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ON BOURLETIELLA (CASSAGNAUDIELLA) PRUINOSA (TULLBERG, 1871) AND ITS

ALLIES (COLLEMBOLA: SMINTHURIDAE)

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ABSTRACT

In dry dune vegetations in the Netherlands a species of Bourlettella occurs that is closely related to B. pistillum Gisin, 1946, and B. radula Gisin, 1946. The species is characterized by a virtually obligatory sexual neutralisation of all males throughout the summer. A study of type material proved the identity of this species with Bourletiella pruinosa (Tullberg, 1871). A lectotype is selected for B. pruinosa as well as for B. agreni Stach, 1956. B. agreni, created for B. pruinosa sensu Agren, 1903, Linnaniemi, 1912, is proved to be a junior synonym of B. pistillum. B. pistillum incisa n. ssp. is described from the Pyrenees and the Ardennes.

Bourletiella cruciata Haybach, 1972, is shown to be a sexually neutralized form of B. pistillum, and is a junior synonym of the latter. Herewith the occurrence of sexual neutralization is established in B. pistillum.

For B. pruinosa (type-species), pistillum and radula the new subgenus Cassagnaudiella is proposed.

the Dutch coastal dunes placed me for considerable difficulties since the secondary sexual characters of the males, essential for a final identification, were constantly absent. The secondary sexual characters in the females, that were present in most adult specimens, pointed towards a relationship with the group of B. radula Gisin, 1946, and B. pistillum Gisin, 1946. The lack of sexual differentiation in the males stimulated me to compare this with the phenomenon of sexual neutralization in B. radula, well known since the work of Cassagnau on this subject, and finally led me to some taxonomic conclusions. The arguments that enable me to designate the species under consideration as B. pruinosa will be given in one of the following sections.

ECOLOGY

As far as I know at present, Bourletiella pruinosa occurs in the Netherlands in the dunes of the Wadden Island of Vlieland, and in the coastal dunes between Castricum and the Hague (Meyendel).

INTRODUCTION

A peculiar species of *Bourletiella*, occurring in dense populations in a relatively dry habitat in

An intensive search farther to the South (Oost Voorne) did not provide the species. Outside the Netherlands B. pruinosa is known to me from its type locality, Gotland in the Baltic Sea. It is possible that Smynthurus fulvus Lie Pettersen, 1896, described from Norway is a (junior) synonym of pruinosa. However, the description is insufficient and the type - in fact Lie Pettersen's whole Collembola collection - seems lost. According to Dr. Fjellberg (personal comm.) no material of Lie Pettersen is present in the Bergen Museum.

The habitat to which the species is restricted is very characteristic: open, unsheltered, dry dune valleys with a very low vegetation, as a rule not higher than 6 cm. Rarely a sparse population of B. pruinosa was met in a vegetation as high as 15 cm. The vegetation is kept as low as that by the joint effect of strong rabbit grazing (their droppings are a striking feature in the habitat) and drought. In phytosociological terms the vegetations would be best described as belonging to the associations Tortulo-Phleetum arenarii and its succesor Violo-Corynephoretum. Dominating plant species are Carex arenaria L., Cerastium semidecandrum L., Corynephorus canescens (L.) P. B., Festuca tenuifolia Sibth., Galium verum L., Koeleria cristata (L.) Pers., Phleum arenarium L., Sedum acre L., the mosses Bryum argenteum (Hedw.), Ceratodon purpureus (Hedw.) Brid., Dicranum scoparium Hedw., Hypnum cupressiforme Hedw. var. lacunosum Brid., Pohlia nutans (Hedw.) Lindb., Tortula ruralis (Hedw.) Crom. var. arenicola Braithw., many lichens of the genus Cladonia, e.g. C. foliacea (Huds.) Willd., and especially unidentified members of the Cladina-section. The substratum consists of fine, almost pure sand with a low humus content and a corresponding low water holding capacity.

In habitats of this type fluctuations in temperature and saturation deficit at ground level are excessive. This, however, does not seem to bother *B. pruinosa*, which, under natural conditions does not show any negative response to heat or drought.

The earliest date at which *B. pruinosa* was swept is 22nd June; the last one 24th September. The species evidently overwinters in the egg-stage, since soil samples taken at various dates in the winter half year at a site where a strong

colony exists in summer time did never produce any Bourletiella.

Bourletiella pruinosa is almost the only collembolan that can live in this habitat; sometimes a few specimens of Entomobrya multifasciata (Tullberg, 1871) were found. In neighbouring higher and denser vegetations Deuterosminthurus repondus (Agren, 1903), and Sminthurus nigromaculatus Tullberg, 1872, were abundant. In small patches of some square meters grown with about 1 m high Salix repens L., that frequently occur isolated in the surrounding low vegetation, only D. repandus could be swept; the vicariance between D. repandus and B. pruinosa at the border of the two vegetations was virtually perfect.

