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**HIGH VITALITY VERSUS LOW FERTILITY IN ARTIFICIAL
INTERSPECIFIC F₁ HYBRIDS OF BUTTERFLIES
(a preliminary report)**

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The method of artificial mating of Lepidoptera permits crossings to be made between species which do not interbreed in nature. The haplogenomes of the F₁ interspecific hybrids are often highly compatible, so that able (in lab) specimens are produced. In spite of such a high compatibility, the hybrids are mostly infertile. Sterility is due to the inability of the F₁ hybrids to produce mature gametes, even in backcrosses. One of the causes of this reproductive incapacity is the irregular meiosis of the ripening gametes. It is due to the disturbed synapsis of the "homologous" chromosomes. The "homologous" chromosomes fail to match not so much because of the new mutations but rather because of the altered linear arrangement of the chromosome loci. It is concluded that the cumulation of discordances between homologous chromosomes, resulting in hybrid sterility, is mainly responsible for the development of reproductive isolation between emerging diversity (species), exceeding its importance in the appearance of new mutations.

Lepidoptera, artificial mating, chromosomes, homologues, meiosis, interspecific hybrids, evolution.

LORKOVIĆ, Z., Velika vitalnost nasuprot sterilnosti umjetnih interspecijskih F₁ hibrida kod danjih leptira. - Entomol. Croat. (1996) 1997. Vol. 2.: Num. 1-2.: 5-10.

Metodom umjetne kopulacije leptira lako se postiže križanje među vrstama koje ne hibridiziraju u prirodi. Oba haplogenoma takvog F₁ hibrida su među sobom tako dobro genetički usklađena (visoko kompatibilni) da proizvode (kod leptira u muškom spolu) normalno razvijene F₁ hibride (križance) koji ni po građi ni po vitalnosti (u laboratoriju) ne zaostaju za primjercima roditeljskih vrsta. Unatoč takvoj visokoj kompatibilnosti križanci su ipak obično neplodni, čak i u povratnim križanjima, jedna okolnost uzeta do sada premalo u obzir. Razlog tako visokoj neplodnosti je nepravilna mejotička dioba kromosoma. Ta pogreška rezultira gubitkom potrebnih gena u gametama 2. mejotičke diobe i time uvjetovanim ugibanjem nezrelih gameta. Izostanak konjugacije "homolognih" kromosoma je više posljedica promijenjenog linearnog rasporeda gena nekada homolognih kromosoma za vrijeme izolacijske faze specijacije nego samih novih mutacija. Čini se prema tome da u evoluciji vrsta nemaju toliki udjel nove mutacije koliko poremećaj rasporeda lokusa na nekada homolognim kromosomima, što postaje uzrok sterilnosti međuspecijskih hibrida kao jedne od bitnih komponenata rasplodne izolacije među novonastalim taksonima (vrstama).

Lepidoptera, umjetna kopulacija, kromosomi, homolozi, mejotička dioba, međuspecijski hibridi, evolucija.

Artificial interbreeding in butterflies, by circumvention of ethological barriers to pairing, permits crossings to be made between species which normally do not interbreed (LORKOVIĆ 1947, 1953, CLARKE 1952, CLARKE & SHEPPARD 1953, 1956). The F₁ hybrids produce in this way a usually high compatibility of the two species' genomes so, that normally balanced specimens are produced not all lagging in their development, behind those of their paternal species. Examples of such lab-produced hybrids are those of *Pieris rapae* ♀ × *P. mannii* ♂ which succeed even better than pure *P. mannii* breeds, so that the viability of the hybrids is not at all reduced. Such specimens are also capable of pairing. The well known intermediary hybrid appearance of their differential characteristics or their incomplete dominance is the

