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Survey of European mites from the suborder Uropodina: II. Morphology, geographical distribution, biology, and ecology of *Trematurella elegans* (Kramer, 1882)

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ABSTRACT

The major aim of this article was to supplement the existing descriptions of the morphology, biology, ecology, and geographical distribution of *Trematurella elegans* (Kramer, 1882) (Acari: Mesostigmata) with a bit of new information about the species. The data available in the literature on this species is scant. The available taxonomic descriptions are based on schematic and very rough drawings. The authors of this article conducted a research study that will shed more light on this species. The study is based on a large set of data (21,741 samples), which have been collected for over 50 years in the area of Poland and a few other European countries. The description of the morphology of the species is based on materials obtained from a scanning electron microscope, and the description of the distribution of the species on the basis of data obtained from the GIS system, which allows the precise localisation of samples to be determined. Finally, the authors have also tried to ascertain the habitat preferences of *T. elegans*, analyzing the phenology and influence of the altitude on the distribution of the species. This study is probably the first attempt to establish the effects of the Pleistocene glaciations on the current distribution of *T. elegans* in Poland and the whole area of Europe.

Keywords *Uropoda elegans*, redescription, habitat preferences, postglacial migration, subcortical species, saprophagous species

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This article is dedicated to the memory of an outstanding acarologist, our colleague and teacher, Dr. Françoise Athias Binche

Introduction

It may seem that European Uropodina mites have been already described so thoroughly that it is virtually impossible to provide any new information about mites from this suborder. Since these mites are quite large and very characteristic, many species had been described in the late 1800's and the early 1900's, but those descriptions are not very precise (see e.g. Müller 1776; Hermann 1804; Haller 1881; Koch 1835, 1839, 1941, 1847; Berlese 1888, 1913, 1917; Michael

1894; Halbert 1915, 1923). At that time the researchers focused mostly on the taxonomy, and they described the species which were new for science and paid less attention to the biology, ecology, and geographical distribution of the species. For this reason the idea of more detail-oriented research into the most abundant European species appeared later. The first publication from a series was published by Błoszyk and Athias-Binche (1998), who described *Polyaspinus cylindricus* Berlese, 1916, a species which has very interesting geographical distribution and ecology.

Nowadays, professor Jerzy Błoszyk, with his co-workers, decided to go back to the idea of a renewed elaboration of the morphology, biology, ecology, and zoogeography of the most interesting European Uropodina species. The current article focuses on *Trematurella elegans*, which was described by Kramer 136 years ago, in 1882, in Germany.

The re-descriptions of selected European Uropodina will be prepared on the basis of the information available in the existing literature published so far, as well as unpublished information, gathered during over 50-year-long research into this group of mites. The next reason is that many of those species were described only in Italian or German, which made the descriptions inaccessible for many readers. Moreover, the authors of the current article also want to make their own contribution towards the research by the use of modern research techniques, like scanning electron microscopy (SEM) for the morphological analysis, and the GIS systems to establish the distribution of Uropodina (Błoszyk *et al.* 2013).

Materials and methods

The study is based on 21,741 quantitative and qualitative samples, which were collected in Poland between 1961 and 2017. The samples were collected in areas with different altitude up to over 2,400 m above sea level. The analysis of the geographical distribution of *T. elegans* in Europe (Figure 14) was carried out on the basis of data available in the literature and data collected through examination of soil samples from Poland and different European countries: Spain (30 samples), France (50 samples), Belgium (40 samples), The Netherlands (100 samples), Germany (50 samples), Denmark (100 samples), Sweden (30 samples), Norway (500 samples), Czech Republic (150 samples), Slovakia (170 samples), and Ukraine (30 samples).

The samples were collected in different seasons from 35 types of habitats, such as open habitats, forests, and merocenoses (Table 1). The samples consisted of soil were collected either quantitatively with a corer (30-90 cm²) to the depth of 10 cm or qualitatively (with a sieve) from the forest floor, as well as unsieved samples from open habitats. The material from dead wood (such as rotten trunks, logs, stumps) was collected with a plastic container with a volume of 0.5–0.8 l.

Mites were extracted using Tullgren funnels for 4–6 days (depending on the level of moisture) just after the material had been collected. The extracted mites were preserved in 75% ethyl alcohol. The specimens were identified using the morphological criteria from the original descriptions and later accounts (Kramer 1882; Hirschmann and Zirgiebl-Nicol 1961; Błoszyk 1983, 1999; Karg 1989; Mašan 2001).

To analyze the preferences towards specific habitat type, altitude, and phenology, over 7,000 qualitative samples were examined. The number of samples slightly varied between the tested phenomena, since the complete set of data necessary for the analysis was not always present. Therefore, 7,476, 7,190 and 7,506 samples were used to analyze habitat preferences, phenology, altitude preferences, respectively. The map of distribution of *T. elegans* in Poland was drawn on the basis of all collected samples (21,741) on the UTM grid (10×10 km).

To visualize the fine details of morphology of the mites, scanning electron microscopy (SEM) techniques were used. The specimens were air-dried, mounted on a pin stubs with a double-sided sticky tape, coated with gold in a sputter coater and observed in a Zeiss Evo 40 Scanning Electron Microscope (Carl Zeiss SMT Ltd., Cambridge, UK) at 16.5 kV.

The analysis of frequency of *T. elegans* in Uropodina communities was based on the index of frequency. The following classes were used (Błoszyk 1999): Frequency: F5, euconstants

(>50%), F4, constants (30.1–50%), F3, subconstants (15.1–30.0%), F2, accessory species (5.0–15.0%), and F1, accidents (<5%).

Systematic status

Genus *Trematurella* Trägårdh, 1942 *Trematurella* Trägårdh, 1942: 111.

Type species *Trematurella stylifera* Trägårdh, 1942: 111, by monotypy.

Diagnosis — Medium size mites, highly sclerotized, with characteristic sculpture. The idiosoma is oval and flat at the dorsal part. The unique characteristics of this species: the large dorsal shield is surrounded by a rather narrow marginal shield. The dorsal setae are serrated, very long and massive, of the same width at the whole length. The female genital shield is large, wide at the base and becomes more and more narrow towards the front (the shape resembles the foot of the iron), with a long narrow appendix at the front, intensively sculptured. The male genital shield is oval, smooth and has no paragenital setae. They have five pairs of sternal setae, two pairs of adanal setae (*Ad1-Ad2*), and single postanal seta (*Pa*). There are cavities for the leg hiding, the last ones, hiding the fourth pair of legs, are located across and do not overlap with the opisthosoma. At the first pair of tarsus there is a single claw. The first pair of hypostomal setae (*h1*) is needle-shaped and smooth, the other ones (*h2-h4*) are feather-like. Also the setae at the trochanters of palps are feather-like.

Trematurella elegans (Kramer, 1882)

Uropoda elegans Kramer, 1882: 406-407

Urodinychus elegans var. *gallica* – Berlese, 1917: 144-145.

Trematurella stylifera – Trägårdh, 1942: 109-112; Trägårdh – 1945: 1-10; Hirschmann & Zirmgiebl-Nicol, 1961: 10; Wiśniewski, 1979: 37.

Trematurella elegans – Błoszyk, 1984: 70; Wiśniewski & Hirschmann, 1991: 174; Błoszyk, 1999: 136-137; Błoszyk & Krysiak, 2000: 117, 119; Błoszyk *et al.*, 2002a 25, 29, 31; Błoszyk *et al.*, 2002b 63, 67, 69-70; Błoszyk *et al.*, 2004: 1507; Błoszyk & Napierała, 2004: 287-288; Błoszyk *et al.*, 2006: 28, 32-33, 35; Napierała *et al.*, 2006: 157; Napierała, 2008: 61, 90, 109, 111, 116, 149; Napierała *et al.*, 2009: 291, 295, 299, 302; Kontschán, 2013: 103, 122; Napierała & Błoszyk, 2013: 166, 169, 175; 176; Błoszyk *et al.*, 2015: 7, 10.

Trichouropoda elegans – Kontschán, 2002: 346; Kontschán, 2003: 186; Fenda & Ciceková, 2007: 30-31; Kontschán, 2008: 6; Kaczmarek *et al.*, 2011: 33; Kazemi & Kontschán, 2014: 12; Huhta, 2016: 132.

Notes — Berlese (1917) in his work described this species as *Urodinychus elegans* Kram. var. *gallicus* Berl. n. var. This variation was also noted by Wiśniewski and Hirschmann (1991) in their catalogue. However, from the taxonomic point of view, it seems that there is no reason to distinguish this variation. With no doubt there is only one such species in Europe, and the differences stem from the range of geographical variability of the species.

Detailed morphology of adults and developmental stages of *T. elegans*

The size of the body (original units used by the authors):

Kramer 1882: length 700 µm, width 560 µm;

Berlese 1917: length 650 µm, width 420 µm;

Błoszyk 1983, 1999: female 650 – 730 µm x 415 – 480 µm; male 650 – 700 µm x 400 – 450 µm;

Karg 1989: female length 670 µm; male length 640 µm;

Wiśniewski & Hirschmann 1993: female 670 x 470 µm; male 640 x 420 µm; deutonymphs 660 – 725 x 420 – 485 µm; deutonymphs (W) 535 – 565 x 335 – 345 µm; protonymphs 570 x 310 µm; larvae 330 x 220 µm;

Mašan 2001: length 535 – 625 µm;

The size of the body measured in this study:

Female (N=30) length 608 – 730 µm, width 401 – 480 µm, average: length $656 \pm 44,1$ SD µm, width $425 \pm 25,9$ SD µm

Male (N=27) length 596 – 700 µm, width 383 – 450 µm, average: length $630 \pm 29,4$ SD µm, width $416 \pm 25,1$ SD µm

Deutonymph (N=32) length 511 – 654 µm, width 332 – 479 µm, average: length $587 \pm 36,2$ SD µm, width $391 \pm 35,2$ SD µm

Protonymph (N=33) length 405 – 580 µm, width 246 – 356 µm, average: length $480 \pm 42,8$ SD µm, width $294 \pm 30,9$ SD µm

Larva (N=17) length 330 – 368 µm, width 189 – 239 µm, average: length $340 \pm 13,4$ SD µm, width $207 \pm 17,0$ SD µm

Female.

The dorsal side (Figures 1 and 2A, B). An oval-shaped idiosoma with a triangle-like vertex at the front edge (Figures 1A and 1B). The dorsal side is flat, highly sculptured. The narrow decorated marginal shield surrounds the big dorsal shield. Both shields fused at the anterior of the body. The whole surface of the dorsal shield is sculptured (Figures 1A and 1C-E). This sculpture is made of polygonal relief of chitin (Figure 2A). The dorsal setae are long, linear, serrated. The number of the setae can be different on each side of a specimen (cosmotrichy).

The marginal setae are similar in length (>40 µm) to the dorsal ones, located on a narrow thickening of chitin, which lies along the external edge of the shield (Figures 1D and 2B); at the posterior part of the body these setae are significantly shorter and located on cylindrical elevations.

The dorsal shield is flat, which can be easily seen from the side view (Figure 2C). The vertex is lowered. There are two pairs of long setae on it (Figure 2D). There are tiny thorns / spikes on the marginal shield – the function is unknown. These structures can be easily seen and they are visible at the posterior part of the idiosoma (Figure 3).

