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Epitoky in *Scutisotoma stepposa* (Collembola; Isotomidae)

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Abstract

Reproductive males of *Scutisotoma stepposa* Martynova from two basins of Vitim Plateau (Russia: East Siberia) display epitoky in three forms. 'Supermales' are armed with strong macrosetae, brushes on ventrum of abdomen, callosities on tube and legs, bent and thickened antennae. 'Modest' males have only strong macrosetae and slightly thickened antennae. 'Neutral' males are indistinguishable from females. In the Vitim Plateau, the species often forms mass aggregations. Population sizes of *S. stepposa* are usually depressed during the first half of the summer and increase as of August. The reproductive individuals occur during the entire vegetative season, and all three types of males can occur together. 'Neutral' males are more frequent under low population densities, while 'supermales' are seen only in aggregations. Taxonomic remarks and new records of *S. stepposa* from the Palearctic are given.

Keywords: Polymorphism, aggregations, sexual dimorphism, life cycle, swarm

1. Introduction

Collembola is a group where males normally deposit their spermatophores and have no direct contact with females. Contact between the sexes, i.e. sexual behavior, is known only for a few families, mostly in Symphypleona, and, with very few observations, in the families Isotomidae and Poduridae. During sexual behaviour a male encourages a female to pick up his spermatophores during simple or elaborate courtship (Schliwa & Schaller 1963, Bretfeld 1970, Betsch 1980, Kozlowski & Aoxiang 2006, Goloshchapova et al. 2006, and others). Visible sexual dimorphism is more widely known and is described in detail for many taxonomically dissimilar species (Palacios-Vargas & Castaño-Meneses 2009), indicating sexual behaviour to be much more common than is observed. The reasons behind strong sexual dimorphism in Collembola remain disputable. It has been shown that it occurs more frequently in Symphypleona and in species living in contact with water (Fjellberg 1988, Palacios-Vargas & Castaño-Meneses 2009).

In the course of our study of collembolan populations of the Vitim Plateau (Russia: East Siberia), we found high density populations and mass aggregations of *Scutisotoma stepposa* (Martynova), including reproductive males with peculiar modifications. In the present paper we describe types of reproductive males of this species, its seasonal dynamics, age structure and discuss some aspects of sexual dimorphism in Isotomidae.

2. Materials and methods

Material used for morphological analysis: Mongolia (central part), Archangaj aimak, Tevshrulekh, steppe, 25.VII.1971, Medvedev leg. (topotypes); Ibidem, in lichens, 23.VII.1971; Russia (European part), Middle Volga, Zhiguli Mountains, near Zhigulevsk, bank of Volga River, mosses on stones of N slope, 3.VI.1988, Potapov leg.; Russia (Middle Ural), Ser'ga River, entrance of Bol'shaya Arakaevskaya Cave, in semidry mosses, 8.VIII.2002, Potapov leg.; Russia (Far East), South Primorye, Shkotovsky area, Livadiysky Range, at the top of Khualaza Mt., 19.IX.2004, Deharveng and Bedos leg. (Ru014); Russia (Far East), South Primorye, middle flow of Bikin River, near mouth of Amba River, N 46,69949, E 135,77142, dry rocky top of hill, forest with *Phellodendron* and *Quercus*, 20.IX.2009, Smirnova leg., Russia (Far East), suburbs of Khabarovsk, Voronez highlands, upper part of sandy bank of Amur River, flotation, 26.IV.2010, Potapov leg.; Russia (E Siberia), E Buryatia, Vitim Plateau, Eravninskaya Basin, sandy-gravel bank of Indola River (in mass), 18.VIII.2008, Chimitova leg.; Russia (E Siberia), NW Buryatia, Barguzinsky Range, ca 5 km W Barguzin, upper flow of Gremyachaya Brook, subalpine belt, ca 1400 m aSL., bare sand and silt on wind erosion areas, 18.VII.2008, Chimitova leg., Russia (E Siberia), Irkutskaya Oblast, W Khamar-Daban Range, Cherskogo Peak, silt and moss on top of a big rock, ca 2000 m aSL., 26.VII.2008; ibidem, steep northern slope, cold mossy shelves in permanent shadow, 26.VII.2008, Potapov leg.; Russia (W Siberia), Khakasiya, Askizskiy Region, 5 km from Berikchul', *Sedum* and *Saxifraga* on rocks, 18.VII.1990, Stebaeva leg. Besides, vast material from several biotopes of Vitim Plateau were considered.

The populations of *S. stepposa* were studied in two neighbouring basins of the Vitim Plateau (eastern part of Buryatia Republic, E Siberia). The climate is highly continental, permafrost soils predominate. The warmest month is July (+16 ^{o}C), and the coldest January (-30 ^{o}C). Temperatures can drop down below zero ^{o}C during all summer months. The annual average precipitation is 300–340 mm, of which 80–85% occurs during periods between May and September. Spring and the first half of summer are dry, while the second half of summer is usually more humid and August rains account for about 60% of the annual precipitation. The landscape of the Vitin Plateau consists of meadow steppes, boggy or dry larch- and birch woods on the flat slopes of basins, and to some extent salt lands at the bottom of basins. Thirteen biotopes of Eravninskaya and Kondinskaya Basins of Vitim Platea were sampled in different seasons with 10 cores for each biotope at one date. More information on the biotopes and methods are given in Chimitova et al. (2010).

