

***Leucozona lucorum* (Linnaeus) – a species complex? (Diptera, Syrphidae)**

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The Central European populations of *Leucozona* (s.s.) are divided into two phenotypes based on a set of characters from adult morphology. For all but two of these characters the two phenotypes exhibit an overlapping variability. The validity of differentiating the two phenotypes taxonomically is demonstrated by biometric analysis. The available data on range, habitat, and flight period do not provide definite differences. The considerable number of differential characters, the lack of intermediate specimens, and sympatric occurrence of the two phenotypes indicate that gene-flow is interrupted. On this basis, these phenotypes are regarded as representing distinct species level taxa. The names *lucorum* (Linnaeus) and *nigripila* Mik are proposed for them. The status of the allopatric taxon *americana* Curran is still uncertain.

Zusammenfassung

Die mitteleuropäischen Populationen von *Leucozona* (s.s.) werden anhand einiger Merkmale der Imaginal-Morphologie zwei Phänotypen zugeordnet. Mit zwei Ausnahmen überschneiden sich die Variationsbreiten aller Merkmale. Durch eine biometrische Analyse werden die Unterschiede bestätigt. Die vorliegenden Daten zu Verbreitung, Lebensraum und Flugzeit lassen keine eindeutigen Unterschiede erkennen. Die beträchtliche Zahl von Differentialmerkmalen, das Fehlen von Übergangsformen und sympatrisches Vorkommen lassen darauf schließen, daß der Genfluß unterbrochen ist. Deshalb werden die Phänotypen als getrennte Arten aufgefaßt, die vorläufig *L. lucorum* (Linnaeus) und *L. nigripila* Mik genannt werden. Der Status des allopatrischen Taxons *americana* Curran ist noch ungeklärt.

1 Introduction

Leucozona lucorum (Linnaeus, 1758) is one of the few taxa among the Syrphinae that are readily identifiable at a glance. It has a Holarctic distribution and is distinctive in its whole range. However, Mik (1888) and Curran (1923) described two new "varieties" of *lucorum*, *nigripila* Mik and *americana* Curran, which differ from the typical form in possessing black pile on tergite 4. Both authors had the vague suspicion that their varieties might in fact represent distinct species: Mik (1888): "... so scheint

es gerathen, die kaukasischen Stücke vorläufig nur als Varietät ... anzusehen." [= it seems advisable to regard the Caucasian specimens provisionally as a variety only]; Curran (1923): "... shows that the American specimens are either a very good variety ... or a distinct species. I am inclined to believe the two distinct, but as the genus is so little known, place our form as a variety." Both taxa have not been recognised by subsequent authors.

The present investigation started from the observation that the 48 specimens of *Leucozona* (s.s.) in my collection are divisible into two clear-cut groups based on differences in the colour of the pile on tergite 4: in one phenotype (12 specimens), in the following called *nigripila* or "black-haired phenotype", it is entirely black while in the other (36 specimens), *lucorum* (s.s.), it is most often predominantly whitish and always pale haired at the sides. This agrees well with the statements of Mik and Curran. However, examination of the other characters given by these authors either proved that they are invalid or of doubtful significance (see 4.2). In order to resolve this inconsistency the following questions have been investigated:

1. Does the examination of additional specimens confirm the existence of discrete phenotypes based on the hair colour of tergite 4?
2. Are there correlations with any other characters?
3. Which taxonomic status is appropriate for the phenotypes?

As the morphology of preserved adult specimens and the data on their labels are the only available information the "distinct species hypothesis" is tested against these data.

The present account deals mainly with Central European populations that comprise two phenotypes provisionally named *lucorum* and *nigripila*, with notes on the Nearctic taxon *americana*.

2 Material

The sample consists of 205 specimens of *Leucozona* s.s. from the private collections of C. Claußen, D. Doczkal, M. Hauser, C.F. Kassebeer, and A. Ssymank, from the Staatliches Museum für Naturkunde in Stuttgart (SMNS) and the type specimen of *nigripila* in the Naturhistorisches Museum in Vienna. The majority of specimens (70 %) is from Germany (various regions). Most of the remaining specimens are from adjacent countries and only a few specimens are from outside Central Europe (table 1). The Canadian specimens have been caught in the vicinity of Montreal and Ottawa. The material consists of dry pinned adults mostly in good condition.

	Σ	<i>lucorum</i>		<i>nigripila</i>		<i>americana</i>
		♂	♀	♂	♀	♂
Austria	19	5	11	1	2	-
Canada	8	-	-	-	-	8
Caucasus	1	-	-	-	1	-
France	5	3	2	-	-	-
Germany	142	48	56	19	19	-
Italy (Alps)	22	6	16	-	-	-
Kirghizia	2	-	2	-	-	-
Sweden	1	-	1	-	-	-
unknown (Europe)	5	1	2	-	2	-
Σ	205	63	90	20	24	8

Table 1: Number and geographic origin of studied specimens.

3 Investigation methods and terminology

3.1 Procedure

The primary selection of morphological characters was done "by eye". This is the most efficient method to pick out the "right" characters, i.e. those that will give the best discrimination. In order to minimise the subjective component of the process of character interpretation, a standardised data collecting and analysis procedure was performed as a second step, initially restricted to the 48 specimens from my private collection. The results were then checked using 157 specimens from other collections. In order to minimise the potential for variability due to geographic origin of specimens, character evaluation was first restricted to the 142 specimens from Germany. Subsequent comparison with specimens from elsewhere revealed that the available specimens from Europe and Kirghizia are within the range of variation observed among the German specimens of the respective phenotype. Therefore they have been lumped. A series of eight ♂ from Canada turned out to be consistently different from both *lucorum* and *nigripila* and are therefore treated as a separate phenotype, *americana* Curran. I have not attempted any alternative grouping of the data, or a further subdivision. In chapter 4.1 only characters with a strong discriminatory power, i.e. those with little or moderate overlap of frequency distributions between the phenotypes, are considered.

3.2 Statistics

The results (4.1) comprise only characters for which significance is obvious even without statistic calculations (figs. 10-12). For most of the characters the level of significance has been calculated. The sign-test of Dixon and Mood (Sachs 1997) has been used for some of the qualitative characters (table 3). For quantitative data the arithmetic mean and the standard deviation have been calculated (tables 4, 5). The histograms (figs. 10-12) suggest that in all examined characters the mean values are lower in one phenotype than in the other, so the unilateral t-test has been chosen for the characters "length of eye hairs" (4.1.1) and "L/D ratio of first flagellomere" (4.2.2). As the variances are partly unequal at the $p = 0.05$ level (F-test) the heteroscedastic t-test of Welch (Lorenz 1988) has been used. Because of the unequal distributions, the Kolmogoroff-Smirnoff-test (Sachs 1997) has been chosen for the remaining characters.

