

## SCHISTOSTEGA “POLLINATORS” AND THEIR ATTRACTION

### КАК *SCHISTOSTEGA* ПРИВЛЕКАЕТ “ОПЫЛИТЕЛЕЙ”

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Abstract

*Schistostega* is a moss with long shoots terminated by one group of either male or female gametangia. Although it is usually described as dioicous, the protonemata may link such male and female shoots, and most populations comprise homogeneous mixtures of both sexes. Thus, dispersal of male gametes at a certain distance is important for *Schistostega* to avoid inbreeding. In addition to stochastic dispersal by small arthropods, male gametes of *Schistostega* attract attention of Acari of the order Sarcoptiformes, suborder Oribatida belonging to families Damaeidae, Oribatulidae, Astegistidae, and Ceratozetidae, and springtails (class Collembola) of the family Entomobryidae, genera *Entomobrya* and *Orchesella*. Short videos in supplementary material demonstrate the intentional consumption of antheridial contents of *Schistostega* by these arthropods in forests in the Moscow Province. *Schistostega* is likely the first moss where this type of nourishment is demonstrated. These events seem to be not rare, but rather difficult to overwatch in most mosses where antheridia are well protected in bud-like perigonia. Antheridia of *Schistostega* are scarcely hidden and readily accessible for microarthropods, as well as easy to observe.

Резюме

Верхушка побега у мха *Schistostega* оканчивается собранием гаметангиев одного пола, которые развиваются на общей протонеме, и в каждой дерновинке представлены оба пола. Таким образом, распространение мужских гамет на значительное расстояние, во избежание имбридинга, приобретает для *Schistostega* особое значение. Случайное распространение мужских гамет микроартроподами для мхов было известно. У *Schistostega*, однако, имеет место также привлечение панцирных клещей (из семейств Damaeidae, Oribatulidae, Astegistidae и Ceratozetidae) и коллембол (родов *Entomobrya* и *Orchesella*), поедающих мужские гаметангии – антеридии и их содержимое, которое отчасти остается на их теле и переносится на другие растения. Короткие видео-ролики в дополнительных материалах на сайте демонстрируют целенаправленное поедание содержимого антеридиев *Schistostega* клещами и коллемболами по наблюдениям в Подмосковье. Это, по-видимому, первое наблюдение такого типа питания. Вероятно, он более распространен, однако сложен для наблюдения.

KEYWORDS: Collembola, Oribatida, *Schistostega*, fertilization, microarthropod vectors, antheria content consumption

#### INTRODUCTION

Mosses is a group of plants where dioicous species are more numerous than monoicous. The monoicous condition, i.e. the position of male and female gametangia on the same plant includes a number of variants. Antheridia are either mixed in terminal inflorescences comprising the *synoicous* sexual condition; or arranged immediately around terminal group of archegonia, in this case called *paroicous*; the male inflorescence sitting on the stem at a certain distance below the female inflorescence(s), the *gonioautoicous* case (most frequent among the autoicous cases and usually reported in taxonomic literature simply as ‘autoicous’); confined to branches,

i.e. axes other than those which are terminated with female inflorescences, *cladoautoicous* case. More dubious and least studied are situations where male and female gametophores originate from the same protonemata. This is difficult to prove in nature, as after gametophore formation the protonema in most species disappears. However, at least *Schistostega pennata* (Hedw.) F. Weber & D. Mohr is an example of this condition. Its fertile shoots are terminated with one inflorescence, either male or female (Fig. 1); however, at least sometimes male and female shoots are connected to one caulonemata (Ignatov & Ignatova, 2001). This connection is difficult to demonstrate due to the fragility of the rhizoids and it is usu-

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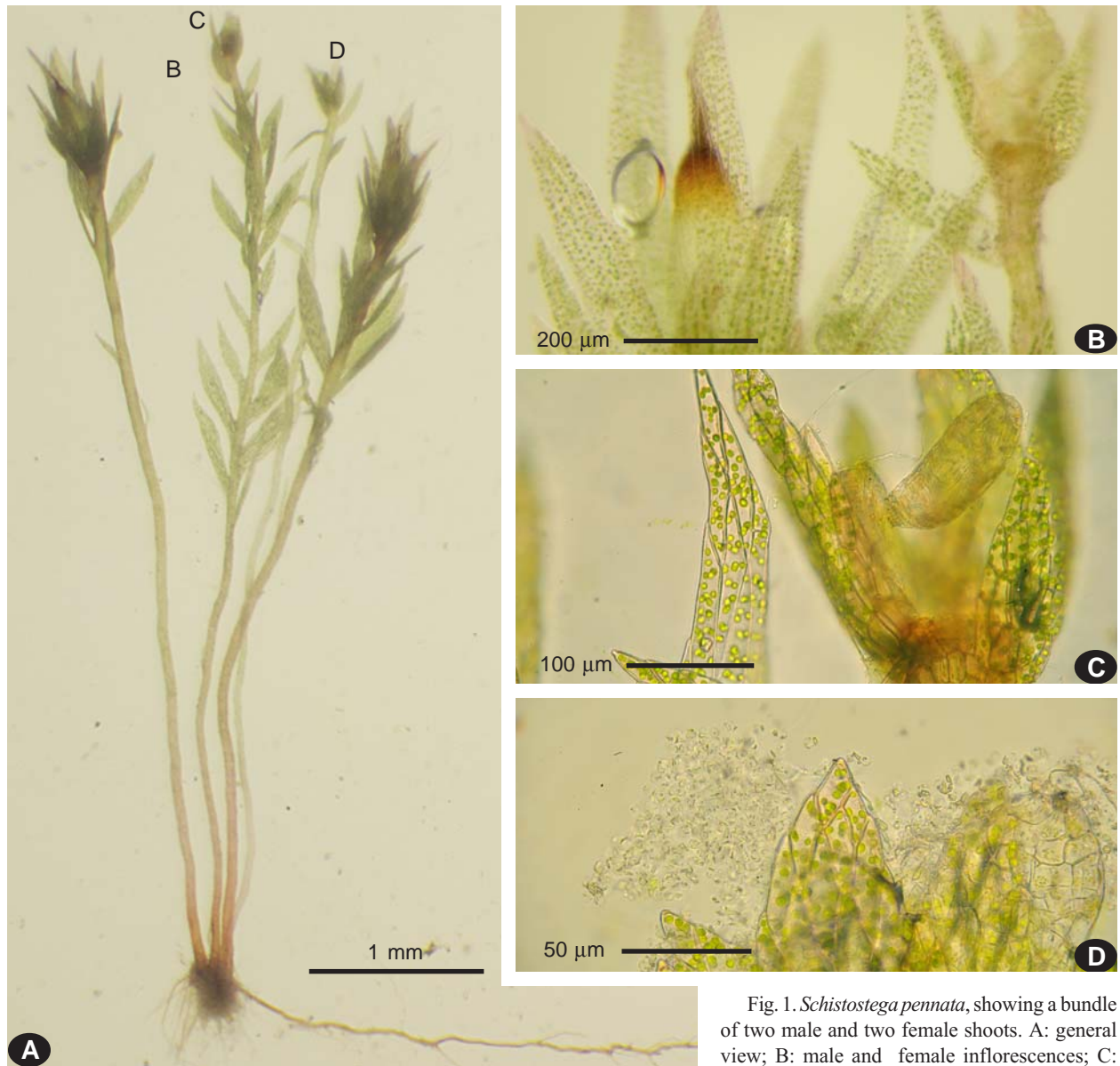


Fig. 1. *Schistostega pennata*, showing a bundle of two male and two female shoots. A: general view; B: male and female inflorescences; C: male inflorescence with two antheridia; D: antheridium with partly released spermatozoa amidst the antheridium medium.

ally difficult or impossible to disentangle their interconnections. However, where the *Schistostega* plants appear as a separate bundles apart from main tuft, they almost always comprise a mixture of male and female gametophores (Figs. 1–2). Also, shortly after fertilization, populations of *Schistostega* look as a very even mixture of male and female plants (Fig. 2). In several square decimetres we failed to find a single group where only one sex was represented.