The ventral side (Figures 4A and 4C) is slightly convex, type of sculpture, length and shape similar to the dorsal side (Figure 4A). The large sculptured genital shield with a long appendix at the front occupies the majority of the intercoxal region (Figure 4B). Four pairs of needle-like sternal setae are placed at the sides of the genital shield. They are of various lengths (*St1* 15 µm, *St2* 17 µm, *St3* 28 – 34 µm). The last pair are the longest (*St4* 52 – 62 µm). In females setae *St5* are reduced. The peritreme has a short poststigmatal sector. The stigma is situated between the coxae of the second and the third pair of legs. The prestigmatal sector is elongated and bent. Cavities for legs are present. The pedofossae for the fourth pair of legs are located transversally and they do not overlap with the opisthosoma (Figures 4A and 4E). The ventral setae (usually 12-13 pairs) are long linear and serrated. They form some transversal rows. The two pairs of those setae are placed a little bit below the back edge of the genital shield (Figure 4C). There are two pairs of needle-like adanal setae. The second pair is significantly longer (*Ad1* 23 µm, *Ad2* 31 – 35 µm) and gently serrated (Figure 4D). The single postanal seta (Pa) is very short (10 µm), needle-like, and gently serrated.

The tritosternum has a narrow base (covered by coxa of the first pair of legs). It also has a strongly feathery, single lacini. The corniculi resembles the rutellum of Opilioacarida. The hypostomal groove is narrow with some teeth (oligodontic type). The hypostomal setae: *h1* needle-like (about 20 µm), *h2-h4* highly serrated (15, 20, 20 µm, respectively). The trochanters of palps have a pair of feathery setae (Figure 5). The chelicerae are robust.

Male.

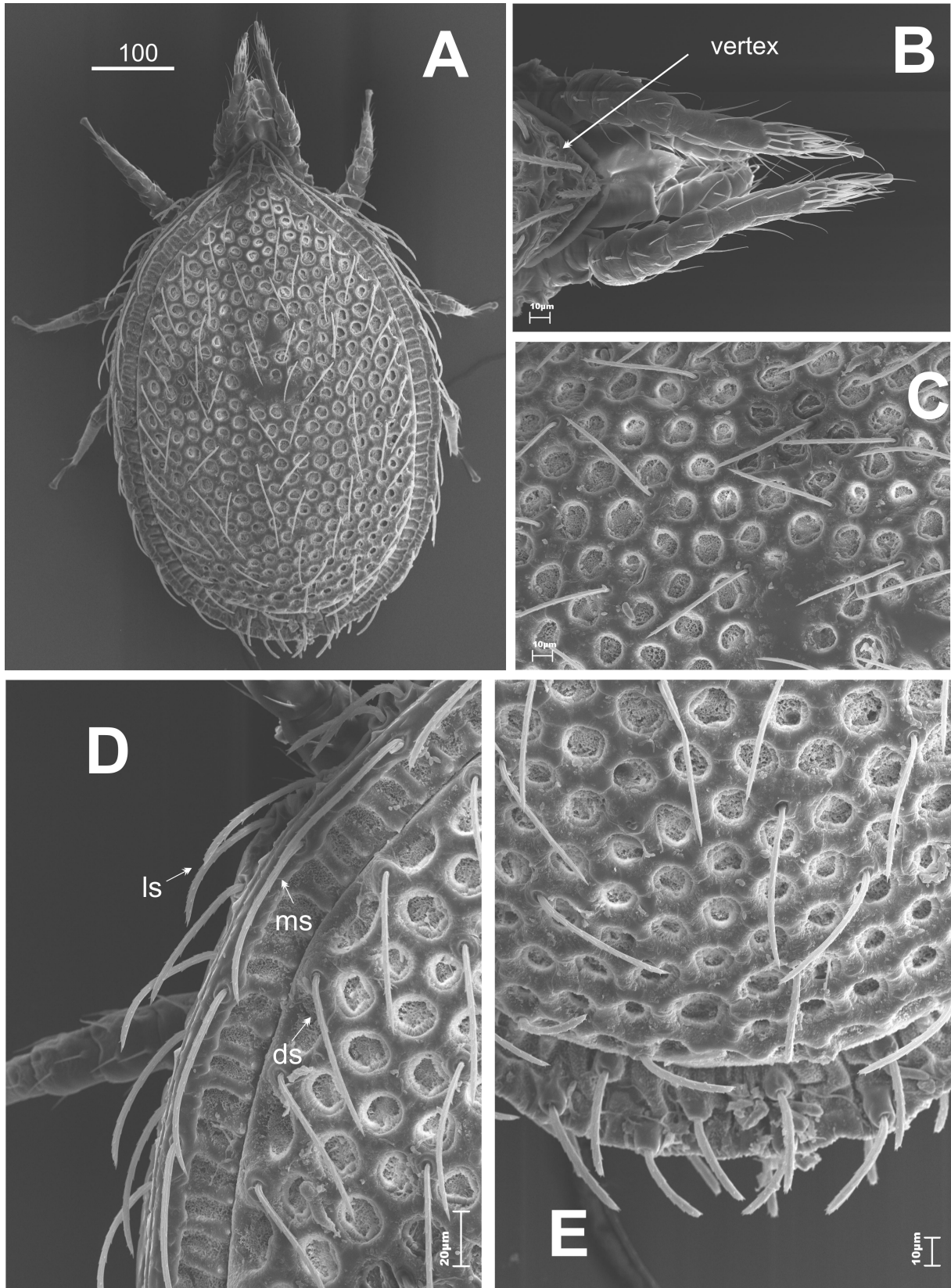


Figure 1 *Trematurella elegans* – Female, dorsal side: A – General view; B – Vertex; C – Dorsal shield, central part; D – Marginal shield, sculpture and setae on lateral part; E – Marginal shield, sculpture and setae on posterior part; ls – Lateral setae, ms – Marginal setae, ds – Dorsal setae.

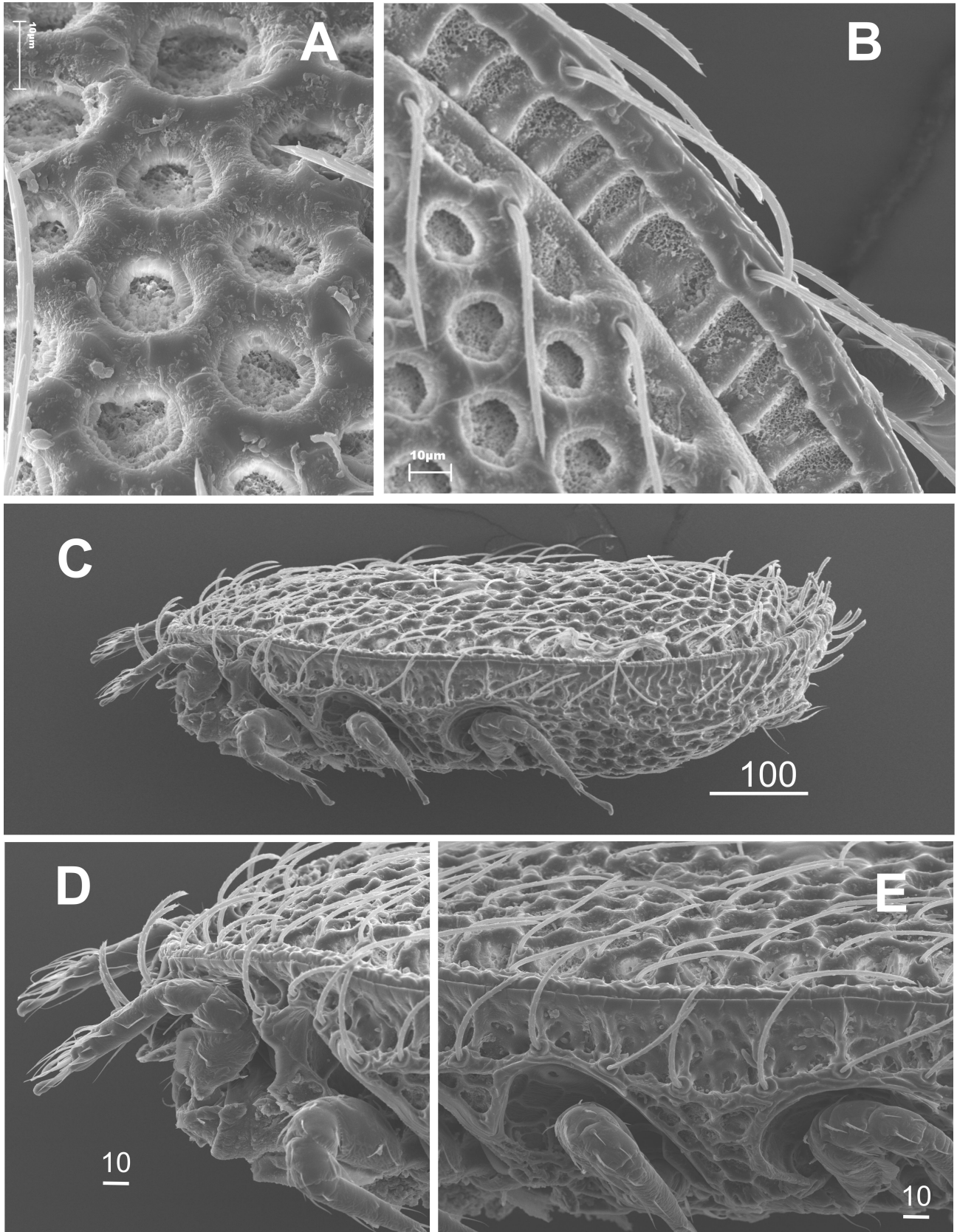


Figure 2 *Trematurella elegans* – Female; A-B – Dorsal side, details of sculpture of central and marginal parts; C-E – Lateral view.

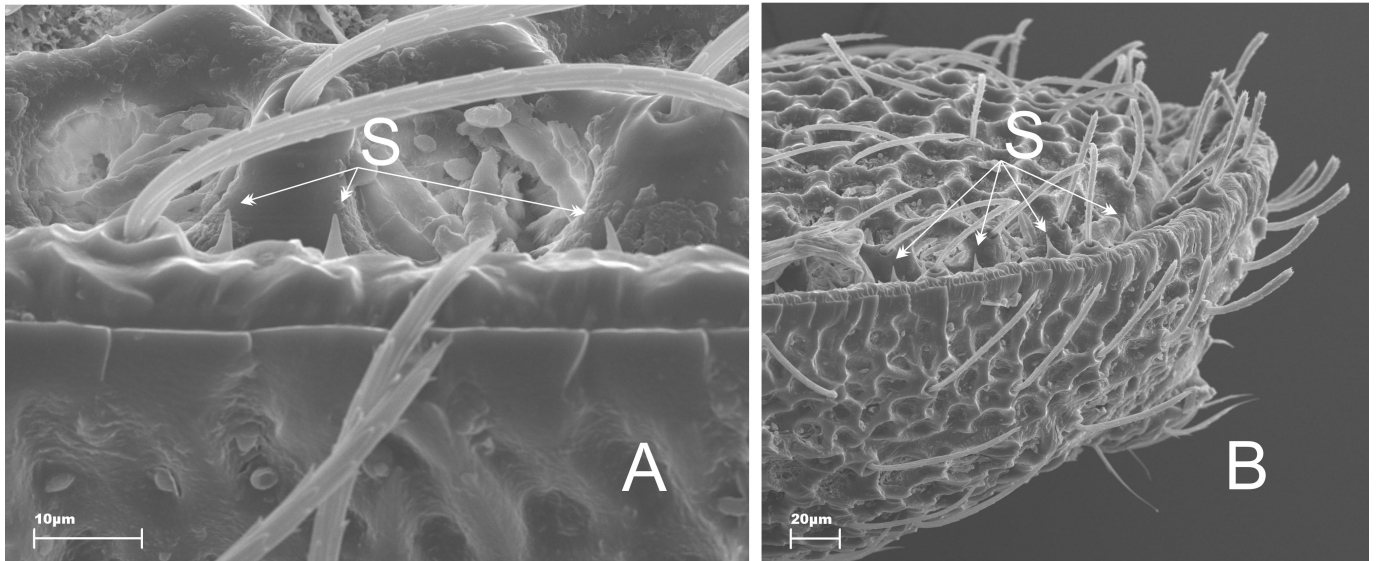


Figure 3 A, B – *Trematurella elegans* – Female, characteristic spines (S) on the marginal shield.

