

Parthenogenesis as a life strategy among mites of the suborder Uropodina (Acari: Mesostigmata)

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Abstract: This paper presents the results of observations concerning the phenomenon of parthenogenesis among European mites of the suborder Uropodina. An analysis of the sex ratios of 66 Polish species revealed that 18 of them (more than one fourth of the examined species) consisted only of females. The authors observed no significant relationship between geographical distribution and the lack of males in the population. Populations consisting entirely of females were observed among widely distributed species as well as among species characterized by narrow geographical ranges. Nonetheless, an increase in the number of parthenogenetic species, especially as a percentage of Middle European and Scandinavian fauna, was also discernible. Species that reproduced without males were associated with forest litter and soil, whereas bisexual species “eagerly” inhabited various relatively unstable and temporary microenvironments (for instance, dead wood, birds’ or small mammals’ nests). The authors aim to define the biological role of occasionally appearing males for the species consisting almost entirely of females and discuss ecological and evolutionary aspects of parthenogenesis in mites of the suborder Uropodina.

Résumé : Nous présentons nos observations sur la parthénogénèse chez les acariens européens du sous-ordre Uropodina. Une analyse des rapports mâles:femelles de 66 espèces polonaises indique que 18 d’entre elles (plus d’un quart des espèces examinées) ne contiennent que des femelles. Nous n’observons aucune relation significative entre la répartition géographique et l’absence de mâles dans les populations. Les populations constituées uniquement de femelles s’observent chez des espèces à large répartition géographique aussi bien que chez des espèces caractérisées par des répartitions restreintes. Il y a néanmoins une augmentation du nombre d’espèces parthénogénétiques, particulièrement du pourcentage d’espèces parthénogénétiques, dans les faunes d’Europe centrale et de Scandinavie. Les espèces qui se reproduisent en l’absence de mâles sont associées à la litière et au sol des forêts, alors que les espèces bisexuelles recherchent activement divers microhabitats relativement instables et éphémères, par exemple, le bois mort, les nids d’oiseaux et les tanières de petits mammifères. Nous cherchons à définir le rôle biologique des mâles qui apparaissent occasionnellement dans les populations constituées à peu près exclusivement de femelles et nous discutons des aspects écologiques et évolutifs de la parthénogénèse chez les acariens du sous-ordre Uropodina.

[Traduit par la Rédaction]

Introduction

Parthenogenesis is observed in various groups of invertebrates. This phenomenon consists of the development of an organism from an unfertilized egg. There are two major kinds of parthenogenetic reproduction: (1) thelytoky, in which only diploid female progenies are produced, and (2) arrhenotoky, in which progenies are produced by mated or unmated females; fertilized eggs yield diploid female offspring, whereas unfertilized eggs yield haploid males. Parthenogenesis can be a regular (e.g., stick insects), cyclical (a number of parthenogenetic generations precede a bisexual generation; e.g., aphids), or occasional phenomenon (e.g., non-parthenogenetic species such as butterflies of the family Sphingidae) (Razowski 1987).

In comparison with asexual reproduction, sexual repro-

duction offers many advantages. Firstly, it greatly and easily enhances genetic variation within the population. Secondly, sexual reproduction requires as few as two cells to form a zygote. This also saves energy that would otherwise be spent, for example, on the division of a parental organism into offspring. Finally, this phenomenon enables the production of a great number of offspring from the parental generation. On the other hand, parthenogenesis is more efficient than bisexual reproduction because it enables virtually geometric population growth. New individuals are produced by a single organism. Therefore, parthenogenetic reproduction is particularly useful in areas where bisexual reproduction may be hindered by environmental conditions.

Parthenogenesis is quite common among mites (Acari), especially among the oribatid mites. Many works have been devoted to parthenogenesis within the Oribatida (Norton and

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Palmer 1991; Palmer and Norton 1991, 1992; Norton et al. 1993; Norton 1994; Olszanowski and Lembicz 1999), and Budzyńska (1998) reviewed certain hypotheses connected with parthenogenesis.

Our preliminary observations suggested that the phenomenon of parthenogenesis is more frequent among soil mites of the suborder Uropodina than among moss mites (Oribatida) (Olszanowski and Lembicz 1999). Herein, we present data concerning the geographical distribution, habitat preferences, and systematic status of parthenogenetic and bisexual uropodid mites in Europe. We also present and discuss the possible relationship between geographical distribution and parthenogenesis, the implications of parthenogenesis, and the role of males in populations that consist almost entirely of females. The results are based upon many years of observations of the suborder Uropodina (Acari: Mesostigmata).

Materials and methods

The results presented are based upon material collected by J. Błoszyk since 1974. This material consists of more than 11 000 soil samples collected from 33 habitat types (open habitat, 10 types; forests and shrubs, 12 types; and mero-cenoses, 11 types). The samples, for the most part, consisted of sifted litter and soil. More rarely, they consisted of unsifted material (soil, litter from various swards, and wood dust from tree trunks) as well as material from bird, mammal, or ant nests collected from all parts of Poland. Sixty-six species of Uropodina were found, comprising 96 503 individuals.

The original maps of the distributions of species in Europe are based on the authors' own research as well as the literature (Karg 1989; Wiśniewski and Hirschmann 1993; Mašan 2001).