Such arrangement of shoots, in the frequent dense growths of gametophores, often with more than hundred stems per square centimeter (Ignatov *et al.*, 2012), may cause a high degree of inbreeding, especially if intragametophytic fertilization occurs, i.e., fertilization involving males and females belonging to the same genotype. If so, mechanisms that could increase the fertilization distance – and decrease the risk of inbreeding – would

therefore be expected to be selectively advantageous.

Also, *Schistostega* often occurs in niches, protected from direct rain drops, thus the sperm requires a vector to access females. Microarthropods were proved to mediate in fertilization of mosses (Cronberg *et al.*, 2006), carrying sperms that stuck to their bodies during their crossing of ‘moss forest’ (cf. also Milius, 2006). In another publication on this issue Cronberg *et al.* (2008) suggested that protonema might attract microarthropods, while Rosenstiel *et al.* (2012) showed an effect of volatile compounds and also documented that female plants are more attractive than male ones to microarthropods. This may imply that for microarthropods male plants could be attractive by the reasons other than a volatile compound signals. Recently Shortlidge *et al.* (2021) demonstrated an even more complicated potential ability of microarthropods to provide a fitness benefit for mosses



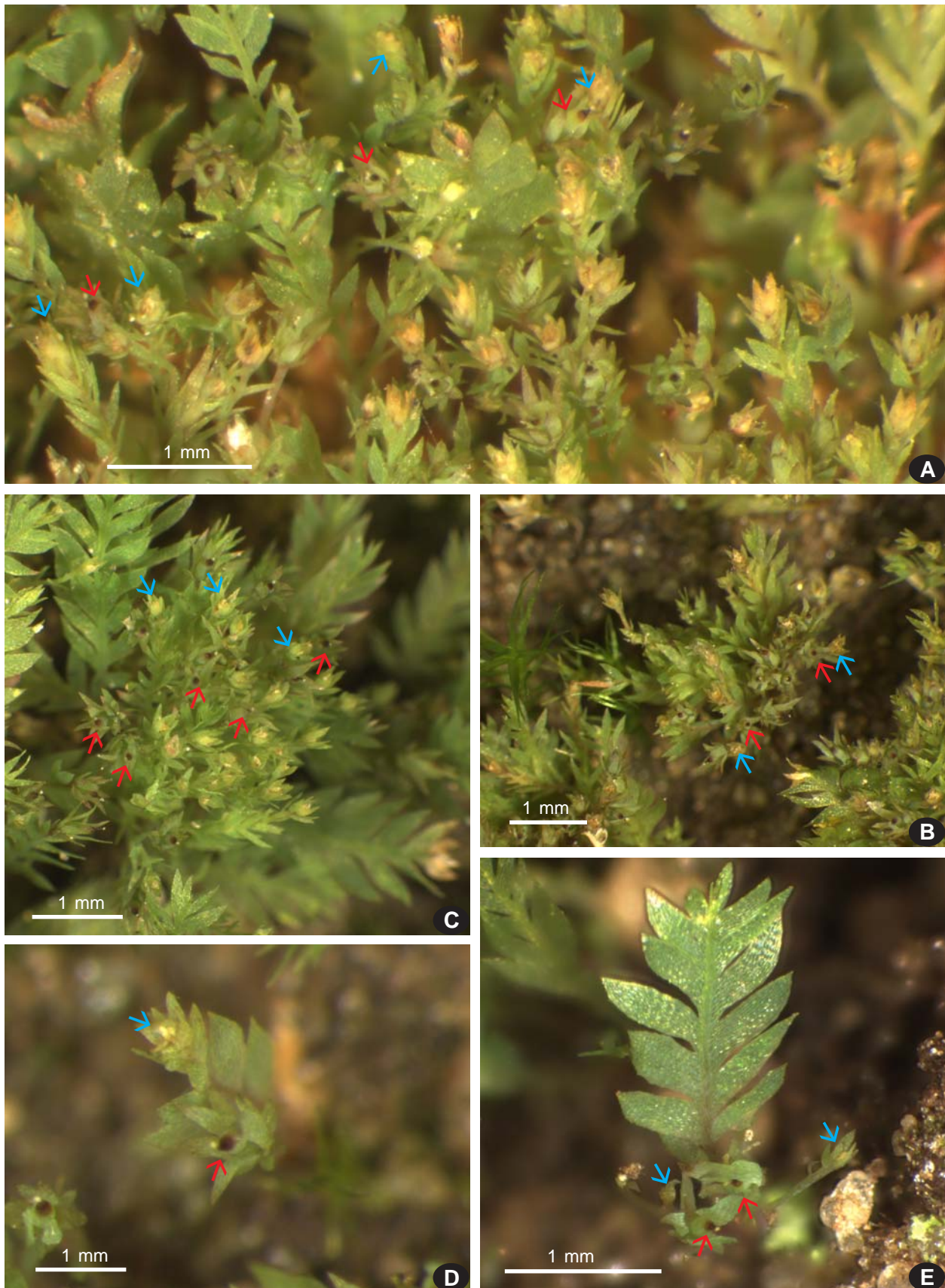


Fig. 2. *Schistostega pennata* population, showing the even proportion and fairly homogeneous arrangement of male (↙) and female (↘) gametophores. The photograph is taken four days after collecting soil pieces in the forest, where only male plants were well-seen, while fertilized archaegonia appeared and became visible during these four days of cultivation.

at genotype level. Some indirect evidence on microarthropods as vectors for sperm dispersal and likely attracted by sperm were summarized by Glime (2017a,b). There are only two modern studies based on field observations by Bisang & Hedenäs (2015) and Fjellberg *et al.* (2017). The former authors found the springtail *Xenylla humicola* (O.Fabricius, 1780) in great abundance on the moss *Tortula cernua* (Huebener) Lindb. in a place with abundant immature and mature antheridia and mature archeogonia, thus suggesting that these springtails are attracted by moss gametangia. The springtails, in return, may increase the fertilization success in this case.

Fjellberg *et al.* (2017) reported another species of the same springtail genus, *Xenylla maritima* Tullberg, 1869, curled up in an antheridial cup of *Polytrichum piliferum* Hedw. after sperm release, when the splash cup was already producing new growth from the center, indicating that the sperm had already been dispersed much earlier. Hence, we are left to wonder what attracted the springtails to this location, and do they facilitate the dispersal of sperm in the right season.

