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THE SCIENTIFIC HERITAGE OF ZDRAVKO LORKOVIĆ (1900-1998)

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The development of the evolutionary thought has been connected with the scientific work of several outstanding lepidopterologists: O. Staudinger, S. S. Četverikov, B. L. Astaurov, E. B. Ford, H. B. D. Kettlewell, G. de Lattin, E. Suomalainen. The scientific work of Professor Lorković worthily can be associated to these important researchers.

He has been well known: in fine karyological techniques experimental hybridisation of critical species, as one of the pioneers of cytotaxonomy, he recognised very early the enormous variability of chromosome, best field experts of the Balkanic high mountains, as describer of the intermediate stages of the process of speciation and create the concept „semispecies", often cited by the classics of the evolutionary biology, he created a new term - the "eco-surface" etc and etc. In his quite long life, and also scientific long work his scientific personality and humanity deeply fascinated.

Z. Lorković, *Lepidoptera*, fauna, genetics

Z. VARGA, Znanstvena baština Zdravka Lorkovića. Entomol Croat., 2009 Vol.13 Num. 1: 85- 94

Razvoj i evolucija misli u ovom dijelu entomologije usko je povezana sa znanstvenim radom izuzetnih leptirologa kao : O. Staudinger, S. S. Četverikov, B. L. Astaurov, E. B. Ford, H. B. D. Kettlewell, G. de Lattin, E. Suomalainen. K njima se sigurno može pribrojati i znanstveni rad profesora Lorkovića.

On je bio poznat po znanstvenom radu na mnogo polja u leptirologiji a posebno: finoj kariološkoj tehnici eksperimentalne hibridizacije kritičnih vrsta, kao pionir citotaksonomije, on je vrlo rano uočio veliku varijabilnost kromosoma, bio je najbolji terenski istraživač balkanskih visokih planina, kreator pojma semispeciesa, kao i eko plohe itd itd. U svom dugom životu ali i dugom znanstvenom radu njegova znanstvena i humana osobnost duboko je fascinirala.

Z. Lorković, *Lepidoptera*, fauna, genetika

The development of the evolutionary thought has been intimately connected with the scientific work of several outstanding lepidopterologists. Even Otto Staudinger, one of the most productive taxonomists of the „fin du siècle", at the turn of 19-20. centuries, often used the term „*species darwiniana*" for such species of Lepidoptera which he considered as being in formation („in statu nascendi"). S. S. Četverikov, the pioneer of the Russian experimental genetics and one of the founders of the modern, mathematical population genetics, published also some significant lepidopterological papers. The classical objects of the research on the sex determination were often Lepidoptera, e.g. the Gipsy moth (*Lymantria dispar*) by S. S. Četverikov and the silk moth (*Bombyx mori*) by B. L. Astaurov. The long-term observation of variation and evolution in natural populations (e.g. in *Euphydryas aurinia*) was initiated by E. B. Ford in Great Britain. The survey of phenomena of melanism in Lepidoptera (e.g. in *Biston betularius*) has resulted in some classical perceptions on variation and selection, e.g. by H.B.D. Kettlewell. G. de Lattin, a student of the evolutionary geneticist Curt Kosswig, has recognised very early the importance of the genetic markers in the biogeography, in the unravelling of glacial refugees and patterns of postglacial re-population. His seminal papers have recently greatly influenced the emergence of the phylogeography. Problems of chromosomal evolution have been intensively studied by the doyen of the Finnish zoology, E. Suomalainen in connection with the evolution of the parthenogenesis in weevils and Psychid moths.

