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Variability of wing venation of the dragonfly

With 7 text figures

Introduction

For the last few decades special attention has been paid to interspecies populational variability of different characteristics in many groups of animals. This trend is connected with the problem of objective interspecies systematics as well as with more general microevolutionary problems. The population (a panmictic unit which is in some way isolated from similar groups of the same species) is considered as an elementary unit of the evolutionary process. This causes the general interest in the study of its genetic, morphological, physiological and other peculiarities.

The investigation of the population by different methods offers the possibility to elucidate the interaction of different elementary factors of evolution and the character of its trigger mechanisms and thus to establish the general laws of microevolution. A morphological approach to the investigation of the population is important for the study of phenotypic variability from the evolutionary point of view (Tchetvericoff 1926, Dobzhansky 1951, Schmalhausen 1968, Simpson 1944 and others).

Studying phenotypic variability of animals in nature we face two groups of problems: on the one hand, we must obtain the description of the greatest number of various characteristics within the population of a given species; on the other hand, we must study the greatest possible number of species (Yablokov 1965, 1968). Certainly, the most general laws of evolution can be equally applied to the insects and mammals as well as to all other groups of organisms. This permits us to choose for evolutionary investigation any species of organisms convenient for study.

All these considerations together cause the interest in the study of the phenotypic variability of insects. Insects as compared to other large groups of the animal kingdom are one of the ancient groups, and at the same time this is the group with the most complete onto- and phylogenetic differentiation. The fact that it is easy to gather mass population material, that numerous characteristics are clearly defined, and the suitability of the characteristics for laboratory treatment — all that makes the microevolutionary study of insects very promising in spite of the difficulties due to the incomplete description of the fauna.

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It is impossible to give even a short list of the papers concerning interspecies systematics and genetics of insects. From the point of view of microevolution, insects have attracted the attention of investigators for a very long time. As an example we can cite the papers of J. J. LUS (1932), K. W. ARNOLDY (1939), S. R. ZARAPKIN (1934, 1937), N. W. TIMOFEEV-RESSOVSKY (1969), V. A. ZASLAVSKY (1966), W. E. BEREGOVOY (1967) and others. But dragonflies have not been studies from this aspect although their biological peculiarities are a promising object for such investigations. Among these peculiarities are a strict localization of populations (connection with concrete water reservoirs), a comparatively large size which facilitates the precise registration of characteristics, a simple and effective way of catching with very simple equipment and finally a structure of the wing most suitable for study. The only works on dragonflies concern the population variability of wing venation of *Libellula, Leucorrhinia* and *Aeschna* in Latvia (SPURIS 1958, 1960, 1962).

These works have demonstrated the possibilities of the precise registration of the cell number in many areas of dragonfly wings and have shown the general character of variability of 15 different characteristics of the wings. It is important that dragonflies have few species as compared to other groups of insects and that their classification is already complete.

It is very attractive for microevolutionary investigations that in nature the material for characterization of variability of dragonflies can be obtained from many populations which are isolated either territorially or in some other way. Finally, the order Odonata is one of the oldest among insects and has existed since the carboniferous period, i.e. for more than 300 million years. The modern suborders of dragonflies were formed in the jurassic period (120—150 million years ago). In wing pattern and the degree of perfection the jurassic dragonflies do not differ essentially from the present ones.

All that determines the interest and makes promising the study of the populational variability of this group, dragonflies being used as models for the microevolutionary problems to be solved. The first inevitable step in this study is to elucidate the general character of variability of different characteristics and to choose some of them for further investigation. At this stage the data on the exact morphological characteristics of the dragonfly population are of importance for the taxonomy of the group.

Materials and methods

In the period from 1965 to 1968 the field material on the populational variability of dragonflies (*Sympetrum danae* SULZER, *Sympetrum flaveolum* LINNAEUS, *Sympetrum vulgatum* LINNAEUS, *Lestes sponsa* HANSEMANN, *Lestes virens* HARPER, *Leucorrhinia albifrons* BURMEISTER, and *Aeshna grandis* LINNAEUS[1]) was gathered on the bank of Gorbatoye lake,

[1] Determination of the species was carried out by Mrs. G. I. RJASANOVA (Department of Entomology, Moscow State University) or by one of us (L. N. PRITIKINA).

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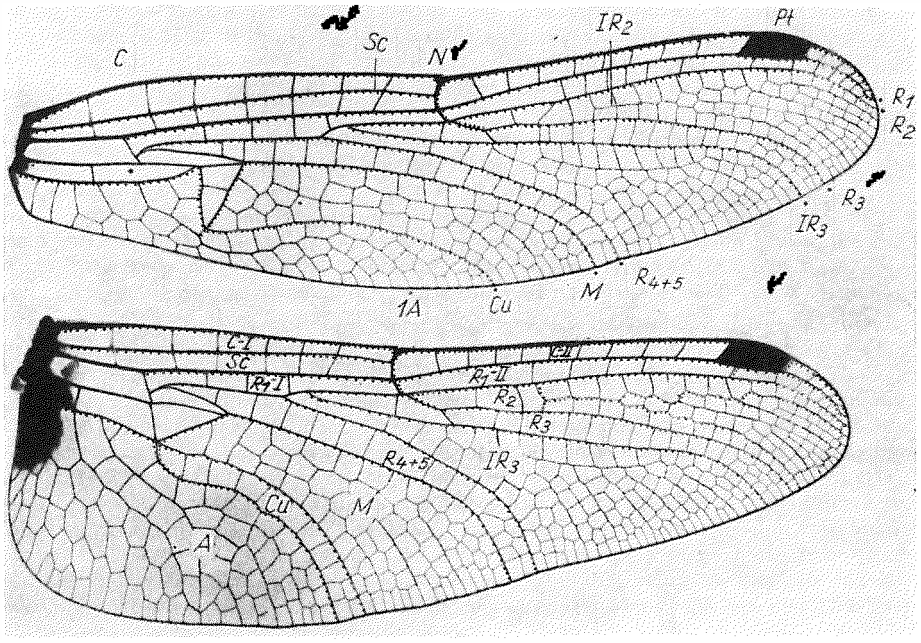

Fig. 1. Designations of the areas of the dragonfly wings between the main longitudinal veins

Abbreviations

C-I – costal area proximal nodal

Sc – subcostal area

R_1-*I* – area between R_1 and R_S proximal nodal

C-II – postnodal part of costal area
1. proximal pterostigmae (*Pt*)
2. distal *Pt*
3. The whole area *C-II*

R_1-*II* – area between R_1 and R_2
1. proximal *Pt*
2. from 1. to the last cell near border of wing
3. row of cells on border of wing
4. the whole area R_1-*II*.

R_2 – area between R_2 and R_3
1. proximal IR_2
2. row of cells near R_2 distal IR_2
3. row of cells near R_3 distal IR_2
4. row of cells on the wing's border
5. the whole area R_2

R_3 – area between R_{2+3}, R_3 and IR_3
1. proximal subnodal transverse vein (*SN*)
2. proximal additional longitudinal vein
3. row of cells along R_3 distal 2.
4. row of cells along IR_3 distal 2.
5. row of cells on the wing's border
6. the whole area R_3

IR_3 – area between IR_3 and R_{4+5}
1. proximal additional longitudinal vein
2. row of cells along IR_3 distal 1.
3. row of cells along R_{4+5} distal 1.
4. row of cells on the wing's border
5. the whole area IR_3

R_{4+5} – area between R_{4+5} and M
1. proximal additional longitudinal veins
2. the whole area R_{4+5}

M – discoidal area
1. row of cells along *M* (without the border cells)
2. row of cells on the wing's border
3. the whole area *M*

Cu – cubital area
1. row of cells along *Cu* (without the border cells)
2. row of cells on the wing's borders
3. the whole area *Cu*

A – anal area
1. row of cells along *IA*
2. row of cells on the wing's border
3. the whole area *A*

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10 km south-west of Orechovo-Zuevo, near Moscow (we shall call this area "lake") as well as in the valley of the Yachroma river (about 10 km south of Dmitrov, near Moscow) and on the flooded meadow (200—250 m²) between the villages Ilyinskoye and Svistukha (we shall call this region "meadow"), the distance between the places of gathering material being a bee-line of one hundred kilometers.

The dragonflies were caught always in the same months of the year, from late July to early September, i.e. at the same phenological regime. The insects were divided according to sex and studied either in the dry state (on cotton wool plates) or after fixation in 70 per cent alcohol. The preparations of the wings were made by pressing the wings between two slides. Enlarged photographs of the wings were obtained. On the photographs the wings were magnified 6—7 times, which made possible the exact count of the wing cells in different areas of the wing. The data were treated statistically to determine mean values with standard error ($\overline{X} \pm S_{\overline{x}}$), standard deviation ($\sigma$) and variation coefficient (C. V. $\pm S_{\text{c. v.}}$).

The following characteristics were chosen for study: the number of subcostal and costal antenodal crossveins, intermedian crossveins and cells in different areas of the wing. These characteristics were sufficient for our task and convenient for registration.

Below we enumerate the wing areas and their regions in the order in which the cells were counted, i.e. from the anterior to the posterior edge of the wing.

The areas were named according to the symbols of the longitudinal veins, limiting the corresponding areas from the front, as it is usual in odonatology. The areas located more proximal or more distal than the node were designated with Roman numerals, different regions of the areas being designated with Arabic numerals.

