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ON THE REPRODUCTIVE BIOLOGY OF PTILIUM CRISTA-CASTRENSIS (PYLAISIACEAE, BRYOPHYTA)

К РЕПРОДУКТИВНОЙ БИОЛОГИИ PTILIUM CRISTA-CASTRENSIS (PYLAISIACEAE, BRYOPHYTA)

VIKTORIA V. TELEGANOVA[1,2] & MICHAEL S. IGNATOV[2]

ВИКТОРИЯ В.ТЕЛЕГАНОВА[1,2], МИХАИЛ С. ИГНАТОВ[2]

Abstract

Ptilium crista-castrensis – dioicous pleurocarpous moss with ascendent to erect stem; mature gametangia are situated on parts of shoots of the second year, and sporophytes occur on parts of shoots of the third year. Female gametangia-bearing plants are 20% larger on average than male gametangia-bearing plants, while sterile plants of both genders do not differ in size from each others. At the same time, the percent of sterile plants within male populations is smaller than in female populations. In most parts of Russia the proportion of male and female collections in herbaria is close to equal; however, in the severe climate of Arctic and Yakutia, male plants are very rare and female plants prevail.

Резюме

Ptilium crista-castrensis – двудомный бокоплодный вид с восходящим до прямостоячего ростом, у которого развитые гаметангии располагаются на участках побегов второго года, развитые спорофиты – на участках побегов третьего года. Показано, что женские растения в среднем на 20% крупнее мужских, но в то же время стерильные мужские и женские растения сходны по размерам, то есть женские генеративные отличаются от женских стерильных сильнее, чем мужские генеративные от мужских стерильных. При этом процент стерильных мужских растений в мужских популяциях значительно ниже, чем процент стерильных женских в популяциях женских растений. В большинстве районов России соотношение полов примерно равное, однако в наиболее суровых условиях Арктики и Якутии количество мужских растений резко сокращается.

INTRODUCTION

About half of the mosses are dioicous (Longton & Schuster, 1983; Wyatt, 1982), but the description of sexual dimorphism is a subject that remains almost unexplored in mosses. In acrocarpous mosses with terminal gametangia, the appearance of male and female plants is often obviously different, as their perigonia and perichaetia contribute much to plant habit. Perigonial leaves are in general shorter and more shortly acute or acuminate comparatively with perichaetial leaves, thus male and female plants of many *Bryum*, *Dicranella*, *Polytrichum*, etc. can be easily recognized by their habit in the field. At the same time, perigonia and perichaetia in pleurocarpous mosses are lateral and usually quite inconspicuous, especially in plants with relatively large leaves. The difference between male and female plants of pleurocarpous taxa probably was never a subject of special studies, as they are thought to be identical in structural and dimensional vegetative characters. At least taxonomic treatments never include separate descriptions of male and female plants unless the male is a dwarf male.

[1] – National Park “Ugra”, Prigorodnoe lesnichestvo, Kaluga 248007 Russia – Россия 248007 Калуга, пос. Пригородное лесничество, Национальный парк “Угра”; teleganovavika05@rambler.ru

[2] – Main Botanical Garden of Russian Academy of Sciences, Botanicheskaya, 4, Moscow 127276 Russia – Россия 27276 Москва, Ботаническая, 4, Главный ботанический сад РАН; misha_ignatov@list.ru

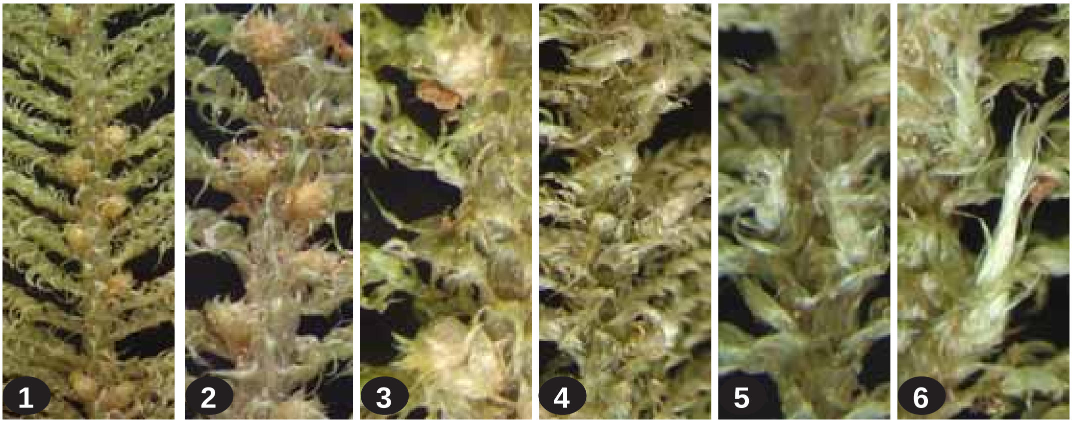


Fig. 1. *Ptilium crista-castrensis:* 1-3 – perigonia (from lower side of shoot); 4-6 – perichaetia (from upper side of shoot).

