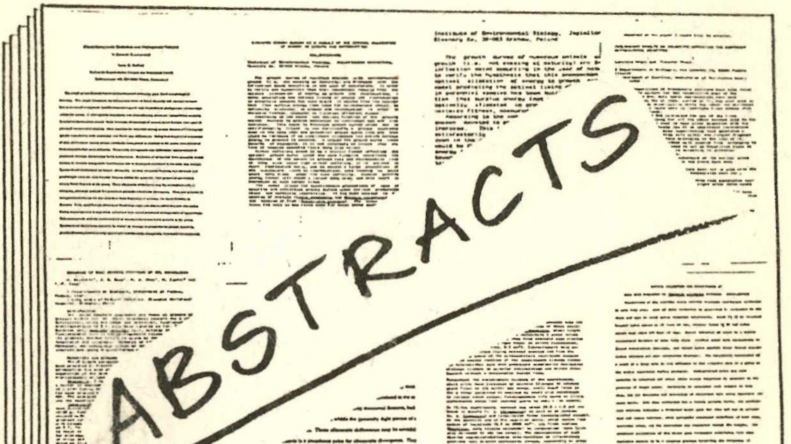
3rd CONGRESS OF E.S.E.B.



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ABSTRACTS

The cover was designed by Zsolt Farkas.

PLENARY LECTURES

PL3 ANALYTIC AND CONSTRUCTIVE APPROACHES TO EARLY EVOLUTION

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The evolutionary origin of the current genetic mechanism is a notoriously difficult problem. Three, interrelated aspects of this will be discussed through the author's contributions: (i) the evolution of enzymatic activity before encoded proteins; (ii) the size of evolutionarily optimal genetic alphabets; and (iii) the origin and evolution of the genetic code.

It is widely thought that enzymatic RNA molecules (ribozymes) preceded protein enzymes. I suggested that *in vitro* RNA breeding could be applied to test the general applicability of this idea. Replication of RNAs is straightforward, and independent selection is possible by affinity chromatography, presenting the stable transition state analog of the reaction to be catalyzed as the affinity center. Since then, RNA molecules binding to various ligands were artificially selected by other groups.

The extension of the genetic alphabet by novel base pairs is chemically feasible. My model shows, however, that the present genetic alpabet may be at a frozen optimum, which at an early evolutionary stage maximized the product of copying fidelity and metabolic efficiency of ribo-organisms, i.e. fitness. Whereas copying fidelity decreases exponentially with alphabet size, the metabolic efficiency increases with diminishing returns for a genome of fixed length. I suggest that the size of the genetic alphabet subsequently became frozen with the evolution of the genetic code and translation.

The code is still evolving by means of codon captures (reassignments). I showed that this is possible up to the point of complete swapping of the codon repertoires of neighbouring amino acids. This can explain how sub-optimal codes (implying a high mutational load) may have evolved to the present near-optimal one. Coding itself may have arisen before translation, as a means to evolve and maintain non-confusingly assigned nucleotide handles to amino acid coenzymes of ribozymes. Testing theories of the code's origin can be done by either experiments, or statistical means.

Szathmáry, E. (1990) *Nature* 344, 115.
Szathmáry, E. (1991) *Proc. R. Soc. Lond. B.* in press.
Szathmáry, E. (1991) *J. Mol. Evol.* 32, 178-182.

PL4

Coevolution to the edge of Chaos

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Coevolution among species is modeled using a spin-glass like model of epistatic interactions among genes within one organism to specify its fitness landscape. Coupling between genotypes of different species assceres that adaptive moves by one species typically alters the adaptive landscapes of other species. The model can exhibit "Red Queen" behaviour on final states similar to Evolutionary Stable Strategies. A selective metadynamics, changing landscape ruggedness and couplings between landscapes may typically lead to a poised state on the boundary between Red Queen and ESS phases, hence on the edge of chaos.

PL5 SPECIATION AND HYBRIDIZATION IN DARWIN'S FINCHES.

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Estimates vary for the number of metazoan species that have evolved on earth, centering on 5 to 10 million. How were all these species formed? Accounting for patterns of organic diversity requires an answer to this question. Field and laboratory studies of extant populations can contribute to an answer by demonstrating how differentiation of populations occurs, in behaviour, ecology and genetics.

Darwin's Finches are a particularly suitable group of organisms for examining ideas about speciation processes. There are several species (14), they were derived from a common ancestor fairly recently (<1 MYA), and their populations are discrete and often small. They occupy about 55 islands and islets in the Galápagos archipelago, and the single Costa Rican Cocos island. Electrophoretic analysis of protein polymorphisms confirms that they constitute a weakly differentiated group, biochemically. Morphological differentiation has been much more pronounced, especially in beak structure. Since beaks are instruments for gathering and dealing with food, variation in beak size and shape can be interpreted in terms of diet. Correlation analysis provides evidence for an adaptive basis to the morphological differentiation, and repeated demonstrations of directional natural selection in three populations substantiate the adaptive argument.

According to the classical allopatric model of speciation, the secondary contact of partly differentiated populations can lead to fission or fusion, in different ways. First the populations may have become completely reproductively isolated in allopatry, and different enough in feeding ecology that they can coexist without interbreeding. Speciation in this case will have occurred entirely in allopatry. Second, reproductive isolation may have evolved in allopatry but ecologically the populations may be weakly differentiated at the time of secondary contact, in which case speciation will have occurred but coexistence is not permanent. The resident species is likely to outcompete the invader. Third, differentiation in allopatry may have been limited, and at secondary contact the populations may interact reproductively and ecologically; they interbreed and compete for resources. If this happens the two extreme results are complete fusion, if the differences acquired in allopatry were minor, or complete fission under natural selection, if the initial differences were already substantial at the time of contact.

The third situation is potentially the most illuminating because processes can be observed and the dynamics measured. It is exemplified by circumstances on the small Galápagos island of Daphne Major (34 ha.). Daphne has a resident population of 35-200 pairs of _Geospiza fortis_ (medium ground finch). The island occasionally receives immigrants of a closely-related species, _G. fuliginosa_ (small ground finch). Some of the immigrants stay to breed, and some of these hybridize with _G. fortis._ The outcome, either the maintenance of two largely separate species or their fusion into one, is determined by the balance of interbreeding and selection. A ringing program, begun in 1973 and continuing to the present, enables us to estimate the evolutionary trajectory of the two species through a determination of the fates of all individuals and their offspring. I will discuss the relevance of our observations to an understanding of speciation and differentiation in Darwin's Finches in general, and beyond those limits to other organisms elsewhere.

PL6 Deleterious mutations as an evolutionary factor

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Most mutations are either neutral or deleterious. While the evolutionary role of beneficial and neutral mutations attracted much attention, deleterious mutations were traditionally neglected and considered as nonessential noise, which is counterbalanced by purifying selection, causing a small mutational load. This view is correct if the genomic deleterious mutation rate $U<<1$, so that selection against mutation can hardly influence other processes in a population.

Recently, however, larger values of U were proposed as a plausible way to resolve the difficulties in a theory of the evolution of reproduction. Simultaneously the data suggesting that $U>1$ in many multicellular Eukaryotes began to accumulate. If true, this means that deleterious mutations have an important 'positive' evolutionary role, in the sence that a general design of amphimixis, as well as many of its more specific features such as crossing-over, mate choice, and outcrossing, originated and has been maintained as an evolutionary consequence of selection against deleterious mutations.

Large values of U also imply that most deleterious mutations have very slight effects and probably are not selected against in civilized human populations. The genomic deleterious mutation rate is the most important parameter in population genetics and its experimental determination deserves much more attention than it has attracted heretofore.

PL7 Evolutionary explanations of phenotypic design

Stearns, S.C.
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For many years, the central elements of evolutionary theory were genetic. However, some of the most exciting modern developments in evolutionary biology deal directly with phenotypes, which form the subject matter of evolutionary and behavioral ecology. This contrast raises several questions that still deserve attention, including (1) What role do phenotypes play in the general theory of evolution? (2) How do genes connect to phenotypes? (3) What distinguishes genetic from phenotypic evolution? The anwsers to these questions involve the role of the phenotype in natural selection, the plastic responses of phenotypes to heterogeneous environments, the quantitative genetic model of the organism, the organism conceived of as a tradeoff structure, and the origin and consequences of constraints on phenotypic evolution. These themes will be illustrated with examples drawn primarily, but not exclusively, from life history evolution, and organized to anwser the more general question: What constitutes a satisfactory evolutionary explanation of phenotypes?

PL8 EVOLUTIONARY THEORY AND PROCESSES OF ACTIVE SPECIATION AND ADAPTIVE RADIATION IN SUBTERRANEAN MOLE RATS, *Spalax ehrenbergi* SUPERSPECIES IN ISRAEL

EVIATAR NEVO

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The inter- and multidisciplinary evolutionary model of active ecological speciation and climatic adaptive radiation of blind subterranean mole rats of the Spalax ehrenbergi superspecies (Spalacidae, Rodentia) in Israel, is overviewed in the light of the synthetic theory of Darwinian evolution, and its current challenges.

The *S. ehrenbergi* superspecies in Israel comprise four chromosomal species (2n=52, 54, 58 and 60) displaying progressive stages of late chromosomal speciation. Their adaptive radiation in Israel from Early Pleistocene to Recent times is closely associated with the mediterranean and steppic climates, subterraneity, and an environmental gradient of increasing aridity stress, hence with distinct climatic diversity: 2n=52 (cool-humid); 2n=54 (cool-semidry); 2n=58 (warm-humid) and 2n=60 (warm-dry).

The ecological speciational trend of *S. ehrenbergi* into increasingly arid environments initiated apparently peripatrically in small peripheral isolates by rapid random fixation of Robertsonian chromosomal mutations. This emergence was followed by gradual genic accumulation of positive assortative mating based on premating ethological species-specific isolating mechanisms involving olfaction, vocalization, seismic (vibrational), aggression and mating (via bacular variation) cues. The speciational trend budded off a sequence of daughter species with increasingly higher diploid chromosome numbers (2n) towards the desert, each species displaying a syndrome of adaptations at all organizational levels. These integrate genotypic-molecular (DNA, nuclear and mitochondrial, as well as proteins), and phenotypic- organismal (morphological, physiological and behavioural) levels as multiple adaptive strategies to the following major challenges: (i) Temporal (seasonal annual division into dry summer and wet winter); (ii) Local (subterranean ecotope with its stresses of low productivity, energetics, hypoxic-hypercapnic burrow atmosphere, and total darkness), and (iii) Regional (gradient of increasing aridity and predictability southwards; 2n=52->58->60; and eastwards: 2n=52->54).

S. ehrenbergi represents a pluralistic example where chromosomal and genic mutations, genetic drift, migration, isolation, and natural selection all interact in producing new adaptive species to environmental diverse challenges. The evolution of *S.ehrenbergi* is explicable by the Synthetic Theory of Evolution, and defies many of its current challenges.

SYMPOSIA

Sy1	Paleontological approaches to evolution org.: A. Hoffman
Sy2	The consequences of molecular evolution for organismal evolution org.: G.A. Dover
Sy3	Toward a modern definition of recapitulation org.: T.J. Horder
Sy4	Complicating factors in the analysis of selection org.: G. de Jong
Sy5	Coevolution org.: V. Loeschcke
Sy6	Evolution in metapopulations org.: P-H. Gouyon

Sy1.1

BIOGEOGRAPHY AND MACROEVOLUTION IN MARINE BIVALVE MOLLUSCS: LEARNING FROM THE RECENT

Karl W. Flessa[1] and David Jablonski[2]

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We are compiling information on distribution of Recent genera of marine bivalve molluscs from throughout the world. Species-level data are gathered from the primary literature and generic nomenclature is updated and corrected to a uniform standard. We record only genera occurring in waters shallower than 200 meters.

To date, we have compiled 115 standardized faunal lists for genera in seven superfamilies: Arcacea, Limopsacea, Mytilacea, Pteriacea, Cardiacea, Carditacea and Veneracea. These superfamilies contain approximately thirty percent of the global marine bivalve fauna. The 115 faunal lists include localities in high and low latitudes, oceanic islands, marginal seas, and continental shelves.

These data permit an actualistic approach to the biogeography and taxonomic structure of extinction and survival. We simulated extinctions by eliminating whole regions, oceans or latitudinal belts from our global generic database.

Extinctions equal in magnitude to those of the Permo-Triassic, Late Triassic, or Cretaceous-Tertiary can be produced only when the geographic scope of an extinction is very broad. If the Recent is a good model, mass extinctions must affect both high and low latitudes, ocean basins as large as the Indo-Pacific, or all continental shelf habitats.

Despite model scenarios that cause extinctions of sixty percent of the fauna, geographically restricted extinctions do not produce significant changes in the relative proportion of taxa in surviving biotas.

Our actualistic model suggests that generic extinctions of at least eight-five percent are required before the taxonomic composition of the surviving biota is affected.