As the vein patterns markedly differ in various sub-orders we slightly deviated from the standard scheme, given above, in the counting of the wing cells: in *Lestes* the area $C-I$, Sc, R_1-I were not counted, R_{4+5} and M were counted together, in *Sympetrum* and *Leucorrhinia* the areas Cu and A were counted together, the regions of the areas IR_3, R_{4+5}, M, A were not counted.

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Table 1

Interpopulation variability of the cell number of the fore right wing of *Sympetrum danae* ("meadow", 1965, males, n = 50)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
IC		7.0 ± 0.05	0.37	5.3 ± 0.53
Sc		6.0 ± 0.03	0.20	3.3 ± 0.33
IR_1		4.1 ± 0.04	0.30	7.3 ± 0,73
II C	1.	7.0 ± 0.10	0.73	10.4 ± 1.04
	2.	3.1 ± 0.07	0.47	15.2 ± 1.32
	3.	10.1 ± 0.14	0.96	9.5 ± 0.95
$II\ R_1$	1.	4.7 ± 0.08	0.54	11.5 ± 1.15
	2.	3.4 ± 0.08	0.57	16.8 ± 1.68
	3.	1.6 ± 0.07	0.48	30.0 ± 3.00
	4.	9.8 ± 0.13	0.93	9.5 ± 0.95
R_2	1.	3.7 ± 0.09	0.63	17.0 ± 1.70
	2.	10.2 ± 0.14	1.01	9.9 ± 0.99
	3	9.2 ± 0.12	0.88	9.6 ± 0.96
	4.	9.5 ± 0.15	1.08	11.4 ± 1.14
	5.	52.0 ± 0.64	4.55	8.8 ± 0.88
R_3	1.	1.02	0.	0.
	2.	10.5 ± 0.16	1.10	10.5 ± 1.05
	3.	2.5 ± 0.14	1.02	40.8 ± 4.08
	5.	2.1 ± 0.05	0.36	17.1 ± 1.71
	6.	16.2 ± 0.22	1.58	9.8 ± 0.98
IR_3	1.	3.0 ± 0.06	0.40	13.3 ± 1.33
	2.	11.4 ± 0.11	0.81	7.1 ± 0.71
	3.	7.2 ± 0.08	0.58	9.4 ± 0.94
	4.	12.5 ± 0.18	1.28	10.2 ± 1.02
	5.	54.1 ± 0.66	4.64	8.9 ± 0.86
R_{4+5}	1.	14.2 ± 0.14	0.98	6.9 ± 0.69
	5.	14.6 ± 0.17	1.22	8.4 ± 0.84
M	2.	3.8 ± 0.11	0.75	19.7 ± 1.97
	3.	36.2 ± 0.36	2.58	7.1 ± 0.71
Cu + A	1.	22.7 ± 0.24	1.71	7.5 ± 0.75
	2.	47.0 ± 0.52	3.66	7.8 ± 0.78

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Table 2

Interpopulation variability of the cell number of the hind right wing of *Sympetrum danae* ("meadow", 1965, males, n = 50)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
IC		5.0 ± 0.03	0.19	3.8 ± 0.38
Sc		5.0	0.	0.
IR_1		3.0 ± 0.03	0.24	8.1 ± 0.81
II C	1.	7.8 ± 0.10	0.70	9.0 ± 0.90
	2.	3.0 ± 0.07	0.49	16.3 ± 1.63
	3.	10.9 ± 0.13	0.90	8.3 ± 0.83
II R_1	1.	5.0 ± 0.06	0.45	9.0 ± 0.90
	2.	3.6 ± 0.08	0.60	16.7 ± 1.67
	3.	1.6 ± 0.07	0.50	31.3 ± 3.13
	4.	10.2 ± 0.13	0.92	9.0 ± 0.90
R_2	1.	4.0 ± 0.07	0.53	13.3 ± 1.33
	2.	10.0 ± 0.15	1.06	10.6 ± 1.06
	3.	9.1 ± 0.12	0.83	9.1 ± 0.91
	4.	9.3 ± 0.12	0.87	9.4 ± 0.94
	5.	52.8 ± 0.59	4.20	8.0 ± 0.80
R_3	1.	1.0	0.	0.
	2.	11.3 ± 0.16	1.13	10.0 ± 1.00
	3.	1.9 ± 0.17	0.83	43.7 ± 4.37
	5.	2.0 ± 0.05	0.35	17.5 ± 1.75
	6.	15.8 ± 0.18	1.30	8.2 ± 0.82
I R_3	1.	2.5 ± 0.07	0.50	20.0 ± 2.00
	2.	11.8 ± 0.14	0.98	8.3 ± 0.83
	3.	6.5 ± 0.09	0.61	9.4 ± 0.94
	4.	15.5 ± 0.23	1.65	10.7 ± 1.07
	5.	63.2 ± 0.75	5.31	8.4 ± 0.84
R_{4+5}	1.	12.2 ± 0.14	1.02	8.4 ± 0.84
	5.	13.0 ± 0.15	1.09	8.4 ± 0.84
M	2.	9.8 ± 0.24	1.68	17.1 ± 1.71
	3.	45.9 ± 0.63	4.47	9.7 ± 0.97
Cu + *A*	1.	27.2 ± 0.29	2.07	7.6 ± 0.76
	2.	79.1 ± 0.90	6.34	8.0 ± 0.80

Table 3 .

Interpopulation variability of the cell number of the fore right wing of *Sympetrum danae* ("meadow", 1965, females, n = 50)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{c.v.}$
IC		7.0 ± 0.05	0.37	5.3 ± 0.53
Sc		6.0 ± 0.03	0.20	3.3 ± 0.33
IR_1		4.0 ± 0.05	0.33	8.3 ± 0.83
II C	1.	6.7 ± 0.10	0.71	10.6 ± 1.06
	2.	3.1 ± 0.08	0.58	17.7 ± 1.87
	3.	9.7 ± 0.14	0.98	10.1 ± 1.01
$II\ R_1$	1.	4.4 ± 0.07	0.53	12.1 ± 1.21
	2.	3.6 ± 0.10	0.68	19.1 ± 1.91
	3.	1.7 ± 0.07	0.47	28.3 ± 2.83
	4.	9.6 ± 0.14	0.96	10.0 ± 1.00
R_2	1.	3.8 ± 0.07	0.47	12.5 ± 1.25
	2.	9.8 ± 0.14	0.99	10.1 ± 1.01
	3.	8.7 ± 0.10	0.72	8.3 ± 0.83
	4.	8.8 ± 0.15	1.05	11.9 ± 1.19
	5.	48.0 ± 0.51	3.60	7.5 ± 0.75
R_3	1.	1.0	0.	0.
	2.	10.0 ± 0.17	1.22	12.2 ± 1.22
	3.	2.1 ± 0.20	1.39	65.6 ± 6.56
	5.	2.0 ± 0.05	0.34	16.7 ± 1.67
	6.	15.0 ± 0.31	2.18	14.5 ± 1.45
$I\ R_3$	1.	3.0 ± 0.06	0.40	13.5 ± 1.35
	2.	10.9 ± 0.11	0.78	7.2 ± 0.72
	3.	5.9 ± 0.07	0.47	7.9 ± 0.79
	4.	11.9 ± 0.16	1.10	9.2 ± 0.92
	5.	49.8 ± 0.58	4.08	8.2 ± 0.82
R_{4+5}	1.	14.2 ± 0.14	1.02	7.2 ± 0.72
	5.	14.4 ± 0.15	1.06	7.4 ± 0.74
M	2.	3.9 ± 0.10	0.72	18.4 ± 1.84
	3.	34.9 ± 0.50	3.51	10.1 ± 1.01
Cu + A	1.	21.5 ± 0.22	1.55	7.2 ± 0.72
	2.	43.3 ± 0.44	3.14	7.3 ± 0.73

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Table 4

Interpopulation variability of the cell number of the hind right wing of *Sympetrum danae* ("meadow", 1965, females, n = 50)

Area		$\overline{X} \pm S_{\bar{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
IC		5.0 ± 0.02	0.14	2.8 ± 0.28
Sc		5.0 ± 0.03	0.20	4.0 ± 0.40
IR_1		3.0 ± 0.02	0.14	4.7 ± 0.47
II C	1.	7.6 ± 0.11	0.77	10.1 ± 1.01
	2.	2.9 ± 0.06	0.44	15.2 ± 1.52
	3.	10.5 ± 0.12	0.88	8.4 ± 0.84
$II\ R_1$	1.	4.9 ± 0.07	0.48	9.8 ± 0.98
	2.	3.5 ± 0.09	0.64	18.5 ± 1.85
	3.	1.5 ± 0.07	0.50	32.5 ± 3.25
	4.	9.9 ± 0.13	0.89	9.0 ± 0.90
R_2	1.	4.1 ± 0.08	0.56	13.9 ± 1.39
	2.	9.9 ± 0.15	1.07	10.8 ± 1.08
	3.	8.9 ± 0.14	0.98	11.0 ± 1.10
	4.	8.6 ± 0.14	1.00	11.6 ± 1.16
	5.	48.7 ± 0.68	4.84	9.9 ± 0.99
R_3	1.	1.0	0.	0.
	2.	11.1 ± 0.19	1.34	12.1 ± 1.21
	3.	1.6 ± 0.12	0.82	50.0 ± 5.00
	5.	1.9 ± 0.04	0.31	16.0 ± 1.60
	6.	15.0 ± 0.19	1.37	9.1 ± 0.91
$I\ R_3$	1.	2.7 ± 0.07	0.52	19.0 ± 1.90
	2.	11.4 ± 0.13	0.90	7.9 ± 0.79
	3.	6.3 ± 0.10	0.73	11.6 ± 1.16
	4.	15.2 ± 0.19	1.33	8.8 ± 0.88
	5.	58.8 ± 0.80	5.63	9.6 ± 0.96
R_{4+5}	1.	12.1 ± 0.12	0.88	7.3 ± 0.73
	5.	12.8 ± 0.17	1.21	9.5 ± 0.95
M	2.	8.6 ± 0.21	1.48	17.2 ± 1.72
	3.	42.2 ± 0.66	4.70	11.1 ± 1.11
Cu + A	1.	25.4 ± 0.28	1.99	7.8 ± 0.78
	2.	72.1 ± 0.90	6.88	8.9 ± 0.89