However, no direct observations were published on attractions of microarthropods by antheridia and/or sperm as food, thus our observations, though limited, could be of interest and direct the further steps in accumulation of similar observations, and enhancing methodology.

#### MATERIAL AND METHODS

##### Study area

All observation reported here were conducted in the Moscow Province, Zvenigorod Biological Station of Moscow University (ca. 55.7 N, 36.6 E). The vegetation consists mostly of hemiboreal spruce forests. Being a protected area, the number of fallen trees has increased during the last decades, and *Schistostega* appeared in the late 1990s and rapidly spread here under upturned roots of fallen trunks (Ignatov & Ignatova, 2001; Ignatov *et al.*, 2012, 2017).

##### Plant

*Schistostega pennata* has a Holarctic distribution, however its habitat requirements make the density of its populations very uneven, both spatially and temporarily. Old publications did not mention the species in Central European Russia at all (Zickendrath, 1900; Warnstorff, 1913), except one place with numerous sandstone outcrops in Kaluga Province (Zhadovsky, 1928). In Moscow Province *Schistostega* became common in 1990–2000s, settling down on soil walls at roots of fallen trees (Ignatov & Ignatova, 2001; Ignatov *et al.*, 2012).

In the Moscow Province, male gametangia become mature in late August to October. Fertilization occurs mostly in autumn, as apparent from the start of sporophyte development (cf. Fig. 2). New antheridia appear on some plants, while in dry shoots they are already dry and empty. Thus, the period of maturation is lasting no less than one month (in cultivation in microcosm no less than month and half).

##### Microarthropods

Despite that various microarthropods were observed in summer in populations of *Schistostega*, we could not see any specific feeding behaviour, except for *Kunstidamaeus*, an Oribatid mite, that climbed on *Schistostega* setae and ate spores (Ignatov *et al.*, 2017). No other species was seen to express any interest in spores of *Schistostega*.

In autumn of 2016 we found that several species of mites and springtails are regularly visiting male gametangia of *Schistostega* and feed on them, which motivated us to expand our observations of these intriguing events.

Observations were done in the laboratory at light period, after bringing big pieces of sand with *Schistostega* in plastic containers disturbing the habitat as little as possible and kept in a Sanyo Environmental Test Chamber MLR-352H: temperature +7°C/+12°C (night/day), light period 10 hours, PPFD - 14 mmolm<sup>-2</sup>s<sup>-1</sup> for three weeks.

In August–September 2021 these observations were repeated, revealing a very similar set of events. The difference in observational conditions was only that the plastic containers were bigger and kept at the open window with temperatures 10–15°C, i.e. similar to the environment in the forest at this time of the year.

Observations were conducted several times for two to six hours in lab conditions no less than one and a half month in microcosms.

As the animals were few and the antheridium feeding events were infrequent and difficult to properly document by still photos, we collected a number of short videos under an Olympus CZX-16 equipped with an Infinity4-4 digital camera, with 0.3x and 1.6x objective lenses. Videos were taken for 1' or 0.5' in the \*.avi files (1': 3 Gb), at 1944 x 2556 px. During video capturing the focus was manually adjusted to show the events more clearly.

Photos in this paper are mostly extracted from these videos, thus being of moderate quality at best.

#### RESULTS

The microarthropods eating gametangia of *Schistostega* are shown in Table 1. Some others were obser-

Table 1. Microarthropodes observed eating antheria content

Family	Species	Observad/Attracted	Eating in minutes (! video taken)
<b>Acari, order Sarcoptiformes, suborder Oribatida</b>			
Damaeidae	<i>Kunstidamaeus lengersdorfi</i> (Willmann, 1932)	50 / 5	>5!, >3!, 0.7!, 0.3!, 0.1
Astegistidae	<i>Furcoribula furcillata</i> (Nordenskiöld, 1901)	4 / 2	>10!, >1!
Oribatulidae	<i>Oribatula tibialis</i> (Nicolet, 1855)	10 / 4	>2!, >2!, >1!
Ceratozetidae	<i>Melanozetes mollicomus</i> (C.L. Koch, 1839)	1	>5
<b>Hexapoda, Class Collembola, order Entomobryomorpha</b>			
Entomobryidae	<i>Entomobrya nivalis</i> (Linnaeus, 1758)	10 / 4	>2!, >1!, >0.5!
Entomobryidae	<i>Orchesella bifasciata</i> Nicolet, 1842	7 / 2?	0.1, 0.1