THE NATURE OF THE SECONDARY SEXUAL NEUTRALISATION

To judge after the fact that full-grown females have 3+3 ribbon-like setae on the ventral flaps of abd, and have elongate anal appendages, abruptly cut and adorned with small fringes, the Dutch material comes close to B. radula and B. pistillum. A comparison of the expression of the secondary sexual structures in both sexes in the Dutch material with those species stresses the following points.

In the male the postabdominal organ characteristic for the genus Bourletiella, is completely absent. The shape of the male postabdomen, the location of the postabdominal setae and their relative lengths are identical with those of immature specimens without evident inner or outer genitalia. In none of the more than 450 males which I studied in detail even a teratological indication of a rudiment of a male organ was found.

Normal mature males of *B. pistillum* and *radula* have on their dorsum a field where the setae are strongly swollen and flame-like. The corresponding setae in *B. pruinosa* are quite normal, and cannot be told apart from other body setae.

Not affected by the neutralisation are the primary sexual characteristics: the genital tubercle with its crown of setae, and the internal genital tract with its thick layer of associated glandular tissue. (This observation is based on cleared specimens and not on histological work).

In the female all transitions could be found between specimens that have their genital papilla opened by a transverse slit, but where the number of hairs on the genital papilla is still very low and where the anal appendages are just hair-like, (1st stage adult of Betsch, 1967), to specimens with a normal hairy genital papilla and well developed anal appendages (2nd stage adults). The degree in which the 3+3 hairs on the ventral flaps of abd₆ are broadened is closely correlated with this gradual transition. Moreover, fully "sexed" females have these setae not only broadened, but the hairs bear a variable number of protracted, often branched lacerations.

Since it seemed that females with poorly or not at all expressed secondary sexual characters were as a rule smaller than normal females, I have measured the material. Because all specimens were mounted, and consequently more or less flattened and stretched, I could not use the total length of the specimens, as Cassagnau, 1964, did in case of B. radula. Instead I have used the length of the dens. A rough estimate of the total length in my material can be derived from the following empirical regression formula: total length (in mm) = 5 x dental length - 0.05.

In table I the dental length is given of juveniles (genital papilla closed), females with genital orifice opened, but secondary sexual characters otherwise absent or nearly so, females with secondary sexual characteristics well developed (in particular as regards anal appendages and setae on genital tubercle) but ribbon-like setae not or almost not differentiated, fully sexed females, and males. This table shows clearly that in the females a completion of the full set of secondary sexual characteristics is coupled with a larger body size.

This fact, and the observation that females with secondary sexual characteristics incompletely expressed are less strongly pigmented, brings me to the conclusion that in the female sex no real neutralisation of secondary sexual characteristics takes place. At most can be spoken of a retardation of the acquisition of the secondary sexual traits. Inhowfar this acquisition is slower than in related species is difficult to decide. So much can be said that in a number of Sminthuridae it is not rare to encounter females with normal, hairy genital papilla, but the anal appendages poorly differentiated (e.g. in Bourletiella viridescens Stach, 1920, and in the "first stage"

adult female" described by Betsch, 1967, for Bo-vicornia greensladei Massoud & Delamare Deboutte-ville, 1967).

I have no data in how far actual sexual activity is linked to possession of a complete set of secondary sexual traits. The interesting discovery of the function of the anal appendages in Arrhopalites females in rotating the eggs while they are covered by a protective faecal coating (Massoud & Pinot, 1973) casts some doubt on the reproductive potentials of incompletely differentiated females. This could mean that a large proportion of seemingly adult females is not reproductively active (see tables II-IV for an indication of the magnitude of this fraction).

COMPARISON WITH SECONDARY SEXUAL NEUTRALISA-TION IN BOURLETIELLA RADULA

Secondary sexual neutralisation in the Bourletiellinae was known until now only in *B. radula*, and has been thoroughly studied by Cassagnau, 1964. Details on the mating behaviour have been given recently by Raynal, 1974a. Although the ecological conditions faced by *B. radula* - alpine meadows in the central Pyrenees - are very different from those met by *B. pruinosa*, it is nevertheless instructive to compare the phenomenon of the neutralisation in both species.

In the Pyrenees, neutralisation occurred in a dry summer mainly in the driest localities; in a subsequent cold summer neutralisation also occurred, but this time basically in the coldest localities (North slopes). Neutralisation thus is essentially facultative, and seems to be triggered by unfavorable conditions. In the Dutch dunes, in contrast, it seems that neutralisation is obligatory, although one could admittedly argue that for B. pruinosa conditions of life are constantly in a pessimum.