Table 5

Interpopulation variability of the cell number of the fore right wing of *Sympetrum danae* ("lake", 1966, males, n = 29)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
IC		7.0 ± 0.04	0.20	2.9 ± 0.38
Sc		6.1 ± 0.06	0.31	4.1 ± 0.67
IR_1		4.9 ± 0.08	0.43	8.9 ± 1.16
II C	1.	7.3 ± 0.11	0.58	7.0 ± 1.05
	2.	3.5 ± 0.12	0.63	17.8 ± 2.35
	3.	10.7 ± 0.15	0.80	7.5 ± 0.99
$II\ R_1$	1.	4.9 ± 0.17	0.90	18.2 ± 2.43
	2.	3.9 ± 0.12	0.62	15.9 ± 2.09
	3.	1.5 ± 0.10	0.51	34.5 ± 4.52
	4.	10.3 ± 0.15	0.80	7.7 ± 1.02
R_2	1.	3.7 ± 0.12	0.61	16.7 ± 2.20
	2.	11.0 ± 0.18	0.97	8.8 ± 1.16
	3.	9.5 ± 0.16	0.89	9.4 ± 1.24
	4.	9.8 ± 0.21	1.16	11.8 ± 1.55
	5.	57.2 ± 1.09	5.90	10.4 ± 1.35
R_3	1.	1.0	0.	0.
	2.	10.1 ± 0.17	0.97	9.6 ± 1.25
	3.	3.5 ± 0.20	1.08	31.2 ± 4.22
	5.	2.2 ± 0.08	0.41	18.6 ± 2.44
	6.	17.3 ± 0.47	2.50	14.5 ± 1.95
$I\ R_3$	1.	3.1 ± 0.065	0.35	11.3 ± 1.49
	2.	11.7 ± 0.20	1.09	9.3 ± 1.24
	3.	6.6 ± 0.13	0.68	10.3 ± 1.35
	4.	13.9 ± 0.26	1.40	10.1 ± 1.42
	5.	58.8 ± 1.03	5.87	9.9 ± 1.30
R_{4+5}	1.	15.0 ± 0.15	0.82	5.5 ± 0.72
	5.	15.0 ± 0.15	0.82	5.5 ± 0.72
M	2.	4.5 ± 0.19	0.50	11.2 ± 0.47
	3.	39.4 ± 0.46	2.48	6.3 ± 0.83
Cu + A	1.	24.0 ± 0.32	1.73	7.2 ± 0.95
	2.	50.6 ± 0.86	4.62	8.1 ± 1.07

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Table 6

Interpopulation variability of the cell number of the hind right wing of *Sympetrum danae* ("lake", 1966, males, n = 25–28)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{C.V.}$
I C		5.1 ± 0.05	0.25	4.9 ± 0.65
Sc		5.0	0.	0.
I R_1		2.9 ± 0.05	0.26	8.9 ± 1.18
II C	1.	8.0 ± 0.13	0.67	8.0 ± 1.05
	2.	3.2 ± 0.13	0.69	21.5 ± 2.83
	3.	11.2 ± 0.11	0.63	5.6 ± 0.73
II R_1	1.	5.3 ± 0.09	0.53	10.0 ± 1.31
	2.	9.0 ± 0.18	0.99	11.0 ± 1.44
	3.	1.5 ± 0.05	0.26	17.9 ± 2.35
	4.	10.5 ± 0.18	0.99	9.5 ± 1.25
R_2	1.	3.8 ± 0.10	0.56	14.9 ± 1.96
	2.	10.9 ± 0.21	1.12	10.3 ± 1.37
	3.	9.5 ± 0.17	0.93	9.8 ± 1.29
	4.	9.7 ± 0.16	0.89	9.2 ± 1.18
	5.	57.0 ± 0.98	5.20	9.1 ± 1.12
R_3	1.	1.0	0.	0.
	2.	11.0 ± 0.16	0.88	8.0 ± 1.16
	3.	2.4 ± 0.15	0.81	33.6 ± 4.42
	5.	2.2 ± 0.04	0.20	9.2 ± 1.20
	6.	15.9 ± 0.29	1.50	9.4 ± 1.25
I R_3	1.	2.3 ± 0.09	0.49	18.9 ± 2.49
	2.	12.0 ± 0.16	0.85	7.1 ± 0.93
	3.	6.6 ± 0.11	0.62	9.4 ± 1.23
	4.	16.7 ± 0.27	1.44	8.6 ± 1.13
	5.	68.8 ± 1.03	5.56	8.1 ± 1.07
R_{4+5}	1.	12.1 ± 0.15	0.78	6.9 ± 0.85
	5.	12.8 ± 0.23	1.23	9.6 ± 1.26
M	2.	11.0 ± 0.22	1.19	10.8 ± 1.44
	3.	47.5 ± 0.77	4.10	8.5 ± 1.13
Cu + A	1.	18.8 ± 0.23	1.23	6.5 ± 0.87
	2.	84.7 ± 1.14	6.09	7.2 ± 0.96

Table 7

Interpopulation variability of the cell number of the fore (right + left) wing of *Sympetrum danae* ("lake", 1966, females, n = 61 – 66)

Area		$\overline{X} \pm S_{\bar{x}}$	σ	C. V. $\pm S_{\text{c. v.}}$
I C		7.0 ± 0.39	0.32	4.6 ± 0.40
Sc		6.0 ± 0.06	0.46	7.6 ± 0.77
I R_1		5.0 ± 0.02	0.19	3.8 ± 0.33
II C	1.	7.1 ± 0.08	0.68	9.6 ± 0.84
	2.	3.5 ± 0.07	0.56	16.1 ± 1.45
	3.	10.6 ± 0.35	2.74	25.8 ± 2.32
II R_1	1.	4.9 ± 0.06	0.49	10.6 ± 0.87
	2.	3.8 ± 0.30	0.72	18.7 ± 1.66
	3.	1.4 ± 0.07	0.52	36.9 ± 3.25
	4.	5.3 ± 0.17	0.90	11.4 ± 1.01
R_2	1.	3.7 ± 0.07	0.53	14.4 ± 0.23
	2.	10.6 ± 0.15	1.19	11.3 ± 1.01
	3.	9.6 ± 0.68	0.54	5.5 ± 0.49
	4.	9.4 ± 0.13	1.05	11.3 ± 1.02
	5.	54.1 ± 0.49	3.79	7.3 ± 0.67
R_3	1.	1.0	0.	0.
	2.	11.4 ± 0.15	1.20	10.5 ± 0.90
	3.	2.8 ± 0.16	1.26	45.1 ± 4.10
	5.	2.1 ± 0.03	0.24	11.4 ± 1.04
	6.	16.3 ± 0.21	1.67	10.2 ± 0.91
I R_3	1.	3.0 ± 0.03	0.29	9.6 ± 0.83
	2.	11.4 ± 0.09	0.78	6.8 ± 0.61
	3.	6.6 ± 0.65	0.52	7.9 ± 0.97
	4.	13.7 ± 0.18	1.42	10.4 ± 0.92
	5.	56.5 ± 0.58	4.16	8.1 ± 0.72
R_{4+5}	1.	14.9 ± 0.11	0.90	6.0 ± 0.52
	5.	15.2 ± 0.14	1.11	7.3 ± 0.64
M	2.	4.6 ± 0.13	0.11	2.4 ± 0.21
	3.	39.2 ± 0.33	2.60	6.6 ± 0.59
Cu + *A*	1.	24.0 ± 0.29	2.01	8.6 ± 0.78
	2.	47.4 ± 0.51	4.10	8.6 ± 0.77

