (c) prodorsum, (d) legs III and IV.

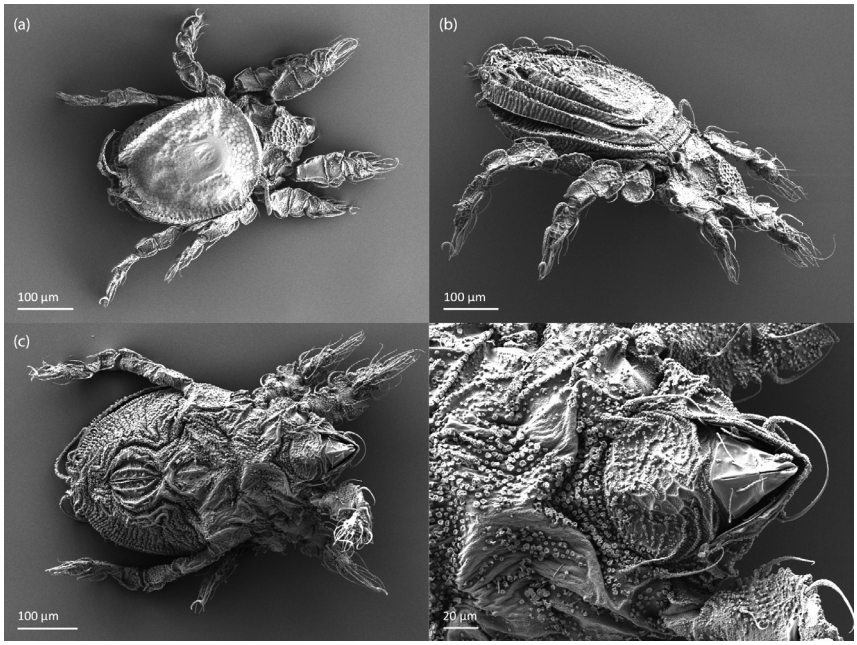


FIGURE 19. *Lopheremaeus mirabilis*, tritonymph. (a) Without exuvial scalps, dorsal view, (b) with exuvial scalps, lateral view, (c) ventral view, (d) hypostomal region.

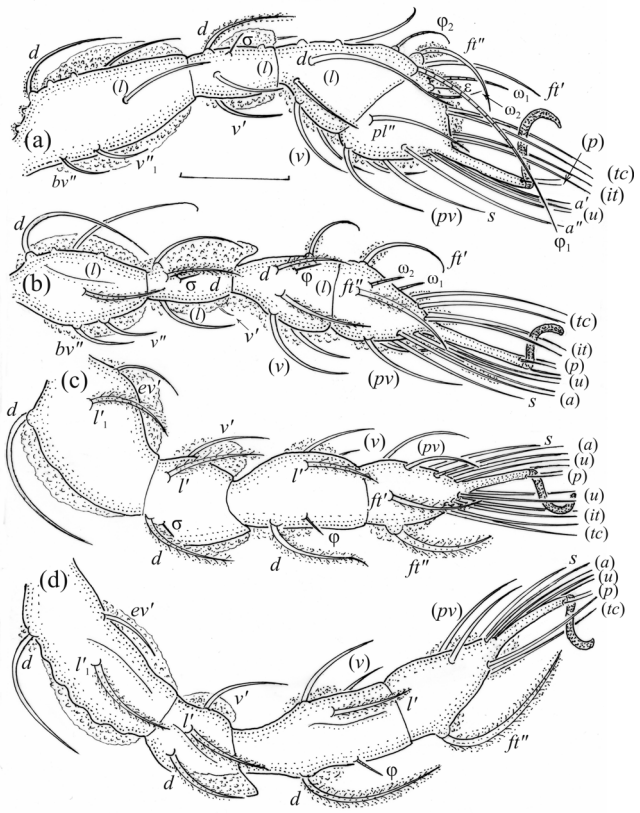


FIGURE 20. *Lopheremaeus mirabilis*, leg segments of tritonymph (part of femur to tarsus), right side, seta on the opposite side not illustrated, but indicated in the legend, scale bar 20 µm. (a) Leg I), tarsus (*pl′*); (b) leg II; (c) leg III; (d) leg IV.

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