Sy1.2 Quantitative-genetic analysis of species-level evolution

Richard A. Reyment
Uppsala

Recently, advances in the theoretical development of Quantitative Genetics have made it possible to apply reasonable methods to the analysis of evolutionary sequences (Lande's models). Originally introduced at the univariate level, the theory is now available in multivariate generalizations. Lande's model was made in terms of truncation selection, but other models of selection can be advantageously considered. The multivariate models turn out to be direct applications of multivariate statistical procedures for multivariate Gaussian variables. Hence, the entire corpus of theory and significance testing is available. Care must be exercised in palaeontological applications of quantitative genetics owing to the problem of obtaining reasonably accurate samples. Size (distance)-measures, those commonly recorded in morphometrical work, can be very deceptive in that any trending sequence of events can have arisen by random walk. An essential accessory for such data is the availability of concomitant variables of some kind. Data on fossil invertebrates are used to support the theory.

Sy1.3 QUANTITATIVE GENETICS OF SPECIATION IN THE FOSSIL RECORD

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&National Museum of Natural History, Smithsonian Institution, Washington, D. C., U. S. A.

The theory of punctuated equilibria relates speciation to random processes such as mutation and genetic drift decoupled from forces of natural selection acting within species. Patterns of phenotypic evolution in the Neogene cheilostome bryozoan Metrarabdotus suggest that new species arise suddenly and persist for millions of years with little or no change, as predicted by punctuated equilibria theory. The possible roles of selection and random change in producing punctuated evolutionary patterns like those of Metrarabdotus were analyzed using methods of quantitative genetics on traits of skeletal morphology in two living species of the cheilostome Stylopoma. Calculations of the minimum mutational input and minimum selection intensity per generation required to account for the phenotypic difference between these species favor random change (mutation plus drift) over selection as the basis for their divergence on time scales consistent with stratigraphic resolution of Metrarabdotus evolution. We also used the extremely close correspondence between phenotypic and genotypic covariance of Stylopoma to calibrate calculations of the probabilities of selection versus random genetic change for speciation of fossil Metrarabdotus. Once again random genetic change was implicated. These results offer strong support for the punctuated equilibria model in cheilostomes, whose life histories make the formation of isolated founder populations likely.

Sy2.1

NATURAL SELECTION AND MOLECULAR DRIVE IN THE EVOLUTION OF COMPLEX BIOLOGICAL FUNCTIONS.

Gabriel A. Dover, Department of Genetics. University of Cambridge. Downing Street. Cambridge. CB2 3EH. U.K. *

I have a strong suspicion (but I could be wrong) that most participants of the ESEB Congress hold the view that molecules are for molecular biologists, and organisms are for real biologists; and that, whilst molecular evolution is undoubtedly occurring, at best it is simply a lower level phenomenon in the fashionable hierarchy of multiple levels of selection, and at worst it has nothing to do with the real stuff of life (evolving complex adaptations).

I will present the evidence and argue the case that there is one level of selection (the organism) and that the causes of selection at this level come from two directions: pressures to survive and reproduce in the external world, and pressures to adjust to molecularly driven changes in populations consequential on mechanisms of DNA 'turnover' in the internal world. The joint activities of natural selection and molecular drive can lead to the gradual establishment of complex biological functions which, in the absence of knowledge of the internal processes and of the genetic basis of given traits, would be traditionally defined as Darwinian adaptations.

Examples will be presented of complex phenotypes (protein translation machinery: egg shell structures) which have arisen via the coevolution of natural selection and molecular drive.

Dover, 1982 Nature 299 111; Dover, TREE 1988 3 81

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Sy2.2

MOLECULAR EVOLUTION OF THE CLOCK GENE *PERIOD* IN *DROSOPHILA*

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The *period* (*per*) gene in *Drosophila melanogaster* determine biological rhythmicity for several temporally programmed phenotypes. Mutations of this locus shorten, lengthen and obliterate circadian (24h) rhythms, ultradian (60s) lovesong oscillation and infradian (10 day) developmental cycles. The *per* gene has been cloned and sequenced in a number of *Drosophila* species, and shows regions of conservation interspersed with regions of high variability. One of these variable regions falls in the middle of the gene and encodes a minisatellite which gives rise to repetitive Threonine-Glycine (Thr-Gly) residues. The Thr-Gly and immediately surrounding area is important for determining the species-specificity of male lovesong cycles and also in providing thermostability for the circadian phenotype. The Thr-Gly tract can be large, virtually non-existent, or replaced by another more complex repetitive amino acid motif within the *Drosophila* and *Sophophora* sub-genus. Within *D.melanogaster*, the Thr-Gly encoding minisatellite shows length variation. Remarkably this length variation reveals a clinal pattern within Europe, with shorter length variants predominating in the south. Consequently natural selection may be playing a role in maintaining this variability. The implications of our findings with respect to function, and evolution of the biological clock are discussed.

Sy2.3 EVOLUTIONARY DIVERGENCE OF SEGMENTATION GENES

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Much is known about the formation of the segment pattern in *Drosophila*, due to the systematic analysis of the genes involved. We are now isolating a number of homologs of the key genes from a range of species in order to understand both, the evolutionary divergence of the genes at the DNA-level, but also their potential role in pattern formation in other species. Sequence comparisons reveal that the genes show usually some very highly conserved domains, which can be implicated with particular functions, such as DNA-binding. Other parts of the coding regions, in particular those showing high levels of cryptic simplicity, are much more divergent. The expression pattern in other species reveals frequently conserved and divergent aspects, indicating a differential rate for the evolution of regulatory elements.

We have complemented the between species comparison by an within species comparison of the gap gene *hunchback* in *Drosophila melanogaster*. The gene was cloned and sequenced from 10 wild type populations. The level of polymorphisms, both in coding and non-coding regions, was found to be very low, about ten times lower than that seen for the ADH gene in *Drosophila melanogaster*. The evolutionary implications of this surprising finding will be discussed.

Sy2.4 ORIGIN AND EVOLUTION OF RUMINANT STOMACH LYSOZYME GENES.

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Two groups of mammals, the leaf-eating monkeys and the ruminants, have recruited the anti-bacterial enzyme lysozyme as a digestive enzyme. Lysozyme breaks open the cell walls of bacteria after they have been transferred from the fermentive foregut to the true stomach of these herbivores. In ruminants the origin of the new biological function is associated with amplification of the lysozyme gene and specialization of expression patterns. Within the family of approximately 10 genes encoding lysozyme in modern ruminants, some retain the ancestral defence role, while other copies adapted to the new digestive role. Multiple amino acid substitutions were necessary for the evolution of the well adapted stomach lysozyme. With the extensive remodeling of lysozyme several coupled amino acid substitutions were probably required. Several molecular events have assisted in the adaptive evolution of stomach lysozyme. Concerted evolution has acted within the gene family upon each exon independently. The concerted evolution thus shuffles exons among genes, which may aid in coupled amino acid substitutions.

Sy2.5 MODULAR AND CONVERGENT EVOLUTION IN SIGNAL PEPTIDES, PROTEINS IN VIRUSES AND MEMBRANES OF GRAM-NEGATIVE BACTERIA

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The general dilemma of convergent versus divergent evolution complicated by modular generation of recombinant structures has been studied on three major groups.

Signal peptides, segments targeting protein transport across membranes, comprise the most abundant protein sequence pattern. Sequences recoded in an 11-letter (instead of 20) amino acid alphabet clearly demonstrate that the majority of the high variation in signal peptides is only oscillation around a few marked patterns. However, it is not necessary to suppose the oligophyletic origin of these patterns, as it was shown by Monte Carlo simulations using amino acid group replacement probabilities computed from closely related signal peptides, a strong convergence is also possible.

Certain proteins of *viruses and of membranes in Gram-negative bacteria* comprise two well-defined groups on the basis of structural similarity due to specific patterns in viral transcriptases, nuclear location signals, bacterial transmembrane, nucleotide binding, gene regulation patterns, etc. Due to the limited size of the genomes and the extremely high intensity of genetic recombination events (insertion into the host genome, plasmids, etc.), modular evolution is more frequent in these taxa than in eukaryotes. The exchange of short gene pieces might be conceived as a vehicle for convergence. An analysis of evolutionary canalization is also presented.

Sy3 Towards a modern definition of recapitulation

Tim J. Horder
Oxford University

In any approach to characterising the relationship between evolution and embryonic development, no concept can be more central than that of recapitulation. This symposium seeks to review the various uses, and abuses, to which this concept has been put, and to redefine it in a way that locates it realistically in relation to current understanding of the phenomena and mechanisms of evolution and development.

The simplest version of the concept -that the phylogenetic sequence is fully and explicitely repeated in individual ontogenetic sequences - is easily disposed of: (i) by heterochronic changes (i.e. paedomorphosis shows precisely the opposite type of relation in that ancestral early developmental stages replace later stages in adult descendents); (ii) even more inconsistent are frequent, rapid phylogenetic innovations (such as specialisations of the egg and the adnexae) prior to stages when the first definitive (Bauplan) embryonic rudiments are established; (iii) genetics and molecular biology now provide the surest grounds for requiring a reformulation of the original Haeckelian concept (DNA - and therefore embryos and adult forms -evolves by loss and substitution, as well as by accumulation of new elements in addition to old as required by literal recapitulation).

It will be argued however, that in a suitably restated form, the concept retains an essential validity and indeed pinpoints a fundamental nature of evolution. The characteristic causal chain of dependent interactions whereby adult forms are hierarchically built up during embriogenesis means, in evolutionary terms, that new characters are most likely to acquired terminally while earlier developmental features will become increasingly stabilised since, without stabilisation of early causal events, later characters could not be expressed. This feature of embryos is merely one manifestation of an inevitable and general feature of the evolutionary process; complexity is built up by gradual acquisition of new characters according to their compatibility with the sum of preexisting characters, some of which themselves become increasingly indispensable. This applies to all characters at all levels. Hence different DNA sequences show variable rates of evolutionary change and degrees of antiquity.

Molecular structure, embryogenesis and adult anatomy are esssentially three ways of displaying the same accumulations of characters uniquely defining a species. But, in being sequential, development has particular evolutionary relevance; the above discribed logic means that early (stabilised) events will dictate overall adult structural organisation and that these "Bauplan" features will be those most closely shared by species of common ancestry. The rules of embryological sequencing can, then, provide taxonomy witha direct, rigorous and rational basis for selecting and weighting combinations of adult characters. These mechanism-based rules will set major limits on, and predict, possible evolutionary change in types and sets of characters; the continuity of all morphogenetic sequences in particular implies continuity of evolutionary transitions and could bridge taxonomic gaps.

No characters are immutable or absolute markers of evolutionary time and developmental stages will never be complete, morphologically identical repetitions of ancestral adult forms or sequences of ancestral embryologies. Evolutionary transitions need only be measured relative to preexisting stages specific to each case. Transitions between between embriological sequences represent the most comprehensive, explicit and direct available measures of evolutionary change. When interpreted relative to phylogenetic and morphogenetic context (using all available sources of data), there is no reason to doubt that embryological sequences repeat evolutionary changes to varying degrees; e.g. that the egg repeats a protozoan stage; the Bauplan of notochordal stages of vertebrates approximates a pre-vertebrate ancestral adult form; the limb-bud reflects fish fin organisation etc.

Individual contributions to this symposium will examine specific examples illustrating the phylogenetic implications of developmental phenomena, and their limits. Key levels are selected from across the phylogenetic scale, including; the limits imposed on evolution by molecular, genetic and cellular organisation; unicellular to metazoan transitions; inferences from rules of vertebrate ontogeny in taxonomy.

Sy4.1

Responses and correlated responses to articial selection on size at eclosion and its plasticity in rich and poor food environments in *Drosophila melanogaster*

S.C. Stearns, E. Hillesheim
University of Basel, Switzerland

To investigate the potential response to natural selection of reaction norms for age and size at maturity, fresh body weight at eclosion was mass selected under rich and poor larval food conditions in *Drosophila melanogaster*. The sensitivity of dry weight eclosion to the difference between rich and poor larval food was selected using differences in sensitivity among families. For both experiments, the correlated response to selection of age at eclosion was examined. The flies were derived from wild populations and had been mass cultured in the lab for more than six months before the experiments started. These flies responded to selection on body weight upwards and downwards on both rich and poor larval food. Selection on increased or decreased sensitivity of body weight was also successful in at least one direction. Sensitivity was reduced by selection upwards in a poor environment and downwards in a rich environment.

Flies that had been successfully selected on rich and poor larval medium for increased and decreased fresh weight at eclosion were then tested for correlated responses in longevity, fertility, and hatchability. Larger flies laid more eggs early in life and lived shorter lives than smaller flies, which not only lived longer but also laid more eggs later in life. This supports the notion of mortality cost of reproduction in *Drosophila*. The total number of eggs laid per lifetime did not differ between the two groups. The number of offsprings hatched followed a similar but more complicated pattern, with some reversals. The percentage of offsprings hatched started at normal levels (about 50% of eggs laid), then declined rapidly in large flies. In small flies, it started at about the same level, but declined much less rapidly. Small flies laid eggs with higher hatchability than large flies and the difference in hatchability of eggs laid by small and large flies increased as the mothers aged. Virgin females lived about twice as long as mated females.

Sy4.2 DECOUPLING PHENOTYPIC SELECTION AND GENETIC RESPONSE.