3. Morphology

Scutisotoma stepposa (Martynova, 1975)
Proisotoma stepposa Martynova, 1975 (synonym)

3. 1. Taxonomical remarks

The species was described from central Mongolia by Martynova (1975) and redescribed by Dunger (1982) based on type materials. Both authors placed it in the genus *Proisotoma* Börner. Recently, *P. stepposa* has been moved to the Holarctic genus *Scutisotoma* Bagnall (Potapov et al. 2006). The species is readily defined by the combination of oligochaetotic furca with generic characters of *Scutisotoma*. Both the manubrium without anterior setae and the dens with only 1/4 setae indicate the similarity to *Subisotoma* Stach and *Folsomides* Stach. More essential characters indicate that this species belongs to *Scutisotoma*. Common characters for the genus include the number (33/22224 s, 11/111 ms) and position (mid-tergal) of sensilla and a full set of elements in the mouth parts (4 sublobal hairs, bifurcate maxillary palp, 4 prelabrol setae, and all papillae and guards in labium). The general appearance and antennae of females are common for the genus (Figs 8, 16). Setae B5 and X on tibiotarsi III are not significantly thinner than other setae, and are markedly thinner in males (Figs 13 and 14). *S. baica* Potapov et al. shares the same furca with *S. stepposa*, but has many more setae on the posterior side of the manubrium and tibiotarsi.

3.2. Sexual polymorphism of males

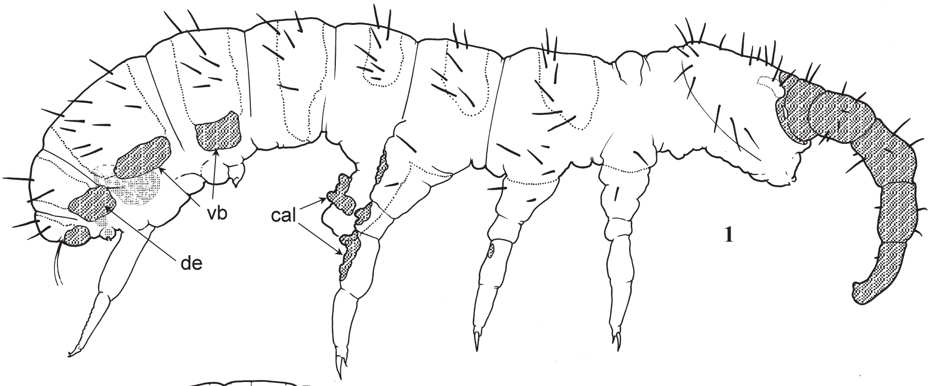
The males of several populations display sexual polymorphism appearing in three types. All three types have a well visible ejaculatory duct terminating at the male papilla, which indicates a reproductive ability. Females are not modified.

1. 'Neutral' males. Size of body from 0.7 to 1.0 mm. Setae of body and appendages unmodified, as in females (Fig. 4). Macrosetae hardly developed, medial pair on Abd.V short and thin, 0.25–0.35 as long as this tergite's length (as in Fig. 9). Secondary sexual characters as common for the genus: antennae with erect male sensilla, as 2,2,>2 (variable) in number on Ant. 2, 3, 4 (as in Fig. 17, notated as 'es'), tibiotarsus III with setae X and B5 slightly thinner than in females.

2. 'Modest' males. Size of body from 0.75 to 1.15 mm. With thick serrated macrosetae on body, head and basal parts of antennae and legs (Figs 3, 11). Medial pair of macrosetae on Abd. V 0.35–0.50 as long as this tergite's length. Proximal half of antennae slightly thickened (Figs 17, 18), relative width of Ant. 1 thus greater than in females and neutral males. Antennae with erect male sensilla (as in neutral males), and thicker setae on dorsal and lateral sides (absent in females and neutral males). Ant. 1 and 2 with a ventral trichobothrium each, other setae of the ventral side unmodified. Tibiotarsus III with setae X and B5 slightly thinner than in females.

3. 'Supermales'. Well recognized by the appearance (Figs 1, 5, 6). Size of body from 1.10 to 1.35 mm. Abdomen curved and armed with strong macrosetae, ventro-lateral brushes and trichobothria. Macrosetae thick and serrated in the distal half, on Abd. V 0.45-0.60 as long as this tergite's length. Abd. III, IV, V, and VI each with a pair of brushes formed by groups of spine-like erect setae. On Abd. III and V, ventro-lateral 'brushes' supplied with ventral trichobothria (one and two, respectively). Ventral side of Abd.VI with two thin and long macrosetae (Fig. 10). Posterior side of the ventral tube and hind leg (coxa, trochanter and femur) with large callosities. Femur of leg II with a small callosity (Fig. 12). Hind leg slightly longer than in females. Head larger than in neutral and modest males because of swollen front, with thickened serrated macrosetae. In addition to normal sensilla, basal microsensilla and setae, antennae also armed with thick serrated macrosetae of different shapes. Several setae on the ventral side and erect male sensilla modified to blunt short spines, in all segments. Distal part of Ant. 4 with two warts (Fig. 15). Antennae bent downwards, unlike in *Rhodanella minos* (Fig. 7), much longer, and in the proximal half thicker, than in other types of males. The antennal segments partly fused and their joints have lost mobility. Tibiotarsus III with setae X and B5 thinner and longer than in females. Callosities and ventral brushes were never seen in males of other species of Isotomidae before.

Sensillar chaetotaxy, furca, claw, outer mouth parts are not affected by polymorphism.



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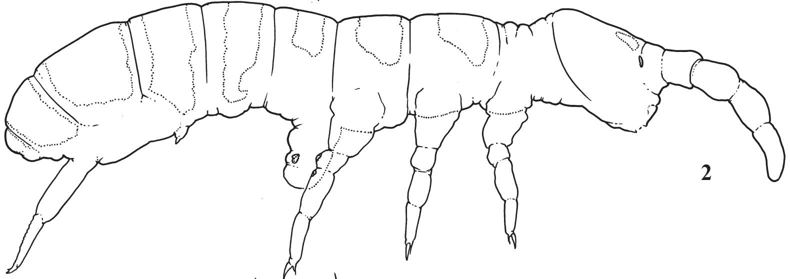