The scientific work of Professor Lorković worthily can be associated to these important achievements of the 20th century evolutionary biology and lepidopterology. He could establish a completely unique unity of the keen laboratory praxis, indefatigable field work and deep theoretical thinking. His fine karyological techniques were quite legendary. The difficult experimental hybridisation of critical species was solved by his discovery of artificial hand-pairing. All his hybridisation and rearing experiments were protocolled with the extreme exactitude and illustrated by precise drawings. He surely was one of the best field experts of the Balkanic high mountains, often acquainted in his mountain trekkings by his friend, the excellent geobotanist Ivo Horvat. These many-sided surveys made possible that he could discover and describe the intermediate stages of the process of speciation and create the concept „semispecies", often cited by the classics of the evolutionary biology as J. Huxley, E. Mayr and others. It was the highest recognition of his scientific achievements that he was invited – in a politically di-

fficult after-world-war period – to the United States (Cold Spring Harbour Symposia, 1958b) and also to Sweden (Uppsala), to the inauguration of the Linnean Bicentenary (1958a).

During his long and honoured scientific career he has worked with many different groups of butterflies. His early papers on the *Leptidia* (1930-31) and *Cupido* (1938, 1942) species were excellent examples how to elaborate difficult groups of sibling species with a full complexity of methods: morphology, anatomy, karyology and also phenology and ecology. Some important topics were repeatedly re-considered by him, e.g. the chromosomal evolution in butterflies. The time-span of these surveys extended about a half of century (1941-1990).

As one of the pioneers of cytotaxonomy, he recognised very early the enormous variability of chromosome numbers in several groups of butterflies, as in *Leptidia, Pieris* and subgenera of *Polyommatus* and also the surprisingly low number of chromosomes in some species of the genus *Erebia*. In this early period the theory of fragmentation (Federley 1938) and the diffuse-kinetochore induced ploidy, suggested by Lorković (1941 and especially: 1949), were the competing explanations of this phenomenon. He introduced the concept of the "modal number" of chromosomes into the survey of chromosomal evolution. The new discoveries on the holokinetic structure of lepidopteran chromosomes (e.g. Maeki 1980, Lukhtanov et al. 2005) essentially confirmed the elucidation of these phenomena given by Lorković. Although the mechanism which leads to the change in chromosome numbers is still unknown, but it seems most probable that low chromosome numbers are caused by fusion and high numbers by fission of chromosomes (Lorković 1990). This is also indicated by the striking reciprocal correlation between the number of chromosomes and their size (Wiemers 2003).

The problem of the interspecific hybridisation and the hybrid fertility vs. sterility was also one of the perpetual problems of Lorković. He carried out a huge number of experiments by his techniques of artificial copulation, and reared numerous generations of hybrid offsprings with statistical evaluation of the change in fertility. One of the results was the recognition of the role of the supernumerary chromosomes, e.g. in the *Pieris napi* superspecies(Lorković 1962b), incl. *P. (napi) bryoniae* and *P. (napi) balcana*, recognised as own species and described by him (Lorković 1970). It was found by a series of experiments that *P. (napi) napi* without supranumerary chromosomes usually gives hybrids with reduced fertility with both "semispecies" *bryoniae* and *balcana*. He could demonstrate

numerous abnormalities in the meioses of the hybrids without vs. with supernumerary chromosomes leading to the incompatibility of karyotypes (Lorković 1974). The discovery of supernumerary chromosomes both in *P. (napi) bryoniae* and *P. (napi) balcana* has also given the possibility to explain the conspicuous lack of *P. (napi) bryoniae* in the Balkanic high mountains which probably became extinct due to the introgression of *P. (napi) balcana* (or *P. (napi) meridionalis* which may be conspecific with *P. (napi) balcana*).

The most famous taxonomical results and theoretical conclusions were connected, however, with the species of *Erebia tyndarus*-group (Figure 1). Based on detailed field surveys and taxonomical studies he described two Alpine endemics of this group, *E. calcarius* from the Julian Alps and (together with de Lesse) *E. nivalis* from the highest parts of the Central Alps (Lorković 1953a,b, 1957, Lorković & de Lesse 1954).