So far the data concerning parthenogenesis in the suborder Uropodina come from field studies exclusively. No laboratory research or culture observations were conducted because of the difficulties inherent in keeping cultures for a long period of time. Estimates of parthenogenetic and bisexual reproduction are based on analysis of sex ratios in the investigated populations. We assumed that species are characterized by sporadic males if the percentage of males in the population was lower than 15% and the majority of tested local populations consisted only of females.

Some individuals, chosen at random from the collected species, were examined with a scanning electron microscope. Specimens were mounted on stubs with double-sided sticky tabs, coated with gold in a Balzers SPC 050 ion coater, and observed in a Philips 515 scanning electron microscope.

Results and discussion

Parthenogenesis among Uropodina

Mites of the suborder Uropodina are widely distributed and occupy various habitats. Many species often inhabit unstable habitats such as holes in tree trunks, rotting trees, ant nests, and nests of birds and small mammals (Błoszyk 1999; Mašan 2001). Within this group of mites, sexual dimorphism is well marked: the structure of the intercoxal region of males and females is different (Figs. 1–4). The male delivers the spermatophore to the female during the sexual act. This

phenomenon was observed and described by Compton and Krantz (1978) and Athias-Binche (1981). Though the majority of species in this group are bisexual, some of the species reproduce without males. The occasional appearance of males in populations of several species has also been observed (Błoszyk and Olszanowski 1985a; Błoszyk and Haliday 2000).

More than 120 species of Uropodina are recorded in Poland, representing ca. 38% of the European fauna and approximately 6% of the worldwide fauna (Błoszyk 1999). The total number of parthenogenetic species is unknown because of insufficient study of the Uropodina. However, the number seems to be high: in Central Europe, for instance, approximately 14% of all species reproduce parthenogenetically (Błoszyk et al. 2003). In comparison, about 10% of all oribatid mites reproduce without males; among insects, less than 1% of species are parthenogenetic, and among all animals the proportion of such species is even lower: 0.1% (Norton and Palmer 1991; Olszanowski and Lembicz 1999).

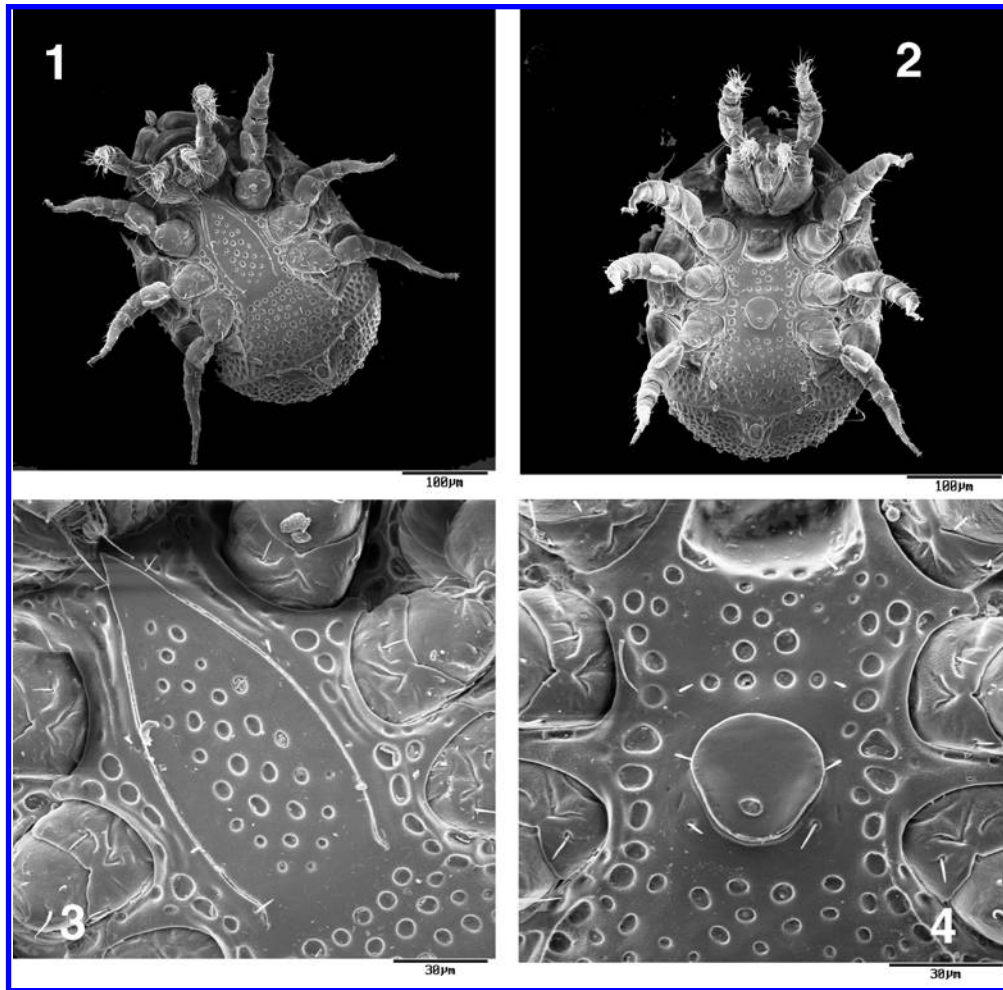
Of 120 species of the suborder Uropodina recorded in Poland (Wiśniewski 1997; Błoszyk 1999), we analysed 66. Among them, 18 species were recognised as reproducing only (or almost exclusively) in a parthenogenetic way: *Trachytes aegrotata*, *Trachytes pauperior*, *Trachytes lamda*, *Trachytes montana*, *Polyaspinus cylindricus*, *Iphidinychus geieri*, *Discourella modesta*, *Olodiscus minima*, *Olodiscus misella*, *Urodiaspis tecta*, *Urodiaspis pannonica*, *Janetiella pulchella*, *Cilliba erlangensis*, *Cilliba* sp. 2, *Uroplitella conspiciua*, *Uropoda italica*, *Uropoda orbicularis*, and *Nenteria stylifera*. Although these species make up only 27% of the examined species, their populations are more numerous (59% of specimens) than those of the other, bisexual species (Table 1). For several species recognised as parthenogenetic, the sporadic appearance of males was also observed (Błoszyk and Olszanowski 1985b; Błoszyk 1999; Błoszyk and Haliday 2000).