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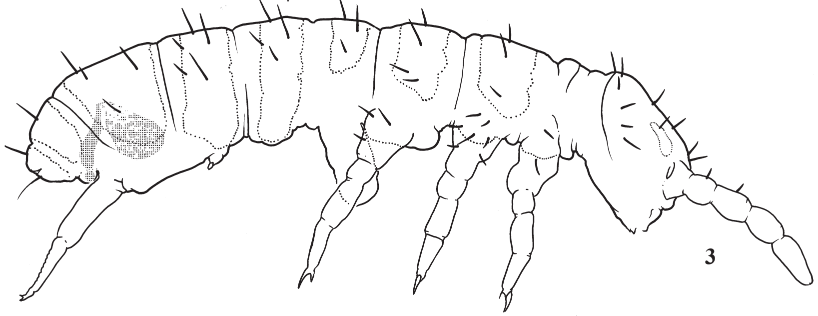

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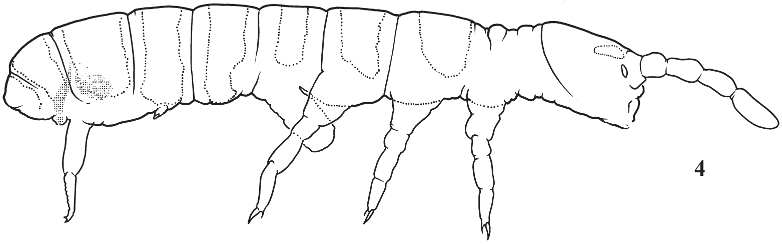

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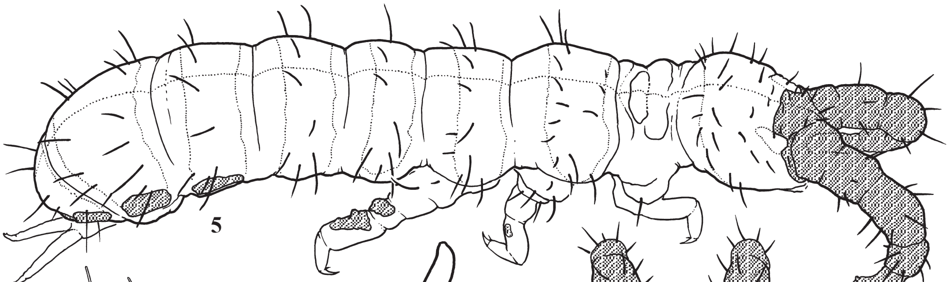
Figs 1–4 Male types of *Scutisotoma stepposa*. Lateral view: 'supermale' (**1, 2**), adult (**1**) and subadult (**2**) (with modified parts of body marked), 'modest' male (**3**), 'neutral' male (**4**). cal = callosities, de = ejaculatory duct, vb = ventral brushes.

Figs 5–9 *S. stepposa* (**5, 6, 8, 9**) *and Rhodanella minos* (**7**). 'Supermale' (**5, 6**): dorso-lateral view of body (**5**) and dorsal view of head (**6**). Head, lateral view (**7**) (after Delamare-Deboutteville et al. 1969). Female (**8–9**): general appearance (**8**) and Abd. IV–VI (**9**). s = sensillum.



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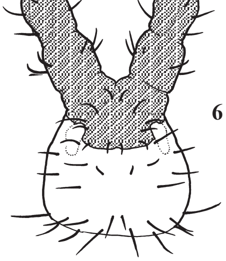

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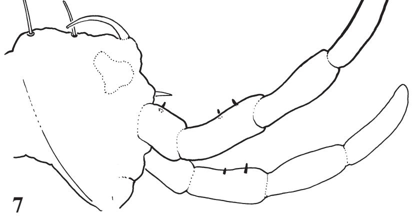

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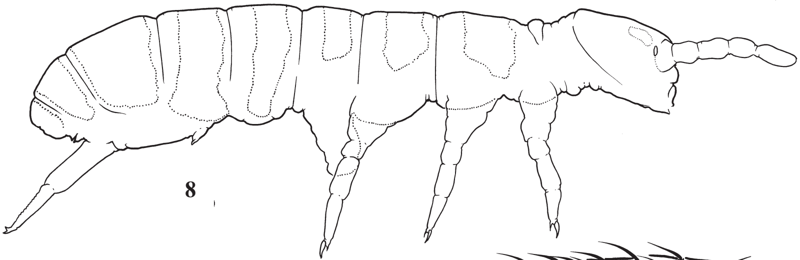

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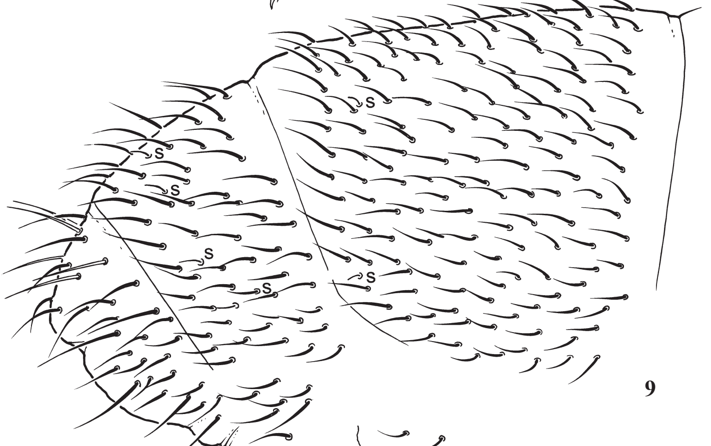