The dorsal side (Figure 6). The sculpture and chaetotaxy of the dorsal side are very similar to those in females (compare: Figure 1 and Figure 6).

The ventral side (Figure 7). The sculpture of the ventral side is like the one found in females. The small oval genital shield is located centrally, in the intercoxal region (at the level of the third pair of legs). There are five pairs of needle-like sternal setae (*st1-st5*) of different length (Figures 7A and 7B): *st1-st3* short (8, 15, 26 µm), *st4* long (32 – 34 µm), *st5* short (26 µm). At the sides of the first three pairs of the sternal setae one can notice characteristically sculptured areas that surround pores. The chaetotaxy of opisthosoma is the same like in females.

There is a gnathosoma. Clearly noticeable sexual dimorphism. Males have reduced *h2* setae and – unlike in females – *h3* setae are long needle-like and not serrated (Figure 7C).

Deutonymph.

The dorsal side (Figure 8). The body is oval with a small triangular vertex at the front (Figures 8A and 8B). The dorsal shield is big and highly sculptured. It is surrounded by the marginal shield, which has a sclerotized narrow band along the edges. The dorsal setae are long (38 – 43 µm) linear and serrated (Figure 8D).

The dorsal part is only partly sclerotized. The marginal shield (very narrow) and the dorsal shield are separated by soft pleura (Figure 8E).

The ventral side (Figures 9B-9D). The sternal shield is intensively sculptured. It has a shape of an elongated cup. The sculpture is made of oval caveoli of various diameters. There are five pairs of needle-like sternal setae and of similar length (32 – 39 µm). Cavities for legs are present, but they are not as arched, as in adults. The peritreme is relatively long, with a short, straight poststigmal sector (Figure 9A). The ventro-anal shield is big oval and has four pairs of long needle-like setae (48 – 51 µm) in a row, placed closely at the front edge, and there are also two pairs of setae in the middle part. The anus is small and round, with two pairs of needle-like setae. The structure of the anal region does not imply phoresy. All ventral shields of newly molted deutonymphs adhere closely to each other. When a mite grows, they begin to grow apart and the space between them is filled by soft pleura. At the last stage, the deutonymph grows to the size of an adult and develops into a male or female.

Protonymph.

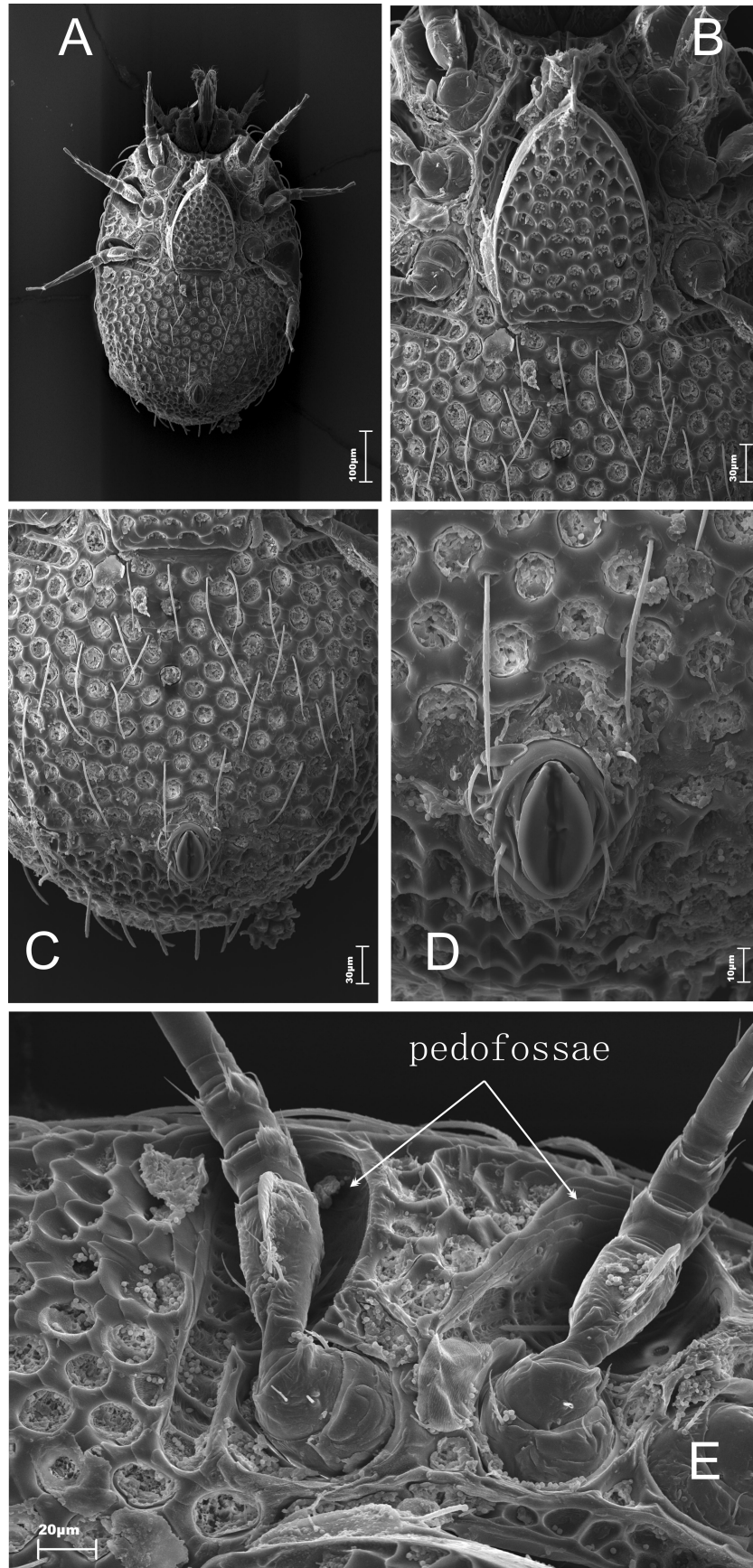


Figure 4 *Trematurella elegans* – Female, ventral side: A – General view; B – Intercoxal region; C – Opisthosoma; D – Anal region, E – Pedofossae III and IV.



Figure 5 *Trematurella elegans* – Female, hypostome: h1-h4 – Hypostomal setae, an arrow indicates a pair of setae on the trochanters of palps.

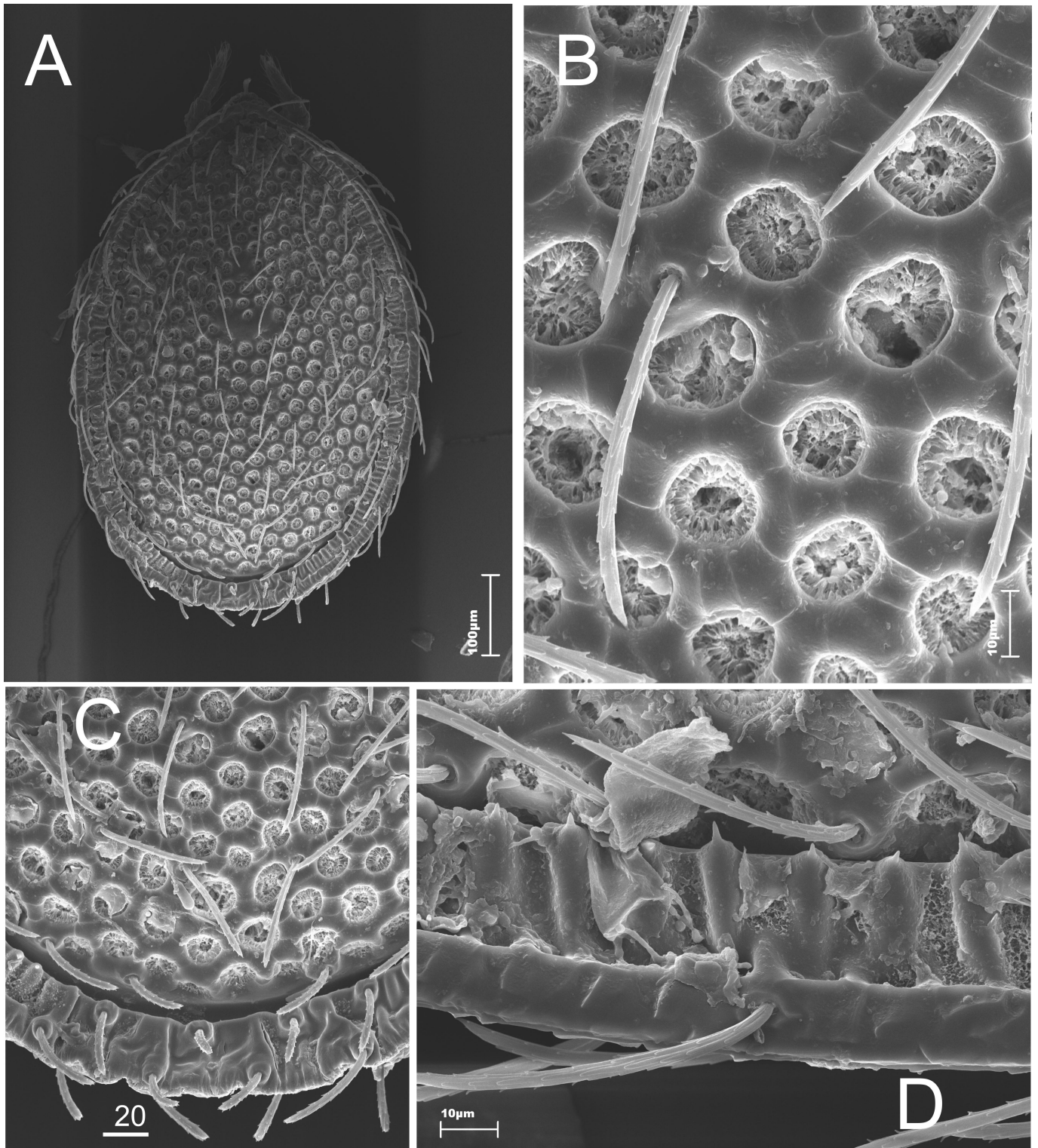


Figure 6 *Trematurella elegans* – Male, dorsal side: A – General view; B – Dorsal setae and sculpture of central part; C – Posterior part of idiosoma; D – Lateral part of idiosoma.