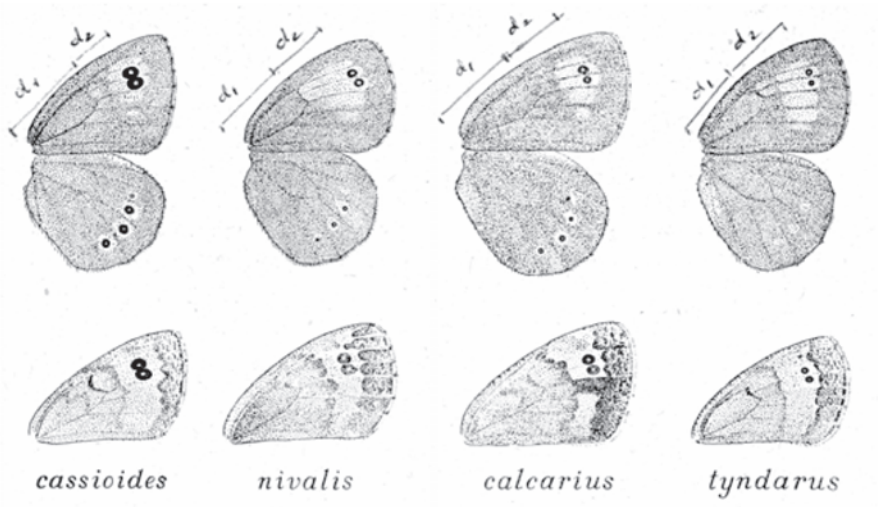

Figure 1. Original drawings of Z. Lorković on the species of the *Erebia tyndarus*-group (1957)

He found that the more ancestral species of this groups have higher chromosome numbers, e.g. the Balkanic *E. ottomana* (n = 51) and the Iberian *E. hispania hispania* and *E. hispania rondoui* (n = 25 and n = 24) while the much more

recently differentiated Alpine taxa have essentially lower numbers, probably due to fusions (*E. tyndarus* and *E. cassioides* n = 10, *E. calcaria* n = 9 and *E. nivalis* n = 11). As a result of numerous hybridisation experiments he could find some degrees of interfertility/sterility (Figure 2) from the complete fertility (e.g. the eastern Alpine and western Balkanic populations of *E. cassioides cassioides* x *E. c. illyrica* or *E. c.*

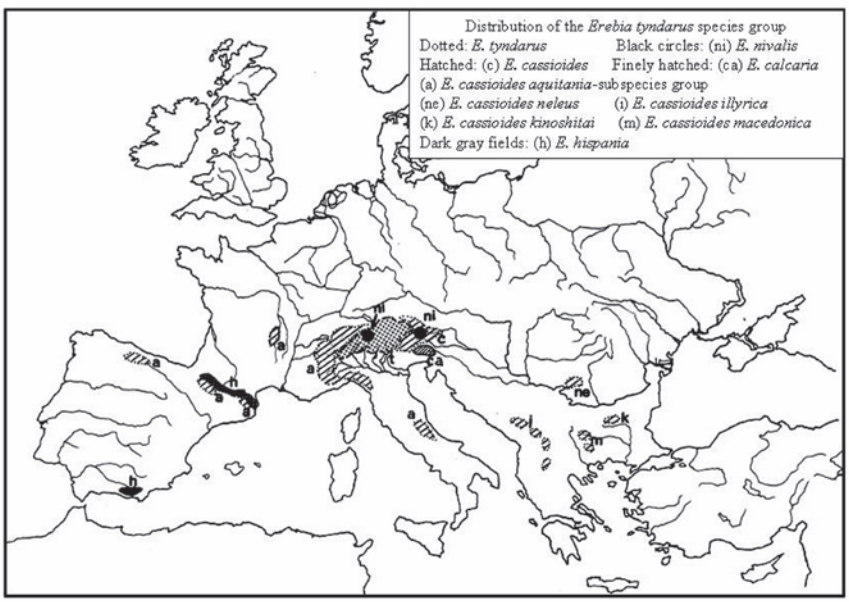

Figure 2. Geographical distribution of the *Erebia tyndarus* species group in Europe