In Poland nearly half of the species of the superfamily Polyaspidioidea are parthenogenetic (46.7%). In the superfamily Uropodoidea only 19.6% of all species reproduce this way. Parthenogenesis is particularly common in the genera *Trachytes* and *Olodiscus*. There are no records of parthenogenesis in the genera *Oodinychus*, *Trachyuro-poda*, and *Dinychus*.

Factors that attend parthenogenesis

The observations of European fauna show that parthenogenetic species constitute various percentages of the Uropodina communities in particular countries. The biggest numbers of such species have been recorded in Norway, Ireland, Lithuania, and Ukraine (Błoszyk et al. 2003). Consequently, the hypothesis of Ghiselin (1974) is partly confirmed. He postulated that organisms reproducing parthenogenetically are dominant in communities in the far north and south. Observations made by other authors have proved that in the northern hemisphere (within a given group), the number of parthenogenetic species increases with increasing latitude (a similar increase in the number of asexual species with increasing altitude is discernible). This phenomenon (with reference to numerous animals and plants) has been described by Vandel (1928), Suomalainen (1950), Glesener and Tilman (1978), Bell (1982), Lynch (1984), Bierzy-

Figs. 1–4. Scanning electron micrograph showing sexual dimorphism of Uropodina species. Ventral side of *Janetiella pulchella*: 1, female; 2, male; 3, genital area of a female; 4, genital area of a male.



chudek (1985), and Hughes (1990), among others. Peck et al. (1998) created a model of the competition between species reproducing sexually and asexually at various latitudes. In 96% of cases, their simulation models generated results in accordance with the aforementioned tendency observable in nature. Of crucial importance in this model was the varied pace of migration, which increased with increasing latitude. Consequently, in the north, species reproducing asexually started to outnumber their rivals as the best-adapted individuals gave rise to optimally adapted clones. In the case of individuals reproducing sexually, there exists a considerable possibility of their coming across “immigrant partners” unaccustomed to the local conditions. The survival chances of such couples’ offspring would be reduced. Therefore, parthenogenesis may be particularly useful in more demanding environmental conditions as well as in places with significant climate changes (for instance, in areas with very hot and exceptionally cold seasons.)

Similar suggestions were put forth by Bell (1982, 1988), who regarded the parthenogenetic species living in drastically altered and unstable environments as better colonizers. An example taken from our material is the uropodid mite community in Norway, where the population of a parthenogenetic species (*T. aegrota*) constitutes more than 40% of the

total uropodid population. A relatively low number of parthenogenetic species has been observed in Central Europe (Wiśniewski 1993; Błoszyk 1999; Mašan 2001). Germany, Poland, and Slovakia are the best-studied countries in terms of the presence of mites in Europe. These countries are further south than Norway, Ireland, and Lithuania and are characterized by a moderate climate. In these countries, *T. aegrota* constitutes less than 30% of the total uropodid population. In the Mediterranean region, this species constitutes less than 3% of the total uropodid population (Błoszyk et al. 2003). The presence of many parthenogenetic species in Ukraine is probably the result of a scantily studied mite fauna in that country. In Poland and Europe, the species recognized as parthenogenetic include the most common and widely distributed species (Figs. 5–8) as well as rare species characterized by limited distributions (Figs. 9–13).

Parthenogenetic uropodid species apparently prefer soil and avoid unstable microenvironments (Błoszyk 1985, 1990, 1992; Błoszyk and Olszanowski 1985*b*, 1986*a*, 1986*b*).

Fujikawa (1987) described the phenomenon of increasing participation of males in a population of the oribatid mite species *Oribatula sakamori* Aoki, 1970 on a cultivated field along with habitat changes. Since uropodid mites inhabit upper soils only (sublevels A_0L and A_1), the abovementioned

Table 1. Sex structure in populations of particular species of Uropodina in Poland.