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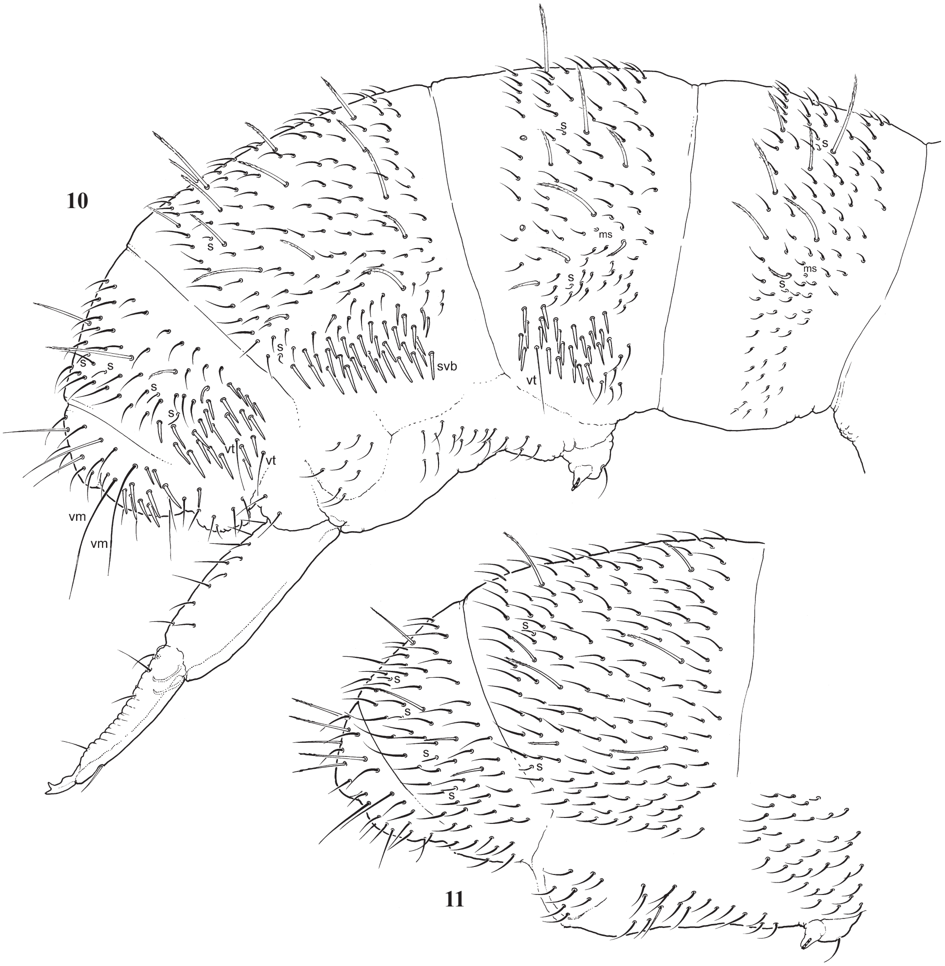
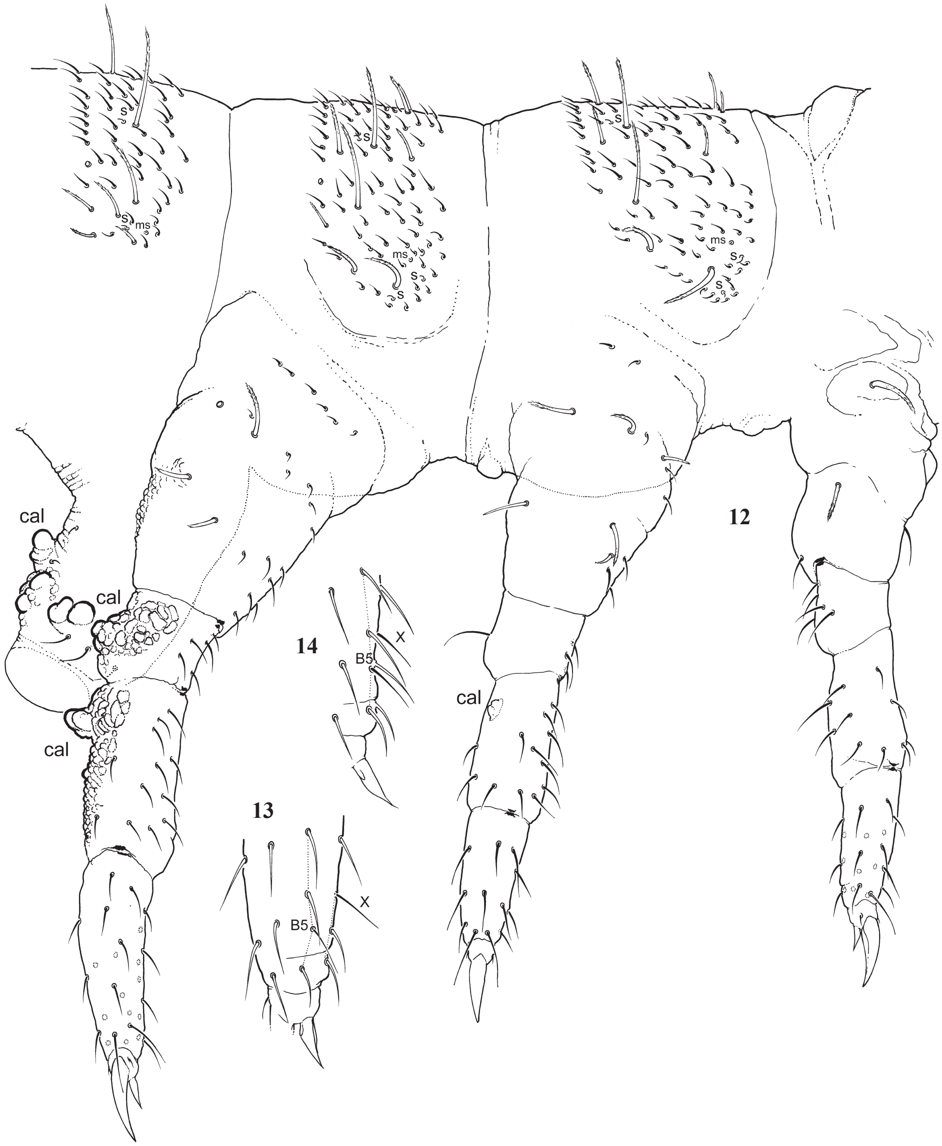
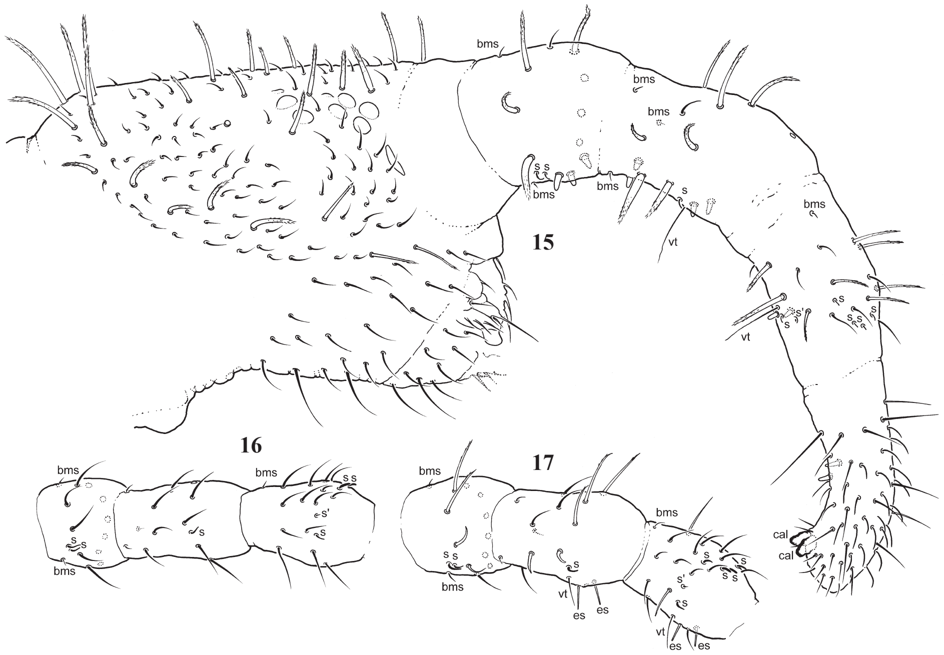