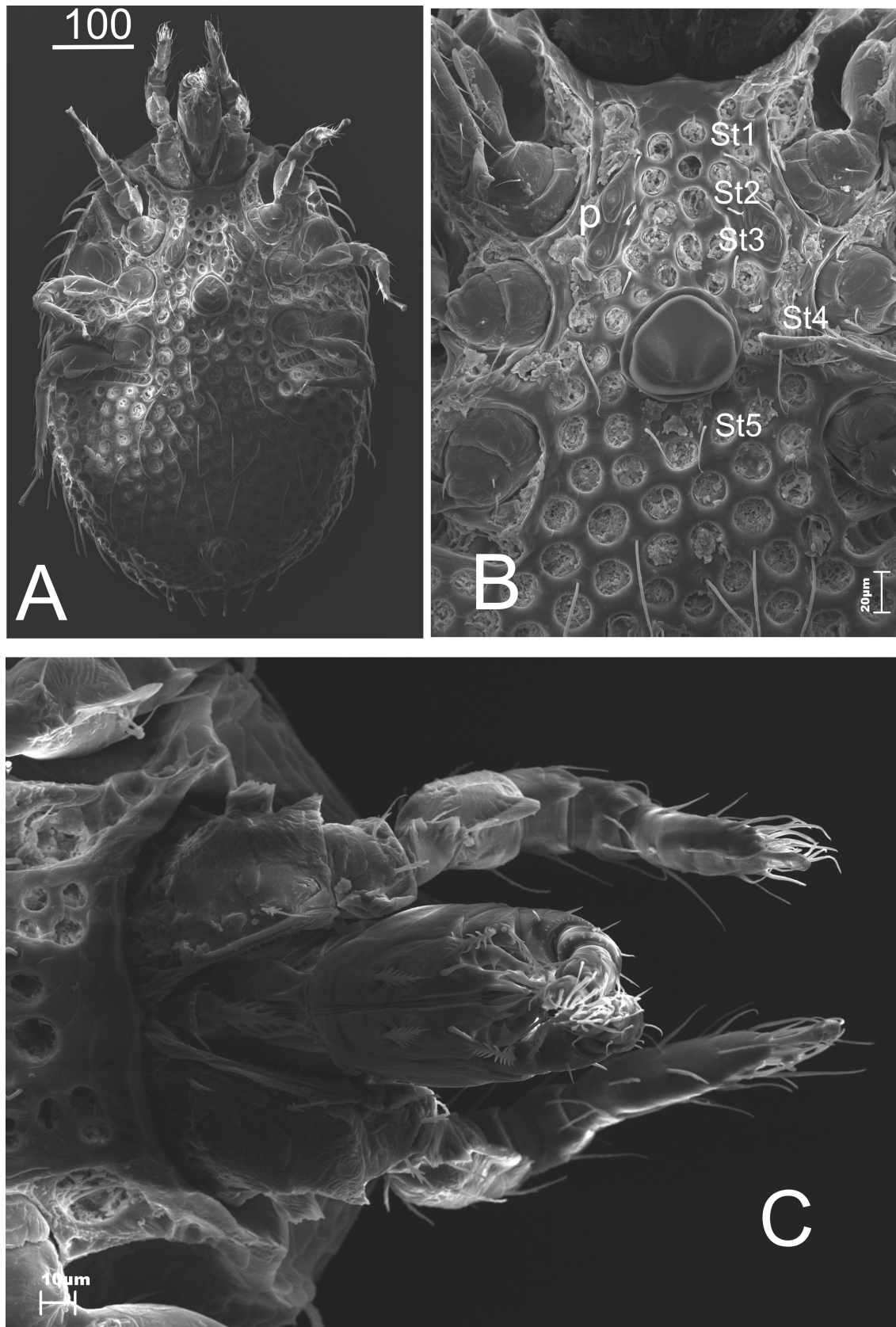


Figure 7 *Trematurella elegans* – Male, ventral side: A – General view; B – Intercoxal region, P – pores; C –Gnathosoma.

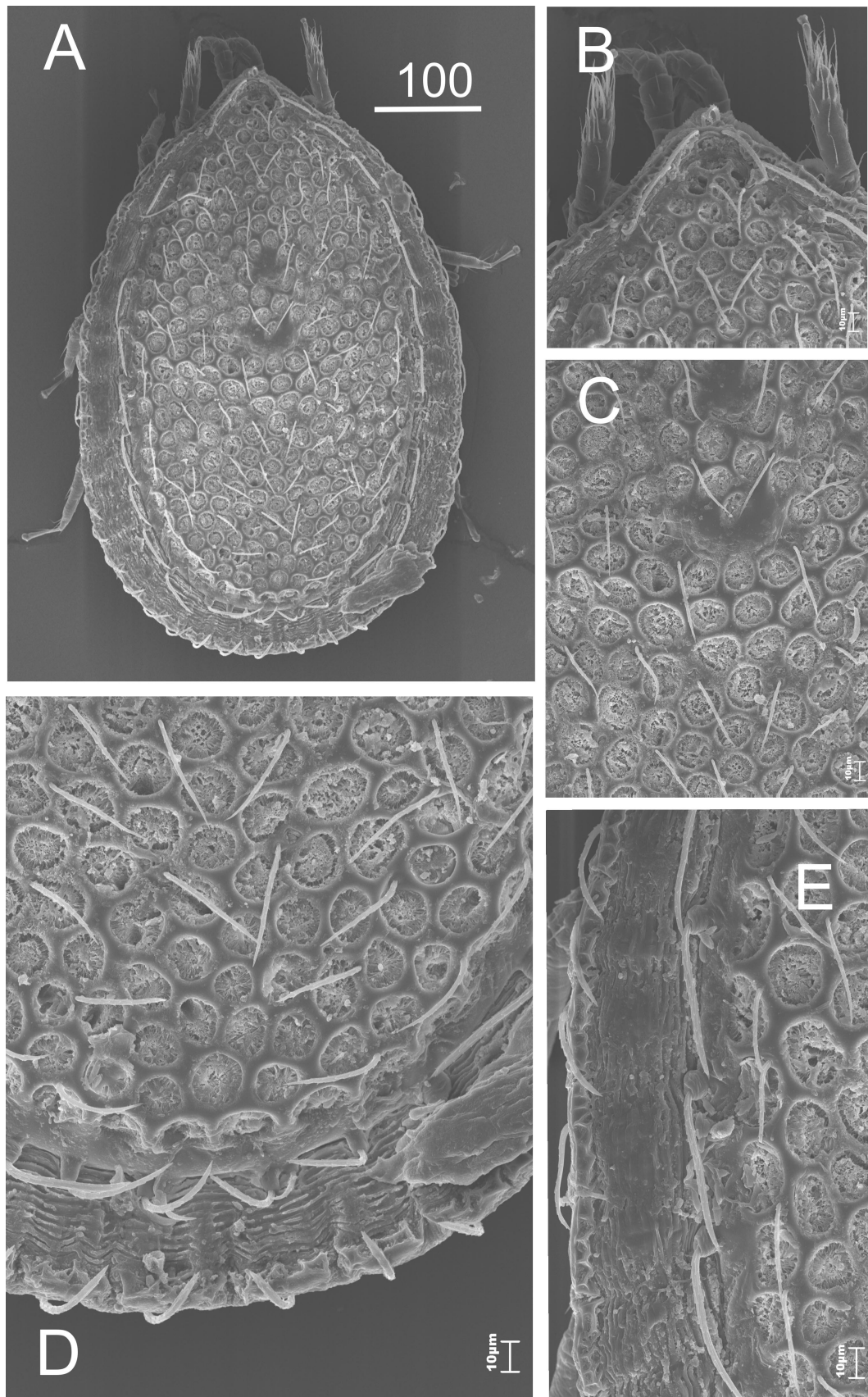


Figure 8 *Trematurrella elegans* – Deutonymph, dorsal side: A – General view; B – Anterior part of idiosoma; C – Central part of dorsal shield; D – Posterior part of idiosoma; E – Lateral part of idiosoma.

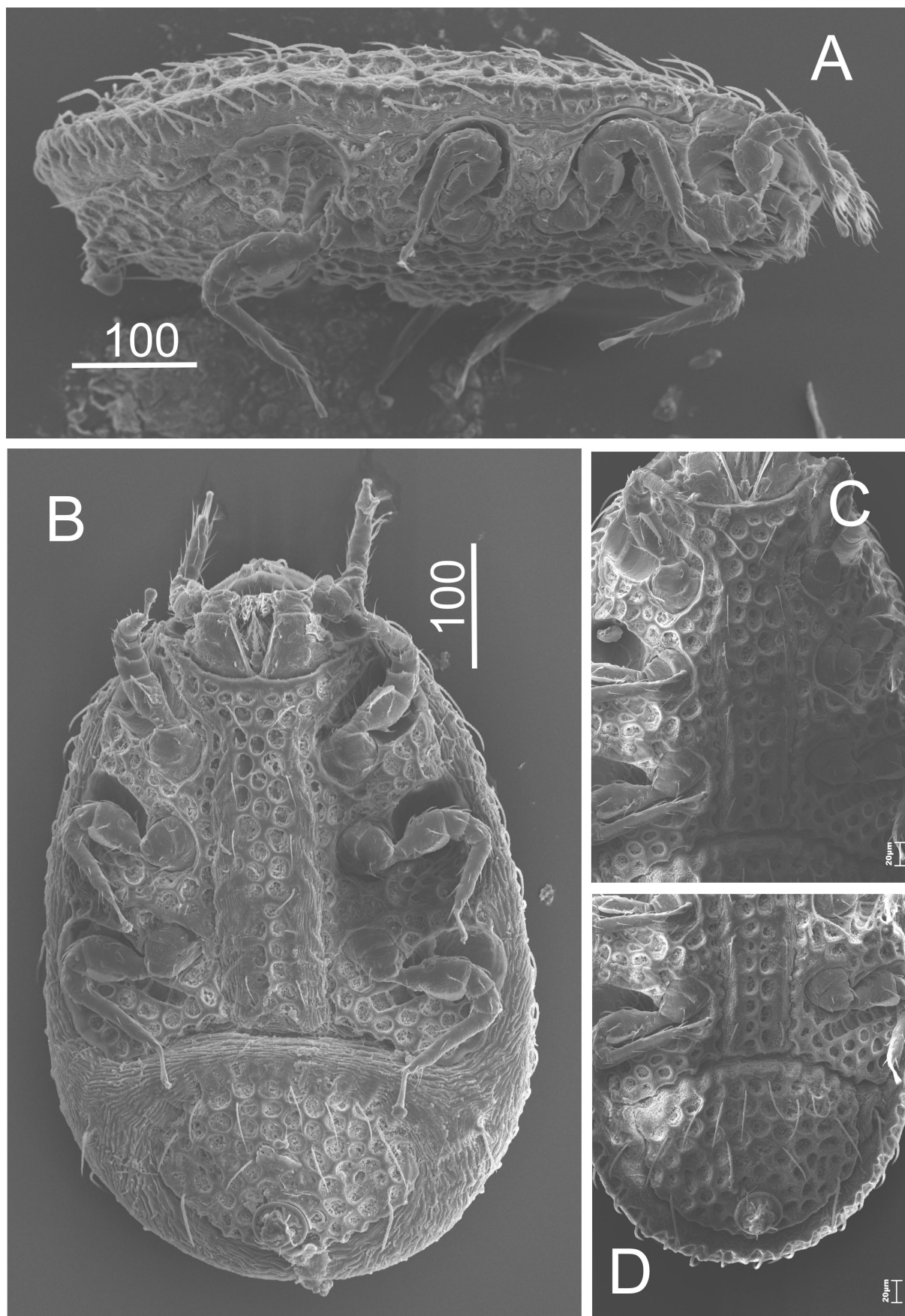


Figure 9 *Trematurella elegans* – Deutonymph: A – Lateral view; B – Dorsal side, General view; C – Sternal region; D – Opisthosoma.