Species	Superfamily	Fertility strategy*	No. of specimens	Sex ratio (male:female) [†]	Phoresy	Ecoelement [‡]
<i>Apionoseius infirmus</i> (Berlese, 1887)	Polyaspidioidea	B	137	1:1,4	+	O
<i>Cilliba cassidea</i> (Hermann, 1804)	Uropodoidea	B	192	1:1	–	O
<i>Cilliba erlangensis</i> (Hirschmann and Zirngiebl-Nicol, 1969)	Uropodoidea	P	84	F	–	O
<i>Cilliba sopronensis</i> Wiśniewski and Hirschmann, 1990	Uropodoidea	B	323	1:0.7	–	S
<i>Cilliba</i> sp. 1	Uropodoidea	B	1 066	1:1	–	P
<i>Cilliba</i> sp. 2	Uropodoidea	P	250	F	–	S
<i>Dinychura cordieri</i> (Berlese, 1916)	Uropodoidea	B	260	1:1	–	O
<i>Dinychus arcuatus</i> (Trägårdh, 1943)	Uropodoidea	B	323	1:1	–	P
<i>Dinychus carinatus</i> Berlese, 1903	Uropodoidea	B	643	1:1	–	M
<i>Dinychus inermis</i> (C.L. Koch, 1841)	Uropodoidea	B	244	1:1	–	O
<i>Dinychus perforatus</i> Kramer, 1882	Uropodoidea	B	1 851	1:1	–	P
<i>Dinychus woelkei</i> Hirschmann and Zirngiebl-Nicol, 1969	Uropodoidea	B	102	1:0.7	–	S
<i>Discourella baloghi</i> Hirschmann and Zirngiebl-Nicol, 1969	Uropodoidea	B	403	1:1	–	O
<i>Discourella modesta</i> (Leonardi, 1889)	Polyaspidioidea	P	284	1:300	–	M
<i>Fuscouropoda appendiculata</i> (Berlese, 1910)	Uropodoidea	B	1	?	–	S
<i>Iphidinychus geieri</i> (Schweizer, 1961)	Polyaspidioidea	P	8	F?	–	S
<i>Iphiduropoda penicillata</i> (Greim, 1952)	Uropodoidea	B	31	1:2	–	S
<i>Janetiella pulchella</i> (Berlese, 1904)	Uropodoidea	P	2 143	1:15	–	M
<i>Janetiella pyriformis</i> (Berlese, 1920)	Uropodoidea	B	964	1:1,3	+	O
<i>Leiodinychus orbicularis</i> (C.L. Koch, 1839)	Uropodoidea	B	1 011	1:1	–	O
<i>Nenteria breviunguiculata</i> (Willmann, 1949)	Uropodoidea	B	241	1:1,4	+	M
<i>Nenteria stylifera</i> (Berlese, 1904)	Uropodoidea	P	15	1:7	–	S
<i>Neodiscopoma splendida</i> (Kramer, 1882)	Uropodoidea	B	2 182	1:0.8	–	P
<i>Neodiscopoma pulcherrima</i> (Berlese, 1903)	Uropodoidea	B	1	?	–	S
<i>Olodiscus kargi</i> (Hirschmann and Zirngiebl-Nicol, 1969)	Uropodoidea	B	224	1:1,7	–	M
<i>Olodiscus minima</i> (Kramer, 1882)	Uropodoidea	P	9 827	1:300	–	E
<i>Olodiscus misella</i> (Berlese, 1916)	Uropodoidea	P	635	F	–	P
<i>Oodinychus karawaiewi</i> (Berlese, 1903)	Uropodoidea	B	3 776	1:1	–	P
<i>Oodinychus obscurasimilis</i> (Hirschmann and Zirngiebl-Nicol, 1961)	Uropodoidea	B	437	1:1	–	M
<i>Oodinychus ovalis</i> (C.L. Koch, 1839)	Uropodoidea	B	9 348	1:1	+	E
<i>Oodinychus spatulifera</i> (Moniez, 1892)	Uropodoidea	B	712	1:1	–	O
<i>Oplitis alophora</i> (Berlese, 1903)	Uropodoidea	B	7	1:1	?	S
<i>Oplitis franzi</i> Hirschmann and Zirngiebl-Nicol, 1969	Uropodoidea	B	1	?	–	S
<i>Oplitis wasmanni</i> (Kneissl, 1907)	Uropodoidea	B	1	?	–	S
<i>Phaulodiaspis borealis</i> (Sellnick, 1940)	Uropodoidea	B	1 649	1:1,2	+	S
<i>Phaulodiaspis rackei</i> (Oudemans, 1912)	Uropodoidea	B	382	1:0.8	–	O
<i>Phaulotrachytes advena</i> (Trägårdh, 1922)	Uropodoidea	B	440	1:1	–	S
<i>Polyaspinus cylindricus</i> Berlese, 1916	Polyaspidioidea	P	772	F	–	P
<i>Polyaspinus patavinus</i> Berlese, 1881	Polyaspidioidea	B	180	1:1,5	–	O
<i>Polyaspis sansonei</i> Berlese, 1916	Polyaspidioidea	B	54	1:1	–	S
<i>Polysapinus schweizeri</i> (Hutu, 1976)	Polyaspidioidea	B	19	1:1	–	S
<i>Pseudouropoda calcarata</i> (Hirschmann and Zirngiebl-Nicol, 1961)	Uropodoidea	B	46	1:1	–	O
<i>Pseudouropoda structura</i> (Hirschmann and Zirngiebl-Nicol, 1961)	Uropodoidea	B	5	1:1	?	S
<i>Pseudouropoda tuberosa</i> (Hirschmann and Zirngiebl-Nicol, 1961)	Uropodoidea	B	2	1:1	?	S
<i>Trachytes aegrota</i> (C.L. Koch, 1841)	Polyaspidioidea	P	17 353	1:6000	–	E
<i>Trachytes irenae</i> Pečina, 1970	Polyaspidioidea	B	11 030	1:0.7	–	P
<i>Trachytes lamda</i> Berlese, 1903	Polyaspidioidea	P	200	1:100	–	S