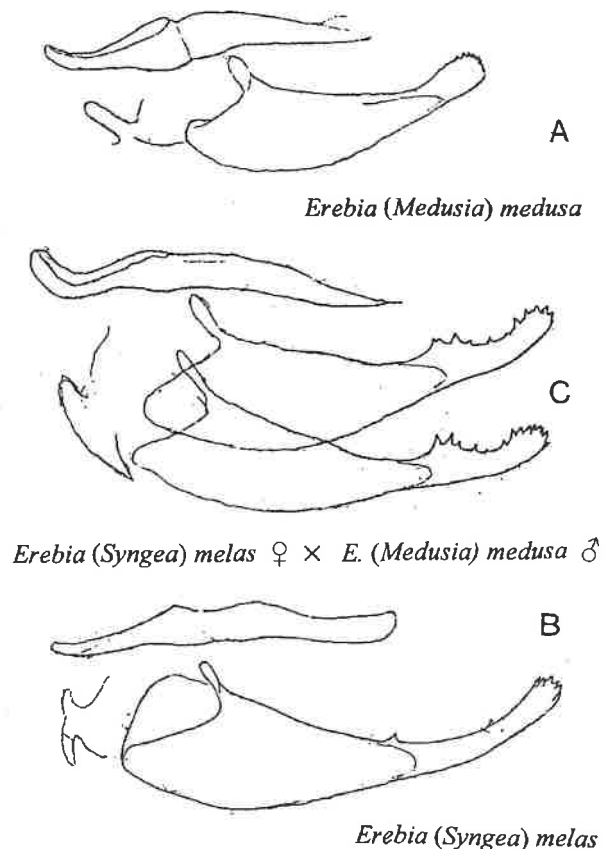


Fig. 1. Valvae of A - *Erebia (Medusia) medusa*, B - *Erebia (Syngea) melas* (Velebit, Croatia), and C - their F₁ hybrid *E. (Syngea) melas* ♀ × *E. medusa* ♂ with its doubly teathed valvae (Lorković, 1954, unpubl.) as the proof that two highly compatible genomes are present and each phenotypically expressed.

proof of the active contribution (Fig. 1) of the genomes of both species involved¹⁾. Similar results were obtained in crossings between *Phyciodes tharos* and *P. batesii* (OLIVER 1979a).

The complete development of many F₁ hybrids of butterflies shows that the genomes of the interbred species are genetically highly compatible and that the differences between them are fewer than usually found for different species. The match of the two hybrids' genomes is even more appreciable considering the fact that the reproductive organs of the hybrids are normally developed in all their parts. This applies in particular to numerous female organs, like the ductus bursae, ductus seminalis, oviductus with the ovipositor and the collateral glutinous glandulae (Fig. 2 and 3). One would expect from such failureless reproductive organs that their function in building the next generation would also be preserved. In spite of the high compatibility of both hybrid genomes, they are incapable to produce ripe hybrid gametes. The gametes are to a high degree, in the female (heterogametic) sex even completely, sterile, and the well developed ectodermal oviductus remains empty more often than not. To a somewhat lesser extent, this applies also to the testicles of the F₁ butterflies in which no or only few ripe sperm bundles can be found, so that even the backcrosses remain infertile²⁾.

How can this be explained? The first answer is given by considering the karyotypes, resp. chromosome sets in the testicles, of the F₁ hybrids. In contrast to the very constant chromosome number in parental species, one can see at a glance that, in the F₁ hybrids, the number and size of chromosomes in the metaphase plates of the first meiotic division of the spermatocytes is usually very irregular (Fig. 4). This irregularity in chromosome number is the result of the default in conjugation (synapses) of homologous chromosomes in the first spermatocytes of the F₁-hybrids. Many of these chromosomes do not reach the first meiotic division as normal bivalents but as univalents which are not to take part in the 1st spermatocytes and remain undivided, randomly distributed between the daughter cells. Thus the cells of the 2nd meiotic division are often rid of the chromosome loci required for further development and remain excluded from further cell division. Such an irregular meiotic chromosome separation is particularly conspicuous in the first order spermatocytes of the interspecific F₁ hybrids of Lepidoptera, e.g. in *Pieris*, *Pontia*, *Anthocharis*, *Euchloe*, *Colias*, *Leptidea*, *Erebia*, *Polyommatus*³⁾ (LORKOVIĆ 1974, 1978, 1985, 1990; SCHURIAN 1989, 1991). Similar results were obtained in many moth species cross-

¹⁾ Such a common (joint) ethological genetic control of both genomes of a hybrid is particularly well expressed in the oviposition of the hybrid females of *Pieris ergane* ♀ × *P. (napi) bryoniae* ♂, where the eggs are not deposited exclusively on *Aethionema saxatile*, as with *P. ergane*, but also on other crucifers, like *Rorippa silvestris* or on many other Brassicaceae (LORKOVIĆ 1978, 1950 unpublished).

²⁾ From among 20 backcrosses of *P. rapae* ♀ × *P. mannii* ♂ F₁ hybrids with *P. rapae* ♀ a total of 970 eggs was obtained. From these, only 7 larvae hatched, all of which reached imago stage (6 ♂♂, 1 ♀). The only developmental error found was a slight malformation of the male wings, which were not as flat as they usually are.

³⁾ In the Satyrinae *Erebia tyndarus* - species - a group with a low number (N = 8 - 11) of mainly large chromosomes, the number in the hybrids is not greater but smaller than in the parental species because of the fact that the large chromosomes are built by the fusion of the smaller ones. Therefore these large chromosomes are only partially homologous and conjugate alternatively with several small chromosomes resulting in the formation of three-, tetra- and even pentavalent long chromosomes, lower in their number than in the original species (LORKOVIĆ 1978, 1990).

ings by the Finnish Lepidoptera geneticist H. Federley in the first half of the century (see SUOMALAINEN 1952).