Figs 10–11 *S. stepposa*. 'Supermale', Abd. II–VI (**10**), 'modest' male, posterior half of abdomen (**11**). ms - microsensillum, s - sensillum, svb - spine of ventral brushes; vm - ventral thin macroseta, vt - ventral trichobothrium.



Figs 12–14 *S. stepposa*. Th. II–III, Abd. I of ‘supermale’ (**12**), inner side of tibiotarsus 3 (**13–14**) in ‘supermale’ (**13**) and female (**14**). For abbreviations see Figs 1 and 10.



Figs 15–17 *S. stepposa*. Head and antenna of 'supermale' (**15**), Ant.1–3 (**16, 17**) in female (**16**) and 'modest' male (**17**). bms = basal microsensillum, s,s' = sensillum, vt = ventral trichobothrium, cal = male callosity, es = erect male sensilla.

3.3. Discreteness of polymorphism

No intermediate forms between the three types were found. Supermales are well discriminated by the body shape and ventro-lateral brushes. Modest males are always armed with well visible macrosetae, their length and serration vary slightly depending on the size of the animal. Two other key characters differentiating the types of males and females are the relative width of the antennae and the length of the macrosetae (Fig. 18). In our populations, these two quantitative characters are possible to use in discriminating the types of males.

In Isotomidae, polymorphism of reproductive males was only described in *Agrenia polymorpha* Fjellberg, while the difference between the types are of another nature than in *S. stepposa* (Fjellberg 1986).

3.4. Relation of types of males

Epitoky is the appearance of certain morphotypes coupled with the reproductive cycle of the individual. In a strict understanding, the different epitokous instars/morphotypes are the conditions of one individual and are separated by moults (Bourgeois 1971, 1981 and others). Later, the term epitoky became applied to any strong modification of males or females related with their reproductive ability (Fjellberg 1976, 1977, 1988). In most observations, the passing of an individual through non-reproductive, reproductive and again non-reproductive instars was not proved, thus epitoky was only assumed. In Collembolae continuing numerous moulting after attaining maturity (protomorphose) and possible alternation between non-reproductive and reproductive instars makes it difficult to discriminate between polymorphism of a reproductive instar and epitoky. We use the latter term in wide understanding here.

The three types of males described above, females and juvenile specimens were recorded together in one mass population (Vitim Plateau, Eravninskaya Basin, sandy-gravel bank of Indola River 18.VIII.2008). Moulting specimens, i.e. having a ‘double skin’, were not found by us. Non-reproductive males were similar to females. In one of the other populations (Vitim Plateau, Kondinskaya basin), the adult males were absent and some of them showed a mixture in morphology of supermale (expanded antennae) and female (short macrosetae). These individuals were large (0.9–1.1 mm) and had neither an ejaculatory duct nor a fully developed male cone and, thus, are considered to be subadult supermales. Subadult supermales have none of the remarkable features of the adult supermales apart from the antennae (which are, however, less extended than in adult supermales) and rudimentary callosities on the hind legs (which vary depending on specimen) (Fig. 2). It would be logical to conclude that the male can become a reproductive supermale through the subadult supermale instar, without passing through neutral or modest male forms. In the model population (Eravninskaya Basin) we found large subadult males without any epitokous characters. Here, these animals would reach maturity and become adult modest (or neutral) males without passing through the supermale form. The possible passings between types of reproductive males, which could run through non-reproductive instars, remain unclear.