Table 1 (concluded).

Species	Superfamily	Fertility strategy*	No. of specimens	Sex ratio (male:female) [†]	Phoresy	Ecoelement [‡]
<i>Trachytes minima</i> Trägårdh, 1910	Polyaspidoidea	B	515	1:1,3	–	O
<i>Trachytes montana</i> Willmann, 1953	Polyaspidoidea	P	22	F	–	O
<i>Trachytes pauperior</i> (Berlese, 1914)	Polyaspidoidea	P	3 208	1:100	–	P
<i>Trachyurogoda coccinea</i> (Michael, 1891)	Uropodoidea	B	123	1:2	–	S
<i>Trematurella elegans</i> (Kramer, 1882)	Uropodoidea	B	509	1:1	–	P
<i>Trichouropoda sociata</i> (Vitzthum, 1923)	Uropodoidea	B	2	?	–	S
<i>Urodiaspis pannonica</i> Willmann, 1951	Uropodoidea	P	1 117	F	–	P
<i>Urodiaspis stammeri</i> (Hirschmann and Zirngiebl-Nicol, 1969)	Polyaspidoidea	B	12	1:0.7	–	S
<i>Urodiaspis tecta</i> (Kramer, 1876)	Uropodoidea	P	5 606	F	–	E
<i>Uroobovella fracta</i> (Berlese, 1916)	Uropodoidea	B	4	1:1	?	S
<i>Uroobovella obovata</i> (Canestrini and Berlese, 1884)	Uropodoidea	B	113	1:1,3	–	O
<i>Uroplitella conspicua</i> (Berlese, 1903)	Uropodoidea	P	19	F	–	S
<i>Uroplitella paradoxa</i> (Canestrini and Berlese, 1884)	Uropodoidea	B	23	1:4	–	S
<i>Uropoda hamulifera</i> (Michael, 1894)	Uropodoidea	B	8	1:1	?	S
<i>Uropoda italica</i> Hirschmann and Zirngiebl-Nicol, 1969	Uropodoidea	P	4	F?	–	S
<i>Uropoda orbicularis</i> (Muller, 1776)	Uropodoidea	P	15 300	1:100	+	S
<i>Uropoda undulata</i> Hirschmann and Zirngiebl-Nicol, 1969	Uropodoidea	B	36	1:2	–	S
<i>Uroseius hunzikeri</i> (Schweizer, 1922)	Polyaspidoidea	B	2	?	–	S
<i>Urotachytes formicarius</i> (Lubbock, 1881)	Uropodoidea	B	21	1:1	–	O
Total			96 503			

*B, bisexual species; P, parthenogenetic species.

[†]F, only females known.

[‡]S, stenotopic species (<20% of habitats); O, oligotopic species (20%–30% of habitats); M, mesotopic species (31%–50% of habitats); P, polytopic species (51%–75% of habitats); E, eurytopic species (>75% of habitats) ($n = 33$ habitats).

phenomenon has not been reported for these mites (Błoszyk 1999).

Among parthenogenetic species, both eurytopic and polytopic species are found. Furthermore, species with a relatively narrow environmental specialization (for instance, *T. lamda*) are also parthenogenetic. According to some authors (e.g., Herbert and Crease 1981), wide ecological tolerance in eurytopic and polytopic groups can be explained as a result of a specific structure of parthenogenetic species populations, where individuals are treated as a number of clones. Each clone is narrowly adapted to the specific conditions of the habitat, and the total number of adaptations determines the general capability for adaptation of the whole species. Nevertheless, this kind of reproduction slows down the processes of speciation and impoverishes the genetic variability. Among parthenogenetic species of Uropodina found in various types of habitat and different geographical regions, a relatively low morphological variability is observed. This indicates that the life strategy based upon offspring “cloning” brings about a reduction in the differentiation of the population.

