What is *Drosophila littoralis* Meigen? (Diptera: Drosophilidae)

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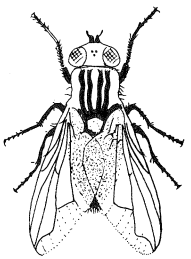

Evgen'ev, M. B., Lakovaara, S., Poluektova, E. V., Saura, A. & Sokolov, N. N.: What is *Drosophila littoralis* Meigen? (Diptera: Drosophilidae).
Ent. scand. Suppl. 15: 337–340. Lund, Sweden 1 July 1981. ISSN 0105-3574.

The name *Drosophila littoralis* has been variably applied to two different species. One of them, *D. littoralis* sensu Sokolov (not Meigen), is commonly used in studies on genetics and developmental biology. Studies on chromosomal gene arrangements, electrophoretic enzyme data etc. show that this species is *D. lummei* Hackman. *D. imeretensis* Sokolov is retained as a synonym of *D. littoralis* Meigen.

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There has been considerable confusion concerning the names of the European species of the *Drosophila virilis* group (Patterson 1952, Evgen'ev 1971, Wheeler & Hamilton 1972). The first species of this group that was formally described was *D. littoralis* Meigen, 1830, from Germany. Meigen's original description is so vague that it covers several species of the *D. virilis* group of the subgenus *Drosophila*. Meigen's (not designated) holotype was reported lost in the Museum of Paris as early as 1902. The nominate species of the group, *D. virilis* Sturtevant, 1916, was described from North America. It has also been found in China and parts of Europe. It is a species associated with human habitation.

In 1940 Sokolov recognized at least three different species of the *D. virilis* group in the Soviet Union. *D. virilis* is found in the southern parts of the country. A species which is common in the vicinity of Moscow has a metaphase chromosome set identical with that of *D. virilis*. Both species have five pairs of rod-shaped and one pair of dot-like chromosomes (2n=12). Sokolov assumed that this species from the Moscow region is *D. littoralis* Meigen, as there were records of it from Germany and Poland (Duda 1935). Sokolov published the results of hybridizing this species with *D. virilis* (Sokolov 1948a) and later in more detail (Sokolov 1959).

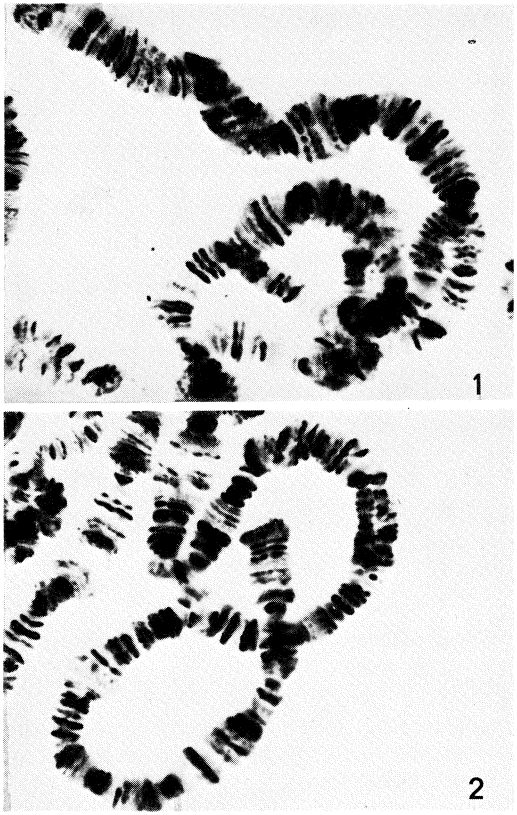
Sokolov also found a single female in 1940 and in 1946 several dozen specimens of a third species resembling *D. virilis*. These flies were found near the city of Kutaisy in the Georgian Soviet Republic. In 1945 flies of this species were also found in the Moscow region. Sokolov demonstrated that this species differed from both *D. virilis* and from *D. littoralis* in the sense of Sokolov. It had a chromosome set of 2n=10, so that it had two pairs of rod-like chromosomes, one pair of metacentric, one pair of submetacentric and one pair of dot-like chromosomes. Sokolov also attempted crossing this species with *D. virilis* and obtained some sterile hybrids. Sokolov incorporated this information in his formal description of this species, which he named *D. imeretensis* Sokolov (1948b).

In the late 1940s Burla had started extensive collections of drosophilids in Switzerland. He recognized that *D. littoralis* Meigen was rather common in his collections and published detailed information on its ecology (Burla 1951). He also described its chromosomes (Burla 1950). He sent Swiss strains of *D. littoralis* to the U.S.A., where Hsu (1952) and Clayton & Ward (1954) again described its chromosome set. All these studies gave 2n=10 for *D. littoralis* Meigen from Switzerland. Patterson (1952) pointed out that both the morphology and chromosome set of the Swiss *D. littoralis* agrees completely with

Sokolov's description of *D. imeretensis*. Patterson proposed that the two forms might either be geographical races of a single species or closely related sibling species. Patterson & Wheeler (in Patterson 1952) redescribed *Drosophila littoralis* Meigen, 1830. A modern description was needed, as several North American species related to *D. virilis* had been described. These species and their relationships are discussed at length by Patterson & Stone (1952).

Evgen'ev (1971) pointed out that the species for which Sokolov had used the name *D. littoralis* "does not correspond to the species with the same name in the Patterson and Stone classification". Similarly, Wheeler & Hamilton (1972) stated that *D. imeretensis*, sent to them by Sokolov, was identical with several western European strains of *D. littoralis* Meigen. In 1970 Lumme in Finland, studying Finnish and Swedish strains labelled *D. littoralis*, found that at least two species were involved in these strains. One species was found to be identical with the western European reference material of *D. littoralis* Meigen. The other species was again found to be identical with a Russian reference strain from the suburbs of Moscow. As this latter species was evidently unnamed, it was called *D. lummei* Hackman, 1972.

The name *D. littoralis* in the sense of Sokolov is, however, continuously used by geneticists working with this species. It is, therefore, apparent that direct evidence is needed to establish that *D. imeretensis* Sokolov is a synonym of *D. littoralis* Meigen and that *D. littoralis* in the sense of Sokolov is *D. lummei* Hackman. We shall in the following give the results of a comparison of chromosome rearrangements and electrophoretic enzyme patterns.



Figs. 1–2. — 1. Two overlapped inversions in the 1 (X) chromosome of a cross between *D. virilis* and *D. littoralis* sensu Sokolov. The limits of the inversions are Nfg-Yef. — 2. The whole second chromosome of a cross between *D. virilis* and *D. littoralis* sensu Sokolov. The inversion Kij-Ua can be seen.

Materials and methods

In order to study the rearrangements within the chromosomes of *D. littoralis* in the sense of Sokolov and *D. lummei*, strains of these species were crossed with each other and also with a wild strain of *D. virilis* from Batumi, Georgian Soviet Republic. Cytological preparations were made of late third-instar hybrid larvae as smear preparations stained with aceto-orcein. The *D. littoralis* sensu Sokolov consisted of flies collected from the suburbs of Moscow. Four strains of *D. lummei* from northern and central Finland were also used.

The starch gel electrophoresis and enzyme assay methods follow those used by Lakovaara & Saura (1971). The assayed material of *D. littoralis* Meigen and *D. lummei* Hackman consisted of about 300 of wild-caught flies studied fresh after capture. The material originate from Finland and Sweden (Lankinen, unpublished). Four strains of *D. imeretensis* from the Georgian Soviet Republic and one strain of *D. littoralis* in the sense of Sokolov from the Moscow region were assayed.

Tab. 1. The approximate limits of chromosome rearrangements in *D. littoralis* sensu Sokolov and in *D. lummei* Hackman. All forms are compared to *Drosophila virilis*, the cytological standard form. Each chromosome has inversions, the breakpoints of which follow the map of Hsu (1952). The triad *D. novamexicana–D. texana–D. americana* as well as *D. littoralis* Meigen are described in Hsu (1952) and in Stone et al. (1960).

	Chromosome (points of break)					
D. virilis	1 –	2 –	3 –	4 –	5 –	6 –
D. littoralis sensu Sokolov	overlapped Cbc-Yef Nfg-Vab	median Kij-Ua	–	distal Ddf-Gf median Idf-Vi	median Kbc-Vfg	Aa-Zk
D. lummei Hackman	Cbc-Yef Nfg-Vab	Kij-Ua	–	Ddf-Gf –	Kbc-Vfg	Aa-Zk

Results and conclusions

A study of the F_1 generation hybrids of both *D. littoralis* in the sense of Sokolov and *D. lummei* Hackman with *D. virilis* as well as when the two forms are crossed with each other shows that the first two carry identical gene arrangements in the first, second, fifth and sixth chromosomes (Figs. 1–2, Tab 1). As for the fourth chromosome, the Moscow population proved to be polymorphic with regard to two inversions, while the Finnish populations had only the short distal inversion in the fourth chromosome. The inversion was also in this case involved in a polymorphism together with the normal gene arrangement.