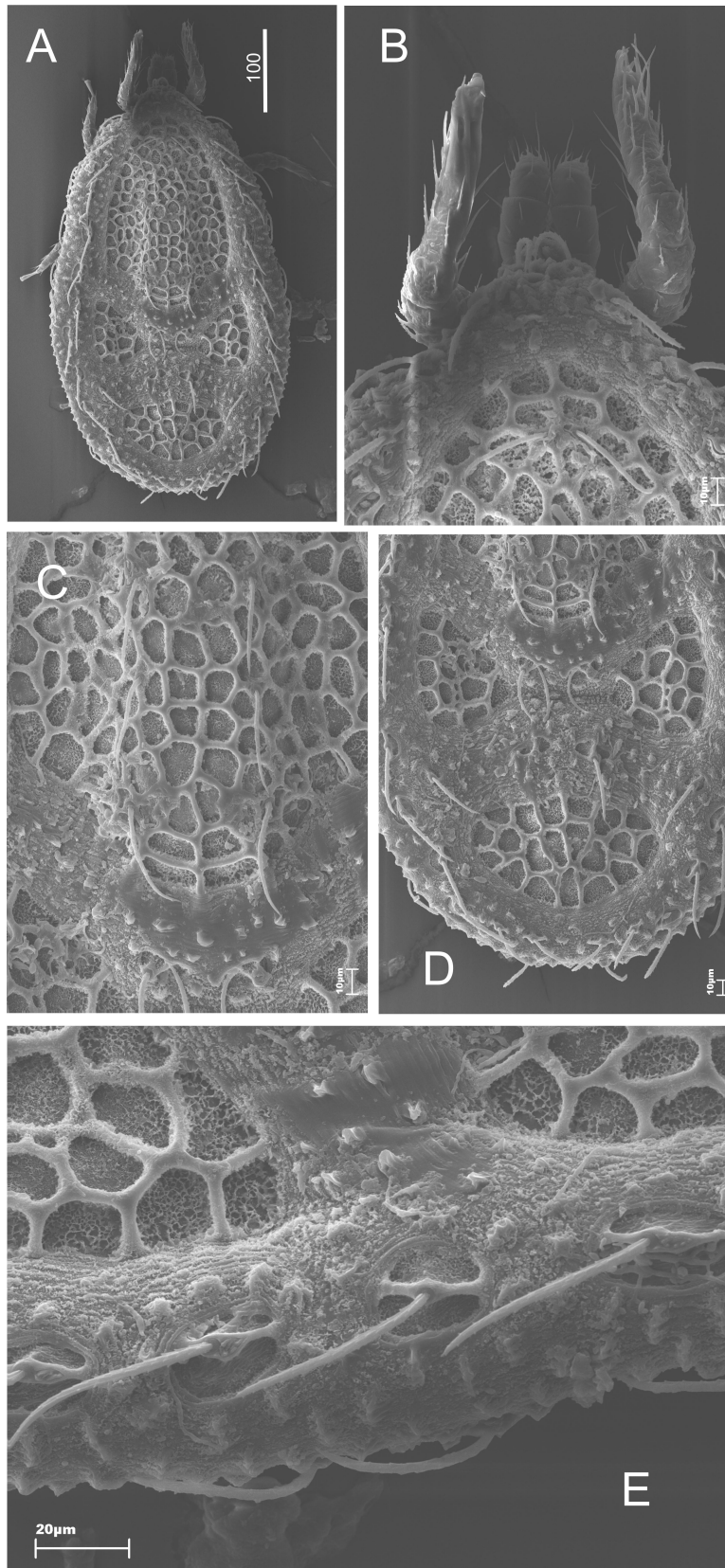


Figure 10 *Trematurella elegans* – Protonymph, dorsal side: A – General view; B – Vertex and anterior part of the idiosoma; C – Sculpture and setae in the midpart of shield; D – Posterior part of the idiosoma; E – Marginal setae.

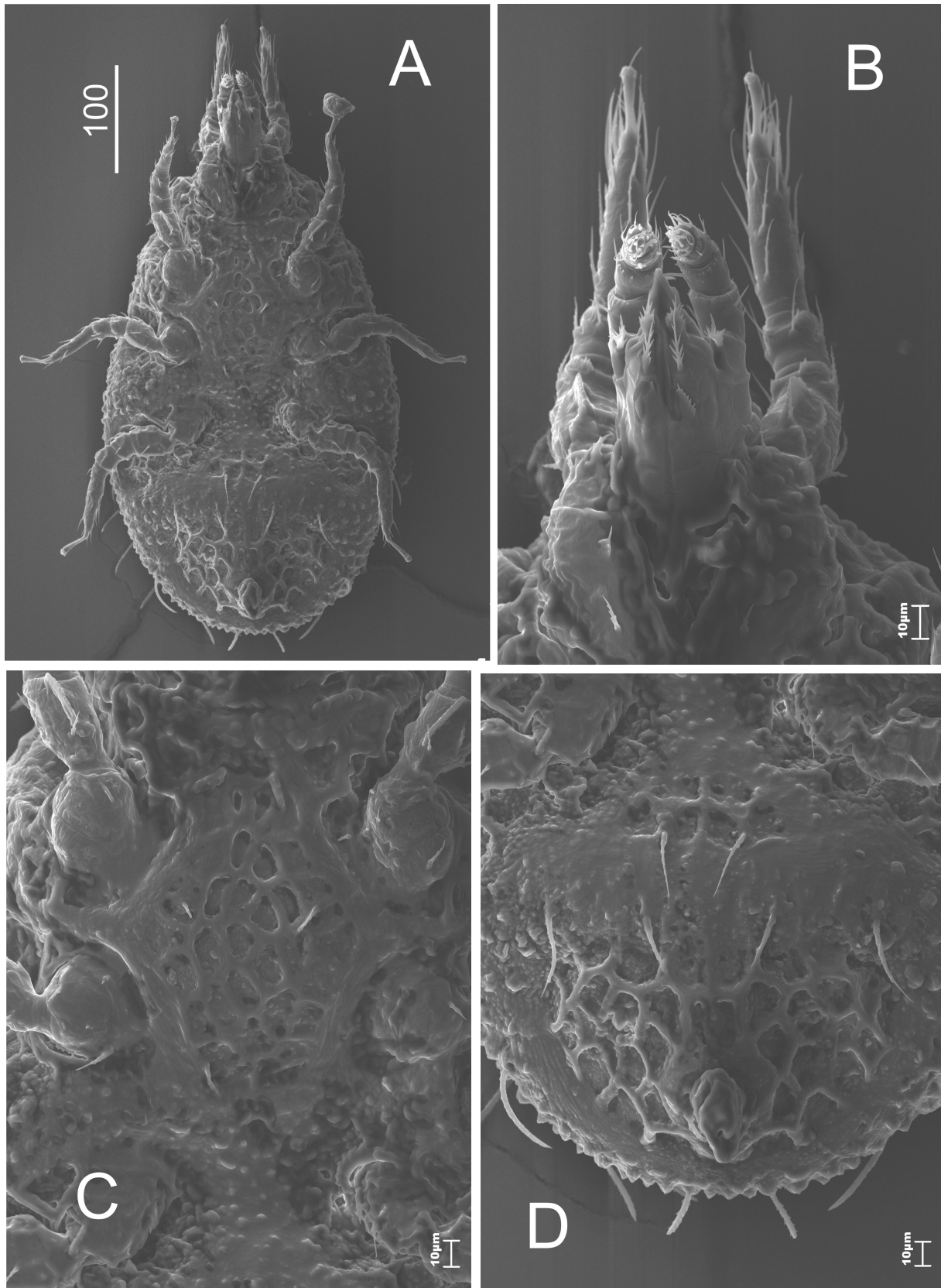


Figure 11 *Trematurella elegans* – Protonymph, ventral side: A – General view; B – Hypostome; C – intercoxal region; D – Opisthosoma.

The dorsal side (Figure 10). The idiosoma is oval with a small triangular vertex at the front. The highly sculptured dorsal shields are separated. The sculpture is made of polygons of various size. They are made of thickenings of chitin. There are large podonotal shields in the anterior part of the idiosoma. The five pairs of the dorsal setae are long. They are arranged in two longitudinal rows in the middle of the shield (Figures 10A and 10C). Below there are two triangular mezonotal shields, which are free from the setae. The large oval pygidial shield is not covered by the setae. The other dorsal setae are placed on the chitinous reinforcements at the base, at the soft pleura (Figure 10E). A row of 11 submarginal setae runs at the sides of the podonotal shield, mesonotal shields, and pygidial shield. Two pair of setae are placed over the front edge of the pygidial shield.

The ventral side (Figure 11). The trapezoid-like sculptured sternal shield reaches slightly beneath the coxa of the third pair of legs. There are three pairs of short needle-like setae. The ventro-anal shield has a polygonal sculpture with a large mesh. The other parts of the opisthosoma and the sides of the body, like in larvae, are covered by characteristic granulation. The ventral setae are long needle-like and slightly serrated (Figure 11D). The first pair of them is located at the border of the podosoma and opisthosoma, the two other pairs are located over the front edge of the ventro-anal shield. The anus is oval, slightly elongated, and located at the back area of the shield.

There are two pairs of hypostomal setae: the *h1-h3* is smooth, the *h4* is feathery. The two pairs of the serrated setae are located on the flattened coxae I, and the first pair of the setae is longer.

Larva.

The dorsal side (Figure 12). The tritosternum has a narrow base, covered by coxae of the first pair of legs, with notched front edge and feathery lacini, which becomes more and more narrow towards the top. There are two pairs of hypostomal setae. The *h1* is smooth, the *h4* is feathery. One can notice a pair of serrated setae on each of the flattened coxae of the first pair of legs; the first seta is two times longer than the second one.

The ventral side (Figure 13). The sternal shield is weakly sclerotized and smooth. It overlaps with the opisthosoma. There are three pairs (*st1-st3*) of needle-like sternal setae. The ventro-anal shield is oval with polygonal sculpture and big mesh. The rest of the opisthosoma and the sides of the body are covered with characteristic granulation. The four ventral setae are short and needle-like (Figure 13D). The oval anus is located at the posterior edge of the shield, without circumanal setae.