3.3 Techniques

The ♂ genitalia have been treated with 10 % KOH at room temperature for about 20 hours, washed in diluted acetic acid and water, examined in water, and stored in glycerol in plastic micro-vials. All other characters have been studied from dry specimens.

The measurements (characters 4.1.1 and 4.2.2) have been performed with an ocular micrometer. The remaining quantitative characters are based on estimates. Specifications are given with the respective character accounts.

The drawings have been prepared from hard-copies of images produced with a Zeiss Stemi SV11 microscope provided with a EHD Kam02 video camera that was connected to a IBM PC computer.

3.4 Terminology

In general, the terminology of McAlpine (1981) has been followed for the morphological features referred to here, but Cumming et al. (1995) have been followed in referring to features of the ♂ terminalia.

Abbreviations: Morphology: MA = anterior branch of media; bc, bm, br, c, cup, r_1 = wing cells (see McAlpine 1981: 30, figs. 68 and 69); f = femur / femora (e.g. f_3 means hind femur); t_3 = hind tibia; T = tergite(s); L/D = ratio length : depth. – Statistics: \bar{x} = arithmetic mean; SD = standard deviation; n = sample size; p = level of significance.

→ **Table 2:** Morphological differences between adults of *Leucozona lucorum* (Linnaeus) and *L. nigripila* Mik in populations from western Central Europe. The characters are sorted in descending order of discriminatory power.

character	<i>lucorum</i>	<i>nigripila</i>
n	63♂ + 88♀	20♂ + 23♀
colour of hairs on T4 (4.1.10)	predominantly white, rarely >50% black, always white at the lateral margins	all black
colour of the rim of the lower calypter (4.1.5)	more or less darkened	yellow
microtrichia on the ventral side of f_{1-3} (4.1.8)	much reduced or absent, always absent on the distal half of f_3	usually (almost) entirely trichose (absent in 1♀)
length of eye hairs in mm (4.1.1) \bar{x} (x_{\min} - x_{\max})	♂ 0.17 (0.15-0.2) ♀ 0.15 (0.13-0.18)	♂ 0.14 (0.13-0.15) ♀ 0.125 (0.11-0.14)
extent of bare area on basal cells in % (4.1.7) \bar{x} (x_{\min} - x_{\max})	♂: c 15 (0-50), bm 64 (40-80) ♀: c 30 (10-80), bm 73 (60-80)	♂: c 0 (0), bm 35 (10-50) ♀: c 1 (0-10), bm 39 (10-70)
♂: black hairs on posterior margin of T2 (4.1.10)	usually absent or only very few present (<50% of posterior margin covered in black hairs)	always present and usually extensive (>50% of posterior margin covered in black hairs)
♂: yellow hairs at the anterior margin of T3 (4.1.10)	usually present	always absent
yellow hairs on anterior and dorsal side of f_3 (4.1.9)	usually ± extensive	most often much reduced or absent
colour of scutal hair (4.1.3)	rufous, ♂ and ♀ concolorous	♂ rufous or tawny, ♀ usually paler
colour of scutal pruinescence (4.1.4)	usually darker, more brownish	usually paler, greenish grey
colour of basal cells (4.1.6)	often distinctly infuscated	not darker than adjacent cells
pruinescence on the bare black area at the sides of the face (4.1.2)	usually missing or only with traces	usually extensive
gonostylus (low n!) (4.1.11)	posterolateral corner not produced, anterior lateral edge hardly receding in upper part, so that the median edge is hardly visible in external view	posterolateral corner usually slightly produced, anterior lateral edge receding in upper part, so that the anteromedian edge is clearly visible in external view
ventral process of the basiphallus (4.1.11)	without a posteromedian carina	with a more or less well-developed posteromedian carina

4 Results from morphological investigations

4.1 Characters with positive results

In overall appearance, *nigripila* and *americana* are very similar to *lucorum*. All have a dark brown spot on the wing, the typical *Leucozona* pattern of pale abdominal markings, a protruding face with a lateral keel on the lower part, and practically identical ♂ genitalia. Specimens of all phenotypes will run to *lucorum* using existing keys and figures. The observed differences are summarised in table 2. They are described and discussed with emphasis on variability, discriminatory power, and practical difficulties.

4.1.1 Length of eye hairs: The length of the eye hairs decreases from the upper to the lower part of the eye. The measurements have been taken from individual hairs on the middle part of the eye observed from above, at a magnification of 169x, and given in classes defined by 1/100 of the micrometer scale ($\approx 8.5 \mu\text{m}$). The results are shown in fig. 10. As the ♂ has longer hairs than the ♀ the sexes are treated separately. The lengths of hairs of a certain part of the eye is somewhat variable, but only one or few hairs have been measured from a single specimen. Furthermore, it is difficult to place individual hairs at an exactly right angle to the microscope axis. For these reasons the error is comparatively high (about 1/100 of the scale) and equals about 4-7 % of the observed lengths. This means that the actual lengths may be \pm one length class. Although this has increased the standard deviation the mean values of *lucorum* and *nigripila* are for both sexes distinct at a high significance level (table 4). The values observed in *americana* are not significantly distinct from *lucorum*.

4.1.2 Pruinescence on the sides of the face: The bare black area between the anterior tentorial sulcus and the mouth edge is usually extensively covered in microtrichia in both sexes of *nigripila*. In *lucorum* and *americana* this area is nearly always bare of microtrichia or at most with traces of dusting. Specimens with extensive dusting are rare. Although some of the specimens of *nigripila* have the microtrichia more or less reduced the difference from *lucorum* is significant (table 3).

4.1.3 Colour of scutal hair: Curran (1923) described the colour of the scutal pile of *americana* as wholly pale yellow while it is "yellow on the disk and rather tawny on the lateral margin and scutellum" in *lucorum*. From the present sample it seems that this difference is valid. All specimens from Canada have a nearly white scutal pile that is paler than in any of the Palearctic ♂ specimens. Fresh specimens of *lucorum* (♂ and ♀) and *nigripila* ♂ have a rufous scutal pile (with a tendency for being more tawny in *nigripila*) while it is much paler in the majority of the *nigripila* ♀ (table 3). The latter may approach the condition observed in *americana* ♂. The colour seems to fade comparatively little in old specimens.

4.1.4 Colour of scutal pruinescence: The colour of the scutal pruinescence varies from pale greenish grey in *nigripila* to nearly black in *americana* and is intermediate

(brown) in *lucorum*. The differences are not entirely consistent (table 3), but they can be observed in the majority of specimens provided the pruinescence is intact.