illyrica x *E. c. illyromacedonica*) through several intermediate levels (e.g. the partial fertility of back-crosses between *E. tyndarus* x *E. calcaria* or between *E. tyndarus* x *E. nivalis*) to the nearly complete intersterility (e.g. between *E. cassioides* x *E. tyndarus*, *E. cassioides* x *E. calcaria* or *E. cassioides* x *E. nivalis*). He also found that the sexual affinity may be strikingly different among these taxa in the reciprocal hybridisation experiments and concluded that some of these allopathic taxa only show an intermediate stage of speciation. These results were recently strongly confirmed by Albre et al (2008). They have found a stronger di-

fferentiation between *E. ottomana* vs. the rather shallow divergence in the "alpine" taxa of the *tyndarus*-group, as a consequence of the supposedly rather recent (Upper Pleistocene) differentiation among the Alpine species.

These experimental data substantiated the elaboration of the semispecies concept for the stages of the unfinished speciation. He re-fined the definition of this category, originally coined by E. Mayr (1940), and repeatedly argued for the necessity and nomenclatorical acceptance of this intermediate taxonomical category (Lorković 1957, 1958a, 1958b, 1962a; Lorković & Kiriakoff 1958; Kiriakoff & Lorković 1958). This suggestion was considered in the Article 6(b) for members of the "*aggregate of species or subspecies within a species*" (ICZN 3rd ed. 1985). The above cited examples from the semispecies of the *Pieris napi* "superspecies" (i.e. aggregate of allopatric semispecies and sibling species with intermediate stages of speciation) clearly show the usefulness of this approach (Varga & Tóth 1978).

Since Z. Lorković spent his long life in a country rich in famous karstic phenomena, the adaptation of butterflies to the karstic substrate was one of the Figure 3. Original figures of Z. Lorković on the hybridisation experiments in the Erebia tyndarus-group (1957) ecological problems which have taken up his attention for a long time. He created a new term, the "eco-surface" (*ekoploh*) for this type of the hiding colouration which is mostly the under surface of the hind wings of butterflies, e.g. in the Ringlets (Satyrinae) spending the most time of the day on the whitish-grey barren karstic surface. The paper on the subspecies of *Hipparchia statilinus* gives a brilliant example (Lorković 1974) on the quantitative-statistical and taxonomical evaluation of this phenomenon.

It was mentioned that Z. Lorković was a perfectionist (Eitschberger 1999). The repeated re-consideration of some basic problems, the re-iterated revision of own earlier results and the continuous following of most recent methods and results were the factors that he could sustain his mental vitality worthily until the last minutes of his life. The varied, partly often discussed (e.g. the different levels of vitality vs. fertility in hybrid butterflies; Lorković 1997) and partly completely new topics of his last publications (e.g. new aspects of habitat preference of *Leptidia morsei major*, the occurrence of the noctuid moths *Chersotis* in Croatia; Lorković 1993, Kucinić & Lorković 1998) clearly demonstrate his famous ability for innovation.

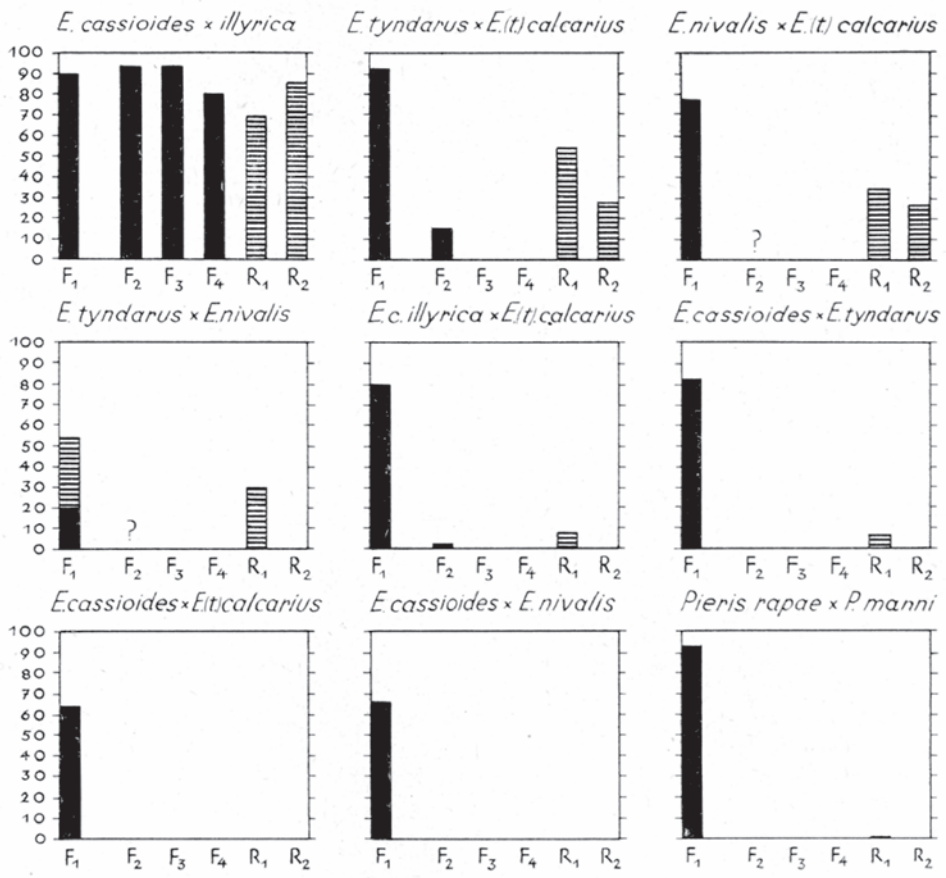

Figure 3. Original figures of Z. Lorković on the hybridisation experiments in the *Erebia tyndarus*-group (1957)

Last not least, I also have to report on my personal impressions connected with Professor Lorković whose scientific personality and humanity deeply fascinated me. I have seen him at first at the Entomological Congress in Moscow, 1968. He was really a central figure of a small international circle of lepidopterologists, discussing mostly in the foyer of the Grand Hotel „Rossiya". He visited Hungary several times with great interest e.g. in the habitats of the *Pieris ergane* in the Vértes Mts. where he could find the eggs of this butterfly on the small succulent

cruciferous species *Aethionema saxatile*, but also in the hybrid populations of *Pieris (napi) napi* and *P. (napi) bryoniae* in the Bükk Mts. Here he could collect some interesting karyological samples and constates the presence of the supranumerary chromosomes in several specimens. It was his interesting observation on this material that he could find malformations in the female genitalia of such hybridogenous individuals accompanied by the sterility of them. Unfortunately, later this hybrid population was transformed into a *P. napi*-population, probably due to the reduced fertility and fitness of such hybrid individuals.

His surveys on *Aricia*, together with his student R. Sijarić (1968) were also helpful for me to evaluate the *Aricia* taxa of the Carpathian basin and Balkan peninsula correctly (Varga 1968). Later, we contacted several times in order to clarify the joint problems of the occurrence of *Apatura metis* in the borderline areas of Hungary and the former Yugoslavia. Since I was intensively interested in the Lepidoptera of the Balkanic high mountains, his fundamental surveys on the genus *Erebia* were highly authoritative for me. It was a great honour for me that he, as chairman of the former Yugoslavian Entomological Society invited me to Postojna to have a lecture on the biogeography and subspeciation which was published in *Acta Entomologica Jugoslavica* (1975). The discussions on these topics essentially shaped my thinking in evolutionary biology and biogeography. Therefore, I think that he was not only one of the greatest lepidopterists of the 20th century but he is also one of the most influential person on the recent development of lepidopterology.

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