Sex distribution in pleurocarpous mosses was recently the subject of an overview of Bisang & Hedenäs (2005) who demonstrated that various ways of evaluation reveal the female bias in most mosses. They did not include in their paper *Ptilium crista-castrensis* (Hedw.) De Not. because of lack of data. This moss attracted our attention because of a relative ease of sex determination in the field and also because a preliminary study revealed that many populations in Moscow Province have strong male bias.

Ptilium crista-castrensis is a widespread moss of boreal forests, occurring on litter or rotten logs at late stages of decomposition. It is known in most regions of Russia, excepting the most xeric ones.

Ptilium crista-castrensis is a dioicous pleurocarp classified in Hypnaceae (Goffinet & Buck, 2004) or Pylaisiaceae (Ignatov & Ignatova, 2004). Plants are rather robust, stems densely regularly pinnate in one plane, ascending to erect, usually inclined making 45-85° with soil surface; this angle, as well as secund leaves, makes unequivocal the understanding of the upper and lower surfaces of the stem. Gametangia are restricted to stems; perigonia are always situated on the lower-lateral surfaces of stems and faced downward, whereas perichaetia develop on lateral or even low-lateral surfaces of stems, but in both cases turn to an upright position (Fig. 1). This distinctive appearance makes the gender determination easy in the field with just a hand lens (or sometimes even by naked eye when mature perigonia are colored and conspicuous on the lower surface of stems).

MATERIAL AND METHODS

Three approaches were used in the present study: (1) 'large-samples study'; (2) study of herbarium collections, and (3) gender mapping in plots.

Large-samples study

In 2006 we studied a number of rather large samples gathered in European Russia (Moscow, Kaluga and Vologda Provinces), and Sakhalin in Russian Far East (Table 1). Altogether 7 male and 8 female samples were studied. Sterile plants from male populations were considered as sterile males and, correspondingly, sterile plants from female populations were considered as sterile females. In the further discussion we will call "sterile males" and "sterile females" for these unisexual populations. 235 male, 151 sterile male, 312 female and 250 sterile female plants were measured during this large-samples study (see Table 1 for details).

In addition to gender identification, we measured length of branches (maximal length for given plant, accuracy 0.5 mm) and determined branch density (number of branches per 1 cm of stem at level of longest branch). Branch length was measured for both gametangia-bearing plants and sterile ones from the same tuft.

Results were analyzed in PAST 1.81 (Hammer et al., 2008); Mann-Whitney test was used for evaluation of differences between genders (α=0.05).

Herbarium study

The spatial distribution of sexes in *Ptilium* and its sexual dimorphism were studied also by herbarium materials from MHA, MW, LE, PTZ, PZV. Altogether 372 specimens with expressed sex from the territory of Russia were investigated (Table 2).

Herbarium collections were analyzed for the

Table 1. Data of ‘large-samples study’. Asterisk * indicates bisexual collection where sterile plants were probably of both genders; M–male; F–female. N – number of plants used for measurements; number of plants used for gender determination is somewhat larger (n, last column); ci – confidence interval of 0.95.

locality	N		**branch length, mm mean±ci**		**number of branches on 1 cm of stem mean±ci**		**difference between branch length in fertile and sterile plants, mm**		**plants with expressed sex, % of studied plants (n)**		
	fert	ster	M	F	M	F	M	F	M	F	n
European Russia	50	50	8.78±0.42		8.74±0.37		0.4		35.37		311
Vologda	55	50		10.47±0.38		10.22±0.26		3.3		11.04	534
60°00’N. 38°30’E	40	50		12.38±0.62		9.05±0.39		3.2		14.49	276
	50	30		11.34±0.48		9.53±0.40		3.3		41.91	303
European Russia	20	20	9.86±0.43		9.6±0.58		1.3		19.8		101
Moscow	37	20		10.69±0.40		10.97±0.59		1.9		36.63	146
(Zvenigorod)	30	20	9.12±0.79		9.23±0.43		2.3		69.86		109
55°42’N. 36°43’E	15	20		11.7±0.57		10.6±0.42		4.4		12.88	101
	35	14	10.67±0.78		9.49±0.36		2.9		87.16		132
	35	20		10.71±0.50		9.4±0.39		3.9		12.57	183
European Russia	35	20	8.1±0.62		10.23±0.39		0.3		85.8		169
Kaluga	30	19		13.32±0.61		10.1±0.47		4.6		30.67	122
53°55’N. 35°45’E	35	20	9.37±0.56		10.13±0.35		1.4		42.11		163
	30	21		11.98±0.62		9.5±0.40		3.4		23.81	210
Asian Russia.	30	7	7.43±0.74		10.97±0.56		1.2		94.57		129
Sakhalin	30	20		10.63±0.49		14.55±0.46		2.1		37.04	108
50°45’N. 143°18’E											
	m/f	sm/sf									
Total:	235/312	151/250	9.01±0.27	11.35±0.20	9.27±0.15	10.19±0.21	1.40±0.87	3.34±0.70	62.10±27.24	24.56±9.43	