4.1.5 Colour of the calypter: In the available specimens of *americana* the colour of the calypter, including its rim, is blackish and the marginal fringe is blackish to auburn. In specimens of *nigripila* the lower calypter is yellowish. Specimens with a darkened lower calypter have not been found. In *lucorum* the lower calypter is distinctly darker even though often not as dark as in *americana*. A few specimens of *lucorum* approach the state observed in *nigripila*. It seems these specimens are teneral. This character separates the material into two rather clear-cut groups. The colour of the rim gives the best result (table 3).

4.1.6 Colour of the basal cells: All specimens of *americana* have bc and the cell proximal to MA dark brown, thus contrasting with the pale yellowish membrane of the adjacent cells. In typical *nigripila* these cells are not darker than the adjacent cells. *L. lucorum* is intermediate. This character is heavily dependent on the age of specimens, since young specimens have paler wings than older ones. The difference between *lucorum* and *nigripila* is often slight and only detectable by direct comparison (table 3).

4.1.7 Extent of bare areas on the wing: All phenotypes have the basal cells bare of microtrichia to some extent. Bare areas are always present in cells r_1 , br above vena spuria, bm, and cup. Cells c, br below vena spuria, and the anal lobe may or may not have bare areas. Typical examples of *lucorum* and *nigripila* are shown in figs. 1 and 2. The extent of bare areas in cells c and bm has been estimated in intervals of 10 %. The mean extent of bare areas in both cells is significantly different in *lucorum* and *nigripila* (table 4). While cell c of almost all specimens of *lucorum* has a more or less extensive bare area at the basal part it is entirely microtrichose in almost all *nigripila*. Concerning bm *lucorum* and *nigripila* both exhibit a wide range of variation with an extensive overlap (fig. 11), but the mean values are clearly distinct (table 4). Differences in the extent of bare areas in the remaining cells are either much less (e.g. r_1) or more difficult to estimate (e.g. cup).

The specimens of *americana* examined have, on average, even more extensively bare wings than *lucorum*. But, due to the considerable variability and small number of specimens available, this difference is not statistically significant.

4.1.8 Microtrichia on femora: The femora of *nigripila* and *americana* are dusted, i.e. covered in microtrichia, whereas they are extensively undusted in *lucorum*. The differences are most marked on the ventral surface. All specimens of *lucorum* have the distal half of f_3 absolutely bare. Its basal half and f_{1+2} are also usually bare, but a few specimens with more extensive microtrichia occur, approaching the condition observed in *nigripila*. In *nigripila* usually all f are completely microtrichose (small bare spots are disregarded). Two ♂ and four ♀ specimens have the microtrichia considerably reduced and approach the condition of specimens of *lucorum* with unusually extensive microtrichia. However, as the distal half of f_3 is always entirely

bare in *lucorum* (figs. 6, 7), a condition observed in one specimen of *nigripila* only, any specimen with extensive microtrichia on this part of the leg belongs either to *nigripila* (figs. 8, 9) or to *americana*. Specimens with an entirely bare distal half of f_3 most probably belong to *lucorum*, but have to be checked for other characters. A reticulate microsculpture (fig. 7) on the bare surface may be confused with dusting when observed at low magnification.

4.1.9 Colour of the leg hairs: A tendency toward reduction of the frequency of yellow hairs on the legs is obvious in ♂ of *americana* and *nigripila*. Specimens of both phenotypes have the anterior and dorsal surfaces of the distal part of f_3 and the basal half of t_3 (almost) wholly black haired. In *lucorum* these parts are mostly yellow haired (table 3). However, this difference is subject to considerable variability and difficult to quantify. Therefore this character has not been studied in detail. The differences are much smaller (insignificant) in the ♀.

4.1.10 Colour of abdominal hair: The proportion of black hairs on T4 and on T5 has been estimated in intervals of 10 % (long erect and short semiadpressed hairs have not been differentiated). Most specimens of *lucorum* have in the median part of T4 a more or less restricted area with black hairs. These may be situated within either the anterior part, or the posterior part of the tergite (short semiadpressed and/or long erect hairs), or both. The proportion of black hairs is usually low (mean value 20 %; fig. 12). The maximum observed is ca. 70 % (2 ♂). The lateral margins, however, are always white haired. All specimens of *nigripila* and *americana* have the pile on T4 completely black. The condition observed on T5 corresponds with that of T4. The type specimen of *nigripila* has a few white hairs at the outermost margin of T4 on the ventral surface, and bears only few black hairs on T5.

All specimens of *americana*, ca. 80 % of the *lucorum* ♂, about half of the *lucorum* ♀, and the majority of the *nigripila* ♀, have no black hairs at all on the posterior margin of T2, whereas 75 % of the *nigripila* ♂ and three ♀ of *lucorum* have more than 50 % of the length of the posterior margin covered in black hairs (table 3). *L. nigripila* ♂ without black hairs on T2 have not been found. All remaining specimens of *lucorum* and *nigripila* are intermediate. The difference is significant for the ♂ of *lucorum* and *nigripila*, but it is not significant for the ♀.

All ♀ of *lucorum* and *nigripila*, the *americana* ♂ and most *lucorum* ♂, have the anterior margin of T3 more or less extensively yellow haired, whereas all *nigripila* ♂ are without yellow hairs on T3. The presence of yellow hairs on T3 is correlated with the absence of black hairs on the posterior margin of T2.

The colour of the hairs on the sternites has not been studied in detail. It seems to correspond with the hair colour of the tergites.

4.1.11 ♂ genitalia: The ♂ genitalia of three specimens of *americana*, eight specimens of *nigripila*, and ten specimens of *lucorum* have been dissected. The phenotypes are extremely similar in all parts of their genitalia. No difference between *americana* and

lucorum has been found. The gonostylus of *nigripila* (fig. 4) is characterised by a slightly produced posteroventral corner and by the structure of the anterior margin, that has the outer edge a little receding at the upper part so that the inner edge is visible there in lateral view. The ventral process of the basiphallus (fig. 5) bears posteromedially a sharp carina. In *lucorum* (fig. 3) the posteroventral corner of the gonostylus is not produced and the entire inner anterior edge is more or less hidden by the outer edge. The ventral process of the basiphallus of *lucorum* lacks a posteromedian carina, but is rounded or angular at the respective spot. The differences are subtle and exceptions occur even within the small sample. Due to the small sample size statistic calculations would be inconclusive.

4.2 Additional characters mentioned by Mik (1888) and Curran (1923)

4.2.1 Shape of facial tubercle: According to Curran (1923) the American specimens have the "facial tubercle longer, less prominent" than specimens from Denmark and England. In a comparison between the head profiles of some of the Central European specimens and the Canadian material, no difference has been observed.