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Table 8

Interpopulation variability of the cell number of the fore right wing of *Leucorrhinia albifrons* ("lake", 1966, males, n = 50)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{C.V.}$
I C		7.3 ± 0.07	0.48	6.5 ± 0.65
Sc		7.2 ± 0.07	0.47	6.5 ± 0.65
I R_1		4.3 ± 0.06	0.44	10.3 ± 1.03
II C	1.	9.3 ± 0.09	0.61	6.6 ± 0.66
	2.	4.9 ± 0.12	0.83	16.9 ± 1.69
	3.	14.2 ± 0.15	1.05	7.4 ± 0.74
II R_1	1.	6.2 ± 0.08	0.54	8.8 ± 0.88
	2.	5.8 ± 0.09	0.64	11.1 ± 1.11
	3.	1.2 ± 0.06	0.40	33.3 ± 3.33
	4.	13.2 ± 0.15	1.03	7.8 ± 0.78
R_2	1.	4.6 ± 0.09	0.64	13.9 ± 1.39
	2.	14.6 ± 0.18	1.25	8.6 ± 0.86
	3.	12.9 ± 0.12	0.85	6.6 ± 0.66
	4.	11.5 ± 0.14	1.02	8.9 ± 0.89
	5.	84.0 ± 0.84	5.96	7.1 ± 0.71
R_3	1.	1.0	0.	0.
	2.	12.9 ± 0.26	1.81	14.0 ± 1.40
	3.	4.7 ± 0.26	1.81	38.4 ± 3.84
	5.	2.7 ± 0.08	0.56	20.4 ± 2.04
	6.	24.3 ± 0.26	1.81	7.5 ± 0.75
I R_3	1.	3.3 ± 0.08	0.55	16.56 ± 1.66
	2.	16.3 ± 0.14	0.97	6.0 ± 0.60
	3.	7.9 ± 0.10	0.72	9.2 ± 0.92
	4.	18.7 ± 0.21	1.46	7.8 ± 0.78
	5.	89.5 ± 0.97	6.85	7.7 ± 0.77
R_{4+5}	1.	15.8 ± 0.16	1.16	7.3 ± 0.73
	5.	19.3 ± 0.20	1.43	7.4 ± 0.74
M	2.	8.4 ± 0.10	0.67	8.0 ± 0.80
	3.	55.6 ± 0.59	4.15	7.5 ± 0.75
Cu + A	1.	26.2 ± 0.24	1.69	6.5 ± 0.65
	2.	58.6 ± 0.65	4.59	7.8 ± 0.78

Table 9

Interpopulation variability of the cell number of the hind right wing of *Leucorrhinia albifrons* ("lake", 1966, males, n = 50)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
I C		6.0 ± 0.02	0.14	2.3 ± 0.23
Sc		6.0 ± 0.	0.	0.
I R_1		3.2 ± 0.06	0.40	12.5 ± 1.25
II C	1.	9.7 ± 0.10	0.69	7.1 ± 0.71
	2.	4.9 ± 0.12	0.83	17.1 ± 1.71
	3.	14.5 ± 0.15	1.06	7.3 ± 0.73
II R_1	1.	6.1 ± 0.07	0.52	8.6 ± 0.86
	2.	5.8 ± 0.12	0.83	14.3 ± 1.43
	3.	1.2 ± 0.06	0.41	33.6 ± 3.36
	4.	13.1 ± 0.15	1.05	8.0 ± 0.80
R_2	1.	4.4 ± 0.09	0.67	15.1 ± 1.51
	2.	14.9 ± 0.14	0.97	6.5 ± 0.65
	3.	13.1 ± 0.12	0.82	6.3 ± 0.63
	4.	12.3 ± 0.16	1.14	9.3 ± 0.93
	5.	88.8 ± 0.81	5.71	6.4 ± 0.64
R_3	1.	1.0	0.	0.
	2.	11.9 ± 0.45	3.18	26.7 ± 2.67
	3.	5.9 ± 0.44	3.13	52.7 ± 5.27
	5.	2.9 ± 0.08	0.55	19.1 ± 1.91
	6.	25.3 ± 0.29	2.03	8.0 ± 0.80
I R_3	1.	3.2 ± 0.06	0.42	13.3 ± 1.33
	2.	16.6 ± 0.14	1.02	6.1 ± 0.61
	3.	7.5 ± 0.09	0.69	8.2 ± 0.82
	4.	23.5 ± 0.24	1.73	7.4 ± 0.74
	5.	106.0 ± 1.15	8.14	7.7 ± 0.77
R_{4+5}	1.	12.2 ± 0.16	1.10	9.0 ± 0.90
	5.	18.5 ± 0.20	1.45	7.8 ± 0.78
M	2.	13.0 ± 0.12	0.87	6.7 ± 0.67
	3.	65.5 ± 0.87	6.16	9.4 ± 0.94
Cu + *A*	1.	30.6 ± 0.25	1.78	5.8 ± 0.58
	2.	94.6 ± 1.19	8.41	8.9 ± 0.89

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Table 10

Interpopulation variability of the cell number of the fore right wing of *Leucorrhinia albifrons* ("lake", 1966, females, n = 49–51)

Area		$\bar{X} \pm S_{\bar{x}}$	σ	C. V. $\pm S_{\text{c. v.}}$
I C		7.4 ± 0.08	0.57	7.7 ± 0.77
Sc		7.3 ± 0.07	0.47	6.4 ± 0.64
I R_1		4.6 ± 0.08	0.57	12.5 ± 1.25
II C	1.	9.2 ± 0.11	0.75	8.2 ± 0.82
	2.	5.0 ± 0.13	0.93	20.2 ± 2.02
	3.	14.1 ± 0.15	1.03	7.3 ± 0.73
II R_1	1.	5.8 ± 0.08	0.54	9.3 ± 0.93
	2.	5.9 ± 0.09	0.62	10.5 ± 1.05
	3.	1.2 ± 0.06	0.43	36.4 ± 3.64
	4.	12.9 ± 0.13	0.93	7.2 ± 0.72
R_2	1.	4.7 ± 0.09	0.60	12.9 ± 1.29
	2.	14.7 ± 0.15	1.09	7.6 ± 0.76
	3.	13.1 ± 0.13	0.87	6.7 ± 0.67
	4.	11.6 ± 0.16	1.14	9.8 ± 0.98
	5.	83.8 ± 0.64	4.51	5.4 ± 0.54
R_3	1.	1.0	0.	0.
	2.	12.5 ± 0.30	2.13	17.8 ± 1.78
	3.	5.4 ± 0.30	2.13	39.2 ± 3.92
	5.	2.4 ± 0.07	0.49	20.4 ± 2.04
	6.	24.6 ± 0.27	1.89	7.7 ± 0.77
I R_3	1.	3.3 ± 0.06	0.45	19.8 ± 1.98
	2.	16.8 ± 0.15	1.04	6.5 ± 0.65
	3.	8.3 ± 0.09	0.64	7.8 ± 0.78
	4.	19.3 ± 0.17	1.23	6.4 ± 0.64
	5.	92.1 ± 0.90	6.33	6.9 ± 0.69
R_{4+5}	1.	17.0 ± 0.19	1.31	7.7 ± 0.77
	5.	19.6 ± 0.20	1.43	7.6 ± 0.76
M	2.	8.9 ± 0.14	0.96	10.8 ± 1.08
	3.	59.7 ± 0.57	4.05	6.8 ± 0.68
Cu + *A*	1.	26.5 ± 0.17	1.20	4.5 ± 0.45
	2.	58.1 ± 0.50	3.52	6.1 ± 0.61

Table 11

Interpopulation variability of the cell number of the hind right wing of *Leucorrhinia albifrons* ("lake", 1966, females, n = 46–51)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{\text{c. v.}}$
I C		6.0 ± 0.02	1.14	2.3 ± 0.23
Sc		6.0 ± 0.02	0.14	2.3 ± 0.23
I R_1		3.2 ± 0.06	0.42	13.0 ± 1.30
II C	1.	9.4 ± 0.09	0.66	7.0 ± 0.70
	2.	5.0 ± 0.11	0.80	16.1 ± 1.66
	3.	14.4 ± 0.15	1.03	7.2 ± 0.72
II R_1	1.	6.0 ± 0.08	0.58	9.7 ± 0.97
	2.	5.8 ± 0.11	0.79	13.5 ± 1.35
	3.	1.2 ± 0.05	0.38	32.2 ± 3.22
	4.	13.0 ± 0.17	1.15	8.9 ± 0.89
R_2	1.	4.3 ± 0.09	0.62	14.6 ± 1.46
	2.	15.4 ± 0.15	1.04	6.8 ± 0.68
	3.	13.5 ± 0.12	0.85	6.3 ± 0.63
	4.	12.2 ± 0.16	1.09	8.9 ± 0.89
	5.	89.8 ± 0.70	4.97	5.5 ± 0.55
R_3	1.	1.0	0.	0.
	2.	11.7 ± 0.38	2.72	23.2 ± 2.34
	3.	5.6 ± 0.43	3.10	55.7 ± 5.57
	5.	2.6 ± 0.08	0.57	21.8 ± 2.18
	6.	24.8 ± 0.32	2.27	9.2 ± 0.91
I R_3	1.	3.0 ± 0.06	0.40	13.3 ± 1.33
	2.	17.2 ± 0.14	0.95	5.5 ± 0.57
	3.	9.0 ± 0.18	1.25	13.9 ± 1.44
	4.	24.3 ± 0.23	1.59	6.6 ± 0.69
	5.	111.9 ± 1.04	7.30	6.5 ± 0.68
R_{4+5}	1.	13.1 ± 0.13	0.90	6.9 ± 0.72
	5.	18.6 ± 0.23	1.56	8.4 ± 0.88
M	2.	13.6 ± 0.14	0.99	7.3 ± 0.76
	3.	70.8 ± 0.70	4.92	6.9 ± 0.72
Cu + A	1.	30.7 ± 0.27	1.82	6.0 ± 0.62
	2.	94.7 ± 0.89	6.02	6.4 ± 0.66