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Selection is usually described as a result of (i) phenotypic variation, (ii) associated differences in fitness, and (iii) inheritance. In standard quantitative genetics notation this becomes $R=h^2S$. This standard model allows decoupling of within-generation selection on phenotypic traits (without doing genetics) and estimating heritabilities (without looking at fitness differences). Recently published data suggest however that this approach is not always valid; for instance, the selection response was absent or in the opposite direction as expected from selective forces and heritabilities.

A second approach to selection is due to Fisher, who saw selection as a result of a genetic correlation between a trait and fitness, without explicit reference to the phenotypic level. In quantitative genetic notation this is written as $R=Cov_g(z,w)$. It is based on a more direct derivation, as it counts the representation of genes affecting the trait in the gene pool of the next generation.

Although these separate descriptions are well-known, a unifying theory from which special cases can be derived appears to be missing. This paper deals with theoretical aspects and practical applications of such a theory, with four main topics:

(1) **A general, unified analysis.**
It can be shown that the 'realized heritability' for a trait (R/S) can be positive or negative. It is equal to the narrow sense heritability (V_a/V_p) only under conditions common to artificial selection, but perhaps uncommon to natural selection.

(2) **Exceptions that invalidate the standard approach.**
Standard theory assumes that genetic and environmental factors affecting the external phenotype are interchangeable with respect to fitness. It will be shown how genetic trade-offs and environmental correlations between trait and fitness may affect results.

(3) **Tests to estimate different expectations for selection response.**
Genetic covariances between trait and fitness can be derived from different kinds of data (parent-offspring regression, sib-analysis). Examples will be given.

(4) **The relationship with multivariate selection models.**
The standard approach treats fitness as an external entity rather than as a trait composed of several components. Consequences of incorporating fitness(-components) are discussed.

Sy4.3 DISCOVERING THE CAUSES AND OBJECTS OF SELECTION: STATISTICAL AND PHILOSOPHICAL METHODS AND INTERPRETATIONS

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Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853-2701, USA (present address)

Natural selection on phenotypes, and ultimately on genotypes and alleles, is the main process resulting in adaptation. Understanding the presence, form, causes and objects of selection requires its measurement in natural populations, and analyzing the relation of phenotypic selection to genetic and phenotypic selection response. Lande, Arnold, and Wade have proposed that multiple regression analysis be used to measure phenotypic selection, and that their quantitative-genetic approach may be used in conjunction with the measurement of genetic variances and covariances to predict phenotypic evolution. More recently, Wade, Kalisz, Mitchell-Olds and Shaw have emphasized the importance of conducting experiments designed to infer the environmental causes of selection. The usefulness of a multiple regression and quantitative genetic framework for measuring selection and predicting selection response depends upon whether or not its assumptions, especially those concerning character independence, constant genetic variance-covariance matrices, and additive, polygenic inheritance, are satisfied. The universality of epistasis, pleiotropy and character interaction indicate that such is often not the case. Moreover, the uniqueness and consequent difficulty in replicating or mimicking selective events suggests that the experimental approach to analyzing selection causes and objects has serious limitations.

I describe an alternative philosophy and methodology for measuring and analyzing phenotypic selection and its relation to genetics. The approach is based on the redefinition of phenotypic characters, the use of Sewall Wright's method of path analysis to infer the causes and objects of selection, and the determination of genetic architecture to understand how selection may lead to phenotypic change and adaptation.

Sy4.4

PHENOTYPIC SELECTION ON A DEVELOPMENTAL CHARACTER

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Classical models of selection on quantitative characters assume or impose additivity of allelic effects within and between loci. This introduces unspecified assumptions about gene action in developmental pathways. Development brings its own models of gene action, in acquisition and allocation of resources or in biochemical pathways. Developmental models easily give rise to epistasis, both through processes that translate into a multiplicative model, and through transformations, e.g., the transformation from the energy devoted to a trait to the trait itself.

Any model of development involves acquisition of resources and allocation of those resources to alternative traits. Allocation of a resource can be repeated, leading to a subdivision of the resource that can be visualized as a dichotomous tree. Despite ubiquitious trade-offs in such repeated dichotomous allocations, negative covariances between traits are not to be generally expected; especially for traits deriving from the higher branchings of an allocation tree, covariances tend to be positive. Phenotypic selection on traits that derive from such an acquisition / allocation process leads to genetic selection that is unequally divided over allocation loci and the acquisition locus. Developmental constraints in the form of allocations of the resource appear phenotypically and genetically as covariances between traits. As the phenotypic covariance between traits need not have the same sign as the genetic covariance between traits, the outcome of selection is not straightforward. Moreover, the epistatic covariances surface to play a role in selection.

Sy5.1

COEVOLUTION

Volker Loeschcke

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A genetically bases conceptual framework of coevolution is given. It includes reciprocity and specificity and separates coevolution from mere evolutionary changes or adaptive processes.

Sy5.2 "CHEATING" IN THE YUCCA-YUCCA MOTH MUTUALISM: THE ECOLOGY OF NON-POLLINATING SPECIES IN THE TEGETICULA YUCCASELLA COMPLEX.

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Yucca moths (Tegeticula, Incurvariidae) and yuccas (Yucca, Agavaceae) interact in an obligate mutualism: yuccas are dependent upon yucca moths for pollination, and yucca moth larvae feed exclusively on the seeds of the yucca. Tegeticula yuccasella is one of three recognized species of yucca moths, but it is actually a complex of host specific species. Most member of this complex exhibit typical mutualistic behaviour: pollination follows oviposition in fresh flowers. However, some members of this complex are non-mutualistic, in that they do not pollinate and they oviposit in fruit rather than flowers.

In my talk I will document (1) the existence of the non-mutualistic yucca moths, (2) their geographic and host distribution, (3) their impact on seed production in yuccas, and (4) their interactions with mutualistic yucca moths. I will also describe the occurrence of non-mutualistic behaviour by yucca moths that usually act as pollinators.

SyS.3

PARASITES AND HOST MACROEVOLUTION

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A characteristic, perhaps definitional, feature of macroevolution is shifting between adaptive peaks. In contrast to elementary landscapes of microevolution, landscapes of large-scale adaptation are likely to be all multi-peaked and at many levels. The traversing of an adaptive valley initiates rapid evolutionary change as the next higher peak is climbed. Coevolutionary side effects of this may cascade into other species that are in close ecological contact.

Sewall Wright's "Shifting Balance theory" based on drift in metapopulations of small semi-isolated demes was the first to address the peak shift problem. *Parasite coevolution* can accomplish the same results as shifting balance without special population structure, although such structure if present will still be favourable. New models of genetical micro-coevolution of sexual hosts with their parasites give special emphasis to (a) multiple parasites countered by multi-locus host resistance, and (b) truncation selection promoting both rapid change and long term conservation of variation.

In these models quasi-periodic dynamical polymorphisms seem to arise even when effects at particular loci are mild. At the microevolutionary level, besides being strongly supportative of recombinant sexuality, such systems provide a hitherto little investigated mechanism for long-term (trans-speciation) persistence of polymorphism in enzymic and other molecules that are connected with resistance.

The macroevolutionary effect of peak abasement and the general genetical seething induced by parasites is discussed with reference to two kinds of evidence: (i) general comparative evidence of the living world and the fossil record including the surprisingly small disadvantage in rate of evolution entailed by longevity and large size; and (ii) evidence from experiments in which sexual "genetic algorithms" (GAs), engineered to have parasites, are applied to solve "artificial intelligence" (AI) problems, the latter serving as models of evolutionary challenge.

Sy5.4 SYNTHETIC LIFE: CO-EVOLUTION IN DIGITAL ORGANISMS.

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Synthetic organisms have been created based on a computer metaphor of organic life in which CPU time is the "energy" resource and memory is the "material" resource. Memory is organized into informational patterns that exploit CPU time for self-replication. Mutation generates new forms, and evolution proceeds by natural selection as different genotypes compete for CPU time and memory space.

From a single rudimentary ancestral "creature", very quickly there evolve parasites, which are not able to replicate in isolation because they lack a large portion of the genome. However, these parasites search for the missing information, and if they locate it in a nearby creature, parasitize the information from the neighboring genome, thereby effecting their own replication.

In some runs, hosts evolve immunity to attack by parasites. When immune hosts appear, they often increase in frequency, devastating the parasite populations. In some runs where the community comes to be dominated by immune hosts, parasites evolve that are resistant to immunity.

Hosts sometimes evolve a response to parasites that goes beyond immunity, to actual (facultative) hyper-parasitism. The hyper-parasite deceives the parasite causing the parasite to devote its energetic resources to replication of the hyper-parastie genome. This drives the parasites to extinction.

Evolving in the absence of parasites, hyper-parasites completely dominate the community, resulting in a relatively uniform community characterize by a high degree of relationship between individuals. Under these circumstances, sociality evolves, in the form of creatures which can only replicate in aggregations.

The cooperative behavior of the social hyper-parasites makes them vulnerable to a new class of parasites. These cheaters, hyper-hyper-parasites, insert themselves between cooperating social individuals, deceiving the social creatures, causing them to replicate the genomes of the cheaters.

The only genetic change imposed on the simulator is random bit flips in the machine code of the creatures. However, it turns out that parasites are very sloppy replicators. They cause significant recombination and rearrangement of the genomes. This spontaneous sexuality is a powerful force for evolutionary change in the system.

One of the most interesting aspects of this instance of life is that the bulk of the evolution is based on adaptation to the biotic environment rather than the physical environment. It is co-evolution that drives the system.

Sy5.5 Genetic aspects of coevolution and coexistence in plants

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Interspecies competition in plants has been widely reported in controlled experiments, and equally frequently it is inferred from the species distribution patterns. The genetic factors have been studied more recently by using several populations within each competitor species and by the measures of "ecological combining ability" in terms of the performance of mixed stands. As noted by Montgomery Slatkin and Volker Loeschcke, among others, models of coevolution under competition should explicitly deal with the asymmetry in competing abilities, genetics of one or several key characters, density regulation, and the evolutionary shifts in both mean and variance. Plant competition literature will be briefly reviewed in relation to these models. Our own work on grassland genera (*Avena, Bromus*) and two vernal pool studies in *Limnanthes* and *Allocarya* will be presented to show some potential examples of character or niche displacement (for seed size and germinability, flowering time and pollination), none of which meet all of the "critical proof" requirements. Several experimental designs and findings by Pierre Jacquard and his colleagues will also be reviewed briefly. Clearly, many excellent opportunities for research are still untapped.

Sy6.1 SOURCE-SINK POPULATIONS IN HARLEQUIN ENVIRONMENTS

Jacques Blondel and Paula Dias

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Most studies on populations, both theoretical and empirical, have been carried out in homogeneous environments. However, most species inhabit heterogeneous habitats where spatial patchiness and temporal variability in resources may have important effects on life history traits. Therefore there should be a large variation according to habitat patches in the contribution of each subpopulation to the demographical and genetical structure of the population at the scale of a landscape.

Here we present a case study in which a population of Blue Tit breeds in a mosaic of good habitat patches (early and abundant food supply) and poor habitat patches (late and poor food supply). Those subpopulations which breed in the rich patches are nicely timed with the food availability whereas those which breed in the poor patches are mistimed. It is hypothezised that rich patches where birds produce many high-quality fledglings operate as a source from which birds emigrate into poor habitat patches where a few low-quality fledglings are assumed to be genetically dead. Such an hypothesis is supported by data from a control poor habitat which is isolated from any rich habitat.

Sy6.2 SELECTION IN HETEROGENEOUS ENVIRONMENTS

Graham Bell
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Species or strains of *Chlamydomonas* cultured in different conditions show a great deal of genotype-environment interaction. This suggests that variation can be maintained by genotype-genotype interaction within mixed cultures grown in a uniform environment, or by genotype-environment interaction when cultures are grown in a range of different environments.
Complementary genotype-genotype interactions were found only when genotypes were sufficiently different (species) and not when they were very similar (sibs). The results of an experiment measuring the response of genetic variance in fitness to selection in uniform and in heterogeneous environments, still running at the time of writing, will be reported at the meeting.

Sy6.3 METAPOPULATIONS: EMERGENT PROPERTIES OR UNNECESSARY COMPLICATIONS?

Chris GLIDDON(1) and Isabelle OLIVIERI(2)

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A study of the evolution of metapopulations necessitates the bringing together of population ecology and population-genetics. Levins (1970) defined a metapopulation as a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear. That is, a metapopulation is a set of local populations connected through migration. The population genetic analogy of this is the Mendelian population which describes a set of individuals connected through parenthood or mating. The similarity of these definitions is obvious, their difference relating simly to the level of the biological hierarchy to which they refer. The metapopulations of geneticists are the models of subdivided populations (e.g. island and stepping-stone models). However, one element is usually missing from the genetic models, namely extinction of local subpopulations. Even when local extinction is added, local demography is not taken into account. The ommissions of the population genetic models are matched by the ecological models failing to take account of the genetic variability of individuals and local populations, which may well have some bearing on their demography.

What is the future of combining life-history parameters for individuals and populations with their genetic basis? Charlesworth (1980) has considered age-structure in single populations but to date the age-structure of populations has not been incorporated into an evolutionary metapopulation model. We shall consider the impact of combining ecology and genetics in a metapopulation model and ask whether this merely results in unnecessary complexity or if a novel evolutionary property emerges.