Our observations indicate that there is no direct relationship between the degree of anthropogenic alteration of the environment and the degree of participation of parthenogenetic uropodid mites. This supports the earlier claims of Walter and Lindquist (1995), who found no significant difference in the number of parthenogenetic acid mites inhab-

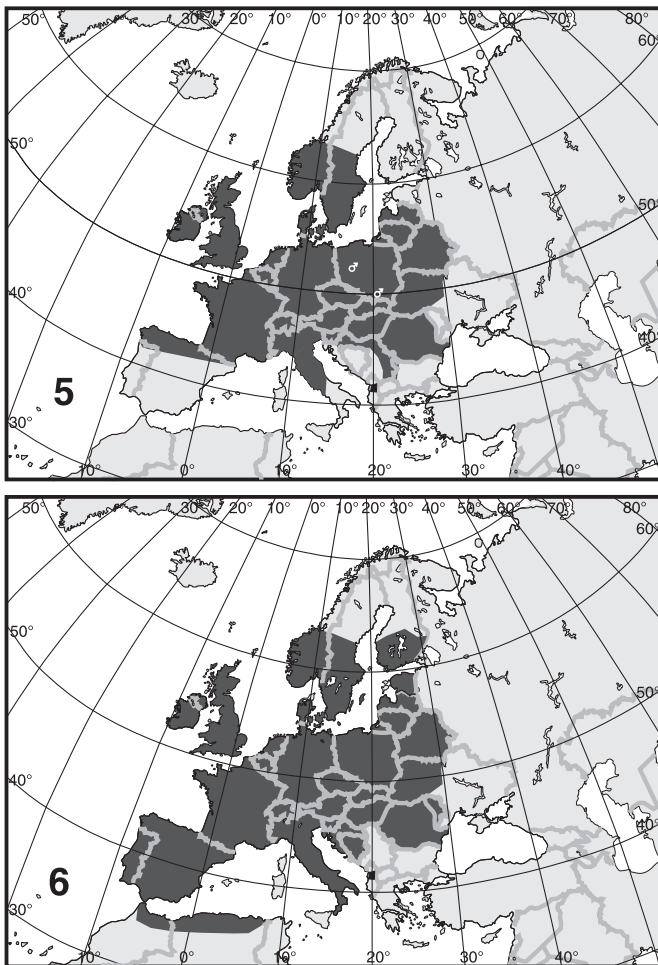
iting synanthropic and natural habitats. Walter and Lindquist (1995) also proved that parthenogenetic species are randomly distributed across various types of habitats. Accordingly, they did not acknowledge the hypothesis of biotic uncertainty.

Olszanowski and Lembicz (1999) maintain that the theory put forward by Olivier (1971) and White (1978), who claim that parthenogenesis cannot exist in all species forming higher taxons (e.g., genus, family), is false for oribatid mites. Nevertheless, the aforesaid theory can be applied to species of the suborder Uropodina. In the majority of known cases, only some of the species of a particular genus reproduce without males. None of the upper taxons of Uropodina is totally parthenogenetic. Therefore, parthenogenesis is typically adaptative and the switch from bisexual to parthenogenetic reproduction presumably improves the process of colonization of pioneer habitats. For example, only parthenogenetic species (*T. aegrota*, *T. pauperior*, *T. montana*, and *I. geieri*) were found in initial habitats located next to the front of the Jonsebergen glacier in Norway and in alpestrine tundra (J. Błoszyk and M. Gulvik, unpublished data).

Appearance of males in parthenogenetic species

Olszanowski and Lembicz (1999) mentioned two factors that can affect the interpretation of results: (1) short lifespan and seasonal appearance of males, which can cause the absence of this sex in scrutinized samples; and (2) the ex-

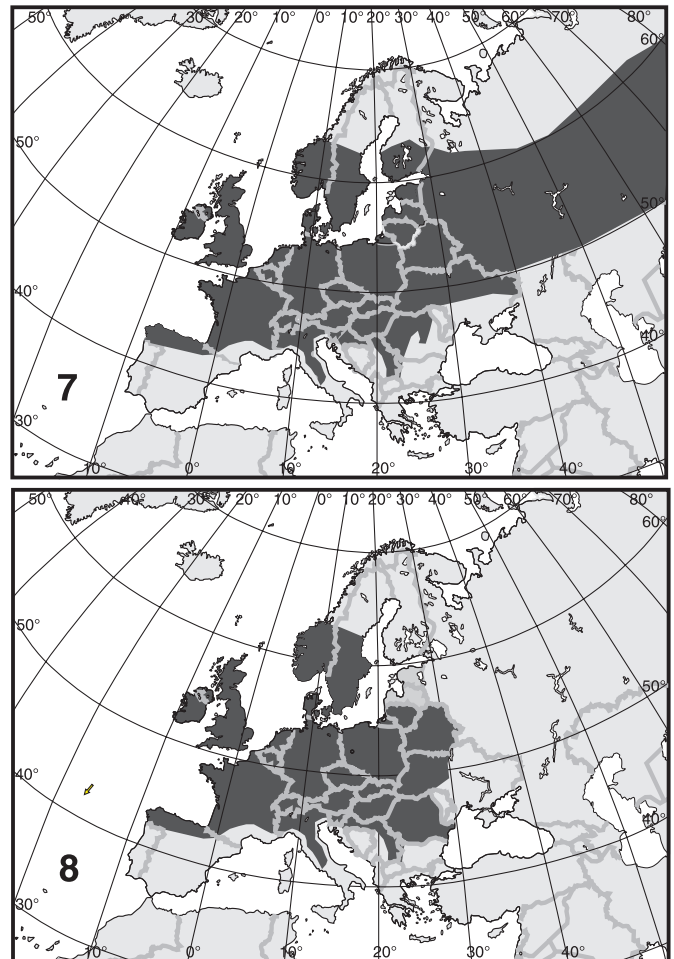
Figs. 5–6. Distribution of common parthenogenetic uropodid species in Europe: 5, *Trachytes aegrota* (locations of populations in which males were sporadically spotted are marked); 6, *Olodiscus minima*.