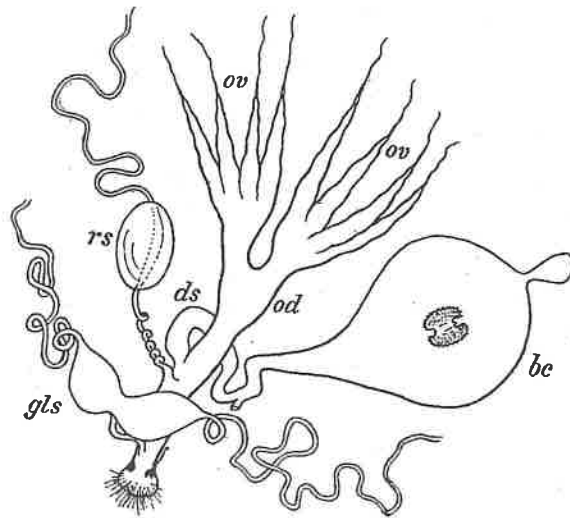


Fig. 2. The female genital organs of F₁ hybrid of *Pieris rapae* ♀ x *P. mannii* ♂. The external genital removed, *bc* bursa copulatrix, *ov* ovarioles, *ds* ductus seminalis, *rs* receptaculum seminis, *gls* gluy glands, *ov* oviduct. (After LORKOVIĆ, 1928)

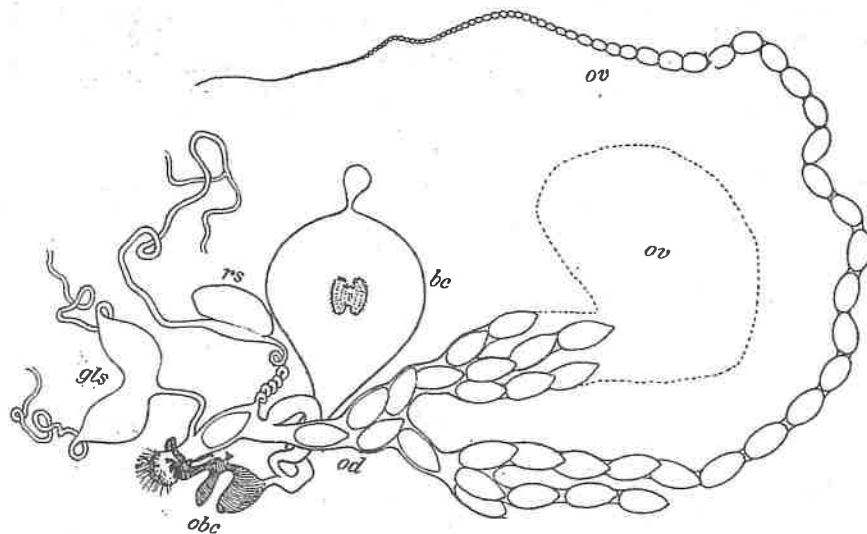


Fig. 3. The female genital organs of *Pieris rapae*. Only one ovariole is presented unrolled. Designation as in Fig. 2. (After LORKOVIĆ, 1928)

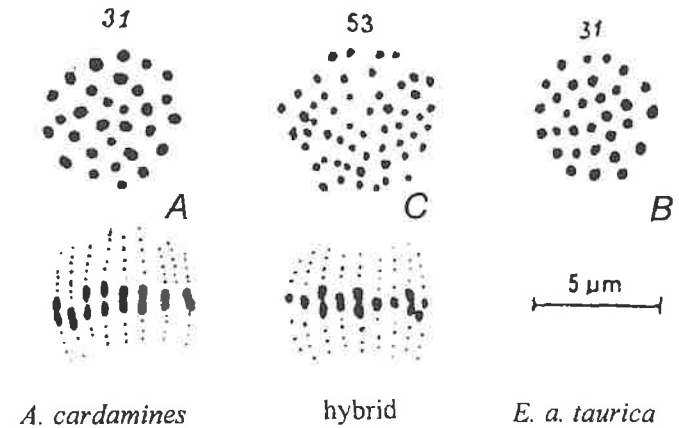


Fig. 4. Metaphase plates of 1st meiotic division in the spermatocytes of A - *Anthocharis cardamines* L. ($n = 31$), B - *Euchloe ausonia taurica* Röber ($n = 31$) and C - one of their F₁ hybrids ($n = 53$ in one plate). The small chromosomes in C are mostly univalents with their easily recognizable simple nature in the side view of the 1st metaphase plate (after LORKOVIĆ 1990, somewhat altered).