Notes — The number of sternal setae changes considerably during the ontogenesis period, depending on the developmental stage. Larvae and protonymphs have three pairs of the setae (*St1-St3*), though larvae the sternal shield is divided into two parts (one on the front part and two pairs on the back part). Deutonymphs have 5 pairs of sternal setae on the long sternal shield (*St1-St5*). This number is the same in adult males, whereas adult females have no *St5* setae.

A similar situation can be observed in the case of the hypostomal setae. Larvae have only two setae (*h1* and probably *h3*). Protonymphs have three pairs of setae on the hypostome (there are no characteristic smooth setae *h1*). Females have all pairs of the hypostomal setae (*h1-h4*), whereas in males the setae *h2* is reduced, and there are also changes in the shape of the setae *h3*.

Geographical distribution

Locus typicus: Thuringia (Thüringen), Germany.

Trematurella elegans was described by Kramer (1882) from Thuringia (central Germany). The species was found in many other countries, not only in Europe. At present, the species occurs in Germany, France, Great Britain, Sweden, Finland, Poland, Czech Republic, Slovakia,

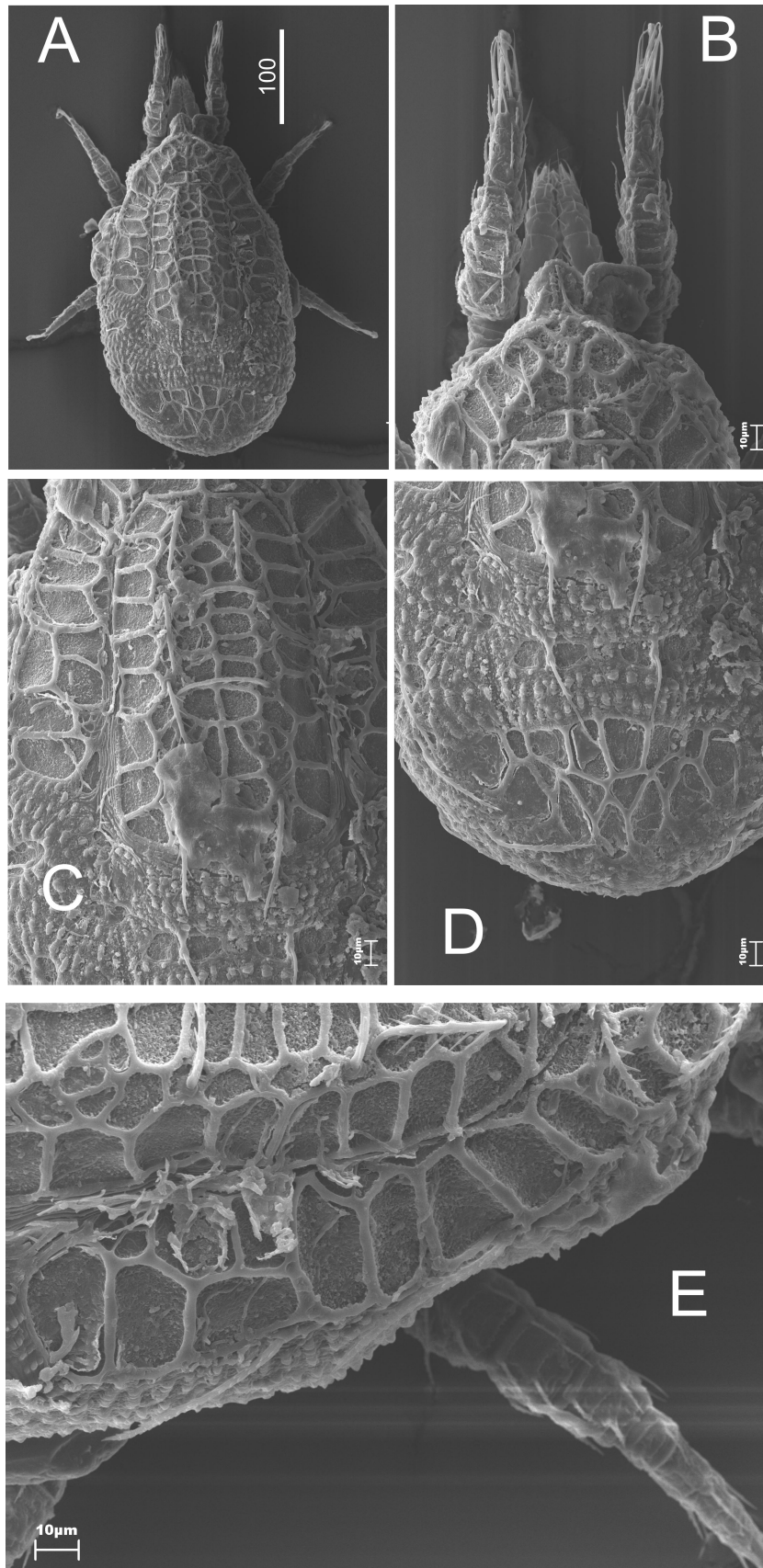


Figure 12 *Trematurella elegans* – Larva, dorsal side: A – General view; B – Anterior part of idiosoma; C – Central part of idiosoma; D – Posterior part of idiosoma; E – Marginal setae.

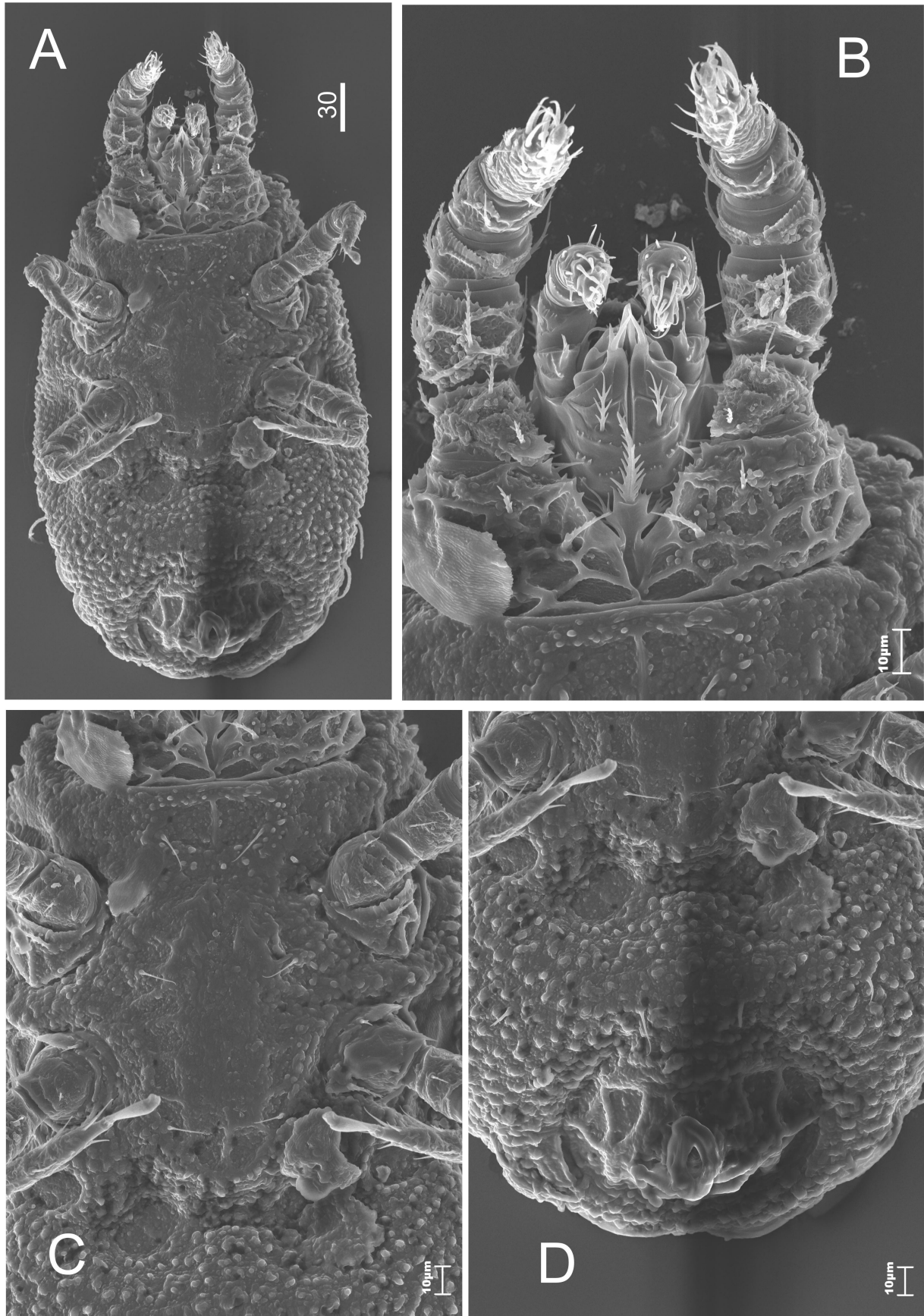


Figure 13 *Trematurella elegans* – Larva, ventral side: A – General view; B – Gnathosoma; C – Intercoxal region; D – Opisthosoma.