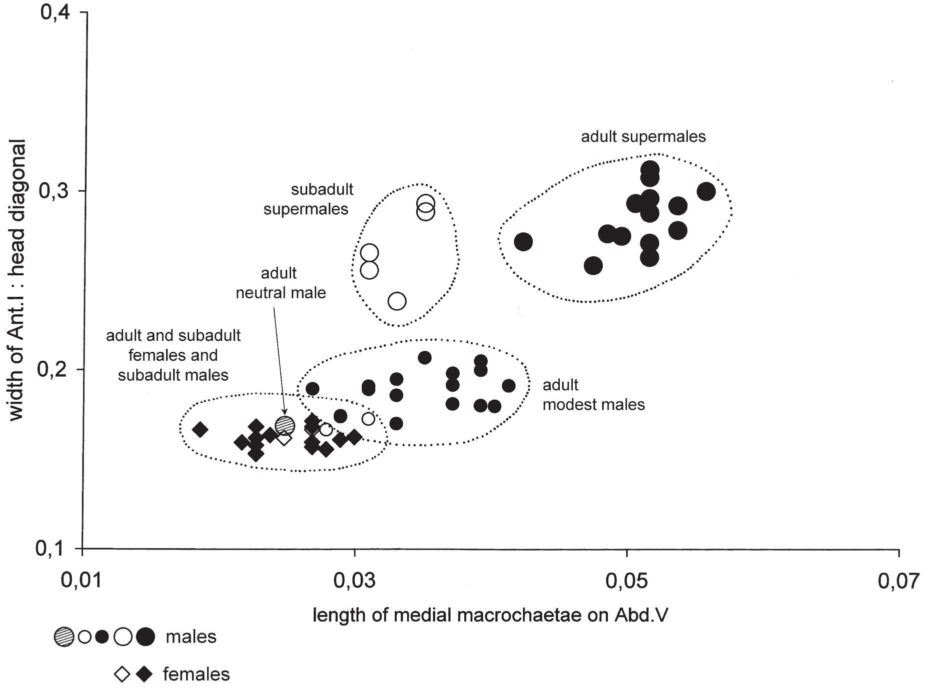
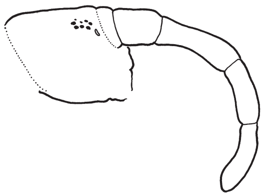


Fig. 18 Sexual polymorphism of males in length of macrosetae and relative width of first antennal segment. Open circles and rhombs: juveniles or subadult animals.

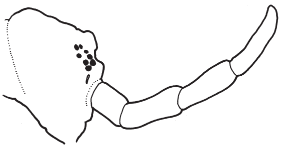
3.5. Possible functions of epitokous characters of supermales

In Symphypleona the modified antennae of males form a clasping organ, with which the male locks up with the female antennae (Betsch 1980 and others). It would be logical to assume the same role in the epitokous modifications in the supermales of *S. stepposa* and morphologically analogous males of Symphypleona. In *S. stepposa* the antennae are bent downwards and their ventral chaetotaxy is also considerably differentiated and presumably serves to fasten the female under the antennae. In this respect all known species of Isotomidae with considerable sexual dimorphism appear in three types:

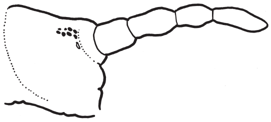


'under-head' grip:

Scutisotoma stepposa, *Dimorphotoma porcella* Ellis, *Vertagopus reuteri* (Schøtt), *Archisotoma pulchela* (Moniez), *Hydroisotoma schaefferi* (Krausbauer) (North American populations)
After Ellis (1976), Schulz (2010), Fjellberg (1982, 2007), Strenzke (1955), Wray (1978)



'over-head' grip:
Guthriella muskegis (Guthrie), *Rhodanella minos* (Denis).
After Palacios-Vargas & Castaño-Meneses (2009), Delamare-Deboutteville et al. (1969)



antennae straight or their orientation is not fully described (grip unknown):
Jestella siva Najt, *J. armata* Potapov et al., *Scutisotoma muriphila* (Grinbergs), *Agrenia polymorpha* Fjellberg (only supermales), *Najtia vicaria* (Arle), *Psammisotoma mariagalanteae* Thibaud, *Isotopenola australis* Potapov et al.
After Najt (1977), Potapov et al. (2005, 2009), Grinbergs (1968), Fjellberg (1986), Arlé & Mendonça (1986), Thibaud (1993).

The epitokous posterior half of the body of supermales of *S. stepposa* (callosities of the ventral tube and posterior legs and abdominal brushes) has never been seen among epitokous Isotomidae. In Symphypleona, the most similar male has been recently described for *Pedonides alcochetensis* Bretfeld, which has two clasping organs: clasping antennae, which are common for Sminthurididae, while the mid legs are also modified for clasping (Bretfeld 2010). In males of Isotomidae, the posterior legs undergo strong modifications in *Vertagopus reuteri* (legs enlarged) and *Jestella siva* (armed with group of expanded ciliated setae on outer side), which probably indicate the same function. Brushes and callosities possibly form the clasping organ as in *Pedonides*.

3.6. Sexual dimorphism of Isotomidae

All sexual dimorphisms in males of the family can be classified as follows:

1. Body size and associated characters. Females are as a rule larger and relatively stouter in Onychiuridae (Pomorski 1998); the same was shown for Symphypleona (Betsch 1980). Males are probably smaller than females in all families of Collembola, however the size difference of sexes is rarely mentioned in the morphological descriptions of species. In our experience, most species of Isotomidae follow this rule. Isotomidae is a polychaetotic group; therefore, when smaller, the males have on average fewer setae on

different parts of their body than females. It is usually disregarded in the descriptions as well. One of the exceptions is the paper of Ding et al. (2006), in which females and males of newly described *Folsomia hubeiensis* Ding et al. have different numbers of setae on the subcoxa.

2. Subtle differences in the chaetotaxy of appendages and body. In Isotomidae, a weak sexual dimorphism is described in the most ordinary genera: *Anurophorus* Nicolet, *Folsomia* Willem, *Vertagopus* Bagnall, *Proisotoma* Börner, *Tetracanthella* Schött and others. It is expressed in the presence of male specific sensilla on the antennae and two spurs on the third pair of legs (Goloshchapova et al. 2006, Palacios-Vargas & Castano-Meneses 2009). In the 'wahlgreni' and 'ethelae' groups of the genus *Tetracanthella*, males have sensilla s' on Ant. 3, which is absent in females (Deharveng 1987). Reproductive males of some *Vertagopus* have shorter macrosetae on the abdomen (Fjellberg 1977). Males of several species of *Isotomurus* Börner are characterized by modified setae on the lateral parts of Abd. III and IV (or only Abd. IV) (Deharveng & Lek 1993, Fjellberg 2007).

3. Considerable modification of males. Males are larger than females and armed with modified appendages, on either or both antennae and legs, and strong spine-like setae or macrosetae. Peculiarities of such males in different species are summarized by Najt (1977) and Palacios-Vargas & Castano-Meneses (2009). Here, we discuss the case in *S. stepposa*.

4. Ecology and geography

4.1. Life cycle and ecology of polymorphism

After Chimitova et al. (2010) *S. stepposa* is formally the second most abundant species estimated in 13 biotopes of the Vitim Plateau (E. Siberia). This reflects very high densities of the species in two open sites: steppe (with *Kobresia, Festuca*, and *Artemisia* as dominants) and dry meadow (with *Kobresia* and *Carex*). In both sites the species shows high aggregations. In the externally homogeneous steppe the number of individuals varies from zero to greater than a thousand per core of 5 cm diameter (Fig. 20), with the average density being ca. 120,000 individuals m^{-2}. During our field observations, we once recorded the mass aggregation of

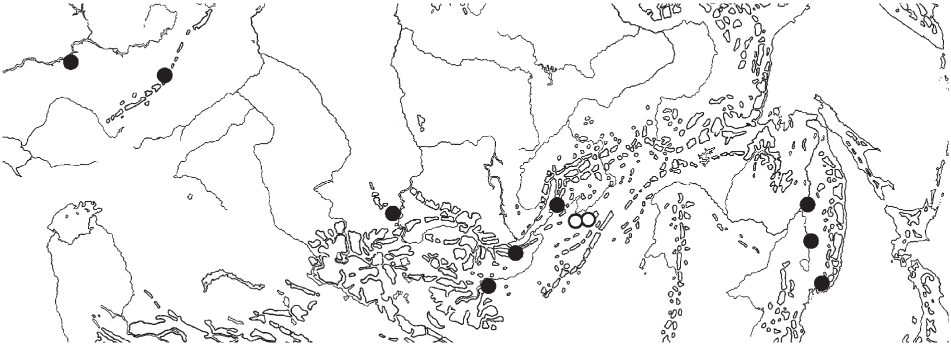


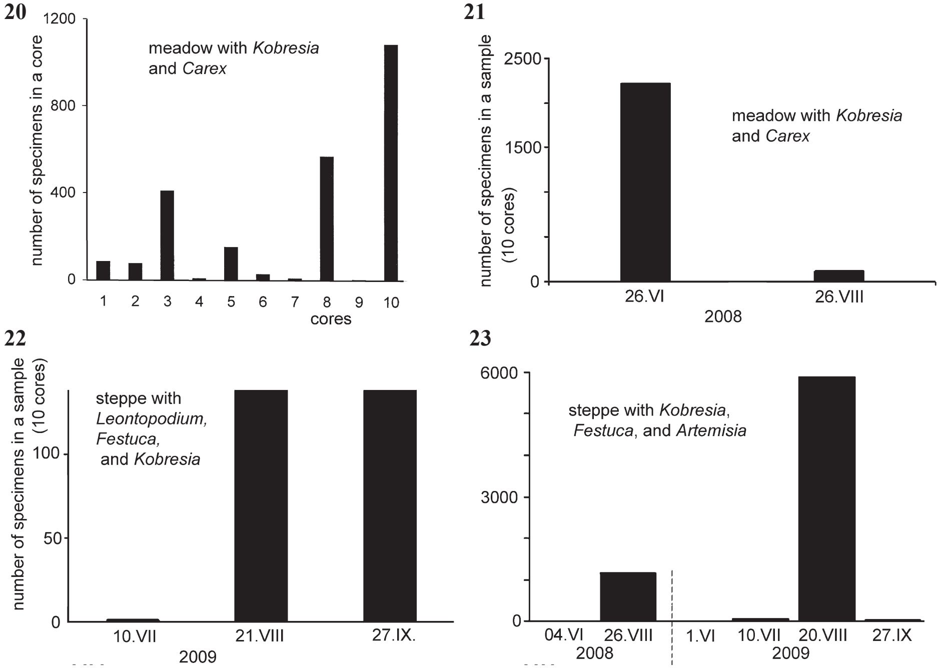
Fig. 19 Records of *S. stepposa*. Open circles represent locations where polymorphism was found.

S. stepposa on the bare surface of the sandy-gravel bank of the Indola River, near the water edge (6.VI.2009. leg. Chimitova). This colony consisted of at least ten thousand individuals and subsequently moved away or disappeared since it was not found at the associated place since. All age instars, including three types of males and juvenile specimens, were recorded in the colony in high abundances; the neutral males were sporadic.

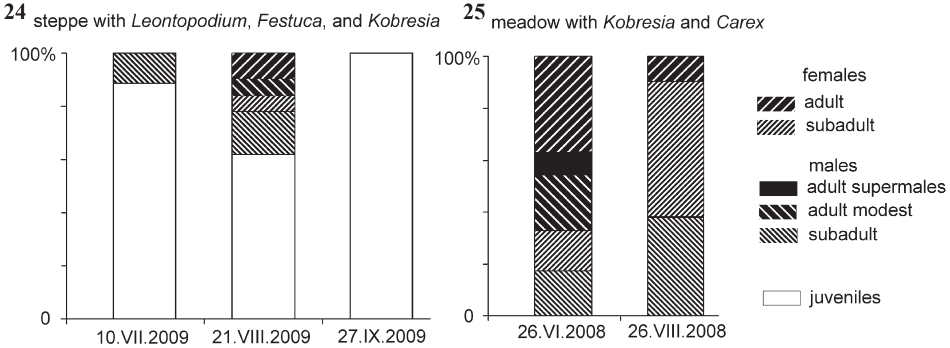
The seasonal dynamics of population densities was studied in three sites (Figs 21–23). The abundance of *S. stepposa* varies greatly: in the two steppe sites the species is depressed in the first, dryer, half of the summer and increases sharply as of August. In contrast, the situation in the more humid meadow (Fig. 22) indicates that the seasonal dynamics is also influenced by the conditions in the biotope.