Sy6.4 THE GENETIC CONSEQUENCES OF RECOLONIZATION

Richard A. NICHOLS

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The rate at which species colonize new habitats is much faster than would be expected from observations of the movement of typical individuals. Similarly the spread of strongly selected genes through a species range is much faster than would be predicted from the average dispersal distance. It would appear that in both these types of invasion are strongly affected by the rare individuals that move expectionally long distances.

In metapopulation models where an area of a species range is recolonized from geographically separate, genetically distinct local populations, the genetic consequences depend critically on the form of the dispersal. In some conditions colonization will proceed as a travelling wave, and the genes from the different origins will become arranged in abutting distributions. In other conditions the main wave of colonization is proceeded by isolated islands set up by long distance colonists and distribution of the genes will be more mixed.

The latter type of colonization may explain the unexpectedly long distance over which genetic introgression is observed in some natural populations. The transition between the two types of behaviour, and the scale over which they are important will be discussed.

WORKSHOPS

Ws1	Molecular, Paleontological, and Morphological Phylogenies in Vertebrates
Ws2	The Evolutionary Significance of Polyploidy
Ws3	Gene Amplification and Evolution
Ws4	Variability and Speciation in Parthenogenetic Organisms
Ws5	Resource - Habitat Selection, Metapopulation and Sympatric Speciation in Animals
Ws6	The Subdivision of Species
Ws7	Genetic Diversity and Microevolution
Ws8	Population Genetics in Conservation: A Re-examination of Models and Recommended Applications
Ws9	Measuring Selection in Heterogenous Environments, How to Aggregate the Data? Are the Problems Different for Spatially and for Temporally Heterogeneous Environments?
Ws10	Host-Parasite Interactions
Ws11	Caenorhabditis elegans Research and Evolution
Ws12	Adaptation in a Stochastic Environment
Ws13	Evolutionary Quantitative Genetics
Ws14	Optimal Energy Allocation
Ws15	The Transformations of Forms and Symmetries in Evolution
Ws16	Mathematical Problems of the Theory of Evolution

Ws1.A RESOLVING OLD AND RECENT NODES IN THE AVIAN TREE USING mtDNA SEQUENCES

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The power and limitations of phylogenetic resolution of mtDNA sequence analysis are exemplified and discussed.

To examine the resolution of old nodes a study of 924 base pair mtDNA *cytochrome b* was performed (with Scott Edwards and Allan Wilson). 13 species representing major groups of Passeriforme birds were included in the analysis. A woodpecker was used as outgroup. The fundamental split, between oscine and suboscine birds, based on the morphology of the voice organ, the syrinx, was reproduced utilizing conservative substitutions at 1st and 2nd codon position. The mitochondrial tree is in broad concordance with the morphological and the DNA/DNA hybridization ones.

Clear demarcation of species can be difficult because morphology provides few characters which are often hampered by subjective characterization and by convergence. To illustrate the potential of DNA sequences at this level of recent nodes, data will be presented from the morphologically indistinguishable, but genetically clearly differentiated Tapaculos (*Scytalopus*) and morphologically different, but genetically nearly identical Canasteros (*Asthenes*).

These and other results will be generalized by relating them to time (years since common ancestor) and taxonomic level. The general pattern emerging is that a period of relatively "free" evolution is followed by a period with beginning multiple substitutions at the same position leading to more and more saturation. There is a hierachy of substitution ratios securing information over a wide very time scale. Therefore according to the kind of questions we pose, we can choose to sequence more or less variable DNA. Furthermore we can take advantage in the phylogenetic analysis of our knowledge of different molecular constraints.

Ws1.B

MAMMALIAN PHYLOGENY AND CONFLICTS BETWEEN MORPHOLOGICAL AND MOLECULAR DATA : A DISCUSSION BASED ON SEVERAL EXAMPLES.

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The most important source of conflicts between molecular and morphological phylogenies comes from the diversity of the methodologies used to interpret the data. When analyzed through phenetic or cladistic method for instance, the same data can lead to different groupings. Moreover the large set of available phenetic methods does not necessarily produce a congruent tree.

By comparing morphological and molecular phylogenies both obtained by cladistic approach, uncongruence give informations on the nature, the place and the amount of homoplasy. On the contrary, the comparison between phenetic reconstructions based on molecular and morphological data cannot provide answers to any phylogenetic questions unless *a priori* assumptions are made on the evolutionary process. Such assumptions remain to be justified by using external data.

An other problem arises because morphological data can include informations from extant as well as from extinct data, while molecular data are from extant data only. In such a case, the comparison between trees having different set of taxa poses theoretical problems solved for the moment only by empirical solutions.

Different methods have been proposed to estimate the congruence between different phylogenies obtained from different set of individual molecular or morphological characters : i) by pooling all of them, possibly with different weightings, and then searching the most parsimonious tree, ii) by drawing a consensus tree according to different procedures, iii) by looking for the tree which is simultaneously present among the best parsimonious trees obtained from the different sources of data analyzed separately ; iv) by searching for the homoplasies produced when the most parsimonious tree for a given set of data is used to reconstruct a tree from an other set of data.

Some phylogenies inferred from molecular and morphological data taken among Mammals are given as an example.

Ws1.C STUDIES ON THE PHYLOGENETIC POSITION OF THE CTENODACTYLIDAE (RODENTIA)

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More than half of all mammalian species belong to the order of the rodents. Although many phylogenetic relationships among rodents have been established beyond doubt, others are not yet established. The phylogenetic position of the Ctenodactylidae (gundis) was discussed in several contributions to a symposium in Paris in 1984 (Luckett and Hartenberger 1985). This is a small rodent family with only four species living in the border regions of the Sahara Desert in Africa. This taxon has been grouped either with the hystricognathous rodents or as a separate branch, as a very early offshoot from the rodent stem. With additional molecular data, it may be possible to shed more light on this controversy and to learn more about the origin of the rodents.

No molecular evidence is yet available on the phylogenetic position of the Ctenodactylidae. Therefore, several tissues and blood of gundis were collected, and a number of proteins were isolated and investigated.

Gundi myoglobin was isolated and its amino acid sequence was determined. This sequence was compared with the 73 other known vertebrate myoglobin amino acid sequences by using computer procedures, described by Czelusniak et al. (1990), that search for the tree or set of trees with shortest nucleotide substitution length. In addition, the amino acid sequences of the alpha and beta hemoglobin chains of gundi were determined (Beintema et al. 1990) and compared with the alpha and beta hemoglobin sequences from 134 vertebrate species. The myoglobin data fail to represent rodents as a monophyletic order.However, when tandemly combined alpha and beta sequences were used, a monophyletic tree of the rodents is obtained, with the first intrarodent divergence separating gundi from all the other rodents. Joining gundi with the hystricognath guinea pig results in a tree with two more substitutions. This is a low number compared with the branch lengths connecting gundi and guinea pig to the rest of the rodent stem.

Studies of other proteins provide little additional evidence about the phylogenetic positions of the Ctenodactylidae. The molecular data confirm that both the Ctenodactylidae and the hystricognathous rodents are early offshoots in the order of the rodents, but - as in classical phylogeny - it is impossible to decide whether they share a common ancestor or are located on separate branches.

Beintema, J.J., K. Rodewald & G. Braunitzer. 1990. Biol. Chem. Hoppe-Seyler 371:1089-1099.

Luckett, W.P. & J.L. Hartenberger, eds. 1985. Evolutionary relationships among rodents: a multidisciplinary analysis. Plenum, New York.

Czelusniak, J., M. Goodman, N.D. Moncrief & S.M. Kehoe. 1990. Methods Enzymol. 183:601-615.

Ws1.D

Workshop on Molecular, Paleontological and Morphological Phylogenies in Vertebrates, Third Congress of European Society for Evolutionary Biology, Debrecen, Hungary, 1991

ORIGIN OF EUROPEAN RABBITS

Comparison of mtDNA diversity with paleontological data

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Differentiation of the genus *Oryctolagus* is estimated, from the first recognizable *Oryctolagus* partial fossils, 6 - 6,5 Million years (MY) old. *Oryctolagus cuniculus*, the only living species within this genus, is thought to have speciated in Spain in early Pleistocene but the origin of present populations are still subject to controversy.

We characterized mitochondrial (mtDNA) molecules extracted individually from 163 European wild rabbits (*O. cuniculus*). Taking into account restriction site polymorphisms we defined 22 different mitochondrial types which can be organized into two quite divergent sub-groups (we willl further refer as lineages A and B). Regarding the lineage they belong to, wild rabbit populations sampled in this study have a well defined geographical distribution over Western Europe: lineage A is found in Southern Spain and lineage B over Northern Spain, France and Tunisia. From nucleotide divergence between A and B (4%) we can infer these two lineages are derived from a common ancestor some 2 MY years ago. At that time, according to paleontological data two species coexisted: one *O. lacosti* had settled over Spain and Southern France and the second *O. laynensis* was found only in Spain. Present rabbits are believed to have speciated from *O. laynensis* 0,7-0,9 MY ago, this means that speciation should have occured in populations with a mtDNA diversity high enough to insure the coexistence of rather divergent molecules. Later on spacial isolation, following an event stilll to be determined, was probably at the origin of the geographical separation of the two lineages. Present mtDNA diversity of each lineage let us suggest that separation must have occurred around 500 000 years ago. The organization of the diversity within each lineage allows to confirm that Southern Spain was a refugee for rabbits carrying lineage A and leads to the hypothesis that Northern Spain, instead of Southern France as usually proposed, was the place for the other lineage (B). Morphometry and cranial discrete character analysis are in progress, they will provide additional arguments for such an hypothesis. Reexamination of fossils, especially in Northern and Central Spain as well as in Southern France, is needed in order to know more precisely the locations of *O. cuniculus* during early and middle Pleistocene.

Ws1.E (Abstract of invited paper for Wokshop #1)

EYE LENS PROTEIN SEQUENCES AND THE PHYLOGENY OF MAMMALIAN ORDERS.

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Analysis of amino acid sequences of the eye lens protein αA-crystallin has previously provided relevant information concerning certain problems in mammalian phylogeny. Most interesting has been the evidence that Tubulidentata form a monophyletic group with the paenungulates Sirenia, Hyracoidea and Proboscidea. αA sequences also provided strong evidence for the monophyletic origin of the Pinnipeda, and for the monophyly of the carnivore families Mustelidae and Procyonidae. They supported in addition the grouping of _Tarsius_ with the Anthropoidea. Additional αA sequences have now been analyzed in order to approach some other disputed mammalian affinities, as well as to corroborate the reliability of αA sequences in phylogenetic reconstructions.

Walrus (_Odobenus rosmarinus_) αA shared with seal and sea lion, as expected, the 3 amino acid replacements which are characteristic for pinnipeds. The beluga (_Delphinapterus leucas_) sequence was identical to that of the earlier studied porpoise. To study the relationship between the Mega- and Microchiroptera we compared the αA sequence of _Pteropus vampyrus_ with the previously determined sequence of _Artibeus jamaicensis_. No synapomorphies were found, nor does either sequence share any convincing replacements with αA from other mammalian orders, making the results inconclusive as to the mono- or biphyletic origin of the Chiroptera.

In contrast, the αA sequence of the elephant shrew _Elephantulus rufescens_ (analyzed by Dr. G.J. Wistow, NIH, and by ourselves) revealed a very surprising pattern. It contains a combination of 4 amino acid replacements which has until now only been found, among the 17 investigated mammalian orders, in the paenungulates. It will be discussed how reliable and significant these shared replacements are as indicators of a monophyletic origin of elephant shrews and paenungulates. Although a relationship of these taxa has never been considered, it should be noted that these specific orders are all of indigenous African origin.

References: De Jong & Goodman (1982) Z.Säugetierk. 47:257; De Jong et al. (1981) Nature 292:538; De Jong (1986) Mol.Biol.Evol. 3:276; De Jong & Goodman (1988) J.Human Evol. 17:575; Wistow et al. (1991) in: Mammalian Phylogeny (Eds. Szalay, Novacek & McKenna) Springer, New York.

Ws1.F MOLECULAR AND MORPHOLOGICAL PHYLOGENIES IN THE GENUS SALAMANDRA

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Until recently, two species were recognized in the genus Salamandra: S.salamandra and S.atra; the former, ovoviviparous, large sized and with a yellow-black colour pattern, was generally considered as ancestral-like; while S.atra, viviparous, smaller sized and fully black, was considered as the derivative one. The picture changed completely when a third species: S.lanzai, was detected in northwestern Italy (Nascetti et al., 1988). This species, formerly included within S.atra, is viviparous, fully black, but larger than S.atra. Nei's genetic distance values, calculated on 34 loci coding for enzymes and other proteins, were found to be: 0.72 between S.atra and S.lanzai; 0.87 between S.salamandra and S.lanzai; 0.66 between S.salamandra and S.atra. Moreover, S.lanzai has been shown to be relatively close to S.corsica (D=0.51),an ovoviviparous, large and yellow-black salamander, often considered as a subspecies of S.salamandra. These data indicate that viviparous reproduction, small body size and black colour pattern have evolved independently in the genus Salamandra, as adaptations to habitat and altitude. This hypothesis is further supported by: 1) the subspecies S.atra aurorae, living in a woody plateau at 1500 m (altopiano di Asiago) and genetically strictly related to S.atra atra (D=0.14), which is viviparous, small sized, but pale yellow-black; 2) the spanish subspecies S.salamandra bejarae and S. salamandra almanzoris: the former lives in a woody habitat at about 1500 m, and is S.salamandra like for the above mentioned characters; the latter,genetically fairly identical to S.s.bejarae (D=0.002), lives near a lake in a rocky habitat at about 2000 m, is ovoviviparous, small sized and almost completely black.