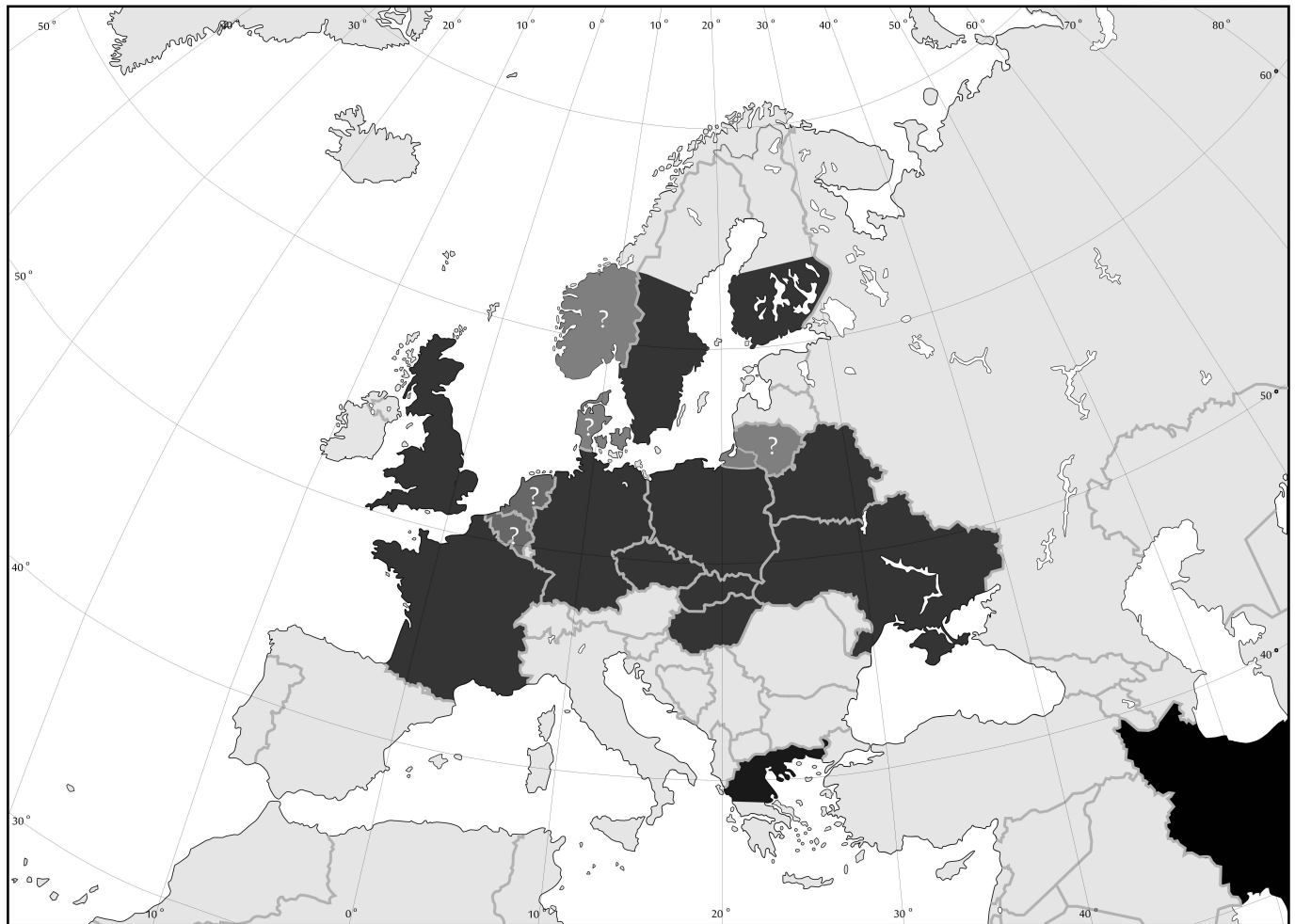


Figure 14 Distribution of *Trematurella elegans* in Europe; ? – Probable occurrence.

Ukraine, Hungary, Greece, Iran (see Taxonomy) (Figure 14). In the majority of these countries the species was found in a few locations. Mašan (2001) found this species mostly in rare locations, mainly in the western and south-western parts of Slovakia.

The authors of this study have tried to obtain all information about the distribution of this species from the available literature, though due to the fact that the species has been found so far in very few countries it is possible that *T. elegans* has much broader range of occurrence than that presented here. This may also stem from the fact that the species is rare and it occurs in low abundance. Thus, the presence of the species in those countries in which it has not been found yet cannot be excluded. This can also be said about the Balkans and the area of the Mediterranean. The presence of this species in Greece and Iran suggests much broader range of occurrence than that presented in the literature. For this reason the information about the distribution of *T. elegans* presented in this study should be considered as a summary of the accounts from the literature on the topic, and not as a new description of the current distribution of the species. The strong preference of the species for bark galleries habitats and occurrence in dead wood of different species of trees in different types of forests suggest that *T. elegans* may have come to the areas of central and northern Europe already in the Boreal or in a warmer Atlantic period from the area of the area of Mediterranean.

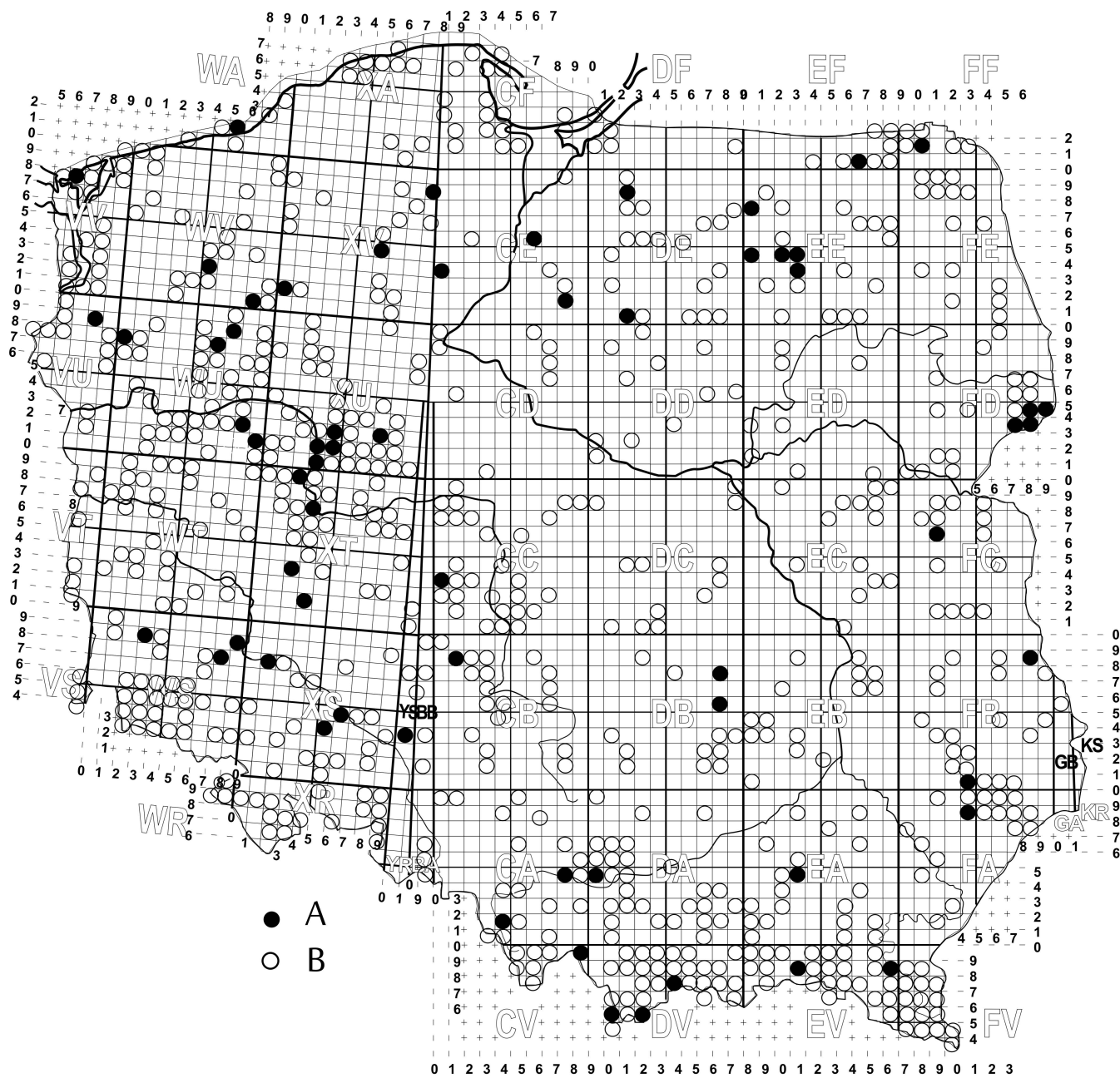


Figure 15 Distribution of *Trematurella elegans* in Poland: A – Localities where *Trematurella elegans* specimens were found; B – All examined localities.

Table 1 Habitat preferences of *T. elegans* in Poland: N – number of samples; F – frequency (%); Ns – number of specimens; X – mean of specimens/per positive sample, Nsp – number of specimens. * in case of woodlands a cumulative number of samples for merocenoses of the dead wood and forest litter and soil was shown.

Habitat	N	F	Ns	X	Nsp
Open habitat					
Xerophilous grasses	78	-	-	-	-
Sandhills	25	-	-	-	-
Rocks grasses (noncalcareous)	168	-	-	-	-
Rocks grasses on limestone	103	-	-	-	-
Meadows	578	-	-	-	-
Moorlands	17	-	-	-	-
Peat-bogs	82	-	-	-	-
Sedgeland	25	-	-	-	-
Agrocenoses	40	-	-	-	-
<i>Schoenoplectus</i> and reed beds	25	-	-	-	-
Forest and shrubs*					
Alder forest	206	1.46	3	1.7	5
Alder forest –soil and litter	142	2.11	3	1.7	5
Marshy forest	314	1.27	4	2.0	8
Marshy forest –soil and litter	213	1.41	3	2.0	6
Hornbeam forest	1,092	3.48	38	0.6	97
Hornbeam forest –soil and litter	497	4.02	20	2.5	56
Mixed deciduous forest	363	2.20	8	1.7	17
Mixed deciduous forest –soil and litter	265	1.89	5	1.6	11
Beech-wood on lowland	182	1.65	3	1.0	3
Beech-wood on lowland – soil and litter	95	2.11	2	1.0	2
Beech-wood in the mountain	598	0.50	3	2.7	8
Beech-wood in the mountain – soil and litter	499	0.40	2	3.0	6
Oak-wood	74	2.70	2	2.0	4
Oak-wood – only soil and litter	58	1.72	1	1.0	1
Pine forest	812	0.49	4	6.8	34
Pine forest – only soil and litter	585	0.51	3	11.0	33
Spruce forest in the mountain	383	-	-	-	-
Spruce forest on lowland	85	24.71	21	13.8	457
Spruce forest on lowland – soil and litter	49	2.04	1	1.8	7
Fir forest	144	0.69	1	2.0	2
Fir forest – soil and litter	126	0.79	1	2.0	2
Larch stand	44	6.82	3	11.3	34
Larch stand – soil and litter	30	14.0	2	6.7	28
Yew-tree stand	163	6.75	11	2.7	30
Yew-tree stand – soil and litter	90	5.56	5	2.2	11
Fir-beech forest	87	3.45	3	2.7	8
Fir-beech forest – soil and litter	66	3.03	2	3.5	7
Mixed forest (with pine)	549	0.55	3	54.0	162
Mixed forest (with pine) – soil and litter	232	1.29	3	54.0	162
Mixed forest (with spruce)	113	0.88	1	14.0	14
Mixed forest (with spruce) – soil and litter	90	1.11	1	14.0	14
Dwarf pine	55	-	-	-	-
Brushwood	120	-	-	-	-
Parks	459	3.49	16	12.3	196
Parks – soil and litter	171	5.85	10	18.0	180
Merocenoses					
Ant-hills	43	-	-	-	-
Nest of small mammals	220	0.45	1	1	1
Nest of birds	821	0.37	3	28.0	84
Rot trunks	1,224	2.45	30	0.5	64
Hollows in tree	173	2.89	5	1.3	13
Bark of tree	88	25.00	22	7.5	458
Total	7,476	2.47	185	9.2	1,699

Detailed analysis of distribution of *T. elegans* in Poland and its migration after the period of glaciations

The detailed analysis of distribution of *T. elegans* in Poland (Figure 15) showed that the species is uniformly distributed in the country, except West Pomerania (NW). The range of occurrence is situated on the meltwater channel of Noteć, which is a part of Eberswalde –Torun meltwater channel. Such a distribution suggests that this species did not manage to colonize the area covered by the last glaciation (Wechselian, syn=Würm), which took place in the area of Poland in Pleistocene and finished c.a. 12,000 years ago (Stankowski 1978; Kondracki 2011). After the Mindel (=Elsterian, 730 and 430 years ago) glaciation and the Saalian (=Riss), which took place between 300 and 170 thousands years ago (Stankowski 1978; Kondracki 2011), this species could disperse on the ice-free areas from two directions – from south-west (through the present Germany territory) and from south-east (through the present Slovakia and Ukraine territory). However, one cannot exclude that the species survived the glaciations in this part of Poland, which was not under the glacier (namely, southwards from the line of Cracow – Przemysł), and it started the expansion from there to the north.

Ecology

The research into habitat preferences of *T. elegans* conducted in Poland is based on 7,476 samples, from 35 types of habitats and microhabitats (Table 1), which show more precisely habitat preferences of this species.

The frequency of the species in the samples was low (2.47%). Therefore, the occurrence of the species can be regarded as accidental ($F < 5\%$). The percentage of *T. elegans* in the fauna of Uropodina of Poland is low (0.87%). Hence, the species is regarded as rare and not numerous.

Trematurella elegans can be classified as a typically forestal species. As it is shown in Table 1, it avoids open and non-woody habitats (Table 1). It has been found neither in the upper subalpine of spruce forests, mugo pines, or other scrubs, nor in anthills. The highest frequency has been recorded in natural and planted spruce forests of the Polish part of the North (Middle) European Plain. The species often inhabits larch stands and yew-tree stands. Furthermore, hornbeam forests, mixed deciduous forests, oak-woods and fir-beech forests can be regarded as favorable habitats. In these forests *T. elegans* can be found under the tree bark (frequency c.a. 25%), in litter, soil, dead wood, and in tree hollows. However, the frequency is many times lower in those habitats than in the most frequent ones. Interestingly, spruce-containing woods are inhabited with lower frequency than other coniferous woods (Table 1).

Phenology of *T. elegans*

The appearance of the life stages of *T. elegans* in various seasons was analyzed on the basis of 7,190 samples (Table 2). The peak of the abundance of *T. elegans* occurs in June (Figure 16).

Table 2 Phenology of appearance of the subsequent life stages of *T. elegans* in Poland: Ns – Number of total samples, Nsp – Number of positive samples (with *T. elegans*), N – Total number of specimens, F – Female, M – Male, D – Deutonymphs, P – Protonymphs, L – Larvae.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Ns	133	211	295	465	1104	1408	813	993	741	557	368	102
Nsp	0	0	0	3	24	54	9	13	16	6	0	1
N				7	146	734	32	139	75	50		1
F				3	64	137	13	28	35	11		
M				3	58	180	10	32	38	11		1
D				1	22	248	7	77	1	11		
P					2	144	2	2		12		
L						25			1	5		

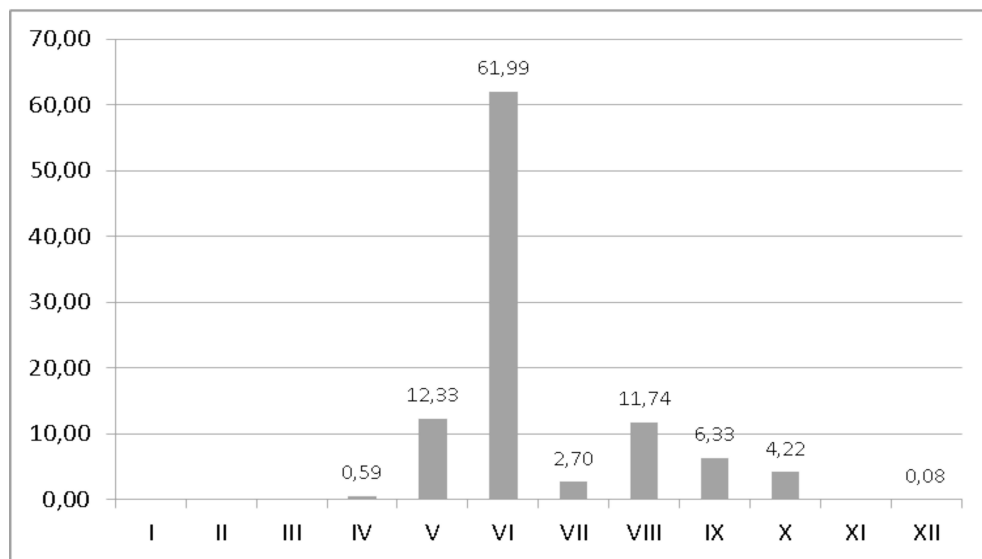


Figure 16 The proportional distribution of individuals of *Trematurella elegans* in collected samples throughout the year.

The number is also high in samples collected in May and August. However, it was very low at the beginning of the phenological season in April and the end of it (December).

The constant presence of adults and deutonymphs in the collected samples was recorded between April and October (Table 2). Single male specimens were found in December, which suggests that these mites overwinter as adults and deutonymphs hidden under bark of trees. Unfortunately, we do not have enough samples collected in winter to support this hypothesis. The diagram shows (Figure 16) that the presence of larvae and protonymphs is limited in time and has two peaks of abundance, i.e. the first in June and the second in October. The larvae were found in May, September, and October, whereas the protonymphs occurred between May and August, and in October.

Vertical distribution of *T. elegans* in Poland

The analysis of ventrical distribution of *T. elegans* is based on 7,506 samples collected at various altitudes in Poland (Table 3). The analysis shows that *T. elegans* is a typical lowland species, which does not inhabit altitudes over 550 m above sea level. The most optimal altitude for the species ranges between 100 and 450 m a.s.l. (Table 3).

Table 3 Vertical distribution of *Trematurella elegans* in Poland. Alt. – Altitudes in m a.s.l, Ns – Number of total samples, Nsp – Number of positive samples (with *T. elegans*), F% – Frequency.

Alt.	0-5	6-50	51-100	101-150	151-200	201-250	251-300	301-350	351-400	401-450	451-500	501-550	551-600
Ns	338	370	2333	1594	472	312	280	130	125	77	163	51	99
N	70	4	90	786	54	15	124	5	17	23	1	1	0
Nsp	1	3	25	67	15	3	8	2	3	1	1	1	0
F%	0,3	0,81	1,07	4,2	3,18	0,96	2,86	1,54	2,4	1,3	0,61	1,96	0
Alt.	601-650	651-700	701-800	801-900	901-1000	1001-1100	1101-1200	1201-1300	1301-1400	1401-1500	1501-1600	1601-1700	>1700
Ns	59	110	134	185	194	155	130	62	34	28	30	22	19
N	0	0	0	0	0	0	0	0	0	0	0	0	0
Nsp	0	0	0	0	0	0	0	0	0	0	0	0	0
F%	0	0	0	0	0	0	0	0	0	0	0	0	0

Discussion

The results shown in this article support the earlier observations of other authors who discuss the distribution and ecology of *T. elegans*. Karg (1989) described *T. elegans* as a European species, associated with litter and soils of leafy forests, bark of trees, and with anthills. In the catalogue by Wiśniewski and Hirschmann (1993) *T. elegans* is described as a species occurring in various environments like mosses, holes in trees, dead wood, forest bed, and anthills of Formicidae (Hymenoptera). However, since the observations mentioned above were rather superficial, it was difficult to establish the preferred habitats of the species on the basis of those studies. These authors described the distribution of the species as northern- and central-European (Wiśniewski and Hirschmann 1993). Mašan (2001) describes the geographical distribution of *T. elegans* in a similar way. He regards this species as a detriticol, which is associated with various types of substrates, such as soil, litter, decaying plants, tree bark, and dead wood. Moreover, he found the species in nests of *Turdus philomelos* C. L. Brehm, and *Clethrionomys glareolus* (Schreber), and in anthills. The last habitat mentioned above was also mentioned by Karg (1989). The studies published by Mašan (2001) also show that the distribution of the species in Slovakia is not regular, in the whole area of the country, similarly like in Poland (Błoszyk 1999). Furthermore, the vertical distribution and preferred altitudes are similar in both countries. Mašan did not find *T. elegans* over 600 meters a.s.l. and he claims that the optimal altitude is lower than 400 meters a.s.l. Fenda and Ciceková (2009) found this species in the south-western Slovakian oak-hornbeam forest in the Little Carpathian Mountains. Kontschán (2008) found *T. elegans* in Hungary, but he did not include any information about the habitat preferences. The species was also described in a similar way by Kontschán (2013). The authors believe that the species *Trichouropoda graeca* Kontschán, 2003, which he found in Greece, should be considered as a synonym of *T. elegans* due to the imprecise description and very schematic drawing, which does not show any significant differences between the two species. The differences probably stem from the geographical variation of *T. elegans*. Also Kaczmarek *et al.* (2011) points out that *T. elegans* is a dominant species in tree hollows in *Tilia cordata*. Lehtinen (1987), followed by Huhta (2016), found this species in dead wood and anthills in Finland. This species had been also found in anthills by Wiśniewski and Hirschmann (1991), but their findings do not conform to the results presented above (Table 1).

The results of the research presented here confirm that *T. elegans* is a European species, which inhabits mainly old forests. This probably stems from the type of the tree stands in which the species occurred most frequently (Table 1). This can be also observed in the case of the Białowieża Forest (NE Poland) – the largest remaining parts of the primeval forest in Europe, where the high frequency and abundance of *T. elegans* was recorded (Błoszyk – unpublished data). One of the most important findings concerning the ecology of the species is the high frequency of *T. elegans* in samples collected under tree bark (25%). This in turn suggests that *T. elegans* is a typically sub-bark species. It seems that this species can be found more often under bark than in litter, soil or dead wood, where it has been usually found so far (Lehtinen 1987; Karg 1989; Wiśniewski and Hirschmann 1993; Kaczmarek *et al.* 2011; Huhta 2016). The results of the analysis of phenology of *T. elegans* indicate that the species probably winters under tree bark as deutonymphs and adults. However, this hypothesis requires further research.

A compilation of both the data from the existing literature concerning biology, ecology, and distribution of *T. elegans* and the new more detailed data presented here is not only a succinct summary of the information about this species, but it also allows to analyze the history of dispersion of the species in Europe, especially in Poland, after the glaciations. The glaciations affected the range of many species of soil fauna, including mites. However, most of the studies focus on insects (e.g. Lunt *et al.* 1998; Fattorini and Ulrich 2012) and springtails (e.g. Werner and Fiera 2009). Little is known about the influence of the glaciation on distribution and range of occurrence of soil mites, though some attempts to solve this problem have been already made (Błoszyk *et al.* 2017). This of course stems from the lack of fossils. Thus, the reconstruction of the migration routes of mites after the glaciation can be possible only on the basis of the

knowledge about the development of the environment that is inhabited by particular species, and on the basis of the knowledge of ecological needs of the species. Among Uropodina there are many species which have their northern range of occurrence in Poland (Błoszyk 1999), and *T. elegans* is also among them. The analysis of the habitat preferences of the species suggests that it reached the northern Europe relatively recently, about few thousand years ago. It probably happened in the boreal interval (c.a. eight thousand years B.P.) because at that time forests were formed in this area, which could provide environmental conditions favorable for *T. elegans*. The presence of the species in southern Europe (Greece) and in Iran is hard to explain. Perhaps these two countries are old relic areas. There is no doubt that this species is not typical for the Mediterranean. It is possible that like in the case of *Trachytes aegrota* (C.L. Koch, 1841), *T. elegans* has its center of occurrence in central Europe, and it migrated from this region to the North and South (Błoszyk 1999; Athias-Binche 1981a,b; 1982a,b).

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