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Table 12

Interpopulation variability of the cell number of the hind right wing of *Lestes sponsa* ("lake", 1966, males, n = 68–74)

Area		$\overline{X} \pm S_{\overline{x}}$	σ	C. V. $\pm S_{C.V.}$
I C		2.0 ± 0	0.	0.
Sc		2.0 ± 0	0.	0.
I R_1		0.	0.	0.
II C	1.	12.2 ± 0.12	1.03	8.4 ± 0.68
	2.	5.1 ± 0.09	0.83	17.3 ± 1.31
	3.	17.3 ± 0.16	1.39	8.0 ± 0.65
II R_1	1.	10.5 ± 0.10	0.85	8.1 ± 0.65
	2.	5.8 ± 0.09	0.77	13.3 ± 1.07
	3.	1.5 ± 0.06	0.49	35.0 ± 2.82
	4.	17.7 ± 0.15	1.36	7.7 ± 0.62
R_2	1.	3.2 ± 0.07	0.64	20.0 ± 1.61
	2.	11.4 ± 0.14	1.22	10.7 ± 0.86
	3.	11.9 ± 0.15	1.30	6.8 ± 0.55
	4.	5.4 ± 0.11	0.98	18.2 ± 1.46
	5.	44.0 ± 0.42	3.72	8.5 ± 0.68
R_3	1.	2.1 ± 0.03	0.27	13.0 ± 1.05
	2.	14.5 ± 0.12	1.07	7.4 ± 0.60
	3.	5.8 ± 0.10	0.84	14.5 ± 1.17
	4	4.6 ± 0.08	0.70	15.2 ± 1.23
	5.	6.1 ± 0.08	0.69	11.3 ± 0.92
	6.	34.4 ± 0.35	3.07	8.9 ± 0.72
I R_3	1.	9.6 ± 0.09	0.78	8.1 ± 0.66
	2.	11.0 ± 0.11	0.93	8.5 ± 0.69
	3.	10.3 ± 0.12	1.04	10.0 ± 0.81
	4.	4.4 ± 0.08	0.74	16.8 ± 1.36
	5.	41.0 ± 0.10	0.84	2.1 ± 0.17
R_{4+5} + *M*	1.	6.9 ± 0.08	0.69	10.0 ± 0.82
	2.	13.9 ± 0.13	1.10	7.9 ± 0.65
	3.	9.1 ± 0.12	1.03	11.3 ± 0.93
	4.	11.0 ± 0.17	1.48	13.6 ± 1.12
	5.	15.7 ± 0.13	1.10	7.0 ± 0.58
	6.	4.2 ± 0.10	0.78	18.6 ± 1.53
	7.	69.9 ± 0.60	5.24	7.5 ± 0.61
Cu + *A*	1.	19.4 ± 0.22	1.56	8.0 ± 0.80
	2.	31.5 ± 0.34	2.40	7.6 ± 0.75

Table 13

Interpopulation variability of the cell number of the fore right wing of *Lestes sponsa* ("lake", 1966, males, n = 50)

Area		$\bar{X} \pm S_{\bar{x}}$	σ	C. V. $\pm S_{\text{C. V.}}$
II C	1.	11.6 ± 0.13	0.93	8.02 ± 0.80
	2.	5.48 ± 0.11	0.75	13.68 ± 1.37
	3.	17.2 ± 0.19	1.32	7.67 ± 0.77
II R_1	1.	9.84 ± 0.11	0.76	7.72 ± 0.77
	2.	6.22 ± 0.10	0.73	11.73 ± 1.17
	3.	1.38 ± 0.07	0.52	37.68 ± 3.77
	4.	17.4 ± 0.18	1.27	7.29 ± 0.73
R_2	1.	3.16 ± 0.09	0.64	20.25 ± 2.03
	2.	12.3 ± 0.19	1.31	10.67 ± 1.07
	3.	13.1 ± 0.19	1.32	10.07 ± 1.01
	4.	5.74 ± 0.14	1.00	17.40 ± 1.74
	5.	43.4 ± 0.20	1.35	3.11 ± 0.31
R_3	1.	2.06 ± 0.03	0.24	11.65 ± 1.17
	2.	11.7 ± 0.15	1.08	9.23 ± 0.92
	3.	6.94 ± 0.15	1.05	15.10 ± 1.51
	4.	5.24 ± 0.11	0.79	15.07 ± 1.51
	5.	7.06 ± 0.14	0.99	14.02 ± 1.40
	6.	34.1 ± 0.19	1.35	3.95 ± 0.40
I R_3	1.	8.96 ± 0.11	0.75	8.37 ± 0.84
	2.	11.5 ± 0.20	1.37	11.94 ± 1.19
	3.	10.6 ± 0.18	1.28	12.07 ± 1.21
	4.	4.72 ± 0.14	0.98	20.76 ± 2.08
	5.	41.8 ± 0.52	3.68	8.80 ± 0.88
$R_{4+5} + M$	1.	6.38 ± 0.11	0.77	12.06 ± 1.21
	2.	14.0 ± 0.19	1.35	9.64 ± 0.96
	3.	8.80 ± 0.13	0.94	10.68 ± 1.07
	4.	11.5 ± 0.23	1.65	14.34 ± 1.43
	5.	13.8 ± 0.15	1.04	7.63 ± 0.75
	6.	4.3 ± 0.12	0.88	20.46 ± 2.05
	7.	67.4 ± 0.83	5.88	8.72 ± 0.87
$Cu + A$	1.	17.4 ± 0.23	1.66	9.5 ± 0.94
	2.	28.2 ± 0.38	2.68	9.5 ± 0.94

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Table 14

Interpopulation variability of the cell number of the fore right wing of *Lestes sponsa* ("lake", 1966, females, n = 48–49)

Area		$\bar{X} \pm S_{\bar{x}}$	σ	C. V. $\pm S_{C.V.}$
I C		2.0 ± 0.	0.	0.
Sc		2.02 ± 0.30	0.20	9.9 ± 1.00
I R_1		0.	0.	0.
II C	1.	12.6 ± 0.12	0.88	7.0 ± 0.71
	2.	5.1 ± 0.30	2.11	36.4 ± 3.70
	3.	17.9 ± 0.18	1.25	7.0 ± 0.71
II R_1	1.	11.0 ± 0.11	0.76	6.9 ± 0.70
	2.	16.5 ± 0.17	–	–
	3.	1.4 ± 0.07	0.23	16.4 ± 1.70
	4.	18.2 ± 0.18	1.24	6.8 ± 0.69
R_2	1.	3.2 ± 0.11	0.81	25.0 ± 2.7
	2.	12.0 ± 0.16	1.16	9.7 ± 0.98
	3.	12.6 ± 0.16	1.15	9.1 ± 0.92
	4.	5.4 ± 0.14	0.98	18.1 ± 1.83
	5.	46.3 ± 0.48	3.39	7.3 ± 0.74
R_3	1.	2.1 ± 0.14	0.96	45.7 ± 4.60
	2.	14.9 ± 0.19	0.97	6.5 ± 0.66
	3.	6.4 ± 0.15	1.05	16.4 ± 1.70
	4.	5.4 ± 0.10	0.71	13.3 ± 1.34
	5.	6.2 ± 0.13	0.88	13.6 ± 1.37
	6.	37.5 ± 0.50	3.46	9.2 ± 0.93
I R_3	1.	10.1 ± 0.13	0.92	9.1 ± 0.92
	2.	11.7 ± 0.17	1.17	10.0 ± 1.01
	3.	10.4 ± 0.12	0.83	8.0 ± 0.81
	4.	4.5 ± 0.11	0.76	17.0 ± 1.71
	5.	43.3 ± 0.41	2.90	6.7 ± 0.68
$R_{4+5} + M$	1.	7.0 ± 0.10	0.72	10.3 ± 1.05
	2.	14.9 ± 0.21	1.48	9.9 ± 1.01
	3.	9.5 ± 0.12	0.93	9.8 ± 0.99
	4.	12.1 ± 0.20	1.39	11.5 ± 1.16
	5.	15.3 ± 0.15	1.02	6.7 ± 0.67
	6.	4.3 ± 0.12	0.80	18.5 ± 1.90
	7.	75.8 ± 0.57	3.99	5.3 ± 0.54
Cu + A	1.	20.7 ± 0.20	1.43	6.9 ± 0.70
	2.	33.9 ± 0.31	2.17	6.4 ± 0.65

Table 15
Interpopulation variability of the cell number of the hind right wing of *Lestes sponsa* ("lake", 1966, females, n = 47—49)

Area		$\overline{X} + S_{\overline{x}}$	σ	C. V. $\pm S_{C.V.}$
I C		2.0 ± 0.0	0.	0.
Sc		2.0 ± 0.0	0.	0.
I R_1		0.	0.	0.
II C	1.	11.8 ± 0.14	0.99	8.4 ± 0.85
	2.	5.7 ± 0.15	1.04	18.4 ± 1.86
	3.	17.4 ± 0.25	1.71	10.1 ± 1.01
II R_1	1.	10.1 ± 0.13	0.86	8.5 ± 0.86
	2.	—	—	—
	3.	1.4 ± 0.11	0.76	51.7 ± 5.20
	4.	17.9 ± 0.19	1.32	7.4 ± 0.75
R_2	1.	3.3 ± 0.09	0.62	18.6 ± 1.88
	2.	12.5 ± 0.16	1.12	9.0 ± 0.91
	3.	13.4 ± 0.15	1.07	8.0 ± 0.81
	4.	5.9 ± 0.15	1.02	17.3 ± 1.75
	5.	50.1 ± 0.50	3.17	6.9 ± 0.71
R_3	1.	2.0 ± 0.03	0.23	11.2 ± 1.40
	2.	14.3 ± 0.12	0.86	6.0 ± 0.61
	3.	7.0 ± 0.17	1.00	14.2 ± 1.43
	4.	5.5 ± 0.14	0.96	17.6 ± 1.78
	5.	7.0 ± 0.10	0.73	10.4 ± 1.05
	6.	38.9 ± 0.51	3.54	9.1 ± 0.92
I R_3	1.	9.2 ± 0.12	0.82	9.0 ± 0.91
	2.	11.7 ± 0.13	0.92	7.9 ± 0.79
	3.	11.0 ± 0.14	0.95	8.6 ± 0.87
	4.	4.7 ± 0.12	0.82	17.6 ± 1.78
	5.	43.4 ± 0.34	2.34	5.4 ± 0.54
$R_{4+5} + M$	1.	6.5 ± 0.09	0.61	9.4 ± 0.95
	2.	15.0 ± 0.18	1.25	8.3 ± 0.84
	3.	9.1 ± 0.73	0.94	10.4 ± 1.05
	4.	12.4 ± 0.15	1.05	8.5 ± 0.86
	5.	13.6 ± 0.13	0.87	6.4 ± 0.65
	6.	4.4 ± 0.11	0.76	17.2 ± 1.74
	7.	71.6 ± 0.68	4.67	6.5 ± 0.67
$Cu + A$	1.	18.0 ± 0.22	1.51	8.4 ± 0.85
	2.	29.2 ± 0.29	2.04	7.0 ± 0.71

Discussion

As the aim of the present study is not taxonomical, attention is paid chiefly to a phenomenological analysis of the variability of the chosen characteristics in wild population. The variability of characteristics in various populations and sex groups within each species was analyzed and compared with that in different species.

I. Analysis of the variability within the species *Sympetrum danae* SULZER (Tables 1—7)

For the analysis of the variability we had at our disposal two samples from the "meadow" (gathered in 1965 and 1966) and a sample of 1966 from the "lake".

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A considerable territorial isolation of the points of sampling suggests that these samples belong to quite different independent populations. While analyzing this material we compared characteristics of the right and left wings, fore and hind wings and those of males and females and of different populations.

As the choice of different characteristics was arbitrary, for the sake of technical convenience we could study characteristics in any sequence. As it was shown earlier (ZARAPKIN 1937), it is rational to classify the characteristics to ascending or descending scale due to their absolute value. Then is it easy to compare the range of variability expressed in variation coefficients with the absolute value of the characteristic (ROGINSKY 1959).

Proceeding from the general conception of a reverse correlation between the variation coefficients and the absolute values of the characters, it is possible to isolate more or less variable characteristics in the general "flow" of variability (YABLOKOV 1966, 1968) and to compare characteristics of the same rank in their strict est form. In this case the "rank" of the characteristic can be defined rather accurately from the data of ontogenetic development. It is clear that the main longitudinal dragonfly wing veins develop at the early nymphae stages and can be considered as more fundamental morphogenetic peculiarities as compared to the venation pattern inside intermedian areas. The number of wing cells in each area can be considered as a general characteristic of it. It is the number of wing cells in different areas that must be compared in the same "flow" of variability whereas more special characteristics must form functional groups which we have not analyzed:

Comparison of the variability of right and left wings

The comparison of the right and left wings in males shows a considerable homogeneity of characteristics both in absolute values and in variation coefficients. There is no noticeable difference in any area of their fore and hind wings, as Table 16 shows.

As can be seen from Table 16, differences in any characteristics compared are not significant and of random character, which emphasizes once more that they are not significant.

The same conclusion can be drawn from the comparison of characteristics of the right and left wings in females of the same population and corresponding characteristics of the population from the "lake".

Thus the comparison of variability of the same characteristics of the left and right wings im *Sympetrum danae* shows that they do not differ markedly.

It should be pointed out that the conclusion about the similarity of the right and left wings refers only to the populational characteristics. In an individual dragonfly the right and left wings may have noticeable differences in any of the characteristics and the number of wing cells may be greater in the same wing area in one insect on the left wing and in another on the right one.

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Table 16

Comparison of characteristics of right and left wings (*Sympetrum danae*, population "meadow", 1965, male) according to criterion

$$t = \frac{\overline{X}_1 - \overline{X}_2}{\sqrt{S^2_{X_1} + S^2_{X_2}}}$$

Area	Fore wing		Hind wing	
	$t_{\overline{X}}$	$t_{c.v.}$	$t_{\overline{X}}$	$t_{c.v.}$
C-I	0	+1.94	0	−2.60
Sc	0	0	0	0
R_1-*I*	0	−0.28	0	0
C-II	−1.76	+0.55	+0.48	−1.58
R_1-*II*	−1.76	+1.48	−0.53	−0.23
R_2	−0.23	+1.25	+0.22	−1.14
R_3	−1.25	−0.33	+0.34	−1.33
IR_3	+0.68	+0.95	+0.50	+0.80
R_{4+5}	0	+0.61	−0.45	−0.33
M	−0.38	−0.39	−0.24	+0.45
Cu+*A*	−0.29	+0.74	0	−0.88

Table 17

Comparison of the number of wing cells in males and females of *Sympetrum danae* (population from the "meadow", 1965, according to the criterion *t*)

Area	Fore wing		Hind wing	
	$t_{\overline{X}}$	$t_{c.v.}$	$t_{\overline{X}}$	$t_{c.v.}$
C-I	0	0	0	+2.12
Sc	0	0	0	0
R_1-*I*	+1.66	+0.91	0	**+3.61**
C-II	+2.00	+0.29	+2.22	−0.08
R_1-*II*	+1.11	+0.36	+1.67	0
R_2	**+4.87**	−1.11	**+4.55**	−1.50
R_3	+3.15	+2.69	+3.08	−0.73
IR_3	**+4.88**	−0.59	**+4.00**	−0.94
R_{4+5}	+0.87	−0.89	+0.87	−0.87
M	+2.09	+2.44	+4.06	−0.95
Cu+*A*	**+5.44**	−0.47	**+5.51**	−0.75

Comparison of characteristics in males and females

The males and females greatly differ according to the absolute value of a number of characteristics of fore and hind wings (Table 17).

It is quite clear that the males have a greater number of cells on both the fore and hind wings as compared to the females (Fig. 2). This conclusion is confirmed also by the "lake" population and by that from the "meadow".

Comparison of characteristics of hind and fore wings

The data given above show that characteristics of the fore and hind wings in most cases differ markedly (Fig. 3). These differences appear most clearly if we

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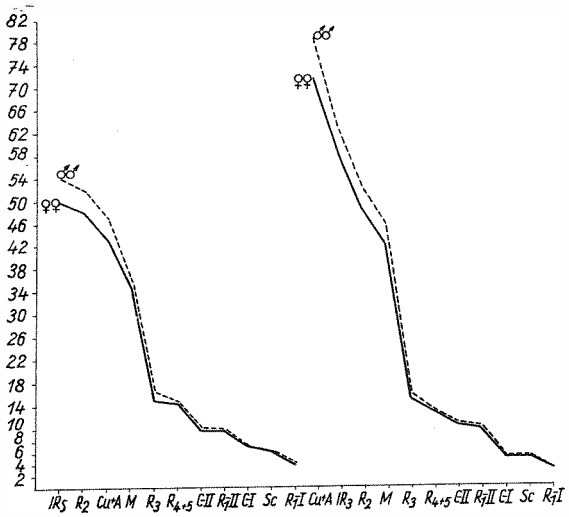

Fig. 2. Comparison of the number of wing cells in males and females of *Sympetrum danae* SULZER. Population from "meadow", 1965

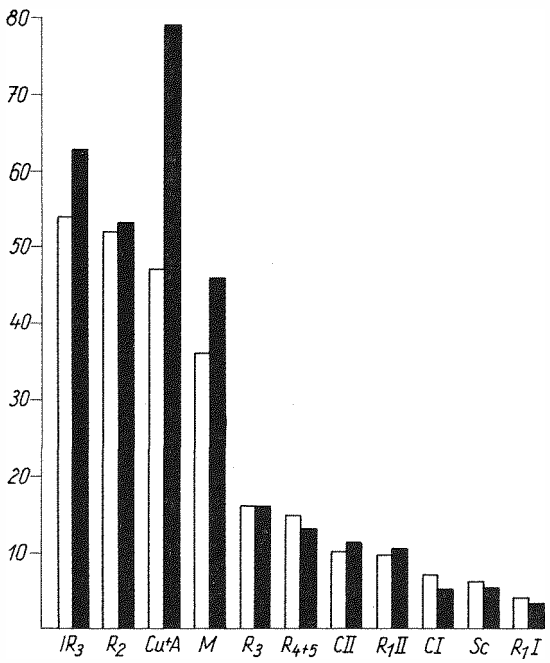

Fig. 3. Comparison of the number of fore (white) and hind (black) wings cells in males of *Sympetrum danae* SULZER. Population from "meadow", 1965