tremely rare presence of males in the population. The possibility of seasonal appearances of males, e.g., during winter when the intensity of sample collection is greatly reduced, can also be an important factor. The first factor (short male life-span) is not applicable here because of the relatively long life-span of uropodid mites (Krasinskaja 1961; Radinovsky 1965a, 1965b; Faasch 1967; Compton and Krantz 1978) and the lack of data indicating differences between male and female life-spans.

Undoubtedly, the occasional presence of males in populations of some species makes the interpretation of reproduction within the suborder Uropodina more difficult (Błoszyk and Olszanowski 1985a, 1985b; Błoszyk 1999; Błoszyk and Haliday 2000). No males were recorded in some of these species, and other species were characterized by a low percentage of males (usually less than 0.5% of the population). In comparison, males in some species of oribatid mites approximated 4%–5% of the population (Grandjean 1941). Therefore, there are three ways in which a species and the importance of males within the species can be characterized: (1) the species is bisexual, with a high level of polygamy (observed in some groups of mites); (2) the species occa-

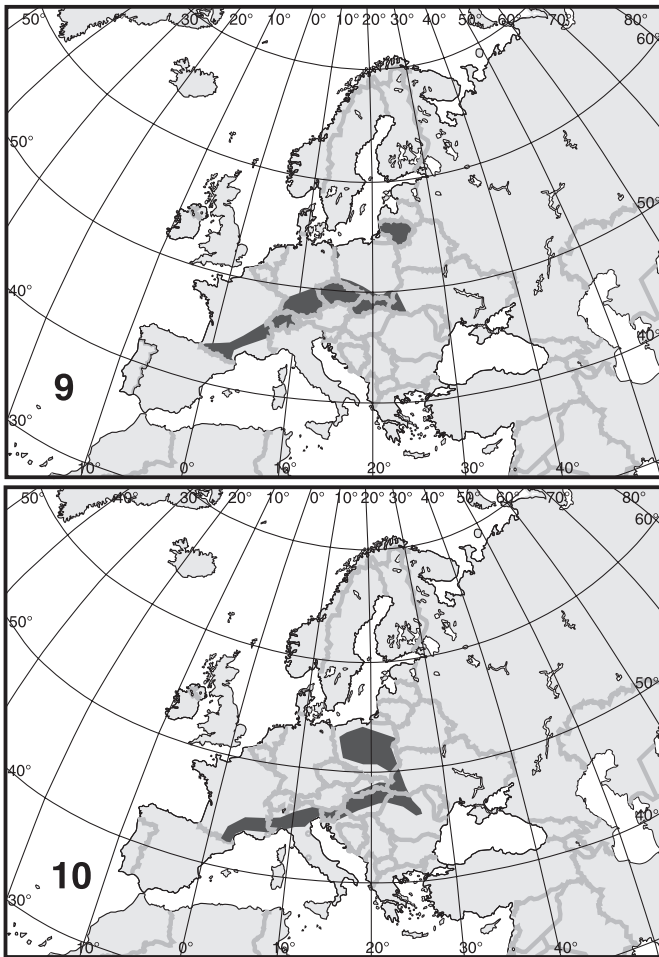
Figs. 7–8. Distribution of common parthenogenetic uropodid species in Europe: 7, *Trachytes pauperior*; 8, *Urodiaspis tecta*.



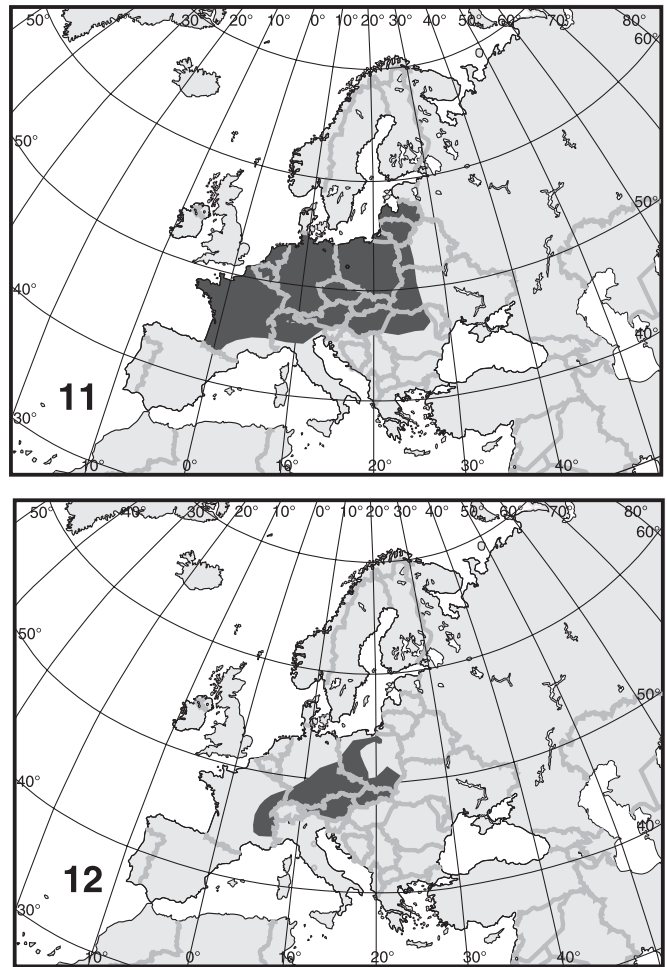
sionally reproduces parthenogenetically, i.e., only some females become fertilized; and (3) in spite of their occasional appearance in the population, males do not take part in reproduction — such a species reproduces only by means of parthenogenesis.