4.2.2 Length of first flagellomere: Curran (1923) observed the third antennal joint in *americana* to be a little shorter than in European *lucorum*. This may be statistically correct, but due to the low number of *americana* specimens examined here and widely overlapping variation this difference has not been found to be statistically significant at the $p = 0.05$ level (table 5). The character may be useful to support *americana* as a distinct phenotype but more data are required. *L. lucorum* and *nigripila* have a practically identical L/D ratio ($p = 0.35$).

4.2.3 Shape of abdomen: Mik (1888) refers to a narrower and more arched abdomen in *nigripila*. The study of a number of Central European specimens revealed that a difference in abdominal shape does not exist. The type specimen is within the normal variation.

4.2.4 Length of abdominal hair: According to Mik (1888) the pile on T4 of *nigripila* is short. In the present sample the hairs on the anterior part are of more or less the same length while on the posterior part long hairs of various lengths are mixed with short and more or less depressed hairs. A quantitative survey has not been conducted. The length of the hairs on T4 is variable in all three phenotypes. There appears to be no correlation between the length of the hairs and any other character.

4.2.5 Colour of tergites: Curran (1923) states that in *americana* the terminal abdominal segments are deep black, while they appear metallic in the European specimens. I have not examined if this is a valid difference or merely an illusion caused by the colour of the hair reflected in the shiny surface of the integument. In *lucorum* the shining parts of T4+5 appear greenish, in specimens of *americana* and *nigripila* more blackish, occasionally with faint purple reflections.

Pair No.	1	2	3	4	5	6	7	8
1	o	+	+	+	o	+	+	+
2	o	+	+	o	+	+	+	+
3	o	+	+	+	+	+	o	+
4	o	o	+	o	+	o	+	+
5	o	+	+	+	o	+	o	+
6	o	+	+	+	+	+	+	+
7	+	+	+	+	+	o	+	+
8	o	+	+	o	+	+	+	+
9	o	+	+	+	+	+	o	+
10	o	o	+	+	+	+	+	+
11	+	+	+	+	+	+	+	+
12	-	o	+	o	+	+	+	+
13	+	+	+	+	+	+	+	+
14	+	+	+	+	o	o	+	+
15	+	+	+	+	o	+	+	+
16	o	+	+	o	+	+	+	+
17	o	+	+	+	+	+	o	+
18	o	+	+	+	+	+	+	+
19	-	o	+	+	+	+	+	+
20	o	+	+	o	+	+	+	+
p	ns	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
21	+	+	+	+	o	o	+	+
22	+	+	+	o	o	o	+	+
23	+	+	+	+	o	o	+	o
24	+	+	+	+	+	o	+	+
25	+	+	+	o	+	o	+	+
26	o	o	+	o	+	o	+	+
27	+	-	+	+	o	o	o	+
28	+	+	+	+	o	o	o	+
29	+	o	+	+	+	o	-	+
30	+	+	+	+	+	o	+	+
31	+	+	+	+	o	o	+	+
32	+	+	+	+	-	-	+	+
33	+	+	+	+	o	o	+	+
34	+	+	+	+	+	o	o	+
35	+	+	+	+	+	o	o	+
36	o	o	+	o	o	o	+	+
37	+	+	+	+	o	o	+	+
38	+	+	+	+	o	o	+	+
39	+	+	+	+	o	-	+	+
40	+	+	+	o	o	o	+	+
p	<0.01	<0.01	<0.01	<0.01	ns	ns	<0.01	<0.01

Taxa		<i>luc</i> ♂	<i>nig</i> ♂	<i>luc</i> ♀	<i>nig</i> ♀	<i>luc</i> ♂ / <i>nig</i> ♂	<i>luc</i> ♀ / <i>nig</i> ♀
n		63	20	90	24	p	p
length of eye hairs (mm)	\bar{x}	0.176	0.14	0.155	0.125	< 0.001	< 0.001
	SD	0.011	0.008	0.011	0.007		
bare area of cell c (%)	\bar{x}	15	0	30	1	< 0.001	< 0.001
	SD	10	0	18	3		
bare area of cell bm (%)	\bar{x}	64	35	73	39	< 0.001	< 0.001
	SD	9	11	5	17		
black hairs on T4 (%)	\bar{x}	20	100	8	100	< 0.001	< 0.001
	SD	14	0	10	0		

Table 4: Differences between *Leucozona lucorum* and *L. nigripila* in selected quantitative characters. The p-values have been calculated from the heteroscedastic unilateral t-test of Welch (length of eye hairs) or (remaining characters) from the Kolmogoroff-Smirnoff-test.

Taxa		<i>americana</i>	<i>lucorum</i>	<i>nigripila</i>	<i>ame / luc</i>
n		8	36	19	p
L/D of 1st flagellomere	\bar{x}	1.57	1.63	1.61	0.055
	SD	0.103	0.074	0.104	

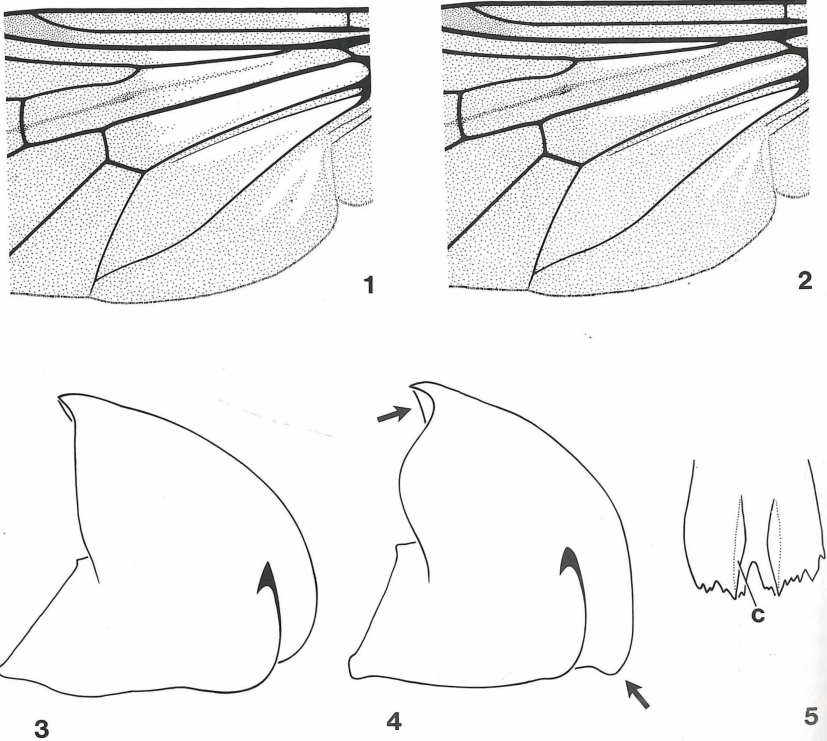
Table 5: Results from measurements of the L/D ratio of the first flagellomere of *Leucozona* ♂. The length refers to the distance between the dorsoproximal end and the apex. The p-value has been calculated from the heteroscedastic unilateral t-test of Welch.

← **Table 3:** Differences between *Leucozona lucorum* and *L. nigripila* in selected qualitative characters. 20 ♂ and ♀ of each taxon have been arranged in pairs with randomly chosen specimens of *lucorum*. Pairs 1-20: ♂, 21-40: ♀. + = character more expressed in *lucorum*; - = character more expressed in *nigripila*; o = no difference. As the characters are continuous it is in principle possible to observe differences in each pair. In order to avoid the overvaluation of extremely slight differences, pairs have been classified as identical if no difference was seen at a glance. The p-values have been calculated from the sign-test of Dixon and Mood (Sachs 1997). ns = not significant at the p = 0.05 level.

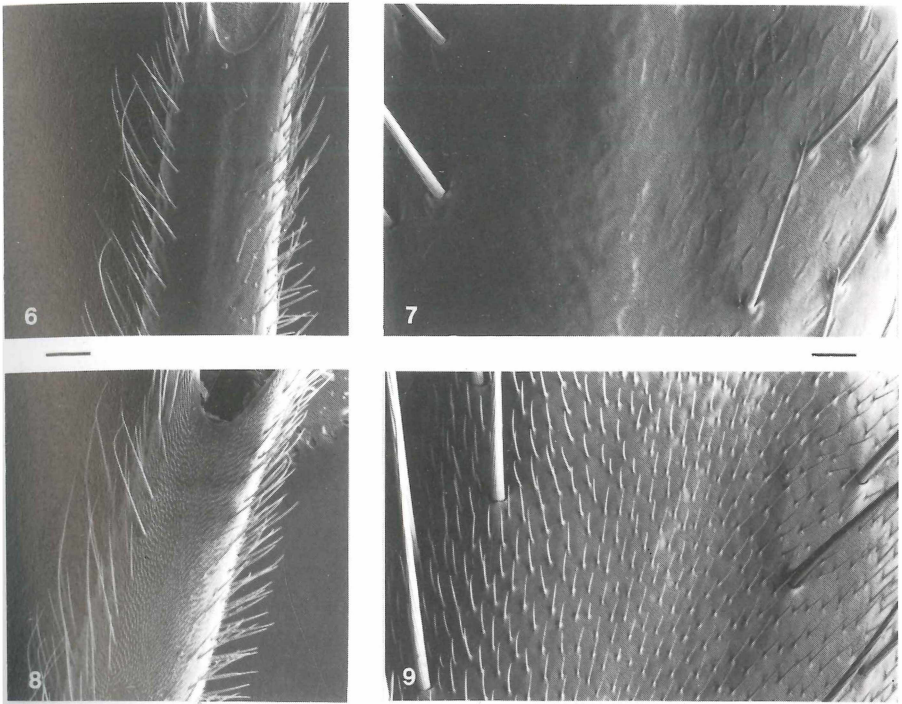
Characters: 1 scutal hair darker; 2 scutal pruinescence darker; 3 rim of lower calypter darker; 4 basal cells darker; 5 yellow hairs on the anterior and dorsal side of f_2 more extensive; 6 posterior margin of T2 with less extensive black hairs; 7 the bare black area at the sides of the face less extensively microtrichose; 8 f_2 ventrally with a more extensive area bare of microtrichia.

combination	frequency			
	expected		observed	
	cases	%	cases	%
<i>lucorum - lucorum</i>	12	60	15	75
<i>lucorum - nigripila</i>	7	35	1	5
<i>nigripila - nigripila</i>	1	5	4	20

Table 6: Expected and observed frequency of combinations between *Leucozonia lucorum* und *L. nigripila* among 20 couples each collected at the same place and day. The sample contains 31 specimens of *lucorum* and 9 specimens of *nigripila*. In order to simplify the calculation the three cases with more than two specimens have been reduced to two specimens; in none of these cases the combination *lucorum - nigripila* occurs.



Figs. 1-5: *Leucozonia* spp. – 1-2: Basal part of the left wing. – 1. *lucorum* (10 % of c and 60 % of bm bare); – 2. *nigripila* (30 % of bm bare). – 3-4: Outline of the right gonostylus, lateral view. – 3. *lucorum*; – 4. *nigripila*. – 5: Apex of the ventral process of the basiphallus of *nigripila*, posterior view. c = posteromedian carina.



Figs. 6-9: SEM photos of the distal part of f_3 , ventral view. – 6-7. *lucorum*; – 8-9. *nigripila*. – 6, 8. overall view, scale = 0.1 mm; – 7, 9. detail, scale = 0.02 mm.

5 Range

While *Leucozona* s.s. is distributed in nearly the entire Holarctic region (map in Vockeroth 1969: 81) the material used for the present account originates from a rather small part of its range (table 1). Therefore the actual range of the individual phenotypes is still unknown. Two ♀ from Kirghizia (coll. C. Kassebeer) differ in no way from Central European specimens of *lucorum* indicating this phenotype has a wide range. Although the only available specimen of *nigripila* from outside Central Europe differs in a few characters from all the central European specimens examined, they are provisionally regarded as conspecific (9.4). If this is correct, *nigripila* has an extensive range, too. The data display no clear chorological difference between *lucorum* and *nigripila*. Rather they are sympatric, at least almost throughout Germany. However, *nigripila* seems to be absent from the (Central) Alps where *lucorum* is abundant:

Among 46 specimens of *Leucozona* examined from the Alps, only one belongs to *nigripila*. This specimen is from Salzburg, i.e. from the N margin of the Alps. In contrast, 38 of the 142 specimens (= 27 %) from Germany belong to *nigripila*.

Because nearly all taxonomic literature misses all the important characters described above it is impossible to decide which of the phenotypes are referred to by previous authors. However, the extensive description in Lundbeck (1916: 243) clearly refers to *lucorum* s.s. (calypter blackish, T4 at least laterally yellow-haired). The same applies to Verrall (1901: 320), where in a short note a possible specimen of *nigripila* is recorded from Britain. Although the description of the latter is rather inconclusive, the colour mentioned for the thoracic pile is typical for the ♀ of *nigripila*.

M. Speight (in litt.) has a specimen of *nigripila* from France (Vosges) and reports *lucorum* from Ireland, Great Britain, Norway and Liechtenstein. M. Jessat (pers. comm.) found in Romania *lucorum* only. T. Nielsen (in litt.) has 2♀ of *nigripila* from Denmark (identification confirmed). From Norway he knows *lucorum* only.