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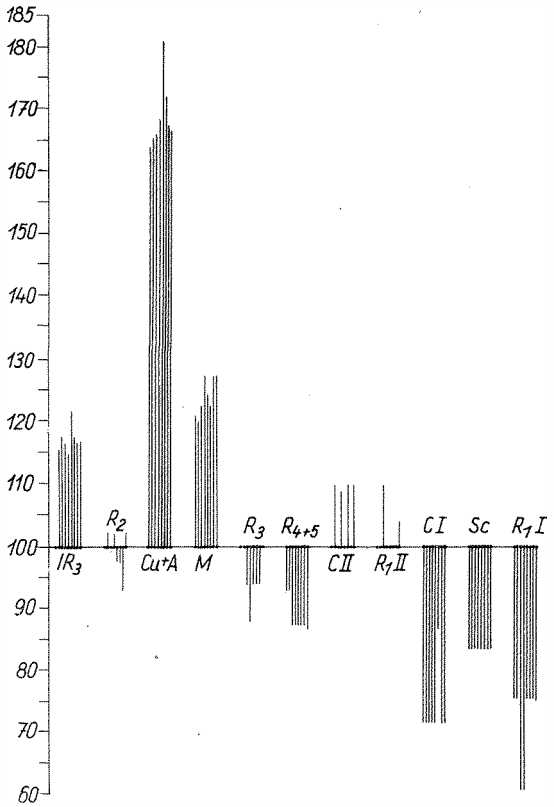

Fig. 4. Comparison of the ratio of values of the corresponding characteristics of the fore and hind wings in males and females in all populations of *Sympetrum danae* SULZER 100. per cent — characteristics of fore wings

compare the ratio of values of the corresponding characteristics of the fore and hind wings (Fig. 4). The functional importance of these differences is still unknown. But even now it is clear that they are not random, as in all 8 cases (see Fig. 4) the comparison of these differences reveals the same trends (with the exception of the characteristics of the areas R_3 and R_2 where the differences are not significant).

Thus the data obtained show that the fore and hind wings differ markedly in cell number in different areas of the wing: some areas have a greater number of cells on the fore wing, others on the hind one, the total number of cells being greater on the hind wing.

Comparison of characteristics of wings of different populations of the same species

Comparison of characteristics of the populations "lake" and "meadow" shows that they differ in the absolute number of cells in different areas of the wing (Table 18).

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Table 18

Comparison (by means of the *t*-criterion) of the cell number in different areas of the fore and hind wings of the males of *Sympetrum danae*

Area	Fore wing		Hind wing	
	Right	Left	Right	Left
C-I	−1.66	−1.42	+10.00	0
Sc	−1.42	−2.00	−0.10	**−3.33**
R_1-*I*	**−8.00**	**−8.18**	0	−1.42
C-II	−3.16	0	−0.48	−4.29
R_1-*II*	−3.18	−1.82	−1.30	−2.27
R_2	−3.11	−1.67	−2.42	−1.24
R_3	−0.94	−1.74	−0.50	+2.00
IR_3	−3.13	**−3.76**	−2.42	−1.24
R_{4+5}	−1.74	0	+0.37	−1.56
M	**−4.60**	**−3.38**	−0.98	−2.34
Cu+*A*	**−3.46**	−2.82	−1.02	+0.82

These data are heterogeneous in some respect. It appears at once that some characteristics greatly differ on the right wing and some on the left, which should not have been the case, supposing a perfect identity of characteristics of the symmetrical wings. This is possibly due to the inadequacy of the criterion (*t*) applied. It adequately characterises only normal distribution. However, one can establish some indubitable trends from the data obtained. Among them are the following: 1. the greater number of wing cells in the "meadow" population; 2. more significant differences in the number of cells between the fore wings than between the hind wings; 3. the most stable differences in the cell number in the areas $R_1 - I$, R_3, M and $Cu + A$. It should be pointed out that from these areas the first has the smallest number of cells, whereas the other three have the greatest. There is no doubt that a comparison of population samples taken during the following years will reveal other general trends which escape our attention when only two samples are studied. This comparison can show the trend and scale of differences between population characteristics. However, even now one can conclude about the existance of pronounced and significant differences between the populations studied.

II. Analysis of the variability within the species *Leucorrhinia albifrons*

(Tables 8—11)

For this species the data were obtained for males and females of the "lake" population sampled in 1966. The analysis of these data shows that neither males nor females have significant differences between left and right wings (Table 19).

There are no differences between either fore or hind wings of both sides. This conclusion confirms the similar one drawn from the analysis of the material on *Sympetrum danae*. Figure 5 shows the difference in cell number of the fore wings and in same characteristics of the hind wings in males and females.

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Table 19

Comparison by means of the *t*-criterion) of the cell number of the right and left wings of *Leucorrhinia albifrons* ("lake" population, 1966)

Area	Fore wing		Hind wing
	Male	Female	Male
C-I	0	+0.90	0
Sc	−1.00	0	0
R_1-*I*	−0.83	0	0
C-II	+0.45	+1.05	+1.00
R_1-*II*	+1.36	−1.36	−0.94
R_2	−0.44	+0.41	+0.33
R_3	−0.54	−0.97	+0.48
IR_3	0	+0.17	−0.62
R_{4+5}	−0.40	−1.33	−1.82
M	−0.47	0	−0.73
Cu+A	−0.23	−0.57	+0.20

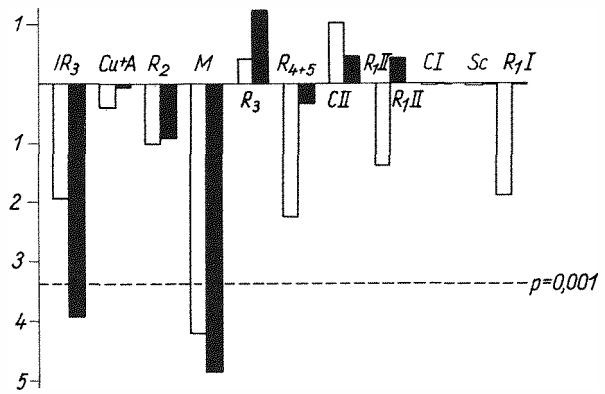

Fig. 5. Comparison (by means of the t-criterion) of the number of wing cells on fore and hind wings in males and females of *Leucorrhinia albifrons* BURMEISTER. Only right wings; white — fore wings, black — hind wings. Population "lake", 1966

The comparison of the structute of the fore and hind wings shows pronounced differences: in the areas $C - I$, Sc, $R_1 - I$ the cell number in females and males is much greater in the fore wing, whereas in the areas I R_3, M, $Cu + A$ the cell number is greater in the hind wing.

Thus *Leucorrhinia albifrons* have no differences between right and left wings, but do have them between males and females and fore and hind wings. All these peculiarities are similar to those described for *Sympetrum danae*.

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III. Analysis of the variability of the venation pattern of the species *Lestes sponsa* (Tables 12—15)

The species *Sympetrum danae* and *Leucorrhinia albifrons* considered above belong to the sub-order Anisoptera.

Genus *Lestes* belongs to the other sub-order, Zygoptera. Accordingly the analysis of the variability of *Lestes sponsa* is of additional interest as it reveals peculiarities of variability of venation that are general for the order as a whole.

Table 20

Comparison (by means of the *t*-criterion) of the cell number of the right and left wings in *Lestes sponsa* ("lake", 1966)

Area	Fore wing		Hind wing
	Male	Female	Male
C-I	0	0	0
Sc	0	0	0
R_1-*I*	0	0	0
C-II	+0.43	−0.36	−2.19
R_1-*II*	+0.45	−0.80	−0.42
R_2	+0.70	+1.47	−0.14
R_3	−0.84	−0.42	−1.32
IR_3	0	+0.70	+0.40
$R_{4+5}+M$	−0.79	+2.21	−0.19
$Cu+A$		+0.44	−0.23

Males and females show marked sexual differences in cell number in most of the wing areas (Fig. 6). Most clearly apparent is the sexual dimorphism in the areas with the greater cell number R_{4+5}, M, R_2, $I\,R_3$, R_3, $Cu + A$, whereas in those with the smallest cell number the differences between males and females are practically absent.

Thus the data on sexual dimorphism in the cell number of the wing areas studied in 3 species show that it is most distinct in *Lestes*.

Comparison of the cell number in the areas of the fore and hind wings shows (Fig. 7) that some of the characters have a clear difference.

Thus it can be concluded that in the population of the species *Lestes sponsa* there are no differences either in the pattern of venation between right and left sides of the fore and hind wings (Table 20) or in the cell number of their areas, but a distinct sexual dimorphism exists.

IV. Comparison of peculiarities of the venation pattern in different genera of the dragonfly

The data on the cell number in different areas of the wing in 3 species of the dragonfly demonstrate some general peculiarities. They are the following:

1. a complete identity of quantitative characteristics of the left and right wings;
2. distinct differences between males and females;

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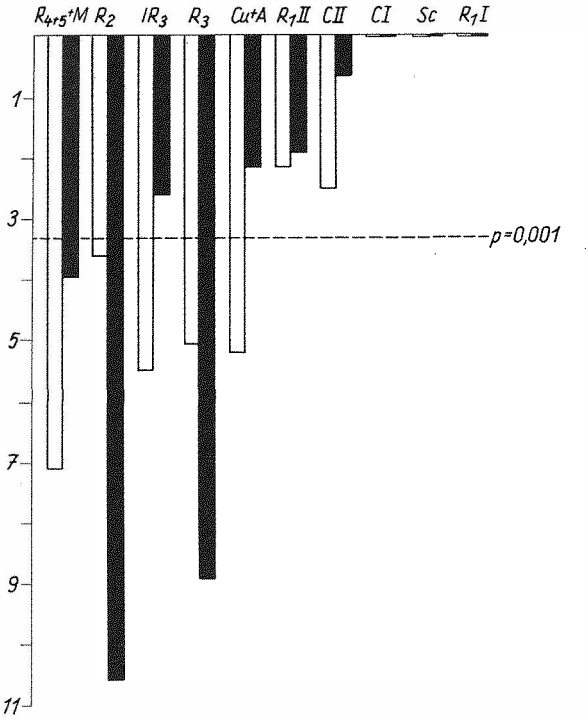

Fig. 6. Comparison (by means of the t-criterion) of cell number in males and females of *Lestes sponsa* HANSEMANN. Only right wings; white — fore wings, black — hind wings. Population "lake", 1966

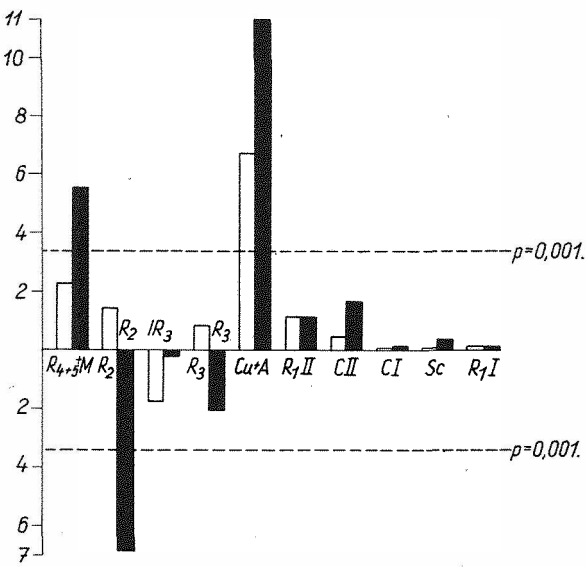

Fig. 7. Comparison (by means of the t-criterion) of cell number of fore and hind wings of *Lestes sponsa* HANSEMANN. Only right wings; white — males, black — females. Population "lake", 1966

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3. differences in the cell number of the fore and hind wings not only in genera which belong to Anisoptera but also in one belonging to Zygoptera.

There are no differences in characteristics of the right and left wings both in males and females in all the species studied.

This permits us in all further investigations of the characteristics described for the wing structure of the dragonfly to take into account characteristics of any pair of wings.

While studying samples with small numbers of specimens for the left and right wings it is possible to obtain more numerous samples suitable for modern methods of statistical treatment.

In agreement with the opinion of many authors (e.g. BARTENEV 1923; SCHMIDT 1929; NEEDHAM & WESTFALL 1955) the cell number in the areas between the main longitudinal veins may serve as a species and genus characteristic. In our opinion, this characteristic can be used for taxonomical aims more widely than it is used now. The data available are not sufficient as yet to give the correct quantitative description of wings of all or most genera of the dragonfly. But in the near future obtaining such characteristics will be quite possible and desirable.

For the 3 species studied this characteristic can be given now in a general form (Table 21).

Table 21

General characteristic of the species studied according to cell number between main longitudinal wing veins

Area	Species					
	Sympetrum danae		*Leucorrhinia albifrons*		*Lestes sponsa*	
C-I	7	5– 6	7	6	2	2
Sc	6	5	7	6	2	2
R_1-*I*	4– 5	3	4	3	0	0
C-II	10–11	11	14	14–15	17	17
R_1-*II*	10	10–11	13	13	18	17
R_2	52–57	53–57	84	88–89	44	43
R_3	16–17	16	24–25	25	34–35	34
IR_3	54–59	63–69	90	106–107	41	67
R_{4+5}	14–15	13	19	19	70–71	67
M	36–39	46–47	56	66		
Cu+*A*	47–51	79–85	59	94–95	32	28

In the future, when similar data are obtained for other species, it will be possible to reveal more accurately the characteristics of the "rank" of interspecies, species and subspecies characteristics, i.e. easily varying within one species, genus or family. Then it will be possible to define more precisely the characteristics of taxonomical significance and those important for the investigation of microevulotionary processes.

It can be assumed that the characteristics $C - I$, Sc, $R_1 - I$ are of taxonomical importance (not lower than "family level"); the other features may be useful in determining species; such characteristics as R_2, $I R_3$, M and $Cu+A$ are promising for a comparison of different populations.

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It should be emphasized that the value of such data which are obtained from the same population increases from year to year with their accumulation as it makes it possible to reveal the phenotypic expression of a current microevolution process. Such a comparison of populational characteristics will permit the clarification of the character of the existing factors of evolution.

Conclusions

Variability of the right and left wings of the dragonfly practically does not differ, accordingly any of them can be chosen.

There is a distinct sexual dimorphism in the wing characteristics. Thus only samples of the same sex can be used for an accurate population comparison.

The structure of fore and hind wings not only of Anisoptera but Zygoptera as well differs markedly in many quantitative characteristics.

The wing of the dragonfly can serve as a convenient object for investigation of variability as it permits us to choose dozens of quantitative characteristics (genus, species, population) which can be easily registered. This makes possible a further development of microevolutionary studies and the obtaining of additional taxonomic characteristics of different species, genera and families of dragonflies.

The data obtained are in full agreement with those concerning sexual dimorphism in the number of the wing cells (at least in some species) of the dragonfly. But if according to SPURIS (1962) *Aeshna grandis* males and females differ only in the cell number of the hind wings, we find distinct differences in the fore wings in 3 other species studied.

Comparison of variability of characteristics chosen concerning cell number within one species (between males and females, different populations and samples of the same population) gives the opportunity to use these features for a precise characteristic of sexual and population differences.

Differences between diverse samples of the same population of different years (different generations) and distinct sexual dimorphism define the importance of the principle of a maximum "pure" comparison while comparing peculiarities both of different species and of populations of the same species. Such a comparison should be carried out between samples of the same sex and within one species — between the samples gathered during the same season.

Comparison of the data obtained from some populations of 3 species and genera of dragonflies shows the existence of pronounced differences practically in all the characteristics studied.

Zusammenfassung

Es wurde die Veränderlichkeit der Zellenanzahl in 35 Flügelabschnitten bei drei Libellenarten (*Sympetrum danae* SULZER, *Leucorrhinia albifrons* BURMEISTER und *Lestes sponsa* HANSEMANN) aus der Umgebung Moskaus untersucht. Innerhalb der Population ist die Zahl der Zellen des rechten und linken Flügels praktisch gleich. In der Regel existiert ein deutlicher Geschlechtsdimorphismus in der Zahl der Zellen sowohl im Vorder- als auch im Hinterflügel aller untersuchten Arten (das erfordert bei weiteren Populationsuntersuchungen an Libellen die Verwendung gleichgeschlechtlicher Individuenserien). Der Vergleich der Variabilität der ausgewählten Merkmale innerhalb einer Art zeigt die Möglichkeit, diese Merkmale zur genauen Charakterisierung nicht nur der geschlechtlichen, sondern auch der Populationsunterschiede zu verwenden. Der Libellenflügel als Organ erweist sich als günstiges Objekt zur Untersuchung von sowohl mikroevolutiven Prozessen, die innerhalb der Art ablaufen, wie auch zum Erhalt taxonomischer Charakteristika beliebiger Ebene (von Populations- bis zu Art-, Gattungs-, Familiencharakteristika).

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Summary

The variability of the cell number in 35 areas of the wings was studied at three species of dragonflies (*Sympetrum danae* SULZER, *Leucorrhinia albifrons* BURMEISTER and *Lestes sponsa* HANSEMANN) from the vicinity of Moscow. Within the population the cell number of the right wing and the left wing is practically the same. As a rule there is a distinct sexual dimorphism in the cell number of both the fore wings and the hind wings of all the species under consideration (thus future studies of populations of dragonflies should use series of individuals of the same sex). A comparison of the variability of the chosen characteristics within a species indicates the possibility of using these characteristics to accurately define not only the sexual differences but also the differences between the populations. The dragonfly wing proves to be a suitable object for the study of microevolutionary processes in a species as well as for obtaining taxonomical data on any level (characteristics of population, species, genus or family).

Резюме

Изучена изменчивость числа ячей в 35 участках крыла стрекоз трех видов (*Sympetrum danae* SULZER, *Leucorrhinia albifrons* BURMEISTER, *Lestes sponsa* HANSEMANN) разных популяций из окрестностей Москвы. Внутри популяции число ячей правого и левого крыла практически не различается. Как правило, существует заметный половой диморфизм в количестве ячей как на переднем, так и на заднем крыле у всех изученных видов (что требует при дальнейших популяционных исследованиях стрекоз пользоваться только однополыми сериями особей). Сравнение изменчивости выбранных признаков внутри одного вида показывает на возможность использования этих признаков для точной характеристики не только половых, но и популяционных различий. Крыло стрекоз, как орган, оказывается удобным объектом для изучения как микроэволюционных процессов, текущих внутри вида, так и для получения таксономических характеристик любого уровня (от популяционных до видовых, родовых, семейственных).

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