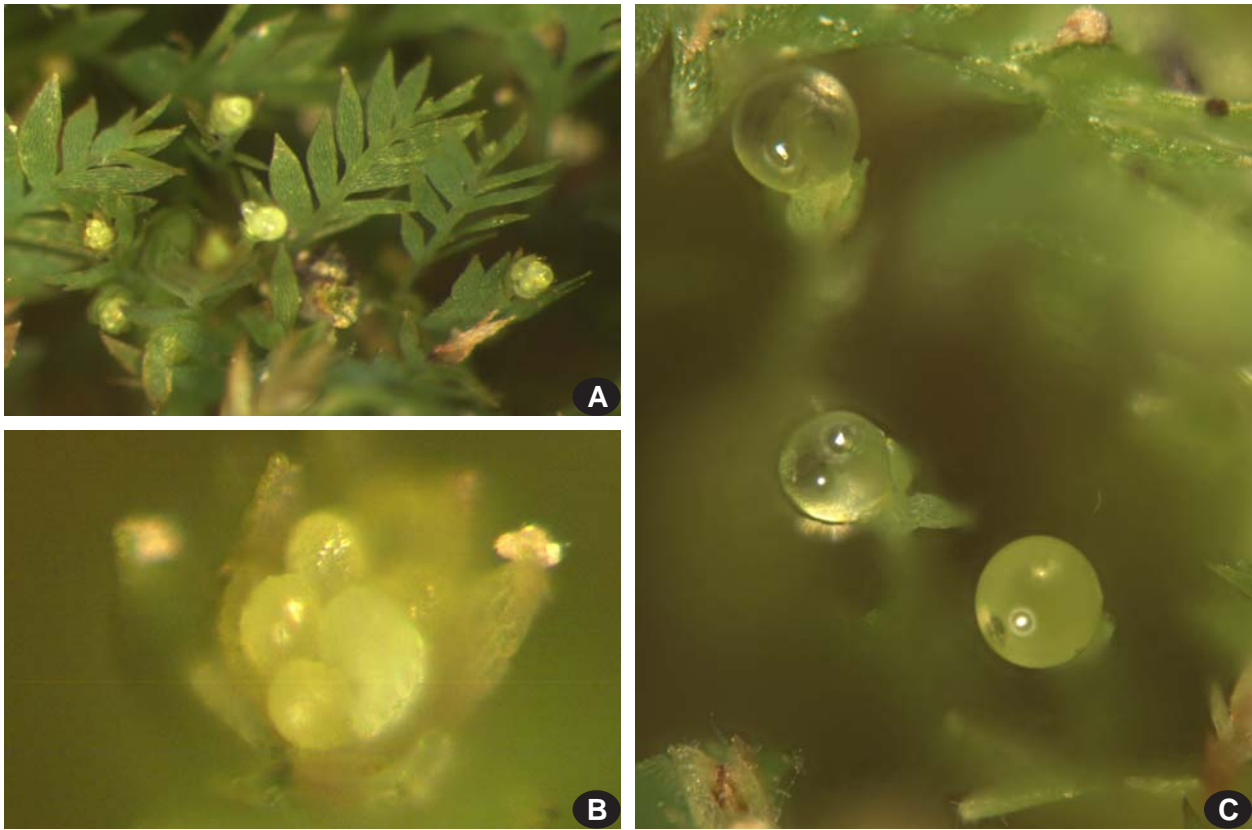
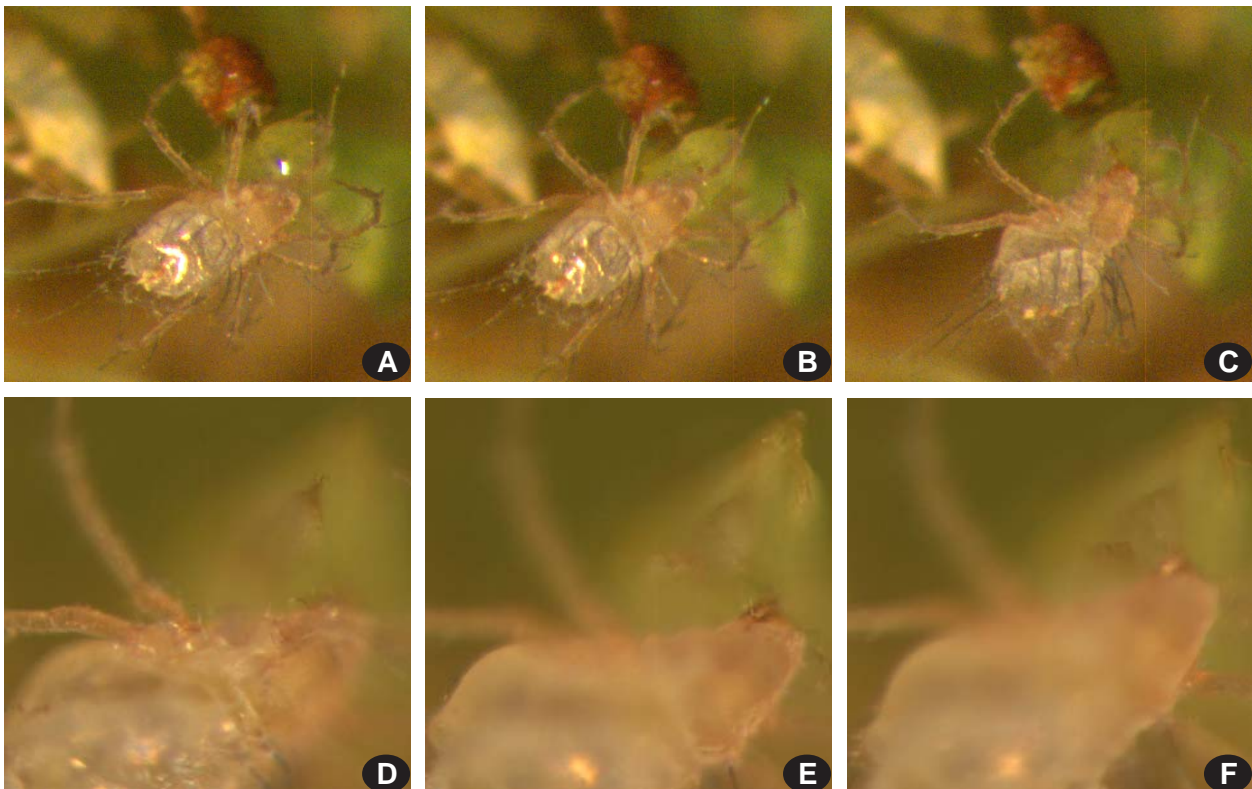


Fig. 3. Male shoots of *Schistostega pennata*, terminated with antheridia, often acquiring a drop, that is transparent at first but after 10–30 minutes becoming muddy because of discharging of antheridia content into water.

Fig. 4. Young *Kunstidamaeus* approaches *Schistostega* antheridia and eats their contents. Video: [https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30\\_451\\_462\\_SM\\_Kunstidamaeus\\_1a.mp4](https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30_451_462_SM_Kunstidamaeus_1a.mp4) (A–C); after 1': same (enlarged)...\_SM\_Kunstidamaeus\_1b.mp4 (not shown here); after one more 1': same (more enlarged)...\_SM\_Kunstidamaeus\_1c.mp4 (D–F).



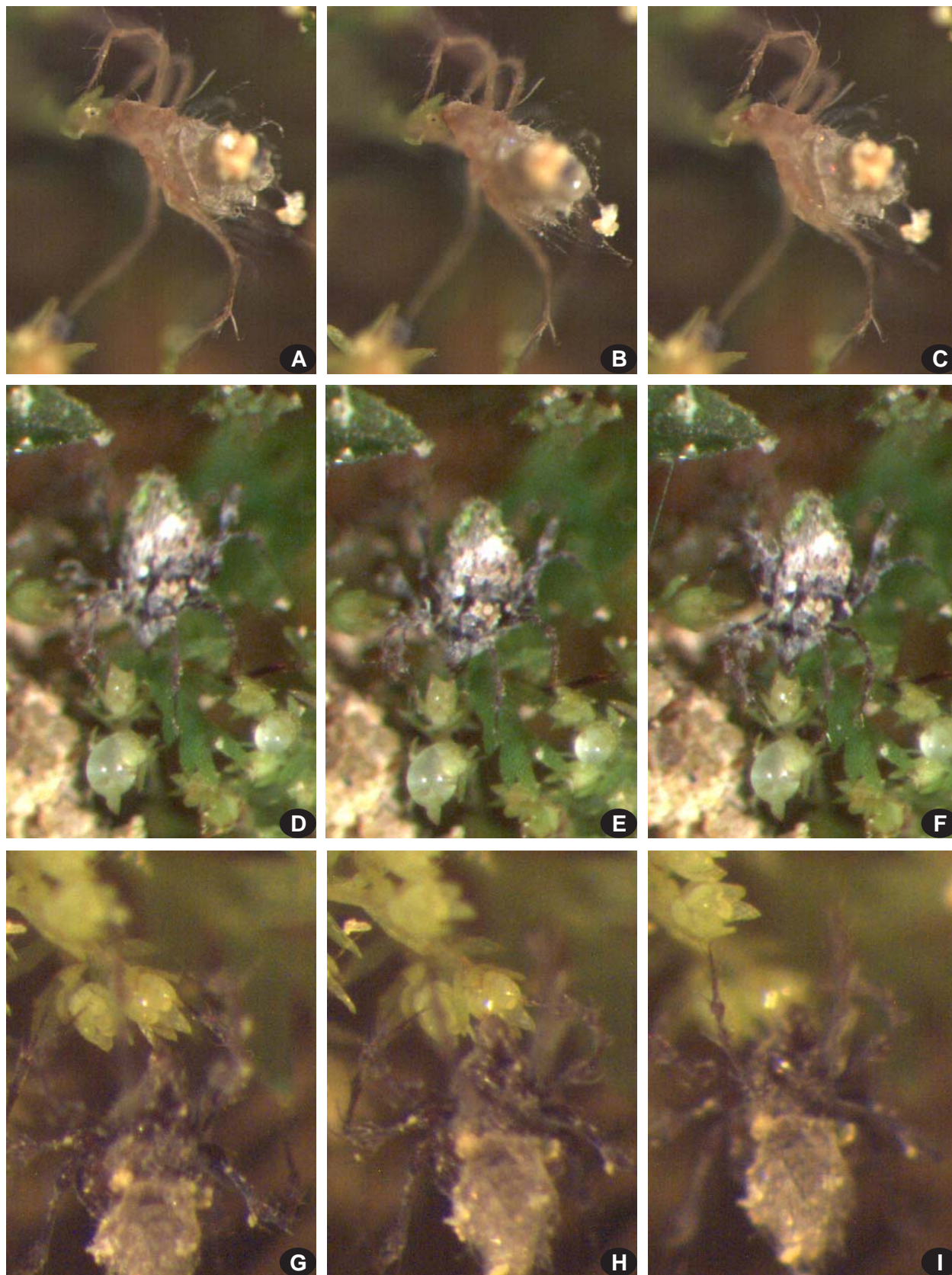


Fig. 5. Young, still pale (A–C) and old, dark gray (D–I) *Kunstidamaeus* mites approach *Schistostega* antheridia and eat their contents. A–C: Video: [https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30\\_451\\_462\\_SM\\_Kunstidamaeus\\_2.mp4](https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30_451_462_SM_Kunstidamaeus_2.mp4); (D–F): same ...\_SM\_Kunstidamaeus\_3.mp4; (G–I): same ...\_SM\_Kunstidamaeus\_4.mp4.



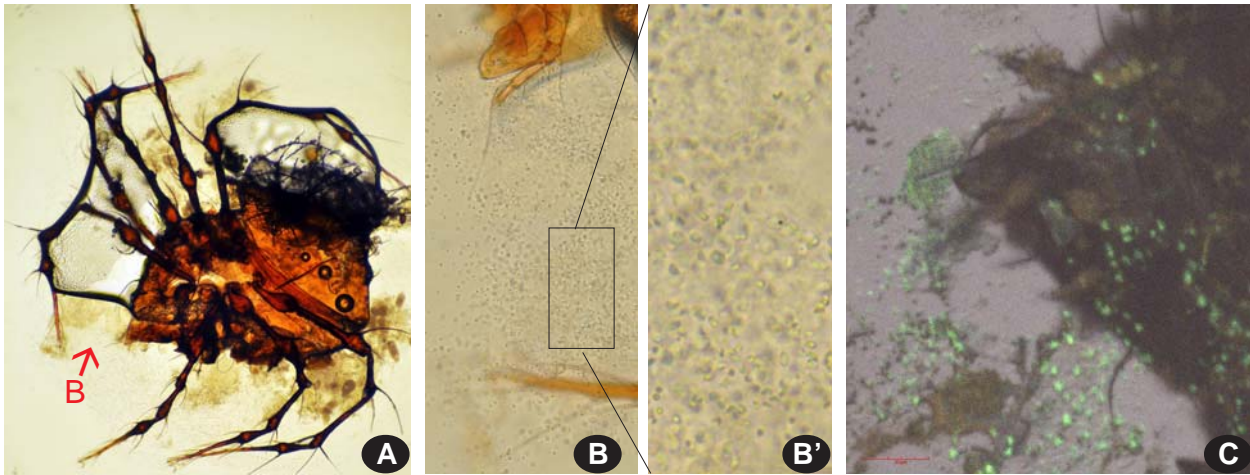


Fig. 6. Adult *Kunstidamaeus* shown in Fig. 5G–I and Video: [https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30\\_451\\_462\\_SM\\_Damaeidae\\_4.mp4](https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30_451_462_SM_Damaeidae_4.mp4), collected immediately after leaving *Schistostega*, put under cover glass (A), showing spermatozooids around its proterosoma (B and magnified B': compare B' with Fig. 1D), and after several hours photographed after DAPI staining, showing DNA-containing units (bright cyan in C).

ved within *Schistostega* at the time of antheridia maturation; they are mentioned in the text. Details of the observations described below. Among them, collembolan species, members of *Entomobrya* and *Orchesella* are atmobionts (i.e. spending considerable time on plant bases, above the litter). Some other species observed on the ground and on *Schistostega*, are mostly litter species (Collembola: *Tomocerus* s.l., Oribatida: *Steganacarus carinatus* (C.L. Koch, 1841), and probably *Kunstidamaeus lengersdorfi*), or hemiedaphic entities (Collembola: *Lepidocyrtus*; Oribatida: *Oribatula*, *Melanozetes*, and *Furcoribula*). Being common among *Schistostega* in our samples, these hemiedaphic species are known among bryophytes elsewhere, while *Furcoribula* (as well as *Orchesella*) occur also on trees.

The observations revealed most events of antheridia eating after several days of keeping living material in the laboratory, when many shoots developed mature antheridia at their apices (Fig. 3). Also drops of fluid were observed on some shoots, being transparent first and becoming opaque during 15–30 minutes, apparently due to discharging of the antheridial contents.

Details of the observations on microarthropods are as follow:

#### **Oribatida, Damaeidae**

*Kunstidamaeus lengersdorfi* was identified by late E.A. Sidorchuk (Ignatov *et al.*, 2017), as a first record from Russia of this Central European strictly cavernicolous species (Mico & Mourek, 2008). It was common in many populations of *Schistostega* in summer time, and for our autumn observation we attributed mites to the same species name (Figs. 4–6). This rather big mite (740–850  $\mu\text{m}$ ), with slow wobbly gait, climbed *Schistostega* with difficulty. When reaching the antheridia, the mite spent several minutes eating them (Fig. 4). However, in many cases *Kunstidamaeus* experienced diffi-

culties in climbing, gave up and moved to the ground. When reaching the soil level, it moved more directly and ‘intentionally’ towards the antheridia on lower shoots shortly above ground (Fig. 5). Feeding often continued half a minute to a minute, i.e. was quite short, probably because at this time, living in an area full of such food, *Kunstidamaeus* mites were simply not hungry.

One individual, shown in Fig. 5G–I, was put under cover glass and photographed in the compound light microscope to show spermatozooids around its “head” or proterosoma (Fig. 6B and magnified B'), and in addition photographed after DAPI staining in a Laser Confocal Scanning Microscope Olympus FW-1000, showing DNA-containing units, likely spermatozooids (Fig. 6C).

Interactions of *Kunstidamaeus* with *Furcoribula* are described below.

#### **Oribatida, Astegistidae**

*Furcoribula furcillata* was observed two times (Fig. 7A–C). Later, one female (from Fig. 7A) was mounted (Fig. 8A, B). This was a rather large female (590–650  $\mu\text{m}$ ). The species is Holarctic in distribution (Weigmann, 2006), living in forests and is regularly recorded within moss cover on trees (Ermilov, 2004; Ermilov & Chistyakov, 2007). Feeding behaviour appeared passive and slow, lasting for more than 10 minutes on one shoot. A big piece of plant tissue, likely a part of a torn antheridium was seen in the mite esophagus. The content of the esophagus includes various spores (10–11 $\times$ 10–11  $\mu\text{m}$ , 12–15 $\times$ 9–12  $\mu\text{m}$ , and small ellipsoidal ones 7–10 $\times$ 4–6  $\mu\text{m}$ ), some of them may belong to *Schistostega*, where they are in average 8–10 $\times$ 6–8  $\mu\text{m}$ . A granular mass in the exofagus looks quite comparable with *Schistostega* antheridium contents shown in Fig. 1D, and in Fig. 6B, where antheridium content was shown from the *Kunstidamaeus* pharynx photographed immediately after this mite ate it ([https://kmkjournals.com/upload/video/Arctoa/Arctoa30\\_451\\_462\\_SM\\_Kunstidamaeus\\_4.mp4](https://kmkjournals.com/upload/video/Arctoa/Arctoa30_451_462_SM_Kunstidamaeus_4.mp4)).

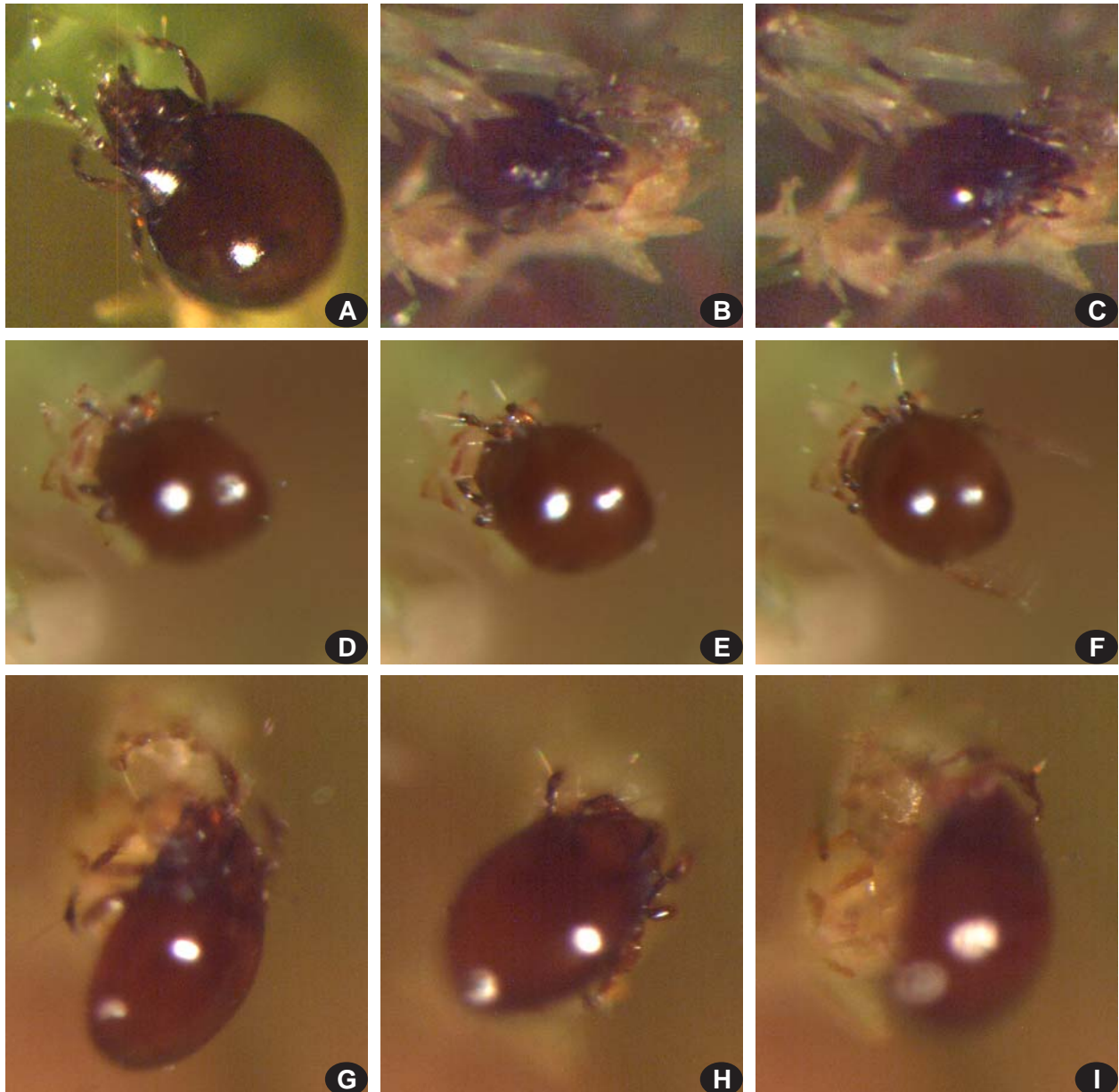


Fig. 7. *Furcoribula furcillata* (A–C) and *Oribatula tibialis* (D–I) mites approach *Schistostega* antheridia and eat their contents. A: Video: [https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30\\_451\\_462\\_SM\\_Furcoribula\\_1a.mp4](https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30_451_462_SM_Furcoribula_1a.mp4) (see also next minute, enlarged ...\_1b.mp4; B–C: ...\_SM\_Furcoribula\_1a.mp4 (see also next minute, enlarged ...\_SM\_Furcoribula\_2.mp4; (D–F): ...\_SM\_Oribatula\_3.mp4; (G–I): ...\_SM\_Oribatula\_5.mp4 (see also similar ...SM\_Oribatula\_4.mp4, not shown here).

#### *Oribatida, Oribatulidae*

*Oribatula tibialis*, a relatively small mite (410–530  $\mu\text{m}$ ), its female was studied (Fig. 8C, D). This species is a cosmopolite and eurybiontic, mainly fungivorous with episodic necrophagy (Antor & Garcia, 1995; Smrž, 2010). Since it is small, it eagerly tried to dig itself into the antheridium mass (Fig. 7D–F), and the event of eating continued for more than five minutes (Fig. 7G–I). As compared with *Furcoribula*, *Oribatula* also moves across the ‘*Schistostega* forest’ faster than any other of the observed mites.

#### *Oribatida, Ceratozetidae*

*Melanozetes mollicomus* was observed once (Video: <https://kmkjournals.com/upload/video/Arctoa/30/>

Arctoa30\_451\_462\_SM\_Melanozetes\_6.mp4), a medium sized female (460–590  $\mu\text{m}$ ). It is Holarctic in distribution, and is mostly the forest and a peatland dweller (Weigmann, 2006), associated with different mosses, and their vegetative parts are palatable food for its development (Shaldybina, 1967; Smrž, 2010) though same tendency to necrophagy also exists (Smrž, 2010). It was collected on peaty soil covering upturned roots in a spruce forest with *Sphagnum*. Feeding behaviour looked passive and slow, lasting for more than 10 minutes.

#### *Mite competition*

A putative competition between mites for the source of this food was observed only once (Fig. 9A), when *Kun-*



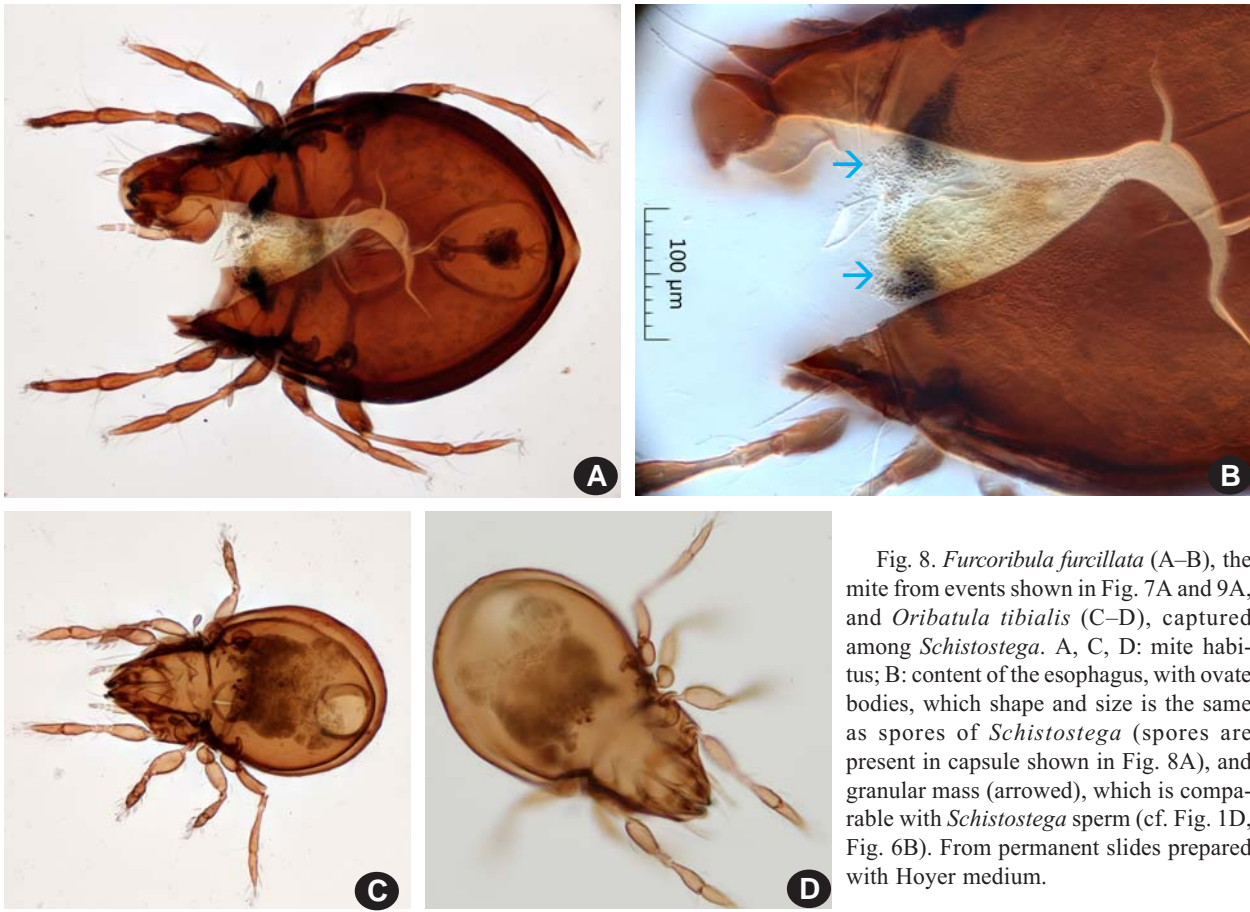


Fig. 8. *Furcoribula furcillata* (A–B), the mite from events shown in Fig. 7A and 9A, and *Oribatula tibialis* (C–D), captured among *Schistostega*. A, C, D: mite habitus; B: content of the esophagus, with ovate bodies, which shape and size is the same as spores of *Schistostega* (spores are present in capsule shown in Fig. 8A), and granular mass (arrowed), which is comparable with *Schistostega* sperm (cf. Fig. 1D, Fig. 6B). From permanent slides prepared with Hoyer medium.

*stidamaeus* slowly climbed up on a moss shoot near *Furcoribula furcillata* (shown in Fig. 7A) and kicked it with its leg, without any obvious success or any other response (*Furcoribula* continued antheridium eating). Immediately after that, *Kunstidamaeus* moved away, but slowly, as usual, by its typical non-hurried wobbly gait.

#### Attraction by female plants

Rosenstiel *et al.* (2012) found that microarthropods are more attracted by female than male plants of the dioicous moss *Ceratodon*.

We noticed intentional visiting of female shoots of

*Schistostega* with unfertilized (?) archegonia only once by *Kunstidamaeus*. However, that plant had some mycelium at the shoot top, and it is thus not clear if the mite was more interested in *Schistostega* or in the fungus. It spent more than a minute picking at something on the shoot top.

*Furcoribula furcillata* climbed the top of shoots with recently fertilized archegonia/juvenile sporophytes (Fig. 9B, C) and spent about a minute there, 'looking for something', then slowly descended and walked away. That was the only observation, not necessarily relevant to the present subject. We decided to mention this because very



Fig. 9. Mite competition and attraction by female plants. A: *Kunstidamaeus* approaching to *Furcoribula* (same as in Fig. 7A) that sits and eats antheridium; then *Kunstidamaeus* attacks *Furcoribula*, kicking it by leg (not shown), but without success. B–C: *Furcoribula* climbing and sitting on the top of female shoot with archaegonium, fertilized few days before.