Raynal, 1974b, has demonstrated recently that sexual neutralisation occurs in *B. radula* only in populations living on a comparatively dry substrate; neutralisation never occurred in populations living near a stream or a marshy zone.

In the Pyrenees it was possible to recognize two rather well-separated generations. Neutralisation, if any, occurred in the second generation, i.e. about from the beginning of August. In the Netherlands no distinct second generation

TABLE I

Measurements of dental lengths of 1972 and 1973 samples

The samples are arranged here according to the progression of the season, irrespective of calendar year or locality. In column 1 the samples are numbered consecutively for reference in tables II-IV; in column 2 locality, author's collection number, date and total number of specimens are given; in column 3 the division of the material is indicated thus: juv. = juveniles (genital papilla closed), (?) = very immature females (genital papilla open and weakly hairy, anal appendages and ribbon-like setae not differentiated), (?)? = slightly immature females (genital papilla and anal appendages fully developed, but ribbon-like setae not differentiated), ? = fully sexed females; in column 4 absolute numbers of specimens of the various categories are given; column 5 provides mean dental length; column 6 the 95 % confidence interval of the mean; column 7 gives the standard deviation; column 8 gives the extreme values; column 9 gives the body length, calculated after the mean dental length with the use of the regression formula given in the text.

The samples from Castricum are collected in the "Provinciale Waterleidingduinen (Geversduin)"; those from Vogelenzang are from the "Amsterdamse Waterleidingduinen", those from Santpoort are from the "Duin en Kruidberg" estate. The sample from Vlieland was taken near the "Posthuis".

1	2	3	4	5	6	7	8	9
sample nr	locality coll.nr. date N	sex	n	mean length of dens in µ	95 % confi- dence inter- val in µ	standard deviation in µ	extreme values in µ	calculated body length in mm
1	Castricum	juv.	11	162	156-168	11	149-188	0.8
	973.098	(♀)	37	205	202-208	9	184-224	1.0
	22.vi.1973	(♀)♀	0				•	
	122	Ş	30	259	256-262	8	243-274	1.2
		đ	44	208	205-211	9	188 - 231	1.0
2	Castricum	juv.	5	168	158-178	11	157-184	0.8
	973.100	(♀)	16	204	198 - 210	11	180-220	1.0
	22.vi.1973	(♀)♀	1	255				1.2
	52	Ç	6	259	247-271	15	231-271	1.2
		đ	23	215	212-218	6	204-228	1.0
3	Castricum	juv.	0					
	973.129	(♀)	20	219	215-223	9	204-243	1.0
	15.vii.1973	(१)	6	233	224-242	12	224-255	1.1
	66	Q	33	277	271 - 283	18	251-341	1.3
		đ	.7	217	211-223	8	204-228	1.0
4	Vogelenzang	juv.	7	170	163 - 177	7	153-180	0.8
	972.105	(♀)	46	219	216 - 222	10	200-239	1.0
	5.viii.1972	(♀)♀	7	238	226 - 250	16	224-271	1.1
	97	Ç	6	293	277-309	20	267-322	1.4
		đ	31	212	208 - 216	10	188-235	1.0
5	Santpoort	juv.	0					
	972.113	(₽)	3	221	207-235	12	208-231	1.1
12.viii.1		2(₹)\$	0					
	51	Ç	25	276	269-283	16	251 - 322	1.3
		đ	23	555	217-227	11	192 - 235	1.1
							Table	continued overleaf

TABLE I - continuation

1	2	3	4	5	6	7	8	9
sample nr	locality coll.nr. date N	sex	n	mean length of dens in µ	95 % confidence interval in µ	standard deviation in µ	extreme values in µ	calculated body length in mm
6	Santpoort	ç	1	247				1.2
	972.114	đ	3	214	207-221	6	208-220	1.0
	12.viii.1972 4							
7	Castricum	juv.	0					
	972.130	(₽)	8	215	207-223	12	200-231	1.0
	2.ix.1972	(♀)♀	0					
	81	ç	50	278	273 - 283	18	243-314	1.3
		đ	23	221	219-224	8	204-235	1.1
8	Castricum	juv.	0					
	972.131	(♀)	2	204	196-212	6	200-208	1.0
	2.ix.1972	(♀)♀	0					•
	100	Q	73	275	271-279	20	235-333	1.3
		đ	25	219	216 - 222	8	200-235	1.0
9	Vlieland	juv.	68	175	172-178	12	122-192	0.8
	973.171	(♀)	67	220	218 - 222	7	204-235	1.1
	17.ix.1973	(\$)\$	13	263	260-266	6	251 - 361	1.4
	423	₽	186	292	289-295	22	251-361	1.4
		ರ	89	226	224-228	9	208-243	1.1
10	Castricum	juv.	0					
	972.150	(♀)	0					
	17.ix.1972	(₽)₽	1	235				1.1
	63	Ş	46	285	279-291	20	239-330	1.4
		đ	16	217	213 - 221	9	196-231	1.0
11	Castricum 972.151 24.ix.1972	ç	1	290				1.4

could be found, but, what is more interesting, neutralisation occurs from the very beginning that adult specimens are present (second half of June).

Not only the males, but also the females are subject to neutralisation in the Pyrenean situation described by Cassagnau. The neutralized females are about as large as normal ones but much more strongly pigmented. These neutralized females were never met with in pruinosa.

The exceptionally large juvenile specimens that Cassagnau found in the second generation, and that might be the precursors of neutralized adults, were also lacking in the Dutch material.

In conclusion, a neutralisation of secondary sexual characters is possible in *B. radula* in both sexes, but only in the second generation, and only under exceptionally unfavourable conditions. In *B. pruinosa*, permanently living under difficult conditions, no neutralisation is evident in the female sex, apart from a probably not very characteristic retardation in sexual development, whereas the males are obligatory neutralized from their first appearance onward.

In her interesting paper on the mating behaviour of *Bourletiella* species, Raynal, 1974a, describes how neutralized *radula* return to an archaic, unspecialized behaviour, without any mutual behaviour between the sexes, in which the spermatophora are placed at random.

It is a current assumption (cf. also Betsch, 1974) that mating behaviour originated in the Bourletiellinae as an adaptation to their epiphytic, i.e. dry, habitat: spermatophora that would otherwise have been exposed overlong and dried, are taken by the female within a short time. However, it is a surprising fact that the morphological prerequisites for a mating behaviour are lacking in exactly that species of the Dutch fauna of Bourletiellinae that occupies the driest habitat. Some details concerning the reproductive biology of *B. pruinosa* will be published separately by Mr. E. Klaver.

THE IDENTITY OF BOURLETIELLA PRUINOSA (TULLBERG, 1871)

Because the Dutch material discussed above did agree with *B. radula* and *pistillum* only insufficiently in morphological aspect, and differred distinctly in its biology, I studied the type ma-

terial of Sminthurus pruinosus Tullberg, 1871, since this species, although very incompletely described, showed in its ecology ("common on short grass in dry meadows of Gotland") and in its general appearance some resemblance with the Dutch animals. Through the much appreciated help of Dr. L. Hedström of the Museum of Uppsala I have been able to study two tubes with syntypes. Both tubes were labelled in Tullberg's handwriting. One tube, containing 4 6, 8 9, 11 immature females, 12 juveniles and 2 fragments was labelled "Sminthurus pruinosus Tullb. Gottl. T. Tullberg" (Gotland was spelled with double t formerly); the other tube, containing only 4 & was labelled "Sminthurus pruinosus Tullb. Gottl. vägen till Snäckgärdet [i.e. way to Snäckgärdet, a place just North of Visby] 11/870 T. Tullberg". The figure 11/870 seems to point to a collecting date November 1870 - a remarkable late collecting time. I have mounted all specimens separately on slides in Marc André II, and selected a male from the first mentioned tube as lectotype, and the remaining specimens as paralectotypes.

The material was in a surprisingly good condition, and almost all specimens could be studied in perfect detail. A study of it made clear that there was no significant difference between Tullberg's material and the Dutch specimens; in particular the male postabdomen was completely "neutral". Thus finally an end has come to the long speculation and resulting confusion of at least one of the classical *Bourletiella* species.

I shall give now a detailed description of the species, basing myself both on the type material, and on Dutch specimens.

DESCRIPTION OF BOURLETIELLA PRUINOSA

Female.- Adult females are 1.2-1.4 mm in length. Pigmentation of living specimens is a pale irregular dirty violet-blue with an irregular pale middorsal line on abdomen. Mounted material is irregularly mottled by blue pigment cloudings, that never are very dense, nor do form any pattern; head and postabdomen are pigmented just as abdomen. The feet are only very feebly pigmented, the antennae are darker, with violet-blue pigment. Immature females are even more feebly pigmented. Outline of body typical for the genus, body covered with short curved setae.

TABLE II

Relative proportions of the sexes and developmental stages.

Samples of the same date and locality are grouped.

sample nr.	juv.	(♀)	(\$)\$	Ş	đ
1+2	9 %	31 %	1 %	21 %	39 %
3	0	30	9	50	11
4	7	47	7	6	32
5+6	0 .	5	0	47	47
7+8	0	6	0	68	27
9	16	16	3	44	21
10+11	0	0	0	75	25

The figures from sample 9, Vlieland, are evidently rather deviating, and may be explained as suggestive of a second generation. Otherwise, the figures suggest that the number of halfmature females rises at first, then decreases, whereas the number of adults rises monotoneously.

TABLE III

Absolute and relative frequencies of developmental stages of the females.

(Samples of the same date and locality are taken together)

sample nr.	date	(₺)	(\$)	Ŷ
1+2	22.vi	53 (59 %)	1 (1 %)	36 (40 %)
3	15.vii	20 (34 %)	6 (10 %)	33 (56 %)
4	5.viii	46 (78 %)	7 (12 %)	6 (10 %)
5+6	12.viii	3 (10 %)	0	26 (90 %)
7+8	2.ix	10 (8%)	0	123 (92 %)
9	17.ix	67 (25 %)	13 (5%)	186 (70 %)
10+11	24.ix	0	1 (2%)	47 (98 %)

These data are - not surprisingly in a time series - strongly heterogenous: G=213.93, with df=12, a highly significant figure (X^2 _{12, 0.005}=28.30). Testing against a probability of 5 % (X^2 =21.03) samples 1+2 and 3 may be grouped (G=13.07) as well as 5+6, 7+8 and 10+11 (G=16.60).

Table III can thus be simplified to table IV

TABLE IV						
sample nr.	date	(♀)	(\$)	Ç		
1+2+3	22.vi-15.vii	73 (49 %)	7 (5%)	69 (46 %)		
4	5.viii	46 (78 %)	7 (12 %)	6 (10 %)		
5+6+7+8+10+11	12.viii-24.ix	13 (7%)	1 (1 %)	174 (93 %)		
9	17.ix	67 (25 %)	13 (5%)	186 (70 %)		

Antennal segments proportionally 2:4:5:10; ant, with 7 indistinct subsegments. Head in the same scale 15 units, ant./head diagonal about 1.4, intermediate subsegments of ant $_{h}$ with whorls of 8 setae + fine sensory hairs. Apex of ant with a small retractile papilla. Labrum with 4 simple cushion shaped papillae. Unguis with internal tooth about halfway, a pair of lateral teeth and a distinct dorsal tooth. Unguiculus strong, about 3/5 times unguis in P2 and P3, narrower and a bit shorter in P1; subapical filament about 0.1-0.2 times unguiculus in P_2 and P_3 , 0.5 in P_1 . Clawate tenent hairs 3, 3, 2 on P₁₋₃. Hairs at unguicular face of tibiotarsi short and spinulose (especially in distal half of tibiotarsus), whereas the hairs at the ungual face are long and slender. This difference is most strongly marked in P, where the longest hairs are about 2 times the thickness of the tibiotarsus, or 1/4 its length. Femur of P, with 15 setae on its outer face and 2 minute setulae on its inner face, one in distal position, another about halfway. Metatrochanter with 2, 3 setae on outer face, moreover an oval organ halfway the anterior face and a small setula proximally on its internal face.

Retinaculum with rami tridentate, corpus with 3 setulae. Furca: relative lengths of manubrium: dens:mucro = 5:10:4. Manubrium anteriorly bare, posteriorly with 8+8 setae (one pair almost at the point of flexure with venter). Outer face of dens with a row of 8 equidistant setae, inner row with 7 equidistant setae. Posterior row with 8 dorsal setae, of which the longest (in the proximal group) is almost as long as the mucro. On the anterior face of the dens one fine proximal hair, and in distal half 1, 1, 2, 2, rather strong, appressed setae. Mucro normal for the genus, toothless.

Abdomen globular, with 3 bothriotriches, inserted on a straight line. Hair cover of abdomen consists of fine, smooth, curved setae.

Abd₅ with bothriotrix D, 2 small curved setae, 8 normal, straight setae and the genital orifice with normal accompanying setae. Setal arrangement of abd₆ is normal for the group; in completely adult females 3+3 setae on the posterior margin of the latero-ventral flaps are broadened bandlike. The dorsal margin of these hairs is fringed to a variable degree: in extreme cases only some faint fringes are visible, but at the other hand

females have been seen where some fringes had been grossly enlarged, and branched. In most cases at least one large - often branched - laceration is present in the most dorsal of these seta.

Appendices anales truncate, with distinct fringes at apex and subapical margin.

Male.- Differs from the female in being smaller (viz., 1.0 mm). The antenna is proportionally somewhat longer, 1.6 times head diagonal. They are somewhat stronger pigmented, and especially the dorsum of abd₁ often has a somewhat rusty tinge. The hair cover of abdomen is identical to that of the female. The chaetotaxy on the postabdomen is indistinguishable from that of an immature or female specimen, except of course in the male genital papilla, that is normally developed, and possesses a mass of small setae.

ON BOÙRLETIELLA PISTILLUM GISIN, 1946

Material seen: holotype & and 1 paratype 9 (Switzerland, labelled "Fops (Zernez) 2400 m. 29-5-46") in coll. Mus. Hist. nat. Genève (I am grateful to Dr. Hauser for kindly loaning me these types and those of B. radula); 10 9 and 2 6 from the Central Pyrenees (Orédon), Cassagnau leg. et don.; 6 and 6 from the Ardennes (Luxemburg, Pont de Bigonville, 4.v.1969, leg. Ellis); 1 9, 3 d and 5 juv. from Norway, Nordland, Saltdal, heath N. of Graddis, (i.e. just North of the Polar Circle) 2.vii.1974 leg. et don. Fjellberg; 57 ♀ and 17 ♂ from Norway, Hordaland, Ulvik, Finse, dry heath 1200 m above sea level (i.e. near the head of the Hardangerfjord), 14.viii.1974, leg. et don. Fjellberg. (All material, except the types, in coll. Z.M.A.).

B. pistillum and radula were both described by Gisin, 1946, in the same paper. The main characteristics for both species taken together are the presence of 3+3 ribbon-like setae on the ventral flaps of abd₆ of adult females, the presence of a dorsal field of strongly thickened, flameshaped setae in the male abdomen, maybe also the short flagellum in the male organ.

B. pistillum was stated to be differentiated from radula by its colour - blue in pistillum, creamy or sometimes rusty in radula. Moreover, the males showed some differentiating characters in the dorsal organ of abd₆, viz. the proportionally high crest, the strong difference in thickness of the two lateral spines, the stout 3+3 anterolateral setae and the posterolateral seta

being curved backward.

The latter character is certainly of no use, since the flexure of the posterolateral seta is variable in both species. The 3+3 anterolateral setae are stout indeed, and maybe somewhat more than in B. radula, but this is not a very reliable character. Very characteristic on the contrary is the strong difference in diameter of the two lateral spines: in all material that I have seen the anterior spine is at least 2.5 times as thick as the posterior one. In the shape of the crest, finally, I found an interesting geographic variability. In the Scandinavian material, and in the type, the crest is high indeed, almost as high as long at base. Moreover, the apex of the crest is gradually curved, only sometimes with a slight notch. All males, however, from Luxemburg and from the Pyrenees have the crest distinctly lower than long at base; moreover the crest is notched for about 1/3 of its height. Of the two lobes that thus result the anterior one is distinctly higher than the posterior one. Parallel to this distinction in males from the Ardennes and the Pyrenees the differentiated setae on the dorsum are much stronger incrassate than in Scandinavian material and in the type.

I therefore consider the Ardenno-Pyrenean material to represent a separate subspecies, that I propose to name B. pistillum incisa n. ssp. Holotype is a male from the Orédon material (in coll. Z.M.A.).

ON BOURLETIELLA RADULA GISIN, 1946

From Dr. Cassagnau I received a sample of normal, and of neutralized specimens of B. radula originating from the Central Pyrenees, Orédon. After studying this material, and the holotype of and 2 paratype ? (labelled "Scarl (He 231)") that Dr. Hauser of the Geneva Museum kindly loaned me I must conclude that the only reliable differential characters of radula against pistillum are the lack of dark (blue or grey) pigment in the body, the eye-patches excepted, and furthermore the proportionally low, not or only weakly notched crest and the feeble difference in thickness of the anterior and posterior lateral spine (at most of a factor 1.5) in the male postabdomen. The shape and length of the lateral setae are not reliable.

This essentially nominal) species was created by Stach (1956: 140 and 154) for Sminthurus pruinosus Tullberg sensu Agren, 1903, and Bourletiella pruinosa (Tullberg) sensu Linnaniemi, 1912. Stach based himself essentially on Linnaniemi's description and figures, and presumably included Agren's interpretation only because Linnaniemi referred to "Bourletiella pruinosa (Tullb., Agren)". Stach's interpretation was evidently based on an erroneous drawing by Linnaniemi, who did not recognize the crest, and misinterpreted the lateral spines.

Through the kind assistance of Dr. M. Meinander of the Zoological Museum of Helsinki, I have been able to study a number of samples from Finland, labelled "Sminthurus pruinosus" mostly by Linnaniemi, but in part also by O.M. Reuter. Unfortunately, the material has on some occasion in the past dried out - evidently for a considerable time, leaving most of the specimens in a very poor condition. Although the material was thus of limited value, the large number of specimens permitted nevertheless some taxonomical conclusions. The blue pigment present in all specimens, the ribbon-like setae in the female postabdomen, the high crest and strongly different lateral spines in the male postabdomen convince me that B. agreni is a junior synonym of B. pistillum s. str.

To settle the matter definitively, I have selected a male from the Linnaniemi collection as lectotype, and the other 24 specimens from the same series as paralectotypes of B. agreni Stach, 1956. (Lectotype - Helsinki Museum type number 6107 - and 3 paralectotypes on 1 slide, remaining paralectotypes on 4 slides, all in Marc André II; the specimens have lost their original blue coloration due to prolonged soaking in Marc André I, necessary for a restoration of morphological details). The locality data are: Sortavala, Kirjavalaks, v. 1902, W.M. Axelson. This is now U.S.S.R. territory, and lies on the northern edge of the Ladozhskoye Ozero (Ladoga Lake). The synonymy of B. agreni with pistillum is not wholly unexpected, since already Stach himself suggested a close relationship of his species with B. radu-

ON BOURLETIELLA CRUCIATA HAYBACH, 1972

Haybach placed this species in the subgenus Deuterosminthurus essentially because the lack of a male organ excluded attribution to Bourbetiella s. str.. But the structure of the unguiculus proves that this allocation cannot be correct, and that B. cruciata might be a neutralized member of the radula complex. (The same suggestion was made to me by prof. Cassagnau in litt.). Upon my request Dr. Haybach kindly sent me a slide containing three paratypes, labelled "Bourletiella cruciata n. sp. Gl 3 Paratypen". Two of the specimens were males, without a trace of a male organ, but the third specimen was a young female at the point of ecdysis. Through the old skin of the postabdomen the ribbon-like hairs characteristic of the radula - group were distinctly visible. This, and the blue pigment of the specimens brings me to the conclusion that cruciata is also a junior synonym of B. pistillum. The interest of this discovery is that herewith secondary sexual neutralisation is established in B. pistillum as well. (It is interesting to note that in the Pyrenees pistillum was never seen neutralized by Raynal, 1974a.)

ON BOURLETIELLA HORTENSIS f. HISPANICA DENIS, 1930

Denis, 1930, described from central Spain a curious form of B. hortensis (Fitch, 1863). Already Stach, 1956, suggested that this form might be unrelated with hortensis and suggests a close relationship with B. arvalis (Fitch, 1863). However, the two thick lateral spines that Denis drew are much heavier than the slender spines of arvalis. The short flagellum (that Denis supposed to be broken) and the incrassate hairs on the male dorsum suggest a close relationship with pistillum and radula (although the very different ecology and olive-green colour are not in favour of an actual synonymy). Dr. Hutasse-Jeannenot was so kind to send me what she had available of this form from the type series: three slides, containing a dissected specimen, apparently only one, a female, labelled "Bourletiella hortensis f. hispanica, Pozuelo de Calatrava. J. M. de la Fuente leg. 1929" in the hand of Denis. The anal appendage of this specimen, which Denis reported he was not able to find, are present, though orientated in a rather

unusual angle in the slide. They are both broadly fan-like and very thin, typical for *B. hortensis*! Since the male depicted by Denis has the lateral spines in the male organ curved parallel, this is certainly no *hortensis*, and I can only guess that Denis had a mixed material before him. A study of topotypical material is imperative for a final answer.

BOURLETIELLA (CASSAGNAUDIELLA nov. subgenus)

The genus Bourletiella Banks, 1899, is essentially characterized by two peculiarities: the possession of an unguiculus that is equal in all feet, and is rather well developed with a small subapical filament, and secondly by the possession of a special organ in the male postabdomen. The first mentioned characteristic is doubtless the most important one for the identification of the genus, since it is useful in an isolated specimen, even a ?. However, it is the second character that has the strongest influence on the biology of the species belonging to the genus, since it is connected with a special type of mating behaviour.

The discovery of an either virtually obligatory, or facultative loss of the second mentioned character considerably disrupts the homogeneity of the genus Bourletiella. I therefore propose to single out the three species in which sexual neutralisation has been observed, and to bring them in a separate subgenus Cassagnaudiella, with as type species Sminthurus pruinosus Tullberg, 1871. The name is chosen in honour of Dr. Cassagnau, who was the first to demonstrate the phenomenon of sexual neutralisation in the Collembola. Bourletiella (Cassagnaudiella) is differentiated by the facultative or obligatory sexual neutralisation, at least in the male sex, and moreover the possession by non-neutralised females of 3+3 strongly broadened setae on the lower flaps of abd, maybe also by the short flagellum in the male organ.

The species of the subgenus can be separated by the following practical key:

- 3a Ribbon-like setae on ventral flaps of abbd6 in full-grown females only with indistinct, fine fringes; pigmentation strong, blue...

 pistillum s.l.

- b These setae usually with some strong, often branching lacerations; pigmentation weak, dirty grey-blue......pruinosa
- ha Dark pigment absent except in eye-patch; secondary sexual traits normally present, and crest on abbd lower than long.....radula
- b Dark pigment present:.....5
- 5a Pigmentation weak, dirty grey-blue; no secondary sexual characters.....pruinosa
- b Pigmentation strong, blue; secondary sexual characters almost always (?) present......6
- 6a Crest on abd higher than long, at most indistinctly notched at apex; flamelike hairs on dorsum proportionally slender..pistillum pistillum
- b Crest on abd lower than long, with two apices, the anterior one the highest; flamelike setae on dorsum thick.....pistillum incisa

As far as present knowledge permits, the zoo-geography could be summarized thus that radula is an alpine species, restricted to the Alps and the Pyrenees. B. pistillum may be called a boreo-alpine species, distributed in Northern Europe, Scandinavia, Finland, maybe also Siberia (Stebaeva, 1974), Alps and Pyrenees, and the Ardennes in between. The occurrence of pistillum incisa in the Ardennes could be explained conjecturally by postulating a repopulation after the pleistocene from the Pyrenees. The Atlantic area of pruinosa is suggestive of a relic distribution.

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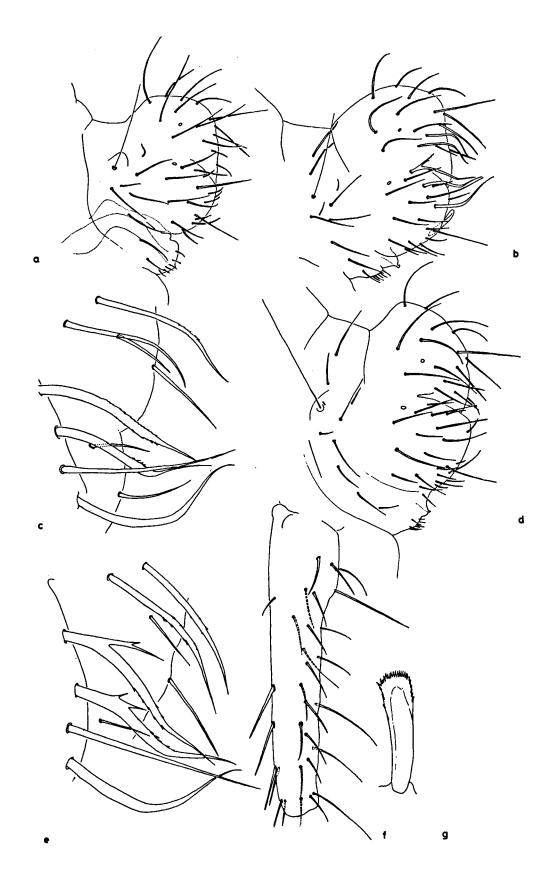


Plate I - Bourletiella pruinosa (Tullberg). a, postabdomen of a male; b, postabdomen of a fully mature female; c, ribbon-like setae of a fully mature female, showing minimum amount of laceration; d, postabdomen of a first stage adult female; e, same as c showing strong laceration; f, dens; g, anal appendage.

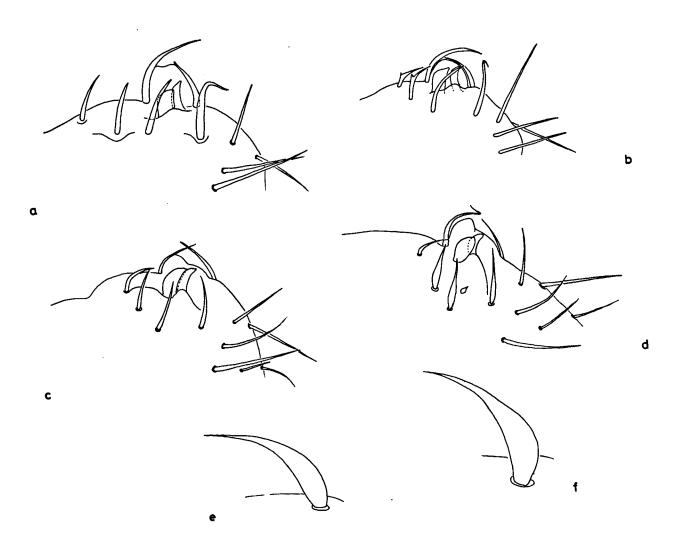


Plate II - Bourletiella pistillum Gisin: a, b and e ssp. pistillum, c, d and f ssp. incisa nov. a, male organ of holotype; b, male organ of specimen from Norway; c, d, male organs of two specimens from Luxemburg; e, incrassate seta on dorsum of holotype male in profile; f, the same of a male from the Pyrenees.