Region	M	F (c.fr.)	mixed (c.fr.)
ARC	1	5	2 (1)
ARC-ESIB	1	5 (1)	0
ARC-FE	1	2	0
ARC-WSIB	4	7	0
ARC-YAK	5	10	0
C	20	21(7)	7 (4)
CAUC	8	6 (1)	0
E-SIB	5	2	5 (4)
NE	5	12 (1)	7 (7)
N-FE	3	2 (1)	0
N-UR	3	2	1 (1)
NW	29	44 (6)	6 (4)
SE	2	0	0
S-FE	10	11 (7)	1 (1)
S-SIB	21	13 (4)	9 (9)
S-UR	16	13 (2)	2 (2)
W-SIB	8	9 (5)	1 (1)
YAK	1	23 (4)	1 (1)
Total	143	187 (39)	42 (35)

Table 2. Herbarium collections of *Ptilium* from regions of Russia, cf. Fig. 2. M – male, F – female, c.fr. – with sporophytes (number in parenthesis indicates how many collections have sporophytes; number before parenthesis – total number of collections). Collections with sporophytes, but without male plants were referred to female (cf. however text).

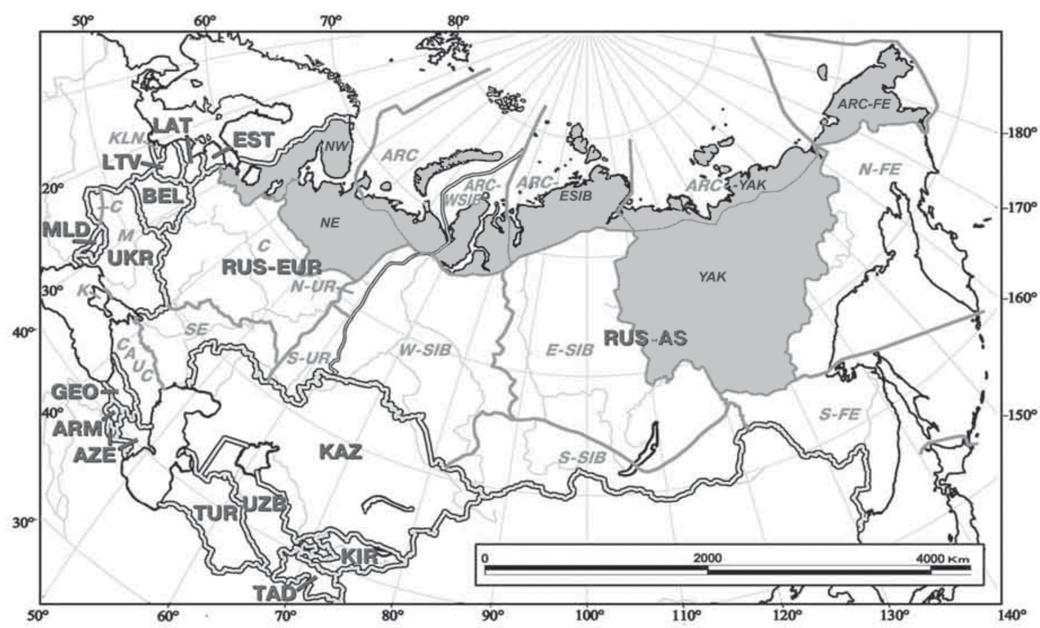
male:female ratio for regions (using subdivision of Russia from Ignatov, Afonina, Ignatova et al., 2006). Maximal branch length per collection with expressed sex was measured in herbarium specimens, but sterile plants were not measured as their gender was impossible to identify.

Gender mapping in plots

Mixed populations, representing both genders, were not found in 2006, but they were found several times in 2007 in Moscow Province, Zvenigirod Biological Station of Moscow University (50 km W of Moscow City). Part of one bisexual population was mapped as follows. The mat was selected in mossy spruce forest where *Ptilium* was abundant and had relatively numerous sporophytes. A portion of a mat of 85 x 25 cm was taken to a box, photographed by digital camera, and then each shoot taken from the mat was related to its digital picture on a computer screen. After gender (or sterile state) was determined, the corresponding shoot was marked in Adobe Photoshop by dots of four colors: male, female, sterile, with sporophyte (Fig. 8).

Similar mapping was made also in unisexual populations 20 x 20 cm (Figs. 5 and 6), in close proximity to bisexual one. During the counting, however, within the male population one female plant and one plant with young sporophyte were

Fig. 2. Regions of Russia, showing (dark) regions where the ratio female:male (by herbarium collections) is no less than 3:2. See table 1 for exact values.



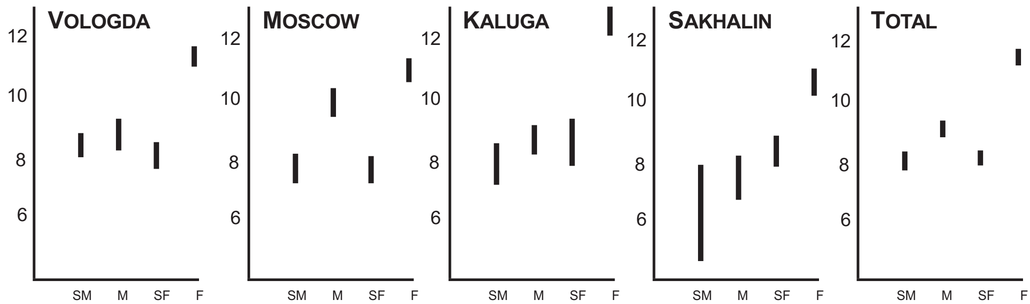


Fig. 3. Branch length (Y axis, mm) in male (m) and female (f) plants of *Ptilium crista-castrensis*, including data on sterile plants from male populations (sm) and sterile plants from female populations (fm). Bars show confident intervals (see also Table 3).

found. As they constitute less than 0.3% of the total number of shoots, we will discuss this mapped plot in Fig. 5 as the male one (not mixed). The counting of plants of each gender and sterile ones was undertaken by 5 x 5 cm squares for both unisexual plots and bisexual plot, thus they were subdivided into 16 and 85 squares respectively.

RESULTS

Distribution of genders

The count of genders in herbarium collections is shown in Table 2 and Fig. 2. Female plants slightly prevail, constituting 56.7% of unisexual herbarium collections, if collections of female plants with sporophytes are counted as female. However, if the latter collection is counted as a mixed one, then female plants will constitute 50.9%. Only 11.3% of the studied collections have plants of both genders. However, if we consider "mixed collection" in a broader sense, including female collections with sporophytes (assuming that male plants grew closer to them), then the number of "mixed collections" will be much higher, 21.8%.

Interesting (although not unexpected) is the presence of sporophytes in most of mixed herbarium collections (83.3%), whereas in collection where only female plants were detected, sporophytes were found much more rarely, in 20.8% of collections.

Most regions of Russia have a nearly equal ratio of genders (Table 2), with the indistinct tendency to male bias to the south (E-SIB is somewhat obscuring this tendency, but there are only few collections from that area and most of them were from the southern part, close to S-SIB). The tendency to female bias to the north is quite apparent (Fig. 2), although these data are rather weakly supported, because in the Arctic this species is rare, and probably also un-

Locality	Male	Female	p
	(1) Branch length of fertile plants		
Vologda	8.78±0.42, n=50	11.30±0.30, n=145	<0.001
Moscow	9.94±0.46, n=85	10.87±0.39, n=87	<0.001
Kaluga	8.74±0.45, n=70	12.65±0.37, n=60	n.s.
Sakhalin	7.43±0.78, n=30	10.64±0.46, n=39	<0.001
Total	9.01±0.27, n=235	11.35±0.20, n=331	<0.001
	(2) Branch length of sterile plants		
Vologda	8.40±0.42, n=50	8.13±0.32, n=130	n.s.
Moscow	7.72±0.50, n=54	7.63±0.45, n=60	n.s.
Kaluga	7.93±0.71, n=40	8.64±0.82, n=40	n.s.
Sakhalin	6.21±1.46, n=7	8.25±0.54, n=50	n.s.
Total	7.93±0.30, n=151	8.12±0.22, n=280	n.s.
	(3) Branch density		
Vologda	8.74±0.37, n=50	9.66±0.22, n=134	<0.001
Moscow	9.60±0.19, n=156	10.28±0.34, n=87	<0.001
Kaluga	10.19±0.26, n=65	9.80±0.32, n=60	n.s.
Sakhalin	10.97±0.56, n=30	14.55±0.49, n=20	<0.001
Total	9.72±0.15, n=301	10.19±0.21, n=301	<0.001

Table 3. Comparison of (1) branch length between male and female plants with expressed sex; (2) branch length between sterile plants from unisexual populations; (3) branch density between male and female plants with expressed sex. Mean ± ci are shown, and p is calculated by Mann-Whytney test.

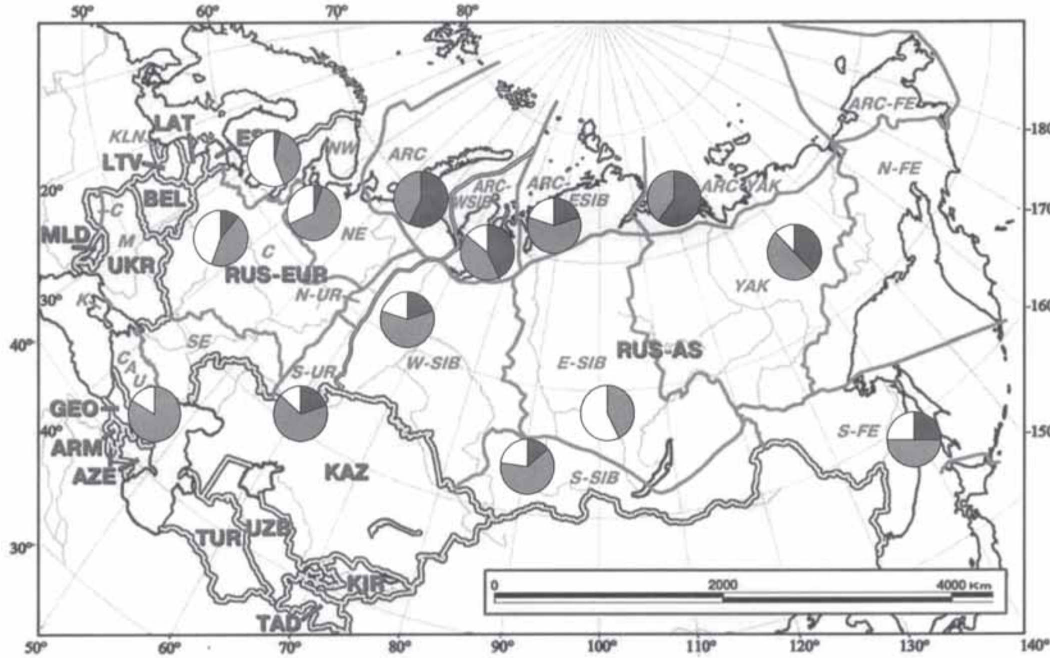


Fig. 4. Proportions of female plants with short, <8 mm branches (black), 8.5-12 mm (grey) and >12 mm (white) in regions of Russia based on herbarium material (regions with only 1-4 female collections not included).

dercollected, e.g. by geobotanists for relevés, because is easy to identify in the field.

Branch length differences

In large-samples study, branches of female plants were found significantly longer than those of male plants, $p<0.001$ for total data (Tables 1&3, Fig. 3).

In herbarium collections branch length of female plants was found also longer, and this difference for combined data from all the regions of Russia was also significant, $p<0.001$.

Table. 4. Mean branch length of plants from herbaria. Only regions with no less than 4 samlpes of each gender are listed (n=305), while total data are calculated by all the measurements (n=433).

Region	female	male
ARC-WSIB	8.9	7.9
ARC-YAK	8.2	7.3
S-UR	10.0	8.7
S-SIB	10.6	8.1
W-SIB	10.7	7.9
S-FE	11.0	8.6
NE	11.6	9.7
C	11.9	9.1
NW	12.1	9.7
E-SIB	13.3	9.5
Total	11.07±0.34 (n=244)	9.01±0.29 (n=189)

Branch length geographic variation

The branch length is apparently correlated with the climatic condition, which is more clearly seen in female plants (Fig. 4). Plants with the shorter branches occur in northern and otherwise climatically severe areas, while the large proportion (>20%) of plants with long branches was found in the boreal zone throughout Russia: in lowland European Russia, Siberia (except Arctic and Yakutia), and south of the Russian Far East. This pattern once more demonstrates that permafrost zone, covering Yakutia, in many respects, is closer to Arctic than to the rest of the boreal zone. Southern mountains, e.g. Caucasus and South Urals, seem to be already affected by the summer drought that makes their living conditions not optimal for mesic and boreal *Ptilium*.

Branch density differences

The branch density data (Tables 1&3) show more variation comparatively with branch length, and they were found singificant not in all the large-sample stidies, but in most samples, as well as in total data female plants have slightly more dense branch arrangement, $p<0.001$. Branch density was studied only in plants with expressed gender.

Difference between sterile and fertile plants

Besides the difference in branch length, male and female plants are also contrasting in their differences between fertile and sterile plants: in male plants this difference is relatively small, whereas female plants differ from sterile plants of the same populations considerably (Table 3). Note, that this pattern has been revealed with the significance of $p<0.001$ in all the sampled populations (Fig. 3). Male and female plants differ significantly in branch length, whereas no difference was found between sterile plants from male and female unisexual populations (Table 3). In average, the difference between fertile and sterile plants in male large-samples was 1.40 mm, while in female large-samples 3.34. This difference has significance of $p<0.005$. In the measurement of herbarium material, the mean difference between male and sterile plants was 2.75, while in females 5.57 mm.

Sex expression in different genders

In addition, the percent of fertile plants in male and female populations was also different (Table 1). In the large-sample study, the mean percent of fertile plants in male populations was 62.1%, while in female populations 24.6%. This difference has however singificance of only $p<0.02$.

The same difference occurred in the two plots with mapped genders. The part of the male population mapped on a 20 x 20 cm square (Fig. 5) had 626 plants, 472 (75.4%) with perigonia, while female one (Fig. 6) had fewer plants, 466, with only 73 (15.7%) with perichaetia.

In smaller squares, 5 x 5 cm, the number of plants with perigonia varied from 8 to 50, with 30 as average, while sterile plants from male population were from 6 to 14, and 11 as average. The female population has corresponding values for squares 5 x 5 cm as follow: plants with perichaetia varied from 0 to 14, and 5 as average, while sterile from 3 to 51, and 25 as average .

Thus, the selected male population differed from the female one (1) in higher density of plants, 1.5 cm^{-1} vs. 1.2 cm^{-1}; (2) in several times higher percent of plants with gametangia. Certainly, these are only two subjectively selected plots that might affect the data considerably. However, the study of the bisexual plot (Fig. 8) shows that these differences remain valid (Tables 5 & 6).

	Male	Female	Sterile
male, n=16	30.36±6.92	—	9.63±1.31
female, n=16	—	4.56±2.27	24.56±7.10
mix, n=85	16.80±2.50	2.09±0.41	10.80±1.67

Table 5. The mean number (±ci) of plants of *Ptilium,* of each sex and sterile ones, in 5 x 5 subsquares in plots with mapped genders (male, Fig. 5; female, Fig. 6; mixed, Fig. 8) .

The subdivision of the 85 x 25 cm plot into 85 subsquares allowed to evaluate correlations of some parameter (Table 6).

Omitting from consideration some obvious correlations of dependent characters (e.g. between number of male and total number of plants), the high correlation was found:

— between the number of female and sterile plants (cf. also Fig. 7).

— between the number of female plants and plants with sporophytes.

— percent of male plants in subsquare correlates ($p<0.01$) with the total number of plants in that subsquare, but the stronger correlation (p><0.001) was found between percent of male plants and the number of plants with expressed sex.

Sporophyte distribution

Sporophytes were found in 36 of 85 squares of bisexual plots, and 35 of them have also male plants, while in one square without male plants the nearest plant with perigonia was at the distance of 3.5 cm from a plant with sporophyte. In all other cases the distance from plants with sporophytes never exceeded 1.5 cm.

Discussion

1. Herbarium collections demonstrate the female bias in *Ptilium*, whereas the studied mixed population (one presented here and some preliminary observation in Zvenigorod biological station) demonstrate that mixed populations have a male sex bias. This incongruence can be explained by the difference of the study method. Similar differences between herbarium and population study were outlined by Bisang & Hedenäs (2005). Cronberg et al. (2003) demonstrated also the difference in the male:female ratio between genets and ramets of *Plagiomnium affine*. At least partly, this incongruence in *Ptilium* may be explained by collector preferences to gather larger plants and plants with sporophytes, avoiding

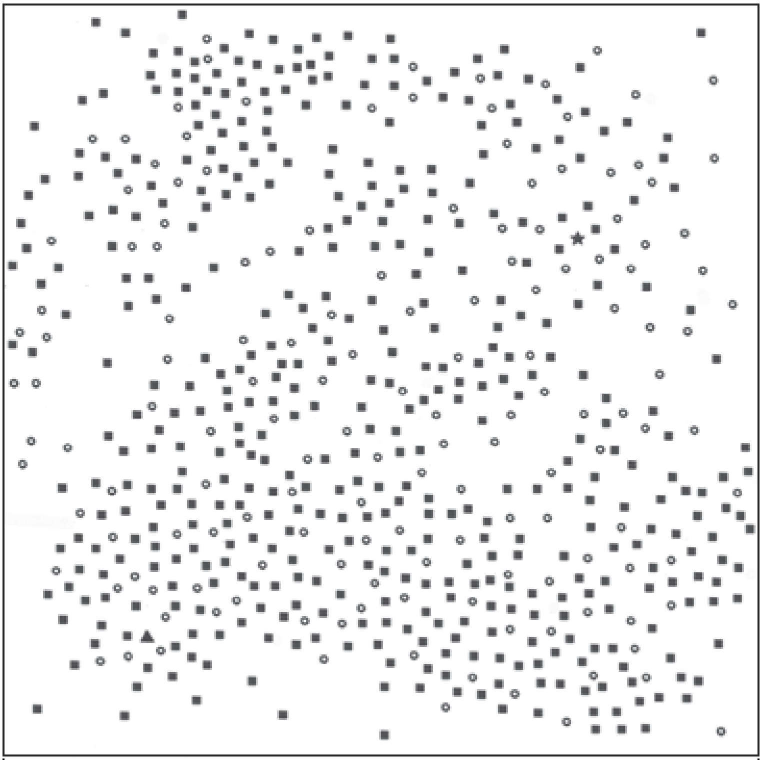


Fig. 5. Map of plot of 20 x 20 cm of almost pure male population of *Ptilium crista-castrensis* from Zvenigorod biological station (50% of natural size): Squares – male plants, open circles – sterile plants (triangule – one female plant, asterisk – one plant with young sporophyte).

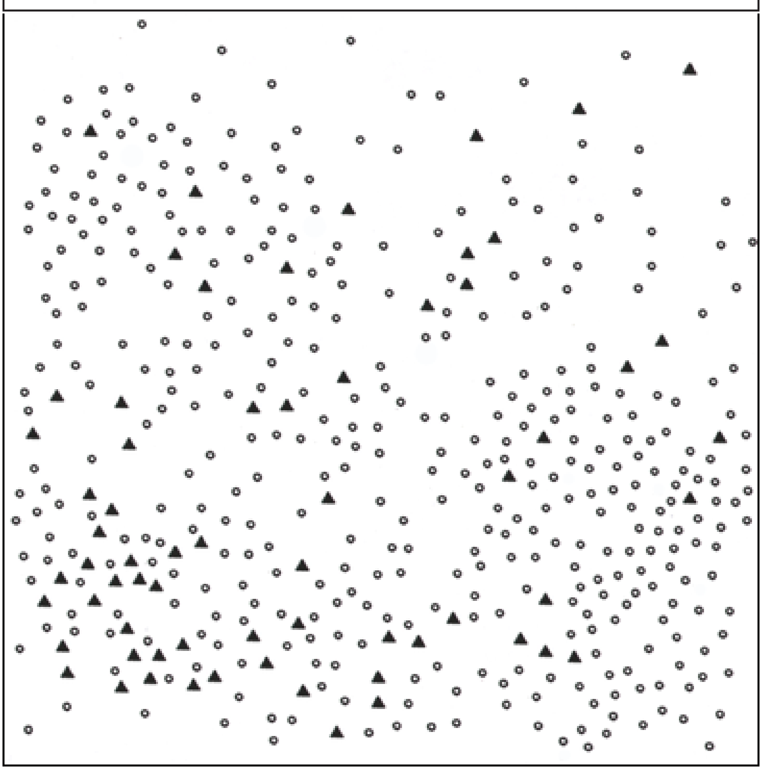


Fig. 6. Map of plot of 20 x 20 cm of female population of *Ptilium crista-castrensis* from Zvenigorod biological station: Triangules – female plants, open circles – sterile plants.

	f	sterile	m+f	m+f+st	S+	%m
male	–0.197 ns	–0.324**	0.976***	0.698***	0.065ns	0.637***
female	—	0.522***	0.022ns	0.348**	0.714***	–0.568***
sterile		—	–0.213*	0.431***	0.260*	–315**
m+f			—	0.790***	0.225*	0.522***
m+f+s				—	0.371***	0.284**
S+					—	–0.260*

Table 6. Correlation found in the 85 subsquares (5 x 5 cm) of the mapped plot of *Ptilium* in Fig. 7. Correlation (r) was calculated in PAST by means of linear model between: (1) number of male plants; (2) number of female plants;(3) number of sterile plants; (4) all plants with expressed gender; (5) total number of plants; (6) plants with sporophytes; (7) percent of male plants; p>0.05 – ns; p<0.05 – *; p<0.01 – **; p<0.001 – ***.

male plants that might be considered simply undeveloped, thus not worthy to collect.

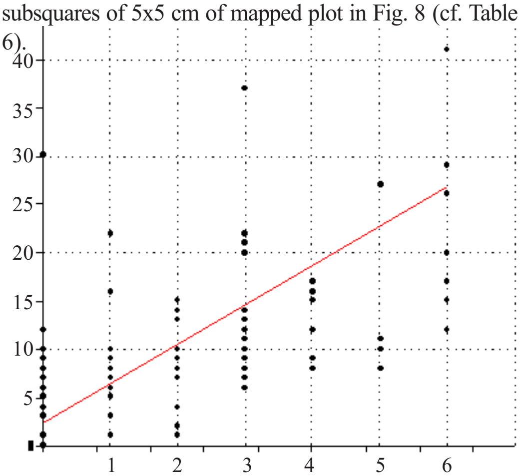
2. The resistance of female sex to more severe conditions was not much discussed, but there are many examples for that. Certain species, e.g. *Hypnum curpessiforme* and *Leucodon sciuroides*, are known with sporophytes in Russia, mostly in Caucasus and western regions of European Russia with a relatively mild climate, whereas throughout most of Siberia only female plants occur (Ignatov, unpublished). Bisang and Hedenäs (2005) also reported declining of male sex in *Hypnum cupressiforme* in high mountains of Africa. This might relate to very short vegetative period that is not enough for development of male gametangia, which require longer time than the development of female ones (e.g. Longton & Schuster, 1983; Milne, 2001; Stark et al., 2005).

3. The larger size of female plants and the bigger difference of fertile and sterile plants (of presumably the same sex) imply that the reproductive effort of female plants is higher than in male plants. There are several ways to explain the difference between sterile and gametangia-bearing plants in male and female sexes. (A) Only better developed and stronger female plants are able to develop gametangia, while virtually any male plant is able to do this; (B) Female plants after considerable effort for gametangia production [that probably correlates with development of longer branches] need a certain time for the recovery, and during this recovery year(s), plants do not waste energy for producing longer branches. These alternative hypotheses probably can be tested in the future.

4. The rare occurrence of sporophytes is explained by the rare occurrence of bisexual populations and spatial segregation of sexes. Even in bisexual populations the grouping of male and female plants is evident (Fig. 8). A similar pattern has been demonstrated for many dioicous species, although the reason for that is not fully understood yet. Cameron & Wyatt (1990) found that in *Splachnum* most populations are female-biased, whereas under experimental conditions, and especially when growing in full sun and on more acid substrate, the male sex becomes more represented and in many cases populations are male-biased. It can be speculated that the micro-mosaic in the forest floor may explain certain differentiation in sexual heterogenity in *Ptilium* populations, although this would be difficult to demonstrate for pleurocarps that are readily spreading vegetatively. Another possible explanation is that the two sexes may compete, resulting in spatial segregation; this mechanism was recently demonstrated in *Marchantia* (Garsia-Ramos & al., 2007).

5. An intriguing parallel can be drawn with the *Tetraphis pellucida* reproductive biology (Kimmer-

Fig. 7. Correlation between number of sterile plants (Y) and female plants (X) of *Ptilium crista-castrensis* in 85 subsquares of 5x5 cm of mapped plot in Fig. 8 (cf. Table 6).



er, 1991). In that species the density of plants in a population (that was studied with removal of 10 to 75% of plants from tufts) affect the proportion of sexes, so the looser tufts develop a higher proportion of female plants. Drawing a parallel to *Ptilium*, this allows one to hypothesize that some female plants may exist among dense male groups, but not develop gametangia there. The experiments with thinning of male populations of *Ptilium* may demonstrate if this takes place or not.

6. About an equal distance from males and fertilized and non-fertilized females was reported for bisexual populations of dioicous *Hyophila involuta* (Hook.) A.Jaeger and *Barbula agraria* Hedw. (Mota de Oliveira, 2005). In *Ptilium* we found the same, however, likely by another, although unclear reason. *Ptilium* differs from these two Pottiaceous mosses that are strongly female biased, in more numerous male plants; the rarity of the latter may be invoked to explain the sporophyte rarity in *Hyophila* and *Barbula*. Glime (2007) reported the maximal distance of fertilizing in pleurocarps to be 6 to 10 cm. In *Ptilium* where the perigonia are always faced downwards, this distance can be somewhat shorter, and this agree with the obtained data of maximal 3.5 cm.

7. Among the further questions should be also the influence of the climatic condition of the given year. In 2006, after a very dry winter (autumn of 2005 was very dry and turned to cold winter very abruptly, thus omitting wet period with temperatures 0 to +10°C), the sporophytes in Zvenigorod forest were very rare. In 2007, however, after 'normal' winter, i.e. with expanded wet and snowless periods in autumn and spring, *Ptilium* sporophytes were obviously more numerous.

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Fig. 8 (see also next page). Map of mat of *Ptilium crista-castrensis* (85 x 25 cm): Blue – male plants; red – female plants; white – sterile plants, red with white dot – plants with sporophytes.

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