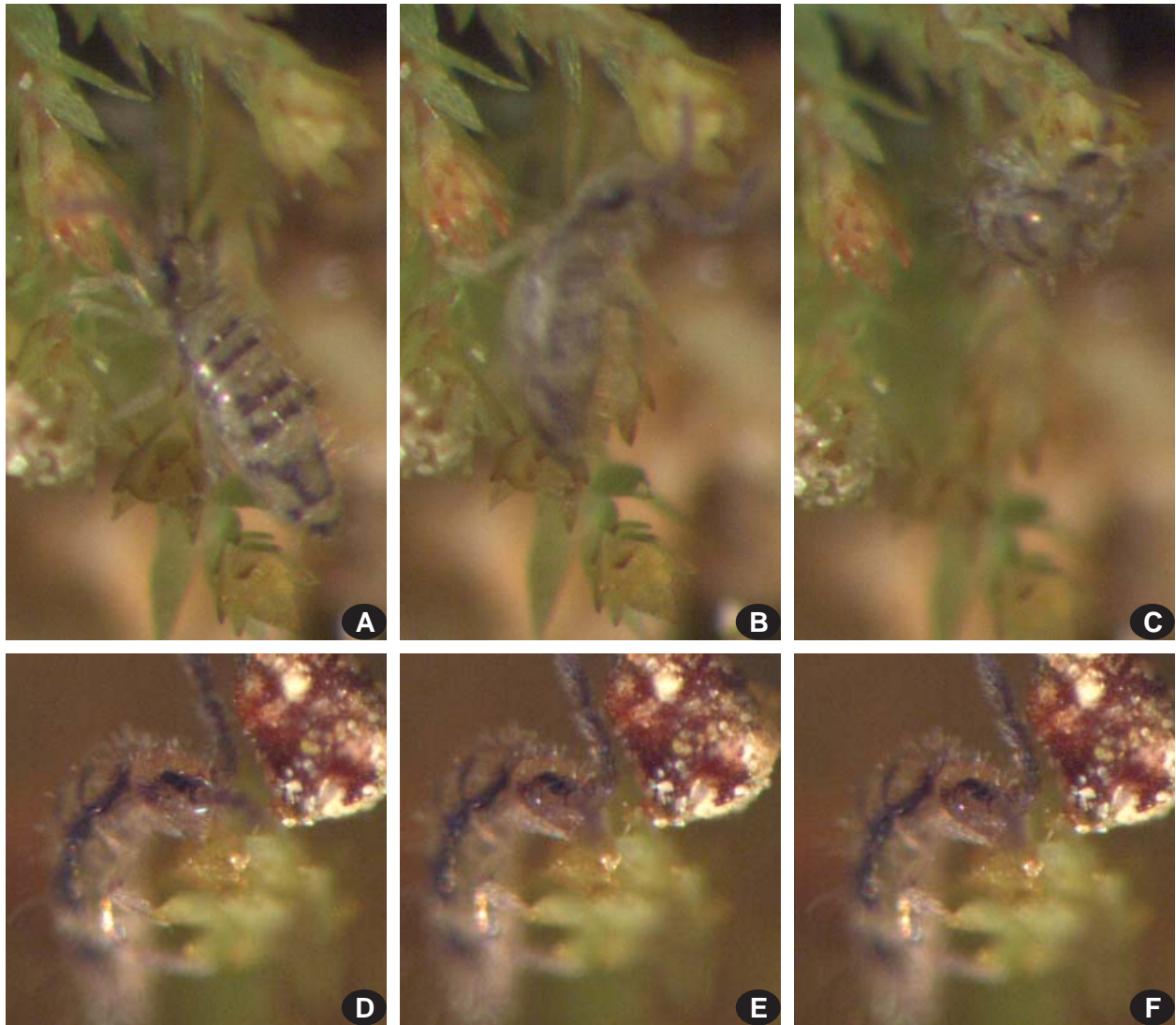


Fig. 10. *Entomobrya nivalis* springtails approach *Schistostega* antheridia and eat their contents. A–C: Video: [https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30\\_451\\_462\\_SM\\_Entomobrya\\_1a.mp4](https://kmkjournals.com/upload/video/Arctoa/30/Arctoa30_451_462_SM_Entomobrya_1a.mp4) and continue, ...\_SM\_Entomobrya\_1b.mp4 (not shown here); D–F: ...\_SM\_Entomobrya\_2.mp4.

close to the female shoot there were two male plants terminated with antheridia clusters at the stage that looked maximally attractive, while the mite was not interested in the latter.

#### *Collembola, Entomobryidae*

We detected interest to antheridia of *Schistostega* in only two species of the genera *Entomobrya* and *Orchesella*, both represented by common species, readily identifiable by photo and video.

*Entomobrya nivalis* is the only species for which we observed several visits of antheridia (Fig. 10A–C) and a rather long period of sitting and eating antheridia of *Schistostega* (Fig. 10D–F).

*Orchesella bifasciata* kicked the antheridial clusters by its head several times when passing them, but it ran too fast for us to take a picture. Although we got the impression that it bit the antheridia, this observation is somewhat uncertain. *Entomobrya* was also fast-moving

and only three short videos were successfully captured at a single occasion.

#### DISCUSSION

Arthropods are the main consumers of plants; however, their damage to bryophytes is far smaller than that of vascular plants. Most records refer to Diptera and Coleoptera larvae feeding on aquatic and stream-side mosses, apparently generalists, not feeding on any particular species (as summarized by Glime (2017).

Obligate bryophagy among terrestrial arthropods is obviously rare, occurs sporadically and is common only in several major taxa of insects and Acari. For most North American pill beetle (Byrridae), the bryophagy is certainly obligate (Johnson, 1991). It is also known for all species of Peloridiidae, Hemiptera (Burckhardt, 2009) and proved for some Boreidae species (larvae and adults), Mecoptera (see Hågvar, 2010; summarized). Other insect cases comprise separate genera or species belonging



to Armatopidae (Coleoptera), Tipulidae and Chironomidae (Diptera), Micropterygidae and Pyralidae (Lepidoptera), Tingidae (Heteroptera) (Johnson, 1987). Among trombidiform mites, the obligate bryophagy is an appanage of the genus *Eustigmaeus* (= *Ledermuelleria*), Stigmaeidae (Gerson, 1972), and family Penthaldodidae (Walter & Proctor, 2013). For oribatid mites, only single evidence of the obligate bryophagy (on liverwort) of the member of *Birobates*, Oripodidae, is known (Colloff & Cairns, 2011).

Reinard Schuster (1956) was likely the first who found the remnants of vegetative moss tissue in the guts of four oribatid mite species. Woodring (1963) reported several oribatid mite species reared on moss. Gerson (1969) observed unidentified oribatids to gnaw the capsules of various mosses and to feed upon the spores. However, the first direct observation of spore consumption was reported by Ignatov *et al.* (2017), who provided evidence that moss spores may be intentionally used as food by *Kunstidamaeus lengersdorfi*.

In studies of gut contents of Collembola (Davidson & Broady, 1996; Ponge, 1986), moss fragments (from *Tortella tortuosa* (Schrad. ex Hedw.) Limpr. and *Pseudoscleropodium purum* (Hedw.) M. Fleisch.) were frequent. The proportion of the fragments is especially high if the collembolan species living in moss cushions (Varga *et al.*, 2020). The mosses are also the common food for Collembola of glacier forelands where the barren ground is covered with the scattered windblown fragments of gametophytes (Hågvar, 2012).

The consumption of antheridium content remains a little-known topic because in most cases such male organs are well packed inside perigonal leaves, which makes them both difficult to access for sperm consumers, and difficult to observe in intact moss carpet. Cronberg (2012) presumed the attraction of microarthropods by lipids from antheridia. Paolillo (1979) provided data on the lipid contents in three moss species.

*Schistostega* is an exceptional moss, lacking the mentioned inconvenience for observations. It is simply surprising how these tiny plants expose their male gametangia with the substance so crucially important for procreation. It seems, however, that the risk is not that big, as potential consumers are few. *Schistostega* is so delicate, that only few microarthropods are able to reach the shoot tops by climbing. For larger insects, the antheridia, which usually occur by 2–6 per plant, are too small. Also, vertical soil banks in the habitats of *Schistostega* are unstable, and few species are able to move there.

Microarthropods that were noticed consuming the antheridium content are polyphagous. Certainly, a specialization to the sperm nourishment cannot be very narrow, as the sperms are only temporarily available, in the Moscow area during a period of about a month to a month and half in the be-

ginning of the autumn, with night temperatures not or only rarely dropping below zero during night.

One of the most striking results was that the species consuming antheridia were the same during the two observation periods in 2016 and 2021. Springtails and mites are also the main arthropods discussed in the literature regarding moss sperm dispersal (Bisang & Hedenäs, 2015; Cronberg, 2012; Cronberg *et al.*, 2006, 2008; Glime, 2017a,b). Although data is limited, it is maybe worthy noting that unlike other mentioned microarthropods, *Kunstidamaeus* consumption of antheridia was observed by both adults and nymphs.

We hope that the present report will increase the interest in the subject and provoke further studies that may reveal more details of the chemistry of attraction and repelling.

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