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An emended description of *Sminthurinus lawrencei* Gisin 1963, with notes on the identification of black *Sminthurinus* species

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Abstract

The black, globular springtail *Sminthurinus lawrencei* Gisin, 1963 has long been thought of as a rare species, known from only few localities in only three countries, up to and including 2020. This work describes the discovery of this species in other countries resulting from identification of newly collected specimens, a re-analysis of older collection material and scrutiny of publicly available high-definition images with location tags. This work includes the first records of this species from Canada, France and the Netherlands. Previously, the brief description of *S. lawrencei* by Gisin resulted in many researchers considering it to be a doubtful species. To identify similarly black-coloured *Sminthurinus*-species without characteristic pigmentation, reliance on the presence or absence of setae on the dentes of the furca is a crucial aid for proper identification. This has previously posed challenging due to the lack of proper systematic description of the positioning of these setae. In this work we describe a recent upsurge of recordings for *S. lawrencei*, describe its morphological characteristics and clarify the dental chaetotaxy (following Bretfeld 1999) to aid in the identification of *Sminthurinus 'niger'*-group, which *S. lawrencei* is a member of. We confirm that *S. lawrencei* is a *bona fide* species, but vastly overlooked and should be looked for in Western Europe and North America. By contrast, *S. niger* (Lubbock, 1870) is likely to be much rarer in Western Europe than currently anticipated, with many past recordings likely representing other species, including *S. lawrencei*.

Keywords *Sminthurinus niger* | dental chaetotaxy | distribution | digital imaging | Collembola

1. Introduction

The Collembola genus *Sminthurinus* consists of small, globular springtails that are distributed worldwide. Currently, a total of 98 species have been described (Bellinger et al. 1996–2022). Of those, 21 species are known to be present in the Western Palaearctic (Bretfeld 1999, Bretfeld et al. 2000). Species belonging to the genus *Sminthurinus* can be divided into two distinct subgroups, the so-called '*aureus*'-group and '*niger*'-group based on several morphological characteristics. In the '*aureus*'-group the fifth abdominal segment is fused with the first four abdominal segments, while in the '*niger*'-group this abdominal segment is clearly separate from the other segments. Moreover, species in the '*aureus*'-group have 1+1 distal seta on the ventral tube, and 1 seta at the sub-apical outer margin of the dens of the furca, while in the '*niger*'-group the ventral tube has 2+2 distal setae, and 2 setae at the sub-apical outer margin of the dens (Gisin 1963, Fjellberg 2007). These two groups roughly distinguish generally colourful, patterned species in the '*aureus*'-group from often more uniformly and

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dark coloured species in the *'niger'*-group. As most species of the *'niger'*-group are uniformly black, they are difficult to distinguish in the field or in large collections of specimens. As a consequence, there are doubts about the distribution of species belonging to these groups as literature records are considered unreliable if not verifiable (Fjellberg 2007, Hopkin 2007)

In North-Western Europe, the *'niger'*-group consists of *S. niger* (Lubbock, 1870), *S. alpinus* Gisin, 1953, *S. domesticus* Gisin, 1963, *S. concolor* (Meinert, 1896), all of which are predominantly uniformly dark grey or black, and *S. trinotatus* (Axelson, 1905), which is characterized by the presence of a whitish lateral spot on a further dark body, and *S. igniceps* (Reuter, 1881), which is characterized by a white-coloured head. A seventh, uniformly black, species known as *S. lawrencei* was described by Gisin (1963). This species is known from only a few locations, including its type locality, collections of soil-extracted Collembola from burnt heath fields (Shaw 1998), from a beech forest in the Belgian Ardennes (Gillet & Ponge 2004), several locations in Germany (Engel et al. 2002, Griegel & Russel 2006) and recently found on bark in a garden in England (McCulloch 2021). *Sminthurinus lawrencei* was thought to be a UK endemic species by Shaw et al. (2013), although the Belgian and German records were not considered in their work. Hopkin (2007) judged that the methodology of permanent mounting performed by Gisin does not allow for a proper resolution of the dental chaetotaxy. As no other specimens were known to exist for validation purposes, these doubts left this species with a status of 'uncertain' on the checklist of the British and Irish Collembola (Hopkin 2007). Bretfeld (1999) did, however, conclude that the few characteristics described by Gisin (1963) are good enough for separating this species from the other species within the (sub-)genus.

New records of *S. lawrencei* following examination of collected material and macrophotographic images contradict the view that the species is as rare as previously thought. The large number of newly identified specimens from various sources presented in this work allows an emended description of the species, bringing its description more in line with modern standards. As identifying species in the '*niger*'-group heavily relies on the analysis of their dental chaetotaxy which contributed to past confusion, we also aimed to provide a comparative analysis of this characteristic to aid in the correct identification of species in the *'niger'*-group. Last, we discuss the status and distribution of darkly coloured species of *Sminthurinus* in Western Europe.

2. Materials and methods

The examined material, both in the form of images and collected specimens, was non-systematically collected from various locations across Europe (Table 1). Collected specimens were examined in temporary glass slide mountings in 70% ethanol, after which the material was transferred and stored in 70% ethanol. To examine the key characters from collected specimens of *S. lawrencei,* material was cleared in NaOH (5–10%), after which key characteristics were examined (at 40-600x magnification, Olympus CHC). Some of the reference material from Belgium and the Netherlands were mounted on glass slides in Euparal, following a modified mounting protocol similar to Hopkin (2007). The modifications included reductions in the number of final washing steps as the synthetic Euparal is known to be more tolerant to residual ethanol than Canada Balsam. In order to ascertain some of the existing British and Irish records of black species belonging to the *Sminthurinus 'niger'*-group, slide-mounted specimens of *S. niger*, *S. concolor* and *S. lawrencei* from the Natural History Museum London (NHML) were requested and examined (details in Table 1). All Belgian and Dutch collection specimens of *S. lawrencei* examined in this work are stored in the collections of the first and last author, while specimens from the UK, other than type specimens from the NHML, are kept in the collection of the second author.

To determine the dental chaetotaxy, collected specimens from *S. aureus*, *S. concolor*, *S. lawrencei*, *S. niger* and *S. trinotatus* were examined to confirm their positions (Table 1). For *S. alpinus, S. igniceps* and *S. domesticus*, drawings in the works by Gisin (1963) and Fjellberg (2007) were used for this purpose. The setae were given names following the chaetotaxic systematic adapted from Bretfeld (1999). Unfortunately, the dental chaetotaxy in *Sminthurinus* is not properly updated in that work, thus we reconfigured the chaetotactic nomenclature. Each seta was scored for presence or absence in the examined species and we drew a map of all possible setae on the dentes. For purpose of comparison, *S. aureus* was included as having the most basal number of setae present in *Sminthurinus*.

Drawings were all made in Inkscape (Inkscape Project 2020).

Use of species-specific characteristics related to the inter-ocular vesicles (i.e. 'eyebrows') between the ocular fields have previously been applied by the third author to identify *Sminthurinus*-species from digital images. As such, publicly available images on the websites Flickr.com and Collembola.org were sourced, and the morphology and location of the inter-ocular vesicles were used to identify further *S. lawrencei* among images of similar species.

3. Results

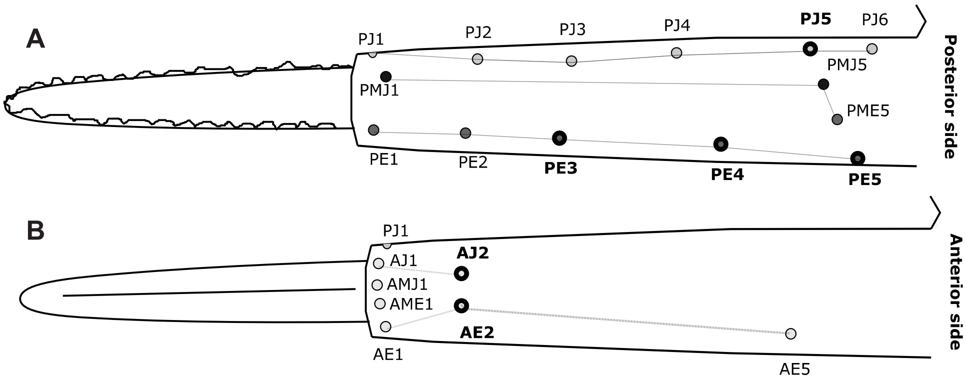
3.1 A systematic description of the dental chaetotaxy of the *'niger'*-group

From the examined specimens (Table 1) and literature work, we drew and named all the possible seta following Bretfeld (1999) and mapped all setae on the posterior and anterior sides of the dentes that showed variation among the examined species (Fig. 1A). A total of six setae are found to vary for their presence, and thus species-specific; PE3, PE4, PE5 on the outer margin of the dentes, PJ5 on the inner margin of the dentes, and AE2 and AJ2 – both anterior sub-apical setae. For *S. trinotatus*, *S. concolor* and *S. igniceps* the arrangement of the setae on the dentes is identical, all with only seta PE4 absent (Fig. 1B). However, colour patterns will usually key them out with *S. igniceps* exhibiting a white head and *S. trinotatus* bearing large white, lateral spots on the abdomens. The highly similar looking species *S. alpinus*, *S. concolor, S. niger*, and *S. lawrencei* require separation of the species based on the specific setae, but there are always at least two setae on the dentes of these species that will separate them with only seta PE3 shared between these species (Fig. 1B). Based on dental chaetotaxy, dark specimens of *S. domesticus* can only be distinguished from *S. niger* by the presence or absence of the second anterior sub-apical seta (AJ2) (Fig. 1B). Images of the dentes with setae annotated as described in Fig. 1A are given for a select number of species: *S. lawrencei* (Fig. 2A, B), *S. niger* (Fig. 2C, D), *S. aureus* (Fig. 2E) and *S. trinotatus* (Fig. 2F, G) as they appear on a glass slide under a compound light microscope.

3.2 An emended description of *Sminthurinus lawrencei*

Synonyms:
Sminthurinus lawrencei Gisin, 1963: 87-88 (original description)
Sminthurinus lawrencei: Shaw 1998: 84
Sminthurinus lawrencei: Bretfeld 1999(107):117,120
Sminthurinus lawrencei: Gillet & Ponge 2004:223, 227
Sminthurinus lawrencei: Hopkin 2007:29, 18 'sd'
Sminthurinus lawrencei: Shaw et al. 2013:164,165 'sd'
Sminthurinus lawrencei: McCulloch 2021(34):201-206
'sd' = status doubtful

Material examined for description; MB 5537, MB 5538, MB 5144, MB 5169, MB6339 SLSTH-1, SL-BDG-1, SL-OPP-1, 012821360 (NHML; paratype), 012821359 (NHML; paratype), 012821358 (NHML; paratype) (For details see Table 1). The Holotype was not examined.



	PE3	PE4	PE5	AE2	AJ2	PJ5
S. aureus	-	-	-	-	-	-
S. lawrencei	+	-	+	-	-	-
S. alpinus	+	-	-	-	-	+
S. niger	+	+	-	+	-	+
S. concolor	+	-	+	+	+	+
S. trinotatus	+	-	+	+	+	+
S. domesticus	+	+	-	+	+	+
S. igniceps	+	-	+	+	+	+

Figure 1. (**A**) all possible setal positions on the posterior side of the furcula in *Sminthurinus*-species (nomenclature follows an adaptation to Bretfeld 1999). All setae that are variably present within the 'niger'-group, the specific setae, are given in bold. (**B**) Presence (+) / absence (-) summary of the specific setae of selected species belonging to the 'niger'-group. *Sminthurinus aureus* is added as a reference, bearing none of the specific setae. The figure was made in Inkscape (Inkscape Project 2020) and drawn by R. F. H. M. van Bezouw.

Table 1. Recent recordings of Sminthurinus lawrencei and other material used in this study. Species; *S.* = *Sminthurinus*. Sample id = ID given as collection systematic by owner of the specimen. X and Y coordinates are given following WGS84 coordinate system. Material, nature of the source; lit = literature record only, coll = specimen stored in collection, img = specimen was identifiable from a digital image with location tag; Source = record had been described in previous publication.

Species	Country	Sample id	Date	*x*	*y*	Count	Leg	Material	Habitat	Source
S. lawrencei Gisin, 1963	United Kingdom	-	??/07/1995	51.157	-0.706	300	Peter Shaw	lit	Burnt heathland	Shaw 1998
		-	25/01/2021	-	-	2	J McCulloch	coll	*Betula* bark	McCulloch 2021
		-	19/12/2022	51.2702	0.0560	4	J McCulloch	coll	Leaf litter in a fern clump	-
		012821360	26/12/1962	-	-	1	PN Lawrence	coll (NHMS)		Gisin 1963
		012821359	25/11/1962	-	-	1	PN Lawrence	coll (NHMS)	Conifer humus	Gisin 1963
		012821358	26/12/1962	-	-	3	PN Lawrence	coll (NHMS)	Bog root hole	Gisin 1963
	The Netherlands	MB 6669	26/01/2002	52.70137	4.69188	5	MP Berg	coll	Moss on tree (oak)	-
		MB 5537	08/03/2002	52.55397	4.86525	200	MP Berg	coll	Moss on roof	-
		MB 5538	080/3/2002	52.55397	4.86525	300	MP Berg	coll	Moss on roof	-
		MB 4597	20/06/2012	52.43282	4.78129	2	MP Berg	coll	Beaten from *Campanula* vegetation	-
		MB 5113	20/05/2017	52.33608	4.82573	1	MP Berg	coll	In litter layer, thick deciduous forest	-
		MB 5144	06/01/2018	52.12796	4.33554	74	MP Berg	coll	On oak, in litter and grass	-
		MB 5169	06/01/2018	52.13212	4.32899	34	MP Berg	coll	Wet stem on grass	-
		MB 5194	06/01/2018	52.13375	4.32772	1	MP Berg	coll	Under bark, dead tree	-
		MB 4965	09/03/2018	52.15712	4.48555	2	MP Berg	coll	Between stone cracks	-
		MB 4966	10/03/2018	52.43282	4.78129	2	MP Berg	coll	Under a stem	-
		MB 4974	11/03/2018	52.15712	4.48555	3	MP Berg	coll	Between stone cracks	-
		MB 5016	26/04/2018	51.26907	5.62385	2	MP Berg, A Krediet	coll	Under bark of a *Pinus* tree	-
		MB 5523	13/02/2019	52.08209	5.64251	5	MP Berg	coll	Moss on trunk	-
		MB 5601	13/04/2019	52.15806	4.38031	3	MP Berg	coll	In moss on steep shore	-
		MB 6176	29/11/2019	52.3491	4.55798	3	MP Berg	coll	On bark (*Crateagus* sp)	-
		MB 6274	20/02/2020	51.96533	5.6522	3	R Majoor	coll	From bark	-
		MB 6276	20/02/2020	51.96533	5.6522	2	R Majoor	coll	From bark	-
		MB 6339	05/04/2020	52.43282	4.78129	16	MP Berg	coll	On wooden fence	-
		MB 6630	29/11/2020	52.22749	4.52072	1	MP Berg	coll	Under tree bark hawthorn	-
		MB 6644	05/12/2020	51.73002	5.51631	1	MP Berg	coll	Between plants and litter	-
		SL-STH-1	27/02/2021 1	51.3958	5.6558	8	RFHM van Bezouw	coll	*Betula* trunk in heath marshes	-
		SL-BDG-1	23/05/2021	52.0819	4.7507	3	RFHM van Bezouw	coll	Trunk in garden	-
		SL-HFD-1	16/08/2021	52.3061	4.6620	1	K van Veen	coll	Trunk in garden	-
	Belgium	-	??/06/2001	49.98	4.86	17	S Gillet	lit	Beech forest soil sample	Gillet & Ponge 2004
		SL-OPP-1	30/04/2021	51.1184	5.6438	17	ML Huskens	coll	In flower pot	-

Species	Country	Sample id	Date	*x*	*y*	Count	Leg	Material	Habitat	Source
		SL-HGV-1	23/10/2021	51.2663	5.4258	2	ML Huskens	coll	Under *Betula* trunk	-
		Ant Mechelen	2021/01/21	51.0281	4.4803	1+	J Soors	img	unknown	Collembola.be
		Lim Kaulille	2019/11/04	51.1902	5.5177	1+	ML Huskens	img	unknown	Collembola.be
		Lim Opitter	2016/2021	51.1184	5.6438	Many	ML Huskens, F Janssens	img (23x records)	in garden, flower pot	Collembola.be
		Lim Neerpelt	10,11/2022	51.2663	5.4258	Many	ML Huskens	img (5x records)	on trunks, in litter in heath field	Collembola.be
		Lim Meeuwen-Gruitrode	22,23/02/022	51.1116	5.6082	Many	ML Huskens	img (2x records)	on trunks, in leaf litter in forest	Collembola.be
	Germany	ID: 19873*	-	48.290649	10.416809	Unknown	Unknown	lit	Coniferous woodland	Engel. (2002)
		ID: 19856*	-	48.467334	7.777	Unknown	Unknown	lit	-	Russell (1998)
		ID: 19866*	-	48.853056	8.123	Unknown	Unknown	lit	Floodplains and woodland	Russel and Griegel (2006)
		ID: 19886*	-	53.33	13.17	Unknown	Unknown	lit	Forests and plantations	Russell (2003)
	Canada	-	23/01/2013	?	?	1	TF Kyron	img	-	Bellinger et al. (1996-2022)
	France	-	08/11/2020	43.2546	1.6716	1	J Joachim	img	Garden	Flickr.com
		-	06/04/2017	46.3648	3.4653	1	J Picard	img	Trunk in forest	Flickr.com
S. concolor (Meinert, 1896)	Jersey (CI)	SC-CIY-1	07/02/2021	-	-	2	S Robson	coll	From garden litter	-
	Great Britain	012821362	22/10/1960	-	-	2	PN Lawrence	coll	Forest	-
		012821361	11/04/1955	-	-	1	PN Lawrence	coll	-	-
S. niger (Lubbock, 1870)	The Netherlands	-	08/06/2011	52.44992	4.72526	4	A Grosman	coll	From plant and upper litter layer	-
		MB 4992	03/03/2018	52.08127	6.07287	3	A Krediet	coll	-	-
		SN-BDG-1	25/05/2021	52.0819	4.7507	31	RFHM van Bezouw	coll	In aquarium in garden	-
	Great Britain	012821357	16/04/1962	-	-	3	PN Lawrence	coll (NHMS)	-	-
		012821356	05/12/1954	-	-	2	PN Lawrence	coll (NHMS)	-	-
		012821354	16/04/1962	-	-	1	PN Lawrence	coll (NHMS)	-	-
		012821353	13/02/1955	-	-	1	PN Lawrence	coll (NHMS)	-	-
	Republic of Ireland	012821355	12/07/1960	-	-	1	PN Lawrence	coll (NHMS)	-	-
S. trinotatus Axelson, 1905	Belgium	ST-OPP-1	30/04/2021	51.1184	5.6438	10	ML Huskens	coll	In flower pot	-
	The Netherlands	ST-STH-1	27/02/2021	51.3958	5.6558	2	RFHM van Bezouw	coll	Grassland humus	-
S. aureus (Lubbock, 1862)	The Netherlands	WB-1-2	29/04/2021	51.3104	5.6868	Numerous	RFHM van Bezouw	coll	Forest ditch	-
		WB-1-3	13/05/2021	51.3104	5.6868	Numerous	RFHM van Bezouw	coll	Forest ditch	-

* Records and coordinates in Edaphobase – https://portal.edaphobase.org/, see Burkhardt et al. (2014)

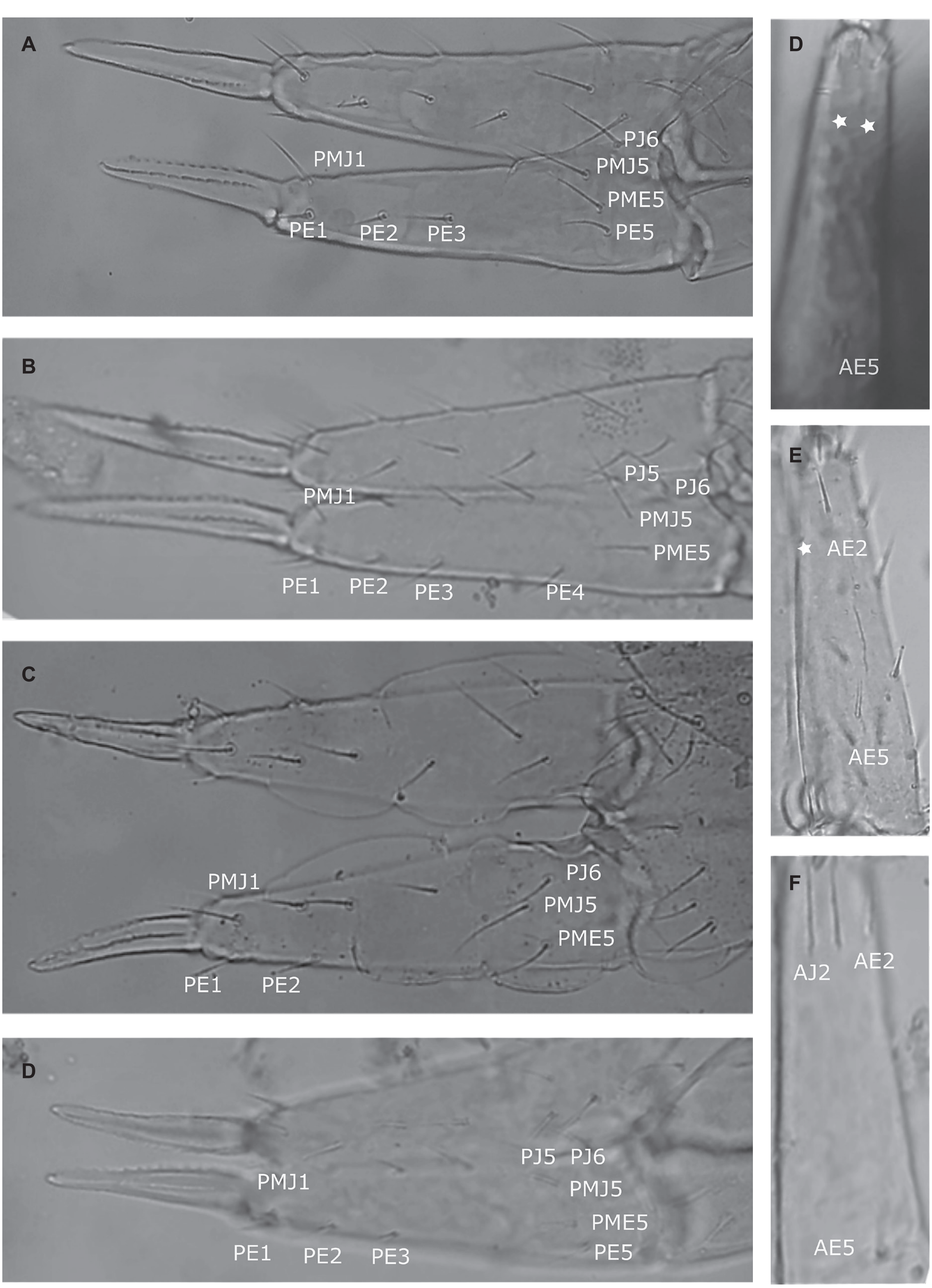


Figure 2. Dental chaetotaxy of *Sminthurinus* sp. (**A**) *S. lawrencei* (material from Belgium), (**B**) *S. lawrencei* ventral view (material from Belgium), (**C**) *S. niger* (material from th Netherlands), (**D**) *S. niger* ventral view (the netherlands), (**E**) *S. aureus* (The Netherlands), (**F**) *S. trinotatus* (Belgium), (**G**) *S. trinotatus* (ventral view) (Belgium). All images were made using an Olympus CHC microscope at 400x magnification, on specimens cleared in NaOH. In B, D and G, asterisk represent positions of missing setae.

Habitus: The size of the largest females extends to 1.2 mm, while males are approximately half that size. The body, head, all antennal segments and legs are all invariably, uniformly grey-black (Fig. 3A), while the furca is pale. Juveniles are more pale.

Head: The ocelli A to H are all present, with ocellus D always reduced in size. The white inter-ocular vesicles are small, and do not extend beyond ocelli G + H. They often come with three teeth pointing inwards in full grown adult specimens (Fig. 3B). The distance between these vesicles is more than two times the width of a vesicle. Between ocellus G and H, setae oc1 and oc2 are invariably present following Janssens (2005–2022). Head ventrally with 2+2 post-labial setae. Six pre-labial setae are present, while the labium contains five posterior, four median and four anterior setae. The third antennal segment has a prominent basal papilla which is undivided. The shape of this organ varies from being triangular, box or more balloon shape-like in examined material (Fig. 3C). Males have enlarged guard setae on the third antennal segment, the upper guard being slightly curved with the tip reaching the undivided fourth antennal segment.

Body: The retinaculum possesses four teeth on each side. The number of apical setae is variable, commonly one, but sometimes two are present (Fig. 3D). The ventral tube contains 2+2 latero-apical setae. Trichobotrium D on the fifth abdominal segment is spine-like (Fig. 3E). Circumanal setae in females are widened at the base, with seta a0 apically split as is typical in *Sminthurinus*. The female sub-anal appendage (SAA) runs out in generally six to seven apical branches. A variable number of these branches is split apically and the SAA includes variation in which up to half of the branching is irregularly subdivided, thus the exact number of branches is variable and hard to define in some specimens (Fig. 3F). However, the outer branches of the SAAs are always longer than the inner branches.

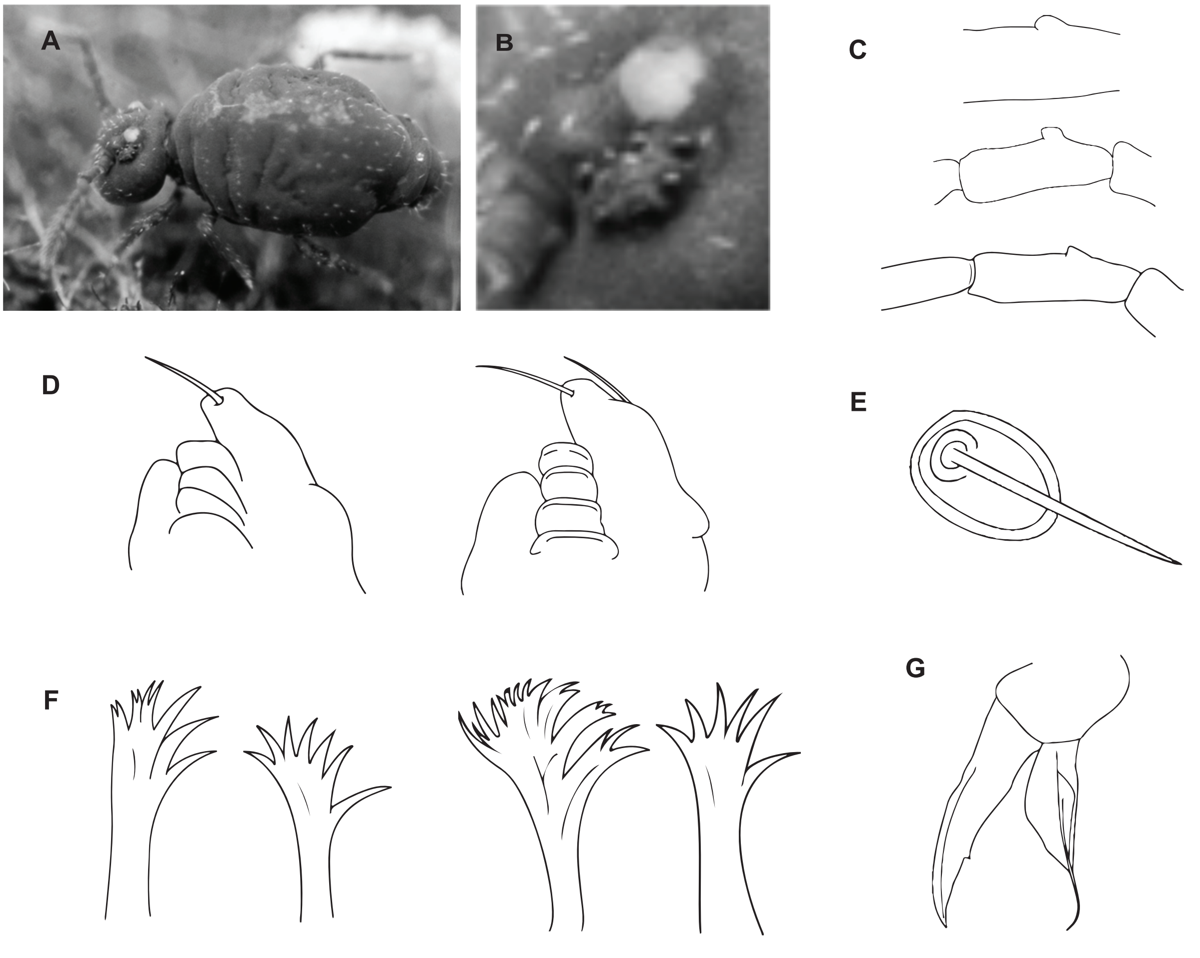


Figure 3. Morphological features of Sminthurinus lawrencei. (**A**) Habitus of adult *Sminthurinus lawrencei* ♀ (NL), (**B**) enlargement of the ocular field of the same specimen. (**C**) Third antennal segment basal papillae (right antennae), from top; material from the Netherlands, Belgium, and Great Britain, (**D**) retinaculum (from left; Belgium and the Netherlands), (**E**) left trichobothrium D on the sixth abdominal segment (material from Belgium). (**F**) female subanal appendages (from left; the Netherlands, Belgium, United Kingdom, and Belgium). (**G**) claw of the third leg, right hind leg (the Netherlands), All drawings were derived from images made using an Olympus CHC microscope at 400x magnification, on specimens cleared in 10 % NaOH. All drawings by James McCulloch (in Inkscape), all images by Jan van Leeuwen.

Legs: Five knobbed setae are present at the distal region of each leg. The unguiculus has a long filament reaching beyond the tip of the unguis on the first leg and is about as long – sometimes slightly longer – than the unguis of the second and third leg (Fig. 3G). The apical filament of the second and third unguiculi are equally long. Claws on all legs bear a single inner tooth, at approximately one third from the top.

Furca: Without variation, among the examined material the dens contained the following setae: two outer (PME5, PE5), one median (PMJ5) and one inner (PJ5 absent, PJ6 present) proximal seta, and two dorsal outer setae (PE2, PE3 present) (Fig. 2A). Anterior, subapical (AE2, AJ2) setae are never present (Fig. 2B). The dorsal median apical seta (PMJ1) is about twice the length of the other setae in the apical whorl. The mucro has both edges unequally serrated over the full length, with the outer edge generally bearing coarser teeth than the inner edge (Fig. 2A). The mucro to dens ratio approximates 0.57.

3.3 New recordings of *Sminthurinus lawrencei*

Summarizing the identification of newly collected specimens, re-examination of previously collected material vastly increased the number of previously published occurrences for *S. lawrencei* over those previously recorded in North-Western Europe (Table 1,

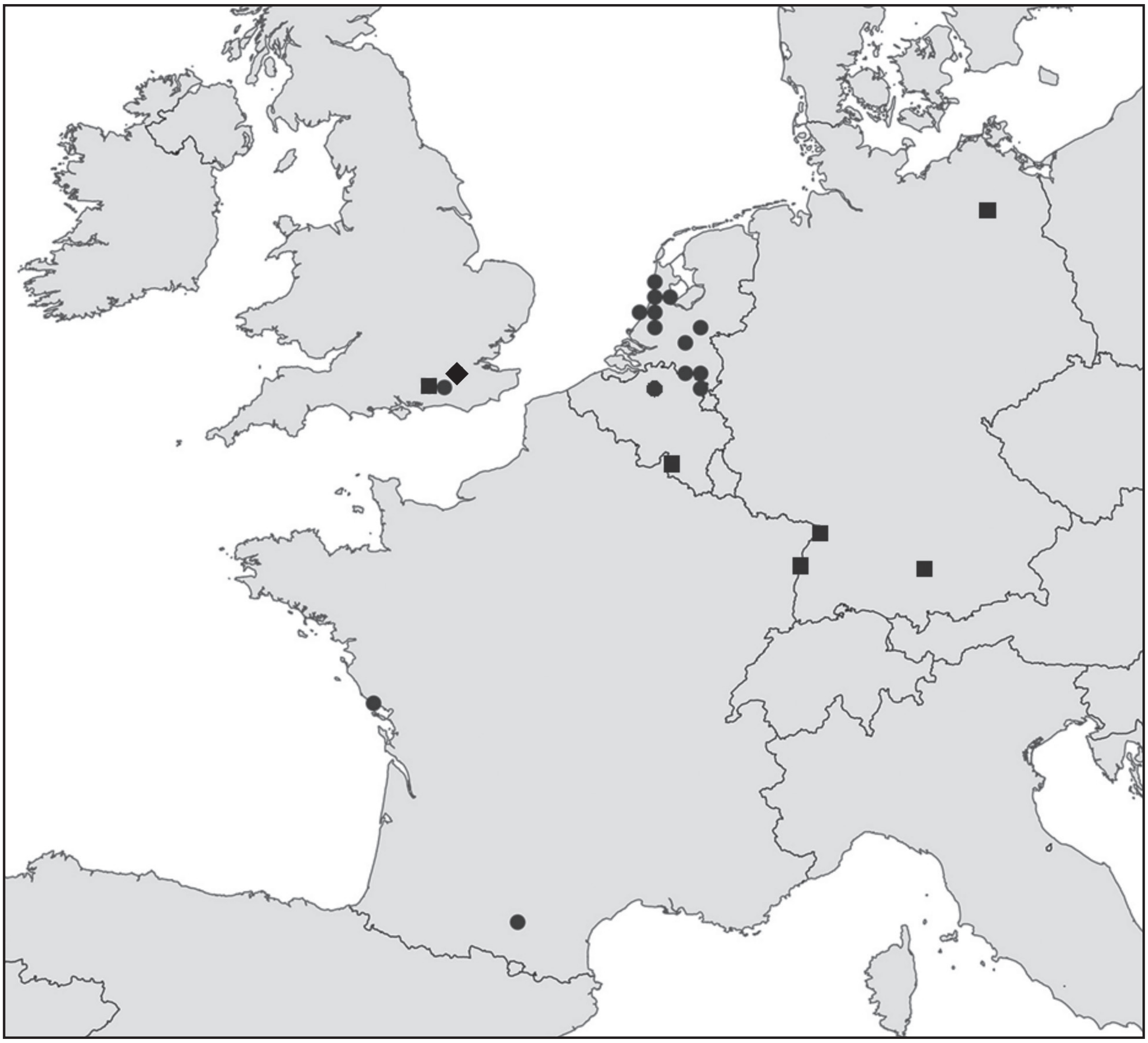


Figure 4. Distribution of localities of verified records of *Sminthurinus lawrencei* in Western Europe. The Canadian record is not shown. Circles represent records supported by collection material. The diamond indicates the location of the type locality (Gisin, 1963; United Kingdom). The squares represent literature records.

Fig. 4). Most of these records are from the Netherlands. Additional records supported by collected material originate from Belgium, thus confirming the presence of the species there, too.

The use of the colouration and shape of the inter-ocular vesicles is a trait that was first used since 2015 by the third author, a character to distinguish between the dark *Sminthurinus*-specieson digital images. By examining the collection material, this character is found to reliably separate the otherwise uniformly black *S. lawrencei* from *S. niger* and *S. concolor*. In *S. lawrencei*, these white inter-ocular vesicles are small, roundish with three teeth pointing inwards in an adult specimen. This inter-ocular vesicle does not advance beyond ocellus C and the distance between the left and right inter-ocular vesicle is more than twice that of the inter-ocular vesicle diameter (Fig. 5A). In *S. niger*, this white inter-ocular vesicle circumvents most of the upper and posterior sides of the ocular fields, creating a large crescent shape in full-grown adults (Fig. 5B). In *S. concolor*, these inter-ocular vesicles are much larger than in *S. lawrencei* and are not crescent shaped. The distance between these inter-ocular vesicles is less than twice that of the inter-ocular vesicle diameter and features a single, large anterior indentation (Fig. 5C). The listing in table 1 is not exhaustive for images from public images due to the large number of records available, which are nearly always misidentified *S. niger*. However, several of such photographs were taken from France and Canada, from which S. lawrencei was not previously recorded and these are thus included in the list (Table 1, Fig. 4).

4. Discussion

4.1 An influx of a long neglected springtail

Almost sixty years after the formal description of *Sminthurinus lawrencei* in 1963 by Gisin we present data indicating that this species is not as rare as previously implied by the few records described in literature until now (Gisin 1963, Shaw 1998, Engel et al. 2002, Russell 2003, Gillet & Ponge 2004, Russell & Griegel 2006, McCulloch 2021). The amount of widespread recordings – both geographically and in time – does not suggest that a sudden, exotic influx of *S. lawrencei* explains the increase in the number of new locations. Also, we do not believe that a recent range expansion of this species, for instance related to climate change, has occurred. Most new recordings of *S. lawrencei* are located south from previously known localities in the UK, which is opposite to what can be expected from a northern range extension as could be predicted from global warming. An important explanation for the

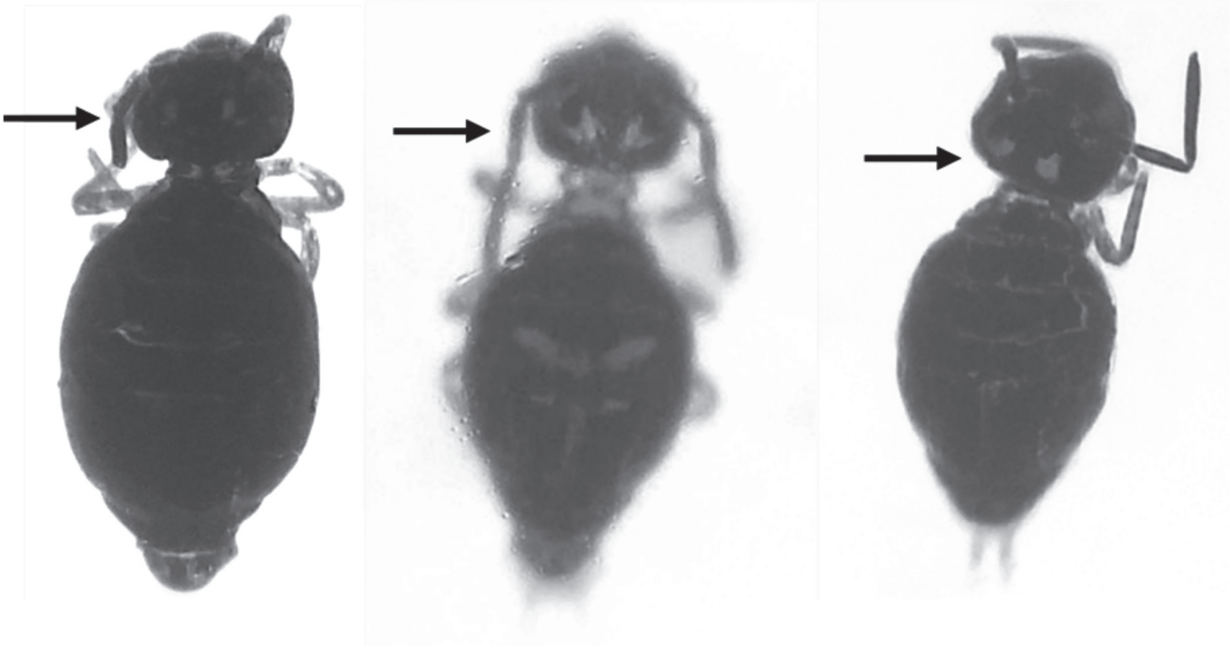


Figure 5. Habitus features of dark Sminthurinus-species fixed in ethanol. (**A**) *S. lawrencei* (material from Belgium), inter-ocular vesicle (i.e. 'eye brow') small, distance > 2x eyepatch diameter, (**B**) *S. niger* (material from the Netherlands) inter-ocular vesicle circumventing the ocular field, distance inter-ocular vesicle smaller than ocular field (**C**) *S. concolor* (material from Yersey Island), inter-ocular vesicle large, with a single indentation, distance < than two 2x inter-ocular vesicle diameter. Images show representative specimens from various locations, collected in 70 % ethanol. Arrows point to the inter-ocular vesicular patches.

increase in recordings is that this species has long been overlooked due to its brief taxonomical description and reliance on dental chaetotaxy which may be difficult to resolve. *Sminthurinus lawrencei* seamlessly keys out as *S. alpinus* in Fjellberg (2007) and as a dark variant of *S. aureus* in Hopkin (2007), two of the most accessible and widely used identification keys to identify Collembola in Western Europe. Consequently, it is likely that *S. lawrencei* remains misidentified in collections this way without further notice.

The arrangement of setae on the dentes in *S. lawrencei*, as described by Gisin (1963), are consistent among all examined specimens. For correct identification among congeneric species, the most important feature is the absence of proximal seta PJ5 in the proximal region of the dentes and simultaneous presence of proximal seta PE5, which reliably separates *S. lawrencei* from all North-Western European members of the *'niger'*-group. Most other characters in *S. lawrencei* are similar as in *S. niger*. A notable difference can be found in the inter-ocular vesicles. In *S. lawrencei,* these are much smaller and distance apart in two of similar species, *S. niger* and *S. concolor*.

The similarity of newly found specimens with previous literature records and verification of characters in paratypes leaves no doubt that the examined material is *S. lawrencei* as described by Gisin (1963). Some characters originally described to be species-specific by Gisin (1963) were found to be variable in the material that we analyzed, now originating from multiple locations. Branching of the SAA, as used by Bretfeld (1999) as a species-specific character in the *'niger'*-group, dictates *S. lawrencei* as being characterized with six branches. However, examination of specimens from various locations, as shown in this study, reveals that this character may not be reliable, with branch number either variable or difficult to determine. We also found the number of apical setae on the retinaculum to vary between one or two apical setae. Ellis (1976) reports on a subspecies of the related *S. alpinus*, *S. alpinus bisetosus* Ellis, 1976*,* in material collected from Crete (Greece), distinguished by the presence of a second apical seta on the retinaculum. However, given the variation of the number of setae on the retinaculum observed among different populations of *S. lawrencei*, this character alone might not be stable enough to describe a new subspecies within *Sminthurinus*. The ant III organ was found to have a variable shape as well. However, the apex of this organ was always undivided which is in agreement with the description provided by Gisin (1963). The here presented material thus provides new insight in the degree of variability of the species and its abundance.

4.2 The systematic description of dental chaetotaxy in *Sminthurinus*-species

The dental chaetotaxy is a reliable characteristic to aid in the identification of *Sminthurinus*- species (Gisin 1963, Bretfeld 1999, Fjellberg 2007), but may in practice be difficult to discern (Hopkin, 2007). For *S. concolor*, we identified a conflict in Fjellberg (2007) during examination which is drawn as having 4 proximal setae (PJ5, PJ6, PMJ5, PE5), but described as having five. Examined material from the NHML and a freshly collected specimen from Jersey confirm that five – including seta AE5 – are present, as depicted in Bretfeld (1999). Curiously, none of the examined species within *Sminthurinus* bears the full arrangement of possible setae present as drawn in this work, thus suggesting independent diverging evolutionary lineages within the genus. A possibility leading to confusion is that while Bretfeld (1999) does provide a sophisticated systematic for naming these setae on the dentes, it is sparsely and inconsistently used, and not described in *Sminthurinus*. Determining variation in *Sminthurinus* species is particularly complicated, due to the importance of correctly assessing the absence and presence of setae on particular positions. In this work we identified a group of six setae (PE3, PE4, PE5, PJ5, AJ2, AE2) that are indicative for different species of *Sminthurinus* in North-Western Europe. By providing a systematic detailing of the arrangement of dental setae based on the work of Bretfeld (1999) and digital images of this character under a compound, light microscope we have contributed to clarify descriptions of dental chaetotaxy of species in the '*niger*'-group. We encourage authors engaged in (re-)describing species belonging to *Sminthurinus* to use a similar approach.

4.3 Usage of digital images to record black *Sminthurinus*-species

High resolution, digital photographic imaging, mostly by macro-photographers, is an increasingly accessible method of recording fauna. Such images are increasingly becoming a valuable tool to assess the distribution and presence of species of springtails in countries (Shaw et al. 2013, Berg & den Ouden 2013). Rather than focussing on characters that can only be reliably discerned under a compound light microscope, we also examined the habitus of *Sminthurinus lawrencei* and two similarly looking species, *S. niger* and *S. concolor*. We were able to verify linking morphological characters with the shape and size of the inter-ocular vesicles. Doing so, we conclude that *S. lawrencei* also occurs in Canada and France, and is very common in Belgium as can be concluded from several tens of verifiable records from digital records in addition to the collected specimens. *S. lawrencei* is also very common in the United Kingdom and the Netherlands, countries with a substantial number of records from macro-photographers in online resources, but we did not exhaustively examine all images. These results confirm the usefulness of digital photography to identify species in this taxonomic clade. The characteristics of the inter-ocular vesicle may require further verification in other uniformly dark species within the *'niger'*-group as an aid to record their distribution as well.

4.4 Status of North-Western European *Sminthurinus*-species

Sminthurinus lawrencei appears to be much more common and widespread in North-Western Europe than previously thought (Shaw et al. 2013), with specimens mostly collected aboveground, from roofs, trees and bark. The species may potentially be regarded as an imported species in Canada as only a single reliable record exists from North America. In collected specimen and collection material, the presence of *S. alpinus* in North-Western European countries has yet to be confirmed. In Nordic collection material examined by Fjellberg (2007) *S. lawrencei* is absent and may be replaced by *S. alpinus*. Its distribution may be restricted to more montane regions in Central and Northern Europe, although the species is reported from Spain and Greece as well (Ellis 1976).

Although we did not structurally analyze all available public images due to the large volume of the data, our records do suggest that *S. niger* is not as common as previously thought. In the Netherlands, *S.lawrencei* is about seven times more frequently found in collection material than *S. niger* (Table 1). In Fennoscandia, Fjellberg (2007) was able to identify only two *bona fide S. niger* specimens among black *Sminthurinus*-species. By contrast, Hopkin (2007) relied mostly on (unreliable) literature records in mapping occurrences of *S. niger* and concluded the species to be common, but it is likely that most of these records mostly represent dark *S. aureus* and/or *S. lawrencei* instead. The availability of digital macro-images may play an increasingly important role in mapping the distribution of species of springtails if colour traits, in this case the inter-ocular vesicular patches as, that do correlate with characters used traditional microscopy.

4.5 Ecology and habitat preferences of *Sminthurinus lawrencei*

Due to the large number of recent records, a habitat preference for *Sminthurinus lawrencei* can be deducted. *S. lawrencei* should be looked for aboveground, on dry surfaces, such as wood, bark or stones, with shelter in the form of cracks and grooves. Regularly mentioned microhabitats include flower pots, but also more natural environments, such in heathfields and forests. All these records combined indicate that *S. lawrencei* is a rather eurytopic species, which is tolerant to disturbances and with a preference for drier microhabitat types, such as on stones and on bark. Noteworthy, the species often occurs in habitats that cannot be sampled by means of soil cores. This may be another reason why the species has been overlooked for such a long time.

5. Conclusion

This study gives an emended description of *Sminthurinus lawrencei*, based on newly and previously collected material. The presence of this species went long unnoticed, which we primarily attribute to the difficulty in discerning it from other uniformly dark *Sminthurinus*-species. Re-examined material, sourced from both collected and photographed specimen, allowed us to describe the species more in line with modern standards and correctly identify *S. lawrencei* among related species. The updated description of the dental chaetotaxy should aid those interested in correctly identifying black *Sminthurinus*-species. This study demonstrates the combined power of digital images and collected specimen to provide novel insights in the distribution and abundance of an under-recorded springtail species.

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