The phenotype *americana* is probably restricted to the Nearctic region, but this will remain uncertain until eastern Palaearctic populations are examined.

6 Adult habitat

Both *lucorum* and *nigripila* are most often found in or near (humid) forests. The available data are insufficient to detect different habitat requirements. However, the data provide a hint that a difference might exist: Among the 197 Palaearctic specimens are 20 couples with identical data on their labels. The observed combinations differ from the values to be expected if both phenotypes were randomly distributed (table 6). One possible explanation is that the phenotypes prefer different situations. The nature of this presumed difference is unknown. Due to the low number of cases this observation may be accidental.

7 Flight period

L. lucorum (s.l.) is regarded as univoltine, with a peak from May to June and a weak partial second generation in late summer (Verlinden & Decler 1987). The phenograms (fig. 13) of *lucorum* and *nigripila* suggest a similar flight period. Due to the low number of records of *nigripila*, in particular, the slight differences in the phenograms may be accidental.

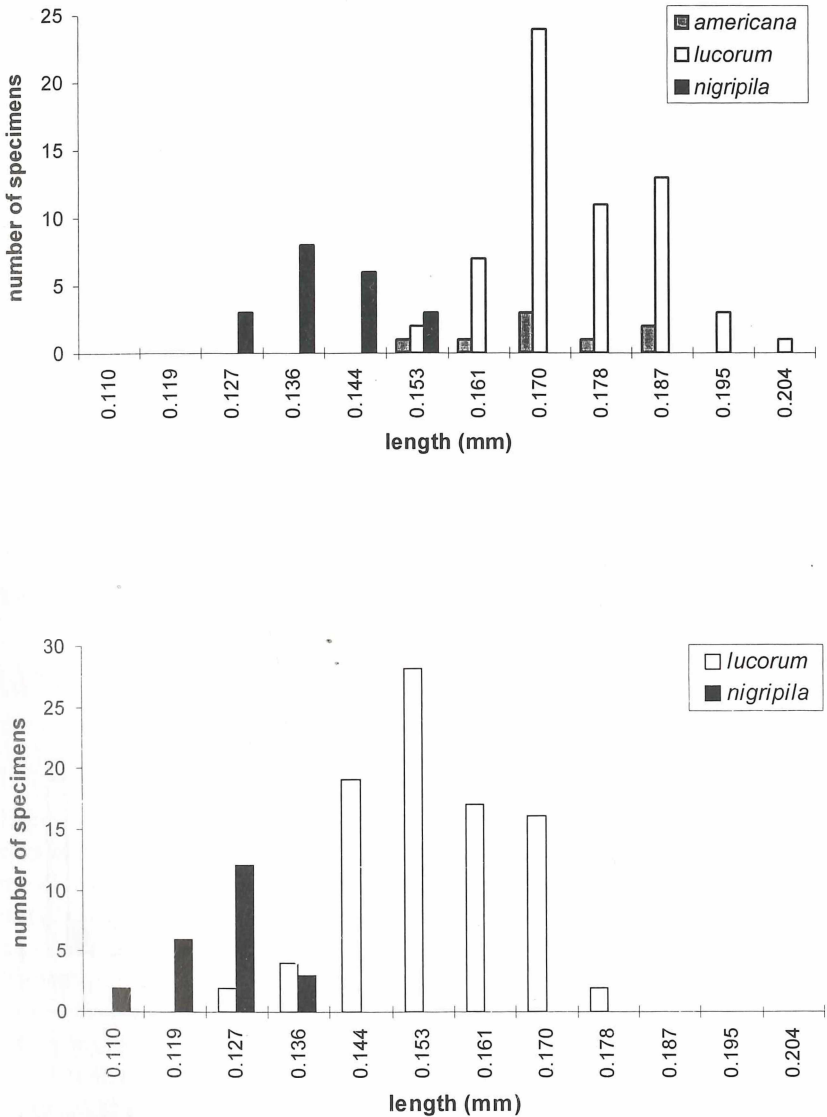


Fig. 10: Length of eye hairs in ♂ (above) and ♀ of *Leucozonia* spp.

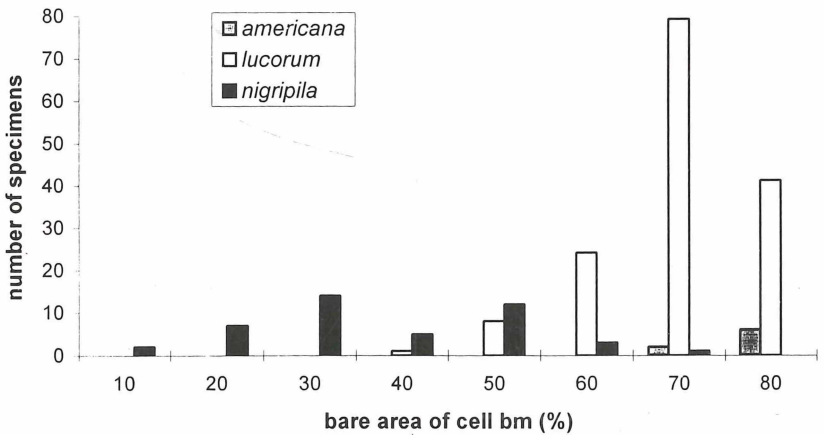
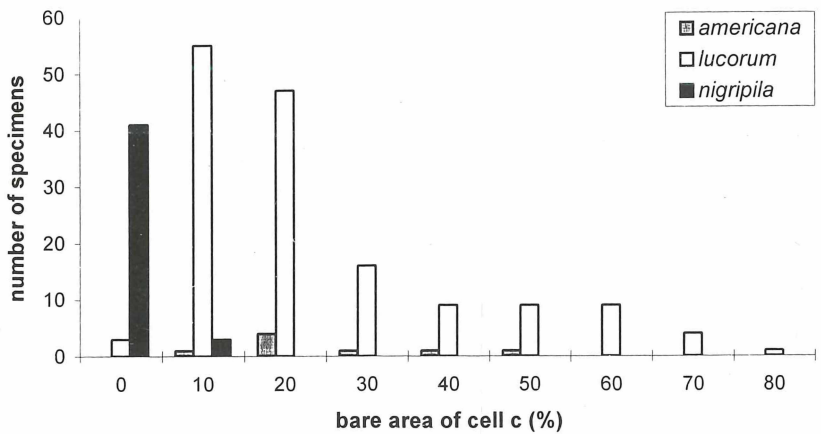


Fig. 11: Extent of bare area in wing cells c and bm. As the differences in mean values between the sexes of *lucorum* and *nigripila* are less than the standard deviation, the data for both sexes have been lumped.

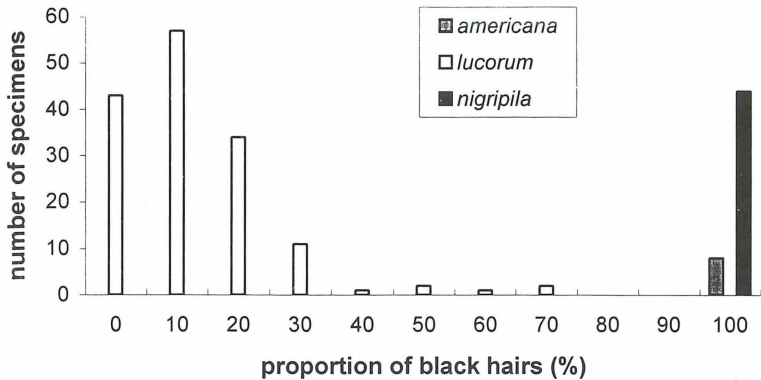


Fig. 12: Proportion of black hairs in the pilosity of T4.

8 Nomenclature

The available names are:

Musca lucorum Linnaeus, 1758: 592.

Conops praecincta Scopoli, 1763: 357.

Syrphus asiliformis Fabricius, 1781: 426.

Leucozonia lucorum var. *nigripila* Mik, 1888: 141.

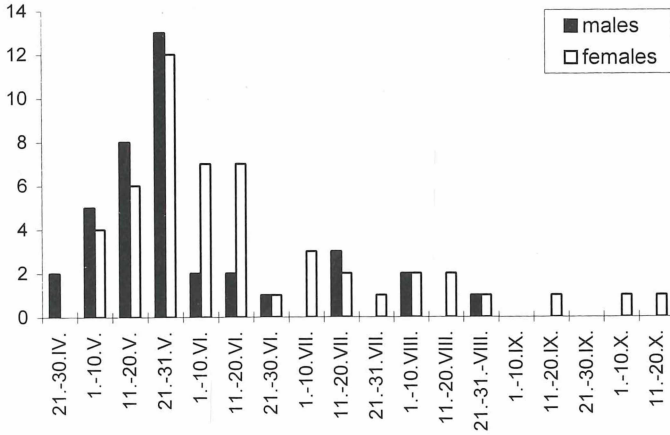
Leucozonia lucorum var. *americana* Curran, 1923: 38.

Leucozonia lucorum var. *differens* Frey, 1946: 158.

Except for *nigripila* and *americana* it is impossible to judge from the original descriptions which of the phenotypes the respective authors had before them since no information concerning the relevant characters are given. The type of *lucorum* has been studied by Thompson et al. (1982: 157) who did not redescribe it. It has not yet been possible to obtain from the Linnaean Society information on the identity of the Linnaean type specimen. The (syn-)type specimens of the taxa described by Scopoli and Fabricius are regarded as lost (Horn et al. 1990; Zimsen 1964).

The name *lucorum* Linnaeus is provisionally adopted for the more common, fair-haired phenotype. The type specimen of *nigripila* has been studied. Despite a few character states not found in any of the Central European specimens of the black-haired phenotype (9.4), it is regarded as conspecific. The only available name for the Nearctic phenotype is *americana* Curran.

lucorum



nigripila

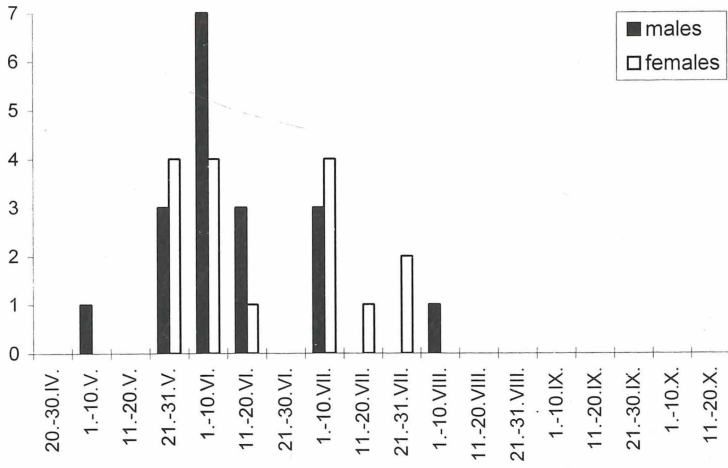


Fig. 13: Flight periods of *L. lucorum* and *L. nigripila* in Germany at altitudes below 1,000 m.

9 Discussion

9.1 Character evaluation

The individual characters are to various degrees diagnostic. One character, the hair colour on T4, divides the material into two clear-cut groups (*lucorum* vs. *nigripila* + *americana*) without any intermediate specimens and with a large gap (4.1.10, fig. 12). The colour of the lower calypter is almost as good. It separates *americana* from *nigripila* by a large gap, whereas the lightest specimens of *lucorum* approach the darkest specimens of *nigripila*. In all remaining characters a varying degree of overlap occurs. However, certain characters always have the same state in one phenotype and the overlap results from the variability of the other phenotypes. For example, the distal half of the ventral side of f_3 is always absolutely bare of microtrichia in *lucorum*. In *nigripila* this part is usually densely trichose but reduction occurs and one specimen is indistinguishable from *lucorum* in the condition of this character (a few additional specimens have the trichia much reduced in number, but not wholly absent). All examined *nigripila* ♂ have T3 wholly black haired. The ♂ of *lucorum* most often have at least some yellow hairs at the anterior margin of T3 but exceptions occur. Other characters are variable within each phenotype, but exhibit only a partial overlap. The assignment of a specimen is possible if its character state falls within a "free end" of the distribution graph (figs. 10-11). Characters with complete overlap are of little use for identification purposes. However, they are useful to support the distinctness of phenotypes if their mean values are significantly distinct. From the characters used in the present account the dusting on the sides of the face and the extent of yellow hairs on f_3 and t_3 belong to this category.

The first problem, whether differences observed between specimens in the colour of the hair covering of T4 represents a valid distinction, has been positively resolved. Most of the remaining characters mentioned by Mik (1888) and Curran (1923) are proved to be invalid or doubtful (4.2). The discovery of several new characters (4.1) raises the number of recognisable differences considerably. However, the number may be artificially large because some of the characters are possibly controlled by a single morphogenetic process (e.g. hair colour of T4 and T5), i.e. actually constitute a single character only. Even so, the number and nature of the differences suggest the existence of several independent characters.

9.2 Intraspecific phenotypes or distinct species?

Each specimen examined can be assigned to one of three discrete phenotypes. Although nearly all differential characters have an overlapping variation the assignment is unambiguous, owing to the high number of characters. The visual impression gained from the character distributions shown in figs. 10-12, as well as the statistical calculations (tables 3-5), demonstrate the high discriminatory power of the characters listed in chapter 4.1. So the existence of distinct phenotypes, based on a large set of characters, is proved.

One might argue that a single diagnostic character is an insufficient basis for recognising phenotypes as distinct taxa. However, hoverfly taxonomy is crowded with similar cases, although authors seem to suppress the exceptions (or examine too few specimens!) when describing taxa or presenting keys. For example, in my experience the only reliable difference between ♀ of *Syrphus ribesii* and *torvus* is the different colour of f_3 . The few additional characters mentioned in keys apply to most of the specimens but outliers occur. Against this background the phenotypes of *Leucozona* are abundantly distinct. They are as distinct from each other as the species recognised in related genera like *Syrphus*, *Epistrophe*, *Scaeva*, or *Eupeodes*. Consequently they should be recognised as distinct taxa, too.

The question remains: Do these taxa represent separate species? As in almost all other species-level taxa, the only available information is that from the external morphology of a limited number of dead adult specimens and the data from their labels. Most species concepts require taxonomic information that is in practice usually unavailable. An essential component of all modern species concepts ["biological species", "phylogenetic species", "evolutionary species", etc.: Claridge, Dawah & Wilson (1997)] is that gene-flow is minimal or non-existent between species. Morphological differences between phenotypes may result from isolated gene pools. However, examples of discrete phenotypes (other than sexual dimorphism) with sympatric occurrence within a single species are already known among hoverflies [e.g. *Criorhina berberina* / *oxyacanthae*: Coe (1950)]. So a difference in only a single character could be regarded as insufficient for recognition of two phenotypes as distinct species. But the more numerous the independent differential characters are, the more probable it is that gene-flow is interrupted. The following grounds may be cited as the basis for supposing the phenotypes in *Leucozona* are actually distinct species:

- The high number of presumably independent characters supports evidence that gene-flow between the phenotypes is minimal. The rate of overlap is too low to explain the observations by any simple mechanism which produces intraspecific variability.
- Particularly, in *nigripila* the scutal hair colour, the presence of black hairs on the posterior margin of T2 and the presence of yellow hairs on the anterior margin of T3 display sexual dimorphism whereas in *lucorum* they do not. Further, while *nigripila* is darker concerning the hair colour of the tergites and the legs there is a reverse trend in other colour characters (calypter, wing base, scutal pruinescence). These observations are difficult to explain if the phenotypes have a common gene-pool.
- *L. lucorum* and *nigripila* occupy a large area of sympatric occurrence. Intermediate populations or specimens are unknown.

In the present case the "distinct species hypothesis" is more parsimonious than any concept of intraspecific phenotypes. For this reason I regard *lucorum* and *nigripila* as distinct species (stat. nov.).

While the taxa are shown to be morphologically distinct in the present account, ecological differences are still uncertain. Nonetheless, the observation reported in chapter 6 and the apparent difference in regional distribution (*nigripila* absent from the [Central] Alps) of the taxa, provide hints that biological differences between them may become apparent when they are subjected to further study.

9.3 The status of *americana*

The Canadian specimens examined exhibit a combination of character states not observed in European populations. The character states are in part as in *lucorum*, partly as in *nigripila*, and are partly unique:

1. length of ocular hair as in *lucorum*;
2. the black sides of the face are (nearly) undusted (as *lucorum*);
3. the third antennal segment is on average shorter than in *lucorum* and *nigripila*;
4. the scutal hair is very pale yellow (nearly white) thus distinctly paler than any of the studied European ♂ of *lucorum* and *nigripila*;
5. the scutal pruinosity is darker (dark brown to blackish) than in any European specimen;
6. calypter, including marginal fringe, blackish (as *lucorum*);
7. the basal cells of the wing are extensively bare (as *lucorum*);
8. cell bc and the cell proximal to MA are infuscated (as *lucorum*);
9. the femora are ventrally largely trichose (as *nigripila*);
10. f_3 and t_3 anteriorly and dorsally at most with few scattered yellow hairs (as *nigripila*);
11. T2 without black hairs along the posterior margin (the usual condition of *lucorum*);
12. T3 anteriorly with more or less extensive yellow hairs (as *lucorum*);
13. T4ff are completely black haired (as *nigripila*);
14. genitalia indistinguishable from *lucorum*.

The characters 3, 4, and 13 are used by Curran (1923) for characterisation of *americana*, and character 6 is mentioned by Vockeroth (1992: 130). The characters 3, 4, and 5 are diagnostic for *americana*. However, the number of examined specimens is too low to generalise from these observations (e.g. the difference in the L/D ratio of the first flagellomere is not statistically significant, table 5). More material has to be studied to confirm or to disprove the present results. At present it is impossible to assign *americana* either to *lucorum* or to *nigripila*. Therefore I propose to regard *americana* as provisionally distinct at the species level (stat. nov.).

9.4 The problem of conspecificity of the type of *nigripila* with the Central European black-haired phenotype

The single specimen from the Caucasus, the type of *nigripila*, is beyond the usual intraspecific variation of several characters observed in Central European populations:

- Cell c is bare of microtrichia for about the basal 1/7 (C.E.: usually 0, at most <1/10).
- The lateral margin of T4 bears on the ventral side a few white hairs (C.E.: without any pale hairs).
- The pile on T5 is predominantly white with only few black hairs (C.E.: entirely black haired).

Due to the lack of more material it is impossible to evaluate the significance of these differences. Perhaps they are characteristics of the Caucasian population or they are accidental. Because of their overall similarity, the Caucasian specimen is provisionally regarded as conspecific with the Central European specimens of the black-haired phenotype. In particular the colour of the pile on T4 – if the very few white hairs on the ventral side are ignored – and the microtrichia on the ventral side of all f are equal.

9.5 Identification

Most of the differential characters for *lucorum* / *nigripila* are subtle or have an overlapping variation. Thus their use for identification purposes is inconvenient. However, identification is very easy using the hair colour of T4. This character is visible even with the naked eye. The error rate is negligible, because transitional specimens are as yet unknown and there is a considerable gap between the character states (fig. 12)¹⁾. As the present account is largely based on specimens from Central Europe the validity of this character (and all other characters) remains to be proved for populations from other regions. The problem with the type specimen of *nigripila* shows that the morphological segregation of the taxa may be more difficult when material from their entire geographic range is brought into consideration. Furthermore, there are additional species at least in the SE Palearctic (Vockeroth 1969, 1992; pers. observ.).

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¹⁾ After the manuscript was finished I received a few specimens of *lucorum* from Norway (coll. T. Nielsen) which have pale hairs on T4 much reduced and restricted to the outermost lateral margin of the tergite.

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