In most biotopes *S. stepposa* reproduces in the second half of August. In the steppe (Fig. 24), the population consists of growing individuals, mostly of small juveniles, at the beginning of July. Later, in August, adult females and modest males reproduce. The population consists only of the newly born individuals at the end of September. One more period of reproduction is possible at the beginning of summer in the meadow (Fig. 25). According to our data, the reproductive individuals occur during the entire vegetative season, from June to August, while the relative abundance of different age groups varies depending on biotope and time.

We examined the association of morphological types of males and population density. Neutral males were rare and recorded in populations with low density values (Fig. 26). In contrast, supermales occur only in aggregations. Modest males are the most common reproductive type and are distributed throughout most populations.



Figs 20–23 Distribution of abundance by cores (**20**) and seasonal dynamics of *S. stepposa* (**21–23**).



Figs 24–25 Age and sexual structure of populations of *S.stepposa* in steppe and meadow.

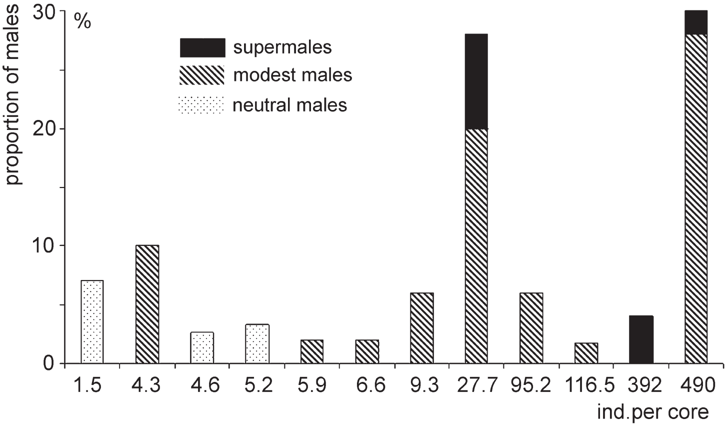


Fig. 26 Relative abundance of male types depending on population density (only populations with reproductive males were considered; the density values are calculated as averages for 10 cores and considering the whole population).

Mass aggregations, or swarms, are widely known in Collembola and different explanations have been proposed for this (Zernecke 1999, Zettel et al. 2002, Zettel 2010, and others). Association of aggregations and strong secondary dimorphism, or even reproduction, is not fully understood in Isotomidae. Mass occurence of *Rhodanella minos*, a species having peculiar males, has been repeatedly noted in the literature: the species was first described from the colony of 'several millions exemplars' (Denis 1928); Delamare-Deboutteville et al. (1969) redescribed in detail this species' dimorphism from an 'abundant population' on the river bank; Goto (1957) represented the sketches of a moving colony and its behavior in time; Cheke (1980) described a swarm fallen into a depression and its subsequent staying position. These observations referred to different species names, but all of them (*Vertagopus minos* Denis, *Rhodanella minos*, *Proisotoma stachi* Goto, *Cryptopygus fasciatus* Carpenter) are possible synonyms (Lawrence 1978). Swarms were also recorded for other species having unusual males (Ellis 1976, Wray 1978, Fjellberg 1982). Large aggregations, however, were also recorded for species of the family Isotomidae without any pronounced sexual dimorphism: *Cryptopygus antarcticus* Willem (by Schulte et al. 2008, Benoit et al. 2009) and *Ballistura filifera* (Denis) (by Ellis 1970).

Hopkin (1997) assumed that pheromone-led aggregation is probably the need for males and females of Collembola to come together during sexual reproduction. Reproduction in aggregations was proven for species of *Orchesella* and *Tomocerus* (Verhoef & Nagelkerke 1977), which increases the chance of finding a spermatophore by the female. However, these aggregations are not initially induced by sexual interactions, but by a higher resistance to desiccation. According to the 'drought hypothesis', copulation and a correspondingly well developed sexual dimorphism in association are also seen to be an adaptation to drier conditions (Stam & Hoogendoorn 1999). An argument against sexual interactions in aggregations is the presence of different developmental stages in aggregations of *S. stepposa*. This agrees with the observations of Benoit et al. (2009) and Schulte (2008) on *C. antarcticus*, which forms aggregations of all ages and are even mixed with another species. According to generalizations on aggregations of non-social insects by Wertheim (2005) and Bengtsson (2008), the high densities in aggregation can lead to competition for mates and selection of high-quality males. We propose that high population densities in aggregations in steppe conditions can be a factor influencing the appearance of epitokous supermales of *S. stepposa*, which are the most high-quality mates in some sense.

4.2. Distribution and ecology

The species is widely distributed in northern Asia, penetrating to eastern areas of the European part of Russia (Fig. 19). Concerning altitude, it occurs from lowland steppes to the alpine belt. *S. stepposa* usually inhabits rocky and mossy sites that are not very dry. In steppe areas of continental Asia, it is abundant in different kinds of xeric grasslands. Detailed biotopical preferences of the species in cold forest-steppe of the Vitim Plateau are given in Chimitova et al. (2010), where it appears to be the dominant steppe species. In swarms, the species can be found in atypical biotopes.

4.3. Geography of polymorphism

At present, the strongly modified males are found only in two localities (Eravninskaya and Kondinskaya basins, Fig. 19). Reproductive males with a neutral morphology were seen by us in Mongolia (topotypes), Middle Volga, and a few localities in Buryatia (Kondinskaya Basin), where epitokous populations also occur. Significant morphological differences between the different geographical populations of *S. stepposa* have not been found by us.

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