There remains the last question: what is the cause of the chromosome conjugation (synapsis) omission? The answer is again in the chromosomes, which are no longer homologous owing mainly to the linear rearrangement of the chromosome loci (translocation, dislocation, deletion, duplications, inversion, etc.) introduced during the isolation phase of evolution which, due to the lack of corresponding equal coupling groups, can no longer be called "homologous". It is precisely this structural difference between the no longer homologous chromosomes, underlying the complex reproductive character of the F₁ hybrids of butterflies and of other animals, that is in the origin of reproductive isolation between the new arising diversity. All the more so since mutations usually do nothing more than enlarge one of the two ends of the already existing polygenic variability of character.

Hohe Vitalität gegenüber niederer Fertilität der Fortpflanzungszellen der künstlichen F₁-Species Hybriden bei Lepidoptera

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Zusammenfassung

Erörtert wird die Frage, warum bei den künstlich gewonnenen F₁-Hybriden zweier nah verwandten Arten trotz höchster äußerlicher und innerlicher gegenseitiger Übereinstimmung, ihre F₁-Genome nicht im Stande sind, reproduktive Fortpflanzungszellen (Gameten) zu bilden, bzw. steril bleiben. Die Antwort liegt 1) in der vergrößerten Zahl und verminderter Grösse der hybriden Chromosomen im Verhältnis zu der konstanten Zahl derselben bei den elterlichen Arten, was wiederum 2) auf der ausgebliebenen Konjugation "homologer" Chromosomen beruht, die nicht mehr normale meiotische Bivalente, sondern mehrere Univalente darstellen, weil 3) die Chromosomen nicht mehr homolog sind, sondern weil es wegen der während der Isolation eingetretenen Translokationen zur Umordnung der linearen Anordnung der Chromosomenloci kam und deswegen zum Verlust der Fähigkeit der Paarung der Chromosomen und somit zur unregelmäßigen Teilung der Reproduktions-Zellen und zum Verlust lebenswichtiger Gene kommt.

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LIST OF PSOCOPTERA (INSECTA) IN CROATIA

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During 1975 - 1995 in nature and in enclosed spaces, on different plants and stored-products a total of 7110 individuals of Psocoptera (males, females, nymphs), of 61 species were collected. The most abundant species in nature was *Ectopsocopsis cryptomeriae* (Enderlein, 1907) and *Liposcelis decolor* (Pearman, 1925) in the enclosed spaces. Species of families Lachesillidae, Trogiidae, Peripsocidae, Caecillidae, Stenopsocidae, Elipsocidae, Philotarsidae, Psyllipsocidae and Trichopsocidae, are less wide spread. All recorded insects of the order Psocoptera in the Republic of Croatia have suitable ecological conditions for their wide spreading.

Psocoptera, lists, faunistic studies, Croatia.

KALINOVIĆ, I., IVEZIĆ, M., Popis Psocoptera (Insecta) u Hrvatskoj. Entomol. Croat. Vol. 2(1996) 1997: Num. 1-2.: 11-16.

Tijekom 1975 - 1995 godine u prirodi i u zatvorenim prostorima, na različitim bilju i u uskladištenim proizvodima sakupljeno je 7110 primjeraka Psocoptera (ženke, mužjaci, nimfe), ukupno 61 vrsta. Najzastupljenije u prirodi bile su vrste *Ectopsocopsis cryptomeriae* (Enderlein, 1907) i vrsta *Liposcelis decolor* (Pearman, 1925) u zatvorenim prostorima. Ostali pripadnici familija Lachesillidae, Trogiidae, Peripsocidae, Psocidae, Caecillidae, Stenopsocidae, Elipsocidae, Philotarsidae, Psyllipsocidae i Trichopsocidae, bili su manje brojno zastupljeni. Svi zabilježeni kukci reda Psocoptera u Republici Hrvatskoj za svoj život i razvoj imaju pogodne ekološke uvjete za široku rasprostranjenost.

Psocoptera, popisi, faunističke studije, Hrvatska.

Introduction

The order Psocoptera is a relatively small one, with about 3800 described species. They are not spectacular insects, because of their small size. In general they are not economically important, but in agriculture they can be significant pests of stored agricultural products. In some species they are medically important (responsible for allergic reactions in man). They could be important in the transmission of some sheep parasites too, and they cause damage to neglected collections of botanical and zoological specimens.

The insects of the order Psocoptera were completely uninvestigated in the Republic of Croatia up to 1975. Since then to 1995 they have been considerably researched in enclosed spaces - domestic psocids (KALINOVIĆ 1995), as well as in nature, living on different vegetation (GÜNTHER & KALINOVIĆ 1975, 1977, 1980; KALINOVIĆ & GÜNTHER 1982, 1985, 1987; KALINOVIĆ et al., 1977, 1978, 1979, 1980, 1980a).

This note is a review of Psocoptera from different regions of the Republic of Croatia.