The comparison of the molecular and morphological phylogenies in the genus Salamandra shows different pictures: this is owing to the fact that at the morphological level taxonomy was built up on characters (such as mode of reproduction, body size and colour pattern) under strong selective pressures, leading to a phylogeny not consistent with evolutionary events. On the contrary, the molecular phylogeny, based on 34 gene loci under generally low selective pressures, agrees much better with the evolutionary history of this genus.

Ws2.A POLYPLOIDY IN THE 80'S : A REVIEW OF WHAT WE HAVE LEARNT IN THE LAST 10 YEARS

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The widespread occurrence of polyploidy in both plants and animals (except birds and mammals) attests to its evolutionary success. However, this is highly variable and is determined by a complex interaction of biological and environmental factors. The ultimate objectives of research into the evolutionary significance of polyploidy has thus been to focus on the need to attain a better understanding of the importance of such factors in relation to the adaptive value and cost of polyploidy. This was the basis for research in the 70's (see the extensive synthesis published in 1980 "Polyploidy, Biological Relevance", Lewis Ed.). How, then, has research advanced our knowledge of the evolutionary significance of polyploidy? During the last decade, research has been increasingly undertaken using modern experimental techniques such as electrophoresis, flow cytometry, whole plant physiological methods and other techniques of molecular biology. These techniques have widely expanded our understanding of the mechanisms of polyploidization (2n gamete production) and of the ecological relations within polyploid complexes. In addition, theoretical models have been developed which more closely simulate natural situations. As a result, ideas are changing and evolutionary research has widened, involving, most often, pluridisciplinary studies. Contacts among scientists who use widely varying approaches to the study of polyploidy are now necessary to facilitate the development of the general concepts arising from the extensive base of theoretical and experimental studies of the evolutionary significance of polyploidy.

Ws2.B

THEORETICAL AND EMPIRICAL CONSIDERATIONS OF POLYPLOID AND DIPLOID COEXISTENCE: THE EXAMPLE OF *ANTHOXANTHUM ALPINUM*

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A contact zone between diploid *Anthoxanthum alpinum* Löve and Löve (Poaceae) and its autotetraploid was investigated in order to determine the level of hybridization, the factors allowing the maintenance of parapatry, and the evolution of the limit of the taxa.

Natural triploids were discovered at the limit of the taxa. In some locations, the limit was located on the ridge of the mountain and in others, both cytotypes grew on the same versant. Hybrids occured exclusively when cytotypes grew on the same versant. Analysis of caryopses from nature showed triploids in the offspring of both diploids and tetraploids. In this latter case, hybridization occured mainly, but not exclusively, at the vicinity of the limit of the taxa. A tetraploid was found in a diploid progeny which prove that introgression between taxa may occur directly, probably by the fecondation of a *2n* ovule of the diploid by a pollen produced by the tetraploid.

No decrease of density, of the number of vegetative tillers, reproductive tillers, flowers and caryopses was detected for diploids and tetraploids growing close to their limit when compared with pure stands. The contact zone is thus probably not maintained by an equilibrium between dispersal and selection against hybridity (tension zone) or selection is against triploids only.

Phenological differentiation was observed in the field. When taxa grow on different versants, the tetraploid (NW) flowered later then the diploid (SE). On the contrary, the tetraploid flowered earlier then the diploid if both taxa occured on the same versant (SE). This latter difference was maintained when the plants were cultivated under uniform conditions in an experimental garden. This phenological differentiation suggests the presence of a barrier against gene flow.

Vegetation analysis showed a differentiation of the habitat of the taxa. Habitat differentiation may correlate with niche differentiation and may contribute to the maintenance of parapatry.

Computer simulations are performed in order to test the influence of dispersal, selection and niche differentiation on the evolution of the contact zone.

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Ws2.C

Genetical and ecological interactions between co-occurring cytotypes in plants

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Interactions with other cytotypes will play an important role in the evolution of new cytotypes in polyploid plant species. Often cytotype hybrids are lethal, which due to minority cytotype disadvantage will restrict the spread of a new cytotype. Although polyploidization by itself may cause some niche differentiation, competition between cytotypes in general is likely to be severe. These negative interactions may be reduced by natural selection, leading to ecological and genetical character displacement. On the other hand, gene flow between cytotypes may have a positive effect on a new cytotype by enriching the gene pool. Secondary cytotype sympatry provides an unique possibility to study these ineractions under natural conditions. Until now such sympatric populations have rarely been studied in autopolyploid plant species. Results from a population study of sympatric 2X and 4X *Plantago media* will be presented.

Ws2.D EVOLUTIONARY SUCCESS OF ALLOPOLYPLOID ANIMAL SPECIES

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Two phenomena have been considered particularly important for the evolutionary success of allopolyploid animal species: the so-called heterotic advantage, resulting from high levels of heterozygosity, and the demographic advantage, resulting from unisexual reproduction (White 1978). Heterozygotes are apparently buffered against environmental variation, and their fitness is increased by widening the range of environmental parameters that a phenotype can tolerate. An example is given by the allotetraploid self-fertilizing snail Bulinus truncatus (Bullini 1982, 1985; Nascetti and Bullini 1980; and unpublished data). Its diploid parental species belong to the B.tropicus group and inhabit Zambia and Kenya, but B. truncatus has extended its range from tropical Africa up to the Middle East, Mediterranean countries, and the Atlantic coast (northern Portugal).The spread of highly heterozygous B.truncatus to new areas took place mainly by 'hitchhiking' on migratory water birds which carry Bulinus eggs or snails on their legs. B.truncatus parental species, which show much lower levels of heterozygosity, have had the same opportunities of passive transport but have failed to widen their range northwards, being apparently poorly adapted to cooler climates.

As to the demographic advantage, all-female allopolyploid species share it with autopolyploid or diploid thelytokous ones. If males and females consume equal amounts of resources, a parthenogenetic population is potentially able to maintain twice as many females on a given area, and each of these will be able to regenerate a population in the event of local extinction or migration to new areas.

The available data suggest that various degrees of both heterotic and demographic advantages have contributed to the evolutionary success shown by most allopolyploid animals. These species frequently overcome their bisexual ancestors (e.g.,hybrid weevils), are associated with reduction of their range (e.g.,the stick-insect Bacillus lynceorum versus B. grandii),or even cause their extinction (e.g.,Clonopsis gallica). Moreover,hybrid species often colonize wide areas,unfavourable to their parental species (e.g. the snail Bulinus truncatus). The role of habitat disturbance by man in favouring both the onset of allopolyploid species and their successful spread is discussed.

Ws2.E

Abstract of paper to be presented at the workshop "Evolutionary significance of polyploidy".

TITLE: Establishment and persistence of the allopolyploid grass Spartina anglica: the importance of individual plasticity. J.D. Thompson (CNRS, Montpellier).

ABSTRACT: Spartina anglica is an allopolyploid, perennial grass which originated in the 19th century on the south coast of England, following hybridisation between the diploids S. alterniflora and S. maritima and subsequent chromosome doubling in the sterile, diploid hybrid S. x townsendii. Whereas the three diploid species have very limited distributions, the polyploid has spread from several sites of introduction to become a dominating feature of coastal salt marshes in the British Isles. In this paper I present results of experimental investigations into the basis of morphological and demographic variation whicih illustrate the importance of individual plant plasticity for the establishment and persistence of populations in the face of naturally occurring environmental variation.

Ws2.G

REPRODUCTIVE STRATEGIES RELATED TO EVOLUTIONARY MECHANISMS OF POLYPLOIDY IN A MARINE BROODING BIVALVE GENUS: *LASAEA*.

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Members of the taxonomically complex marine bivalve genus *Lasaea*, are reproductively specialized, minute, intertidal, crevice dwellers with a near cosmopolitan distribution. A major reproductive/developmental dichotomy exists within the genus. One species, *Lasaea australis*, reproduces by cross-fertilization, releases its progeny as planktotrophic larvae and is restricted in its distribution to the Western Pacific (Ó Foighil, 1988, 1989). This species probably represents the ancestral condition with a diploid complement of 2n=36, including 4 metacentric, 6 submetacentric, 3 subtelocentric and 5 telocentric chromosome pairs. All congeners studied to date are simultaneous hermaphrodites which release their young as crawl-away juveniles and form a complex grouping of nominal species and subspecies of poorly defined systematic status. Genetic studies of European and northeastern Pacific *Lasaea* populations have revealed the existence of a variety of non-hybridizing, sympatric, genetic strains capable of reproducing in isolation. There is currently no evidence for cross-fertilization in this grouping. In Northeastern Pacific *Lasaea* clones, asexual reproduction related to pseudogamy (autogynogenesis) has been observed (Ó Foighil & Thiriot-Quiévreux, 1991). Direct development in this genus is associated with evolutionary mechanisms of polyploidy. In subantarctic Kerguelen strains, chromosome complements of 100-120 were scored (Thiriot-Quiévreux et al. 1988). However, ploidy levels could not be determined. In Mediterranean *Lasaea* strains, chromosome numbers range greatly (63-340) and can be grouped in different ploidy levels of 3, 4, 5, 6 in addition to variable supernumeraries (Thiriot-Quiévreux et al. 1989). In Northeastern Pacific strains, chromosome numbers of 90-100 showed a ploidy level by 3, and variable number of supernumerary chromosomes (Ó Foighil & Thiriot-Quiévreux, 1991). The lack of concordance between the bivalents of *L.australis* and the multivalents of other *Lasaea* strains may support the inference that these polyploid biotopes may well be polyphyletic, having arisen independently in different areas.

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Ws2.H ALLOPOLYPLOIDY AND FACULTATIVE PARTHENOGENESIS AS DETERMINANTS OF CLONAL DIVERSITY IN THE FRESHWATER PULMONATE *ANCYLUS FLUVIATILIS*

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Polyploidy is known to occur in several gastropod taxa, but even in hermaphroditic groups with demonstrated capability of self-fertilization only the minority of species are polyploids. On cytogenetic grounds, all molluscan examples are believed to be allopolyploids, but corroborating evidence is still lacking for most of them. This report draws on an extensive allozyme study of Central European populations of the common stream limpet, *Ancylus fluviatilis* MÜLLER (Gastropoda: Basommatophora), a tetraploid with unknown, presumably extinct diploid progenitors.

Ancylus fluviatilis exhibits a clustered distribution of multilocus genotypes into three distinct "strains", with allelic differences at multiple loci. Most importantly, fixed heterozygosity at several loci is a common feature of all three strains, which argues decidedly for the hybrid nature of extant tetraploid lineages. Jointly, these data provide compelling evidence for polyphyletic origins of tetraploidy, involving successful hybridization events between ancestral diploids of considerable genetic differentiation.

Against this background, I have attempted to utilize allozyme markers to assess frequencies of reproductive modes in natural populations, and to evaluate their relative contributions to genotypic diversity. Outcrossing at low levels demonstrably occurs both within and among strains, which are sympatric at many sites, but self-fertilization and/or functional apomixis predominate. For two of the strains, I frequently observed unbalanced, nonsegregating heterozygous genotypes (with 3:1 allele dosage), which constitutes strong evidence for ameiotic parthenogenesis (possibly gynogenesis). This feature, like polyploidy itself, must have arisen at least twice independently. Recent laboratory breeding experiments have confirmed the field-derived prediction that asexuality in *Ancylus* is facultative. Due to allopolyploidy, sexual outcrossing *per se* does not necessarily generate new genotypes; whether or not it does depends largely on the strain-composition of any given population, and thus very likely on a complex interplay of ecological factors and historical contingencies.

Allopolyploidy is one of several mechanisms expected to severely restrict the erosion of linkage disequilibria, and to effectively "freeze" hybrid genotypes, provided that meiosis is essentially "diploidized" (no intergenomic bivalent formation). In principle, the route to polyploidy outlined for *Ancylus*, and implicitly assumed to hold for other freshwater pulmonates (e.g. *Bulinus*), does not require intermediate asexual stages, thus differing from the sequence of acquisition of a polyploid condition in most animal taxa.

Ws2.I

- Third Congress - ESEB - Debrecen, Hungary - September 1991 -
- WORKSHOP 3: The evolutionary significance of polyploidy -

POLYPLOIDY IN THREE ENTIRELY TETRAPLOID FISH PHYLA.

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Three entirely tetraploid phyla are known to have evolved in fish, in which the irreversibility of the polyploidization can be explained by their slow evolution by fonctional diploidization. In this process, some loci become inactived (silenced) by the accumulation of deleterious mutations or, in the case of genes coding for enzymes, by a mutation of the active site. It is a local return to diploidy.

The Salmonids: This family is assumed to result from autotetraploidy about 100MY ago. The loss of duplicated loci by functional diploidization has reached a rate of 50% of the enzymatic loci. Nevertheless, it is of interest to note that the number of loci has stabilized in each enzymatic system for all the species of Salmonids.