With the exception of the fourth chromosome, the limits of inversions determined here coincide in all cases with the limits described by Patterson & Stone (1952) for *D. texana* and *D. americana*. It has been pointed out previously that *D. lummei* (or *D. littoralis* sensu Sokolov) must be related to the American triad *D. americana–D. texana–D. novamexicana* on several morphological grounds (Wheeler & Hamilton 1972). In the sixth chromosome *D. lummei* has an inversion characteristic of this species (Fig. 3). The inversion has not been found in its American relatives (*D. novamexicana-D. texana-D. americana*). When *D. virilis* is used as a female parent in the cross with *D. lummei*, the *D. lummei* sixth chromosome undergoes elimination at early stages of embryogenesis of the hybrid.

We have also surveyed the electromorph frequencies in various enzyme systems with starch gel electrophoresis. The data are from the extensive survey of Lankinen (unpublished). Table 2 lists the electromorphs shared by the four forms in polymorphic systems. *D. littoralis* Meigen and *D. imeretensis* Sokolov always have the same electromorph established as the most common one (Tab. 2). Again *D. lummei* Hackman and *D. littoralis* sensu Sokolov have the same predominating electromorphs. In particular the enzymes hexokinase-4, malate enzyme and triosephosphate isomerase are more or less completely monomorphic for a species-specific electromorph.

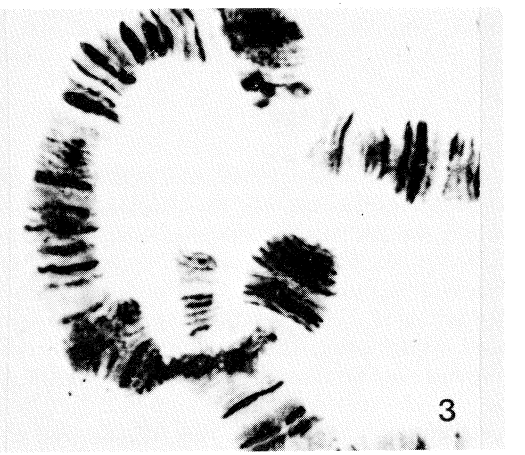


Fig. 3. The sixth chromosome in a *D. virilis* × *D. lummei* hybrid larva. The *D. lummei* chromosome (center right) is inverted with regard to the *D. virilis* chromosome (center left).

We also note that *D. littoralis* Meigen hybridizes freely with *D. imeretensis* Sokolov and also *D. lummei* Hackman hybridizes with *D. littoralis* sensu Sokolov equally well. The morpho-

Tab. 2. Number of electromorphs in common with any two forms (above the diagonal). LI = *D. littoralis* Meigen, IM = *D. imeretensis* Sokolov, LU = *D. lummei* Hackman, LS = *D. littoralis* sensu Sokolov. The X's below the diagonal indicate the most common electromorph shared with any two forms.

Acid phosphatase

	LI	IM	LU	LS
LI		1	2	0
IM	X		0	0
LU	–	–		2
LS	–	–	X	

Malate dehydrogenase

	LI	IM	LU	LS
LI		1	1	0
IM	X		0	0
LU	–	–		2
LS	–	–	X	

Malate enzyme

	LI	IM	LU	LS
LI		1	0	0
IM	X		0	0
LU	–	–		1
LS	–	–	X	

Hexokinase-4

	LI	IM	LU	LS
LI		1	0	0
IM	X		0	0
LU	–	–		1
LS	–	–	X	

Isocitrate dehydrogenase

	LI	IM	LU	LS
LI		1	0	0
IM	X		0	0
LU	–	–		2
LS	–	–	X	

Triosephosphate isomerase

	LI	IM	LU	LS
LI		1	1	1
IM	X		1	1
LU	–	–		2
LS	–	–	X	

logical descriptions of Patterson (1952), Sokolov (1948b) and Hackman (1972) also agree completely with the above conclusions. Accordingly, *D. imeretensis* Sokolov, 1948, is a synonym of *D. littoralis* Meigen, 1830. Likewise, *D. littoralis* in the sense of Sokolov (not Meigen, 1830) is *D. lummei* Hackman, 1972.

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Manuscript received May 1980.

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