Unlike oribatid mites, uropodid mites can fit either of the first two characterizations. A number of clear differences in leg structure among the species of the genus *Trachytes* were observed. Males of the bisexual species (e.g., *Trachytes minima*) lack massive spines on legs II, but these spines occur on legs of related species (species in which males are rarely present, e.g., *T. pauperior*). This difference can be interpreted as an evolutionary mechanism preventing different species of Uropodina from having sexual contact with each other (Błoszyk and Olszanowski 1985b). If the rarely present males had long ago taken no part in reproduction, this difference would probably have been eliminated. Nonetheless, the possibility that the differences in leg structure are only remains from the times when these species were bisexual cannot be excluded. It would mean that such species have rather recently begun to reproduce parthenogenetically. In this case, the group of species with rarely present males should be treated as a relict of the sexually reproducing progenitors (Grandjean 1941).

Figs. 9–10. Distribution of rare parthenogenetic uropodid species in Europe: 9, *Cilliba erlangensis*; 10, *Trachytes lamda*.



Figs. 11–12. Distribution of some rare parthenogenetic uropodid species in Europe: 11, *Discourella modesta*; 12, *Olodiscus misella*.

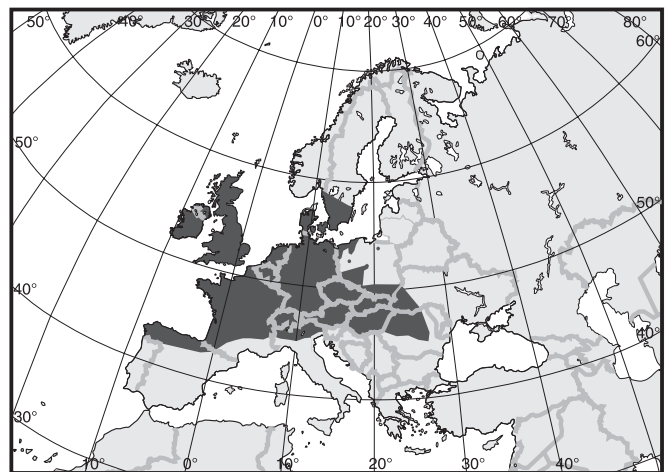


Sporadic appearance of individual males in populations of some species recognized as parthenogenetic is undoubtedly interesting and was suggested earlier (Błozzyk and Olszanowski 1985a, 1985b; Błozzyk 1999; Błozzyk and Haliday 2000). The male to female ratio in these species varies from 1:10 to 1 : 20 000. It is not known whether these occasional males participate in reproduction. However, the production of males under specific conditions could be a method for increasing genetic variety within the population (we found no data on the karyotype of uropodid mites; hence, it was not possible to determine whether or not the scantily occurring males are haploid). Therefore, we believe that this phenomenon of reproduction requires further study.

Some advantages of parthenogenesis

Undoubtedly, a species reproducing parthenogenetically can migrate faster and thus colonize new areas more quickly. Parthenogenetic species can colonize new areas more easily than bisexual species. This may be why parthenogenetic species of the suborder Uropodina are widely distributed and common in both Poland and Europe. They are also characterized by a wide ecological tolerance that allows them to exist in various habitats. For instance, the most eurytopic species of the Polish fauna — *T. aegrota*, *T. pauperior*,

Fig. 13. Distribution of the parthenogenetic uropodid species *Polyaspinus cylindricus* (atlantic element) in Europe.



O. minima, and *U. tecta* — are present in almost all types of habitats (Błozzyk 1999). In some cases parthenogenesis can be an adaptation to extreme conditions, for example, during

the colonization of cold, alpine terrains by *T. montana* or *I. geieri*. Although phoresy is one of the frequent ways in which mites of the suborder Uropodina are spread (Athias-Binche 1994; Bajerlein and Błoszyk 2004), it is not common among parthenogenetic mites (see also Walter and Lindquist 1995). Among the species observed, the authors found only *U. orbicularis* to be phoretic.

If it is assumed that parthenogenesis appeared secondarily (in relation to bisexual reproduction) within the present species of the suborder Uropodina, the sporadic presence of males in some populations probably points to the species' centres of origin, i.e., places from which the species dispersed as parthenogenetic populations. In this case, Poland would be an important area as far as the distributions of *T. aegrota*, *T. pauperior*, *T. lamda*, and *O. minima* are concerned.

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