The Catostomids: This family also appears to have a tetraploid origin 50MY ago. The number and nature of functional diploidization of enzymatic loci vary from 35 to 65% for the different species. This variation has been used to establish phylogenies.

The *Barbus (sensu stricto):* Here tetraploid species have characteristics of tetraploidy very similar to those of the Catostomids, but show signs indicating continued evolution. For example, *Barbus meridionalis* has null alleles with high frequencies (up to 50%) which are thought to show functional diploidization in progress.

The recent observations on *Barbus* spp. suggest that new aspects of the evolution of the tetraploid fish phyla need consideration. Functional diploidization seems to act on particular genes which have no advantage when duplicated. The most logical evolution of a tetraploid phylum would be to reach an equilibrium pattern. The Salmonids, which are considered to be the oldest tetraploid fishes, may have reached this equilibrium. The Catostomids and the *Barbus* species can be assumed to be evolving towards this equilibrium. Hence, even fifty millions years has not been long enough for the process to stabilize.

Ws2.F MULTIPLE ORIGIN OF THE ALLOPOLYPLOID *SENECIO CAMBRENSIS* (COMPOSITAE)

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A survey of allozyme variation was conducted in populations of the newly arisen allopolyploid species *Senecio cambrensis* (Welsh Groundsel) and its two parental species *S. vulgaris* and *S. squalidus* sampled from the 3 locations in Britain where *S. cambrensis* is known to occur i.e. at Wrexham and Mochdre in Wales, and Edinburgh in Scotland. Electrophoretic variation at the Acp-1 and αEst-1 loci provided strong evidence of separate origins of *S. cambrensis* in Wales and Edinburgh. The possibility of two additional independent origins of the species in Wales was indicated by the variation pattern at the Aat-3 locus, although this variation could be explained as a result of segregation from a fixed heterozygote (representative of a single origin) following pairing between homoeologous chromosomes.

Multiple origins of an allopolyploid will combine sets of parental genes at each site of origin which have been subject to selection for local conditions. The potential for successful establishment and spread of the allopolyploid is likely therefore to be enhanced.

Ws3.A

A BIBLIOGRAPHIC DATABASE FOR THE STUDY OF THE ROLE OF DNA AND GENE AMPLIFICATIONS IN THE EVOLUTION OF ALLOMETRIC CHARACTERS

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Using mainly the ASCA service of the Library of the Hungarian Academy of Sciences and other sources as well, an electronic bibliographical database has been compiled in order to monitor the progress in the field of understanding the role of the DNA and gene amplifications in evolution of allometric traits in the case of cultivated plants.

This database comprises now about 10.000 bibliographical entries, a large collection of reprints and case studies on Pisum, Trifolium, Triticum sl., Adonis (Sect. Consiligo) and Galanthus. The field experiments have been carried out in the Laboratory of Ecological Genetics and Evolution of Crops (LEGEC).

Started from the experiments published by LAZANYI (1985) and based on our own set of data, the concept of molecular allometry has been formulated. According to this concept the molecular mechanisms of DNA amplifications are among the basic processes of the the evolution: allometric growth starts with differential growth ie. with the molecular allometry of DNA sequences, components of genes with regulatory or other fuctions. The positive and negative molecular allometry started on the level of DNA and directed by still rather insufficiently elucidated mechanisms interfers with further processes of the molecular allometry during the transcription and translation up to the final gene products identifiable as izoenzymes found in different quantity and quality in different organisms, organs and even in the same organism and organ in different ecological conditions.

The lecture reviews the state of knowledge regarding the sources of the molecular allometry, the mechanisms related with DNA amplifications, data regarding the DNA amplifications in microorganisms and cell organelles, DNA amplifications under the environmental pressures and phenomena of acquired resistance. The possible role of DNA amplifications in pathological and normal (allometric) growth is reviewd, too.

Ws3.B

GENE AMPLIFICATION AND PLANT BREEDING

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Literature data show, that the quantitative characters in cultivated plant species are controlled mostly by polygenes. By micrometer measurements we have found, that in cultivars of older cultivated species, the average chromosome volume is two-three times larger than in their wild ancestor species, i.e. the chromosomal DNA in cultivars is largely redundant.
A working hypothesis was formulated : the genesis of this redundant DNA was in a causal relationship with the selection exerted by man for an allometric growth of the useful plant organs. This redundant DNA may contain for the greater part non-coding repetitive DNA sequences, but should contain also many additional copies of the polygenes controlling the quantitative characters. It is possible, that the polygene loci in the genome of the cultivars are not saturated yet, and further gene amplifications can be efficacius.
By finding of a pure gene-duplication-inducing compound and by reiterated treatments with this compound, applied on different cultivars of crop plants, valuable results were obtained:
a) 30 to 50 % increase of the thousand-kernel-weight;
b) increase of the lysine and HMW-protein content of endosperm;
c) transformation of the shrivelled kernels into plump, vitreous ones in allotetraploid rye and triticale, by harmonizing the different polygenic systems in the genome of these hybrids.
In conclusion : the induced amplification of polygenes is becoming a new plant breeding method.

Ws4.A

POPULATION STRUCTURE DYNAMICS IN PLANTS: GENE EXCHANGE BETWEEN DIPLOID SEXUAL AND TRIPLOID ASEXUAL TARAXACUM SECTION RUDERALIA

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The majority of Ruderalia species are agamospermous triploids (2n=24) reproducing through non-pseudogamous diplosporic parthenogenesis; higher ploidy levels are rare. Extensive cytogeographical studies revealed that diploids are widely spread over large parts of central and western Europe where they generally occur in mixed stands with triploids. The diploid/triploid ratio varies among populations, occasionally pure diploid or triploid populations can be found.

Levels and distribution of genetic variation were studied in Central and West European populations of Taraxacum section Ruderalia containing differing mixtures of sexual diploid and asexual triploid plants. All sexual populations were panmictic with their variation mainly partitioned among populations. Genotypic diversity in triploid samples was very high with few clones widespread and many clones restricted to one or a few populations. In both ploidy levels there was no simple relation between genetic and geographic distance.

Sharing of all major allozyme polymorphisms, intrapopulational homogeneity in genic variation between ploidy level versus strong geographic differentiation at each ploidy level separately, simultaneous occurrence of population-unique alleles at the two ploidy levels, and a general good agreement with Hardy-Weinberg expectations in asexuals indicate an extensive amount of intrapopulational gene flow. Most likely gene exchange occurs bidirectionally by means of mechanisms such as reductional pollen meiosis in all agamospermous plants, facultative agamospermy, and unreduced gamete formation in sexuals. The high levels and organization of genotypic variation in triploids suggest that this component locally approaches an outcrossing species closely tied to the diploid component. Thus the diploid and triploid components probably form a cohesive evolutionary unit with the level at which the gene pools are shared differing by population.

Ws4.B PHYLUM ROTIFERA: PARTHENOGENESIS AND VARIABILITY.

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Phylum Rotifera consists of three classes: Seisonidea, Bdelloidea, and Monogononta. Seisonidea reproduce exclusively by bisexual means. Bdelloidea reproduce only through apomictic thelythoky, males being entirely unknown. Monogononta exhibit cyclic parthenogenesis. In this group only occasionally do parthenogenetic females give birth to haploid males through arrenothoky; such females are called mictic females. These males may mate with other mictic females which result in the production of resting eggs. These different reproductive methods can be related to the environment in which the organisms are found. For example, Seisonidea are marine, Bdelloidea are found in the waterfilms on mosses and in soils, while Monogononta are mostly planktonic.

Phenotypic variability in Monogononta is well documented, consisting of processes such as annual cyclomorphosis, latitudinal variation in size, and predator induced changes in morphology (e.g., spines, appendages). This variability has both genetic and physiological components, and is made more complex by the fact that different clones replace each other with changing abiotic factors. Further, the same genotype can express different phenotypes as a consequence of abiotic factors. However bdelloids, reproducing only by apomictic parthenogenesis, are not expected to exhibit any variation. Comparisons of isoenzymatic patterns among different clones of one species demonstrated significant variability. However, the same study also revealed phenotypic plasticity in terms of life-history patterns. Both enzymatic and life-history traits appear to be related to the environment from which the clones were isolated.

Studies on total protein patterns carried out on both monogononts and bdelloids suggest that physiological differences occur in animals of different age. However, bdelloid specimens (matched for age and controlled for maternal age) exhibit a high variability that currently cannot be explained according to our present model of bdelloids genetics.

Ws4.C ANHYDROBIOSIS: THE RESPONSE OF BDELLOID ROTIFERS AND NEMATODES

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Anhydrobiosis is a particular form of cryptobiosis, characterized by slowed metabolic activities, arrested development and reproduction. These effects are reversible and due to unavailability of environmental water. Three taxa of metazoans are capable of anhydrobiosis at any stage in their life spans: bdelloid rotifers, nematodes and tardigrades. We investigate the effects of desiccation on reproduction and survival of both bdelloid rotifers and nematodes. Two parthenogenetic species, Macrotrachela quadricornifera (Rotifera) and Panagrolaimus rigidus (Nematoda), were desiccated at 4 different ages and kept dried for 7 days. The remaining life cycle of the recovered animals was studied following the life table experimental schedule. For each cohort we ran control cohort to compare with the survival and fecundity of the studied animals. The percentage of recovery was low for rotifers and high for nematodes. The age-specific survival and fecundity of animals that recovered from drying were very similar to controls. It seems that rotifers possess some internal clock that can be interrupted at any time and will resume its program where it was broken. Nematodes have an internal clock which registers the time spent under anhydrobiosis. The cost of anhydrobiosis is mainly paid in survival by rotifers and in fecundity by nematodes.

Ws4.D

RELATIONSHIPS BETWEEN HERMAPHRODITISM AND PARTHENOGENESIS IN GASTROTRICHA

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The primitive sexual condition of the Gastrotricha, phylum of acquatic microinvertebrates that represent an early derivation in the evolution of Metazoa, is simultaneous or proterandric hermaphroditism. In the order Macrodasyida, marine and interstitial, the association of a peculiar type of internal fecondation, the general absence of copulatory organs, the complex accessory reproductive structures and the absence of vitelline cells defines an evolutionary line clearly distinct from that of similar mesopsammic groups. In the order Chaetonotida, the passage from interstitial marine habitat to epibenthic life in fresh water is followed by a remarkable simplification of the genital apparatus and by the passage from simultaneous hermaphroditism of the marine species to obligate thelytokous parthenogenesis of the far more numerous fresh-water species. These ones produce only 4 large eggs of two morphological and physiological types: one developes immediately after deposition and the other, more rare, is a resting egg. Cytological data on parthenogenesis in Gastrotrichs are lacking and the degree of ploidy and heterozygosis unknown. The lack of chromosome pairing in the parthenogenetic oocytes is considered indicative of apomictic parthenogenesis. The only observation on the expulsion of a polocyte in an oocyte of Lepidodermella squamata and the non-fusion between the products of division points to an apomictic mechanism or an automictic one with suppression of the second meiotic division. On the other hand, indications of genetic variations between populations and of intraclonal variability suggest a more complex situation. In particular, hermaphroditic individuals sporadically appear in natural parthenogenetic populations of different species, and animals reared in isolation show a long post-parthenogenetic period, where 1-2 clusters of immobile spermatozoa of various shape and simplified structure appear and coexist with primary oocytes. Fecundation has never been observed and genital pores are not evident. The synaptonemal complexes in postparthenogenetic oocytes and the normal process of spermatogenesis, notwithstanding the very low number of sperm produced (no more than 16), support the hypothesis that a period of amphimictic reproduction is indeed part of the biological cycle, as also indicted by the remarkable duration of the postparthenogenetic period. The switch from parthenogenesis and amphimictic reproduction in Chetonotid Gastrotrichs involves the biological cycle of an individual, in contrast to normal cyclical parthenogenesis in other invertebrates. Furthermore, resting eggs are parthenogenetic and the reproductive strategy thus seems different than that in groups where they represent the product of fecondation, giving rise to genetically distinct populations. Hermaphroditism as well as parthenogenesis in Gastrotrichs may be adaptative for dispersal, considering that this primitively mesopsammic phylum does not possess pelagic larvae nor vegetative means of reproduction.

Ws4.E CURRENT KNOWLEDGE ON PARTHENOGENESIS IN TARDIGRADES

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Parthenogenesis in tardigrades occurs in all fresh-water and terestrial habitats. Meiotic and ameiotic parthenogenesis is known, but only thelytoky has been observed. A multitude of cytological modalities are present, analyzed principally in eutardigrades. Additional premeiotic doubling of the chromosomes, meiotic maturation with or without crossing-over and ameiotic maturation, with regular or irregular arrangements of univalents along the equatorial plane has been identified. It is relatively frequent to find thelytokous populations that cannot be taxonomically distinguished from other amphimictic ones. Moreover, thelytoky is often associated with polyploidy, in particular triploidy. The presence of polyploidy has been shown by the chromosome number and evaluation of Feulgen-DNA content. Regarding geographic distribution, it was noted that thelytokous strains are more widespread but often also sympatric with the corresponding amphimictic strains. Nevertheless, in the same area, specimens of Ramazzottius oberhaeuseri found in lichens collected from tree trunks were only triploid ameiotic females, whereas those in the same species of lichen collected from large rocky outcrops were almost always diploid males and females, often accompanied by ameiotic polyploid females. These findings indicate that different strains can be syntopic and that passive dispersal favors thelytokous strains, which can colonize new territories with a single specimen. On the contrary, amphimictic strains cannot colonize recently formed habitats (lichens on tree trunks) but only substrates of ancient origin. Moreover, the repeated presence of two or more polyploid cytotypes when diploid males (and females) are present and the presence only of triploid females when they are absent suggests the possibility of hybridization of diploid and polyploid strains and the in loco origin of some polyploid thelytokous cytotypes.

Ws4.F PARTHENOGENESIS AND EVOLUTION IN THE CRUSTACEA

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The Class Crustacea represents a relatively diverse assemblage consisting of approximately 35,000 species, most of which inhabit the aquatic environment. Parthenogenesis has been confirmed in several Subclasses, particularly among the Branchiopoda (Orders Anostraca and Cladocera), and Ostracoda, while only a few examples are known from the Subclass Malacostraca (Order Isopoda), and one documented example from the Subclass Copepoda (Suborder Harpacticoida). The majority of cases of parthenogenesis in the Crustacea are restricted to those groups, which often inhabit intermittent bodies of water. A review of the ecology and genetics of these parthenogenetic taxa will be presented, and will be discussed within the general framework of the evolutionary significance of parthenogenesis.

Ws4.G

CYTOLOGY OF THE HYBRIDOGENETIC - PARTHENOGENETIC *BACILLUS WHITEI* (INSECTA PHASMATODEA).

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Within the genus *Bacillus*, Italian taxa have proven quite adequate for the study of a variety of reproductive modes. Actually among them bisexual species (*B. grandii* and *B. rossius*) as well as thelytokous morphs - either automictic diploid (*B. atticus*, *B. whitei*) or apomictic triploid (*B. lynceorum*) - have been reported from Sicily. The latter two, spread in Southeastern Sicily, are hybrids of known parentage, while the former only supposedly so. Furthermore, a hybrid strain reproducing by hybridogenesis (*B. rossius-grandii benazzii*) has been discovered on a coastal belt of Northwestern Sicily, where hybridogens are syntopic with their fathering males (Mantovani & Scali, 1990, Inv. Repr. & Dev., 18:185-188; Mantovani *et al.*, 1990, J. Evol. Biol., in press). Owing to this finding, also some parthenogenetic *B. whitei* demes syntopic with the parental bisexual *B. g. grandii*, have been investigated and found to reproduce even by hybridogenesis (Scali *et al.*, 1991, Frustula Entomol., 12:103-108). We therefore decided to karyologically analyze hybridogenetic females to check whether they differ from strictly parthenogenetic ones.

Actually, both share a 2n = 35 (XX) complement, clearly deriving 17 chromosomes from *B. g. grandii* and 18 from *B. rossius*, but, while in strictly parthenogenetic females the second chromosome of *rossius* derivation is a metacentric, in the hybridogenetic ones is an acrocentric of similar size. Therefore, the latter show a *rossius* set perfectly matching the nowadays karyotype (neo-*rossius*), while the former - also invariably shared by *B. lynceorum* and never found in extant *B. rossius* - appears to keep a paleo-*rossius* set; also some differences between automictic and hybridogenetic females in NOR number and location seem to support this view. It can be concluded that: strictly parthenogenetic *B. whitei* constitute an older hybrid complex, while the hybridogens a more recent one; hybridogenetic females are also exploiting different ways of reproduction (androgenesis, gynogenesis) and they appear to embody the possibility to evolve towards parthenogenesis; this final stage has been reached by the older hybrid by "learning" to segregate and re-utilize the *B. g. grandii* set already present in the hybrid egg thus restoring its F_1 constitution, instead of eliminating and replacing the entire *B. g. grandii* complement through the fertilization by host sperms at each generation; the systematic status of *B. whitei* should be reconsidered.

Ws4.H

SEXUAL AND PARTHENOGENETIC POPULATIONS OF A SNAIL

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The freshwater snail *Melanoides tuberculata* ranges from far-eastern Asia into Africa. Throughout much of its distribution it reproduces parthenogenetically. In Israel however, males have been found. This study investigates whether sex ratios of *M. tuberculata* are related to frequency of trematode infections, faunal diversity and chemistry of water.

34 populations were sampled. Seven of these contained no males, fifteen contained less than 10%, ten had 10-36%, one had 46% and one 66% males.

Male frequency is not related to trematode infection, neither to their overall frequency nor to the frequency of those parasites which could be identified specifically. These results do not support the view that sex is favoured by selection resulting from host-parasite interactions.

Male frequency is not related to habitat diversity either, as expressed by the number of mollusc genera found at a site. It is negatively related to magnesium, pottassium and chloride concentrations in the water.

Several additional findings result from the study:

Very sparse populations lack males;

The most stable, predictable habitats have lower-than average frequencies;

The two highest male frequencies are found in habitats that are highly unstable (water bodies that were dry in the last two years), densely populated and have *M. tuberculata* as the sole or overwhelmingly major genus.

Laboratory cultures were designed to examine the extent to which male frequencies are influenced by population density, temperature, and food abundance. The progeny produced in these laboratory experiments were all female.

Ws5.A GENETIC HETEROGENEITY AND HOST SPECIALIZATION IN _HYALOPTERUS_ APHIDS

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The genetic study of populations of the aphids _Hyalopterus pruni_ living sympatrically on different host plants (plum, apricot, peach, almond trees) has shown marked genetic heterogeneity, with lack of expected heterozygote classes at some loci. Three distinct gene pools (A, B, C) have been detected, characterized by alternative alleles at the loci _Est-1_, _Est-2_ and _Gpi_, exploiting different trophic niches at the primary host level. Specimens with A genotypes were collected on plum and apricot trees; B genotypes were found mainly on almond trees (the so called _amygdali_ form), but rarely also on peach trees; on the contrary, specimens with C genotypes were collected mainly on peach trees, and less frequently on almond trees. The three biological species share the same secondary host, i.e. reeds. The genetic distance found between the three gene poools is low, Nei's _D_ ranging from 0.17 to 0.24; these values indicate that speciation process was recent, as also suggested by the substantial lack of morphological differentiation between them. The data up to now available do not allow to explain how evolution towards trophic specialization has been achieved in this group.

Ws5.B

MORPHOLOGICAL, ECOLOGICAL AND REPRODUCTIVE DIFFERENCES IN TWO ELECTROPHORETICALLY DETECTED SPECIES OF *CLIONA* (PORIFERA, DEMOSPONGIAE).

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The taxonomic status of different morphotypes generally ascribed to the species *Cliona viridis* is until now dubious. In the present study, morphometric, ecological, reproductive and genetic differences between two morphotypes (1 and 2 in the continuation) have been pointed out in order to elucidate this problem. Morphotype 1 is characterized by small, well separated papillae (α stage) and bores exclusively the crusts of coralline algae living on the exposed rocky bottoms of the upper sublittoral. Morphotype 2 shows bigger papillae often connected by portions of incrusting tissue (β stage); this morphotype bores essentially the organogenic concretioning of sciophilous habitats.

The morphometric analysis of the tylostyles indicates that the morphotype 1 has spicules significantly smaller ($p < 0.01$ t test) than the morphotype 2.

The electrophoretic analysis shows that the two morphotypes fix alternative alleles at all the five scored loci. This is a strong indication of a complete lack of gene flow between the two morphotypes and therefore of their status as distinct biological species. Their reproductive isolation is confirmed by the study of the reproductive cycle: morphotype 1 mainly reproduces in the winter period (february, march), while morphotype 2 showed a maximum of reproduction at the beginning of the summer (may).

These data are discussed from the point of view of speciation mechanism, with special regard to the sympatric model.

Ws5.C

MICROSPATIAL VARIATION AND HABITAT PREFERENCE IN DROSOPHILA : MAINTENANCE OF POLYMORPHISM OR SYMPATRIC SPECIATION ?

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In the most studied Drosophila species, *D. melanogaster*, a growing evidence exists that, in spite of the adult dispersal capacities, microspatial genetic variations may be observed, at least in some parts of the world.

An interesting situation is found in Southern Spain. At least 3 enzyme loci allow to discriminate field and wine cellar populations. These two types of samples are not, however, genetically isolated. Studies of genotype frequencies and gametic associations between loci suggest a regular mixing of population, i.e. a Wahlund effect.

In equatorial Africa (Brazzaville) a still more interesting situation is observed, contrasting field and brewery populations. Numerous consistent differences are observed between these populations, which could be considered as "habitat-races". However, intermediate, hybrid populations also exist in the gardens of the city.

it is argued that in both cases, strong selection pressures maintain the genetical differences between the two habitats, in spite of a regular and consistent gene flow. In the Spanish populations, the seasonal demographic fluctuations and the instability of the ressources presumably prevent the formation of stable habitat-races. Such is not the case in Brazzaville where genetic behavioral differences help to maintain the stability of field and brewery populations.

Ws6.A THE HOUSE MOUSE AS A RING SPECIES: RADIATION FROM THE INDIAN CRADLE AND THE FORMATION OF HYBRID ZONES.

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The House Mouse, *M. musculus* is present all over Eurasia and is partitioned into several genetic entities which we call subspecies. These subspecies have been best characterised at the periphery of the species range. *M. m. domesticus* is found around the Mediterranean and in Western Europe while *M. m. musculus* occupies central Europe. Contact and transition between these two forms occurs through a sharp hybrid zone. In China and eastern USSR there is also a discontinuity, between *M. m. musculus* and *M. m. castaneus* (roughly north and south of the Yangtse River, resp.). The modalities of contact and transition are not yet known in detail. The japanese population results from an admixture of these two subspecies. The question of where and when these four subspecies were formed is addressed here. Samples collected in India, Pakistan, Iran and Afghanistan were characterised by protein electrophoresis at 15 polymorphic nuclear loci and by mtDNA RFLP. Both the nuclear genes and mitochondrial DNA were extremely polymorphic and nuclear alleles characteristic of the four subspecies in peripheral populations were found together in these samples. MtDNA diversity shows that these populations have evolved for a long time in this part of Eurasia. Genetic differentiation in this region appeared continuous, as one would expect in the case of primary differentiation. On the basis of these results and of paleontological information we propose that *M. musculus* could be a ring species which has differentiated from an Indian cradle in four directions, with reduced admixture after secondary contact at the peripheries of Eurasia. It is difficult however to determine the exact paths of primary differentiation on the basis of the present data.

Ws6.B

VARIATION PATTERNS AND RACES - SOME FUN AND GAMES IN DEALING WITH ANNUAL PLANT SPECIES

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Several introduced (weedy) and crop-related annual plant species have been desribed in California by the evolutionists and biosystematists. Rapid evolution of infraspecific categories (races, ecotypes, subspecies) has been inferred, especially in relation to recent colonizing episodes, adaptation to changing environments, as well as sources of introductions. Examples will be presented from several genera including *Avena, Trifolium, Limnanthes,* and *Amaranthus* to illustrate the following: Races and subspecies have been often described arbitrarily in terms of a collector's perception of novelties and ease of field identification; ecotypes and clines are equally uncertain due to a lack of detailed genecological evidence. Ecologists are primarily interested in the adaptive processes. I shall briefly review the examples of both adaptive and nonadaptive geographical differentiation and ways to define a race. More efforts are needed to test the concordance of a field biologist's morphological descriptors and of a modern biosystematist's molecular analysis; already we have examples of both concordant and discordant taxonomies.

Ws6.D

NATURAL HYBRIDIZATION AND ITS EVOLUTIONARY CONSEQUENCES IN THE GENUS *ORCHIS*

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In the genus *Orchis*, as well as in other Orchidaceae, a high number of interspecific hybrids have beed described. However, research on the genetic structure of these presumed F_1 hybrids are lacking. A number of cases analyzed by us in this genus by allozyme markers show that quite different situations exist, such as: 1) hybrid zones of different width, with F_1 hybrids, various recombinant and backcross genotypes and more or less widespread introgression (e.g. between *O.morio* and *O.longicornu*); 2) F_1 hybridization and limited backcross, that apparently do not lead to gene flow between the parental taxa (e.g. between *O.palustris* and *O.laxiflora*, or between *Aceras antropophorum* and *O.italica*); 3) F_1 hybrids, with complete lack of gene exchange (e.g. between *O.morio* and *O. papilionacea*).

The evolutionary consequences of these situations are discussed and some data on the correlation between habitat disturbance and patterns of hybridization and introgression are given.

Ws6.E

BUMBLEBEES AND CUCKOO BUMBLEBEES, A PHYLOGENETIC ANALYSIS BASED ON mtDNA SEQUENCES

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In order to analyse the phylogenetic relationship between true Bumblebees (Bombus) and the mimetic Cuckoo Bumblebees (Psithyrus) mtDNA from both have been analysed.

DNA was extracted from the flight musculature, PCR-amplified and directly sequenced.

Approximately 500 bp mtDNA of the *cytochrome oxidase*-1 gene from four Bombus species and from their corresponding inquilines among four Psithyrus species have been sequenced. Phylogenetic analysis indicate that Psithyrus is a monophyletic group closely related to a common ancestor of the four Bombus species. These results support modern phylogenetic analysis based on morphology.

Ws6.F

THE ORIGIN OF BERTHELOT'S PIPIT AND THE SPECIES STATUS OF ROCK AND WATER PIPIT REVEALED BY mtDNA SEQUENCES.

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The origin of the Berthelot's Pipit (*Anthus berthelotii*), endemic to the Atlantic islands, was studied using 1000 base pair *cytochrome b* mtDNA. The sequence was compared to sequences from Tawny Pipit (*A. campestris*), Meadow Pipit (*A. pratensis*), Tree Pipit (*A. trivialis*), Rock Pipit (*A. petrosus*); Water Pipit (*A. spinoletta*) and Grey Wagtail (*Motacilla alba*) as an outgroup. DNA sequences were obtained by PCR amplification followed by direct sequencing.

Preliminary results relates Berthelot's Pipit to Tawny Pipit. This relationship is discussed in relation to morphological, acoustical and ecological characteristics.

Comparison of a 280 base pair sequence from 10 individuals of Berthelot's Pipit revealed no intraspecific variation. The 10 specimen/individuals cover the species north-south range and are from five different islands.

Sequences from a Danish Rock Pipit and a Swiss Water Pipit were nearly identical. This adds new information to the discussion of these species status and recency of common ancestry.

Ws6.G MORPHOLOGICAL AND LIFE HISTORY VARIATION ACROSS A HYBRID ZONE IN FROGS OF THE GEOCRINIA LAEVIS COMPLEX

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The hybrid zone between two species of *Geocrinia* in south-eastern Australia comprises a sharp transition of call types and steep clines at several enzyme loci. Clines at two protein markers are displaced to opposite sides of the hybrid zone.

Osteological investigations did not reveal any character allowing reliable species identification. Skull proportions exhibited a gradual transition across the contact zone. The occurrence of morphological aberrations did not increase in the centre of the hybrid zone.

The significance of ecological gradients for the maintenance of this hybrid zone has been controversial. As an initial step of investigating possible divergence in life history, we studied variation in propagule size. *Geocrinia victoriana* had bigger offspring than *G. laevis*. Hatchling size variation in the hybrid zone showed a complex pattern, not matching clines in call parameters or allozymic frequencies.

We tentatively conclude that neither hybrid breakdown nor ecological factors modulating life history variation are likely to be the prime cause maintaining the narrow hybrid zone.

Ws6.H SPECIES SUBDIVISION WITHIN THE GREEN FROG RANA LESSONAE FROM ITALY

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Two distinct taxa were detected within Italian populations of the green frog Rana lessonae, on the basis of morphological, allozymic and immunological data (Uzzell & Hotz, 1979; Uzzell, 1979, 1983). These taxa were indicated respectively as: 'northern Italian' R.lessonae (so-called from its range), genetically similar to the central and eastern European populations; and 'southern Italian non hybrid taxon' (so-called to distinguish it from its hybridogenetic derivative R.esculenta), from peninsular Italy south of the Northern Apennines, Sicily and Corsica. Further research confirmed the presence of two genetically differentiated taxa within Italian R.lessonae, but their geographic distribution was found to be different (Santucci et al., 1989): the range of the northern taxon was shown to include Corsica and peninsular Italy down to Calabria, whereas the southern taxon was detected in southern Calabria and Sicily; a wide hybrid zone was found between the two taxa, with its highest degree of hybridization in the Catanzaro plain (Santucci et al.,1989).

For three loci (Mdh-2, NADHdh and Ada), diagnostic between the two taxa, the centre of the hybrid zone corresponds to the Catanzaro plain; a fourth diagnostic locus, Got-2, shows a non-coincident cline, with its centre in the Crati-Sibari plain (about 70 km to the north); finally, two differentiated loci, Mpi and Ck, show a 'diffuse' centre, with similar frequencies of the 'northern' and 'southern' alleles in the area between the Catanzaro and the Crati-Sibari plains. This pattern of allozyme variation appears mainly owing to recurrent sea submersions of the Catanzaro and the Crati-Sibari plains. The former caused separations of southern Calabria from the rest of Italy, with their last rejoining about 50,000 years ago;the latter reduced the connection between northern and central Calabria to a land bridge, a few km wide,represented by the 'Catena Costiera' mountains.

Effects of temporary interruptions of gene flow on the genetic differentiation of R.lessonae can be evidenced, on a lower scale, in the Alps and Apennines, owing to Pleistocene glaciations, and in Sicily. In the last case, the present severage of this island from Italy, supposed to have started less than 20,000 years ago, has given origin to a process of divergence, now shown by the fixation of an alternative allele at Me-1 locus in the Sicilian populations.

Ws6.I

INTROGRESSION BETWEEN ITALIAN AND BALKANIC HYLA ARBOREA

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The analysis of genetic variation of various populations of the tree-frog *Hyla arborea arborea* from different countries has shown that Italian samples differ from the Balkanic ones, with alternative alleles at many of the loci tested (*Idh-1*, *Xdh*, *Sod-1*, *Got-2*, *Pk*, *Est-2*, *Ap-1*, *Ap-2*,*Ap-4*, *Ada*). Introgressed populations of the two types were detected respectively to the west and east of the Isonzo river. Neither F_1 hybrids and backcrosses were observed in this area, nor populations in which specimens of the Italian and Balkanic forms coexist. It can be concluded that within *Hyla arborea arborea* two distinct species are present, respectively from the Balkans and Italy, which diverged genetically in geographic isolation. During a secondary contact they formed a hybrid zone in which reproductive isolation was achieved, possibly by reinforcement. The present parapatric distribution of the two species seems to be due to competitive exclusion.

Ws6.J

REPRODUCTIVE ISOLATION AND INTROGRESSION BETWEEN BEETLES OF THE *OCHTHEBIUS QUADRICOLLIS* COMPLEX (COLEOPTERA, HYDRAENIDAE)

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Three biological species were detected by allozyme markers within the rock-pool beetle *Ochthebius quadricollis* (Sallicandro *et al*., 1989): *O.quadricollis* A, *O.quadricollis* B, and *O.steinbuhleri*, till now considered as a subspecies or even a synonymous of *O. quadricollis*. The first two species are widespread along the Mediterranean coasts, whereas the range of *O.steinbuhleri* seems to be limited to the Adriatic Sea. Studies carried out on several sites along the Thyrrenian Sea, where *O.quadricollis* A and B live together, have shown introgressive phenomena between the two species, involving a number of diagnostic loci. Such introgression is low, geographically limited, and differs among the various markers. No F_1 hybrids, backcrosses or recombinant genotypes were detected at any of the syntopic sites, indicating that reproductive isolation, incomplete when secondary contact occurred, is now fully effective, presumably by reinforcement. Sympatric sites have been discovered also between *O.quadricollis* B and *O.steinbuhleri* in Apulia (southern Adriatic coast). Also in this case limited introgression was found, but no evidence of present gene exchange was detected. This finding confirms the status of good species for *O.quadricollis* A, *O.quadricollis* B and *O.steinbuhleri*, and appears promising for the study of two debated problems: 1) the evolution of reproductive isolation after secondary contact; 2) the role of competitive exclusion in species geographic distribution.

Ws7.A GENETIC DIVERSITY IN NATURE AT THE PROTEIN AND DNA LEVELS: PATTERNS AND THEORY

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The evolutionary significance of genetic diversity of proteins and DNAs (nuclear and mitochondrial) in natural populations of plants and animals was reviewed using the environmental-genetic correlation methodology at three geographic levels: (1) local: several species of wild cereals, landsnails and barnacles in Israel; (2) regional: 38 species in Israel; of these, 21 range from the Mediterranean region to the Negev desert; also included were two species of wild cereals in the Near East Fertile Crescent; and (3) global: 1111 species of animals and plants ranging worldwide. The species involved in these local, regional, and global analyses are largely taxonomically unrelated. They vary in their ecologies, demographies, life histories, and other biological variables. They were mostly tested for allozymic diversity by routine horizontal starch gel electrophoresis at 25 gene loci on average (range 14-50 loci). In addition, several studies were reviewed on nuclear and mitochondrial DNA polymorphisms (restriction fragment length polymorphisms, RFLPs) in animals and plants in Israel and the correlation was explored between RFLPs and allozymes.

The following results were found at all three geographic levels: (1) The levels of genetic diversity vary nonrandomly among populations, species, and higher taxa, and (2) genetic diversity is partly correlated with, and predictable, primarily by ecological factors. These results corroborate the adaptive, environmental theory of genetic diversity, and they were confirmed for several allozyme loci in controlled laboratory experiments on pollution biology. The genetic patterns obtained are inconsistent with the neutral theory of molecular evolution. By contrast, natural selection in its various forms appears to be a major differentiating and orienting force of evolutionary change in protein and DNA polymorphisms.

Ws7.B

GENETIC DIVERSITY AND SPECIATION PATTERNS IN *Pinus* and *Picea*

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The presentation includes summary of results from five case studies on genetic diversity and the role of introgressive hybridization in the evolution of *Pinus* and *Picea.*

In the first study, phylogenetic relationships among several *Pinus* species from Asia were inferred from analysis of chloroplast (*cp*) DNA variation. The results confirmed early divergence of the two subgenera *Haploxylon* and *Diploxylon.* In addition, they substantiated earlier evidence suggesting discrete phylogenetic character of *P. bungeana* and *P. gerardiana.*

In the second study, allozyme and *cp*DNA markers were used to assess interspecific gene flow and hybrid speciation comprising *Pinus tabulaeformis*, *P. yunnanensis* and a putative hybrid species *P. densata.* The obtained results revealed that introgression has occurred over a large geographic area and was probably aided by long-distance pollen flow. Normal fertility and widespread character of *P. densata* indicate that the maintenance of this hybrid species is through normal sexual reproduction. Distinct ecological separation of *P. densata* from its putative parents may have assisted in its stabilization.

In the third study, patterns of allozyme diversity have been analyzed in populations representing three varieties of *P. sylvestris* from Europe and Asia. While some geographically distant populations showed little differentiation, unexpectedly large differences were found among adjacent populations from Asia. It is possible that history of Asian populations and possibly interspecific gene flow have contributed to the observed patterns of variation.

In the fourth study *cp*DNA markers were used to assess the extent of hybridization between *Picea glauca* and *P. sitchensis* populations from Alaska and British Columbia. The obtained results are consistent with the notion that hybridization is occurring between the two species in natural, sympatric regions, and that the invasion of foreign genes beyond species boundaries is impeded by factors other than reproductive barriers.

In the fifth study, we have applied restriction fragment analysis to examine *cp*DNA variation in *Picea abies*. Two major plastotypes were detected among the individuals analyzed. Their geographical distribution within Europe was then tentatively determined on the basis of an analysis of 37 individuals from 23 localities. The partitioning observed suggests a parapatric distribution of the two plastotypes within Europe, and a diffuse zone of contact located in Central Sweden.

Ws7.C

HETEROZYGOSITY AT INDIVIDUAL AMINO ACID SITES: EXTREMELY HIGH LEVELS FOR HLA-A AND B GENES

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The amino acid heterozygosities per site for *HLA-A* and *B* loci are determined to be extremely high by combining population serotypic frequencies with amino acid sequences. For the 54 amino acid sites thought to have functional importance, the average heterozygosity per site is 0.301. Sixteen positions have heterozygosities greater than 0.5 at one or both loci and the frequencies of amino acids at a given position are very even, resulting in nearly the maximum heterozygosity possible. Furthermore, the high heterozygosity is concentrated in the peptide-interacting sites whereas the sites which interact with the T-cell-receptor (TcR) have lower heterozygosity. In particular, there is greater conservation of TcR sites at locus *HLA-B* than at *HLA-A*. The extent of parallel polymorphism between the loci is much higher than expected under neutrality. Overall, these results indicate the importance of some form of balancing selection operating at *HLA* loci, maybe even at the individual amino acid level.

Ws7.D MOLECULAR EVOLUTION OF PLANT MITOCHONDRIA AND ITS CONSEQUENCES FOR MATING SYSTEM VARIATION AND COLONIZING ABILITY.

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In contrast to nuclear genes, cytoplasmic genes usually show maternal inheritance. Male sterility (i.e. the lack of male gamete production) is therefore not deleterious for them.

In contrast to the nuclear and bacterial genomes, cytoplasmic genome cannot recombine with DNA from another cell. This has consequences for their molecular evolution, in that their mutation rates (substitutions, insertions and deletions), and their recombination rate are very different from those of nuclear genes.

Genome organization and evolution is different between chloroplast and mitochondria, and within mitochondria, between those of plants, animals and fungi. Plant mitochondrial genome evolves very slowly in sequence, but its evolution in structure is rapid, due to a high rate of recombination. This facilitates the creation of new "chimeric" genes, such as those responsible for male-sterility. The different evolutionary processes underlying the organization of the different cytoplasmic genomes could explain why male-sterility is encoded by mitochondria, and why it is common in plants and almost absent in animals.

Among plant species, the frequency of male-sterile individuals could be linked to physiological properties, and can have significant ecological consequences, in terms of the ability to colonize new open sites. This is illustrated by reference to *Thymus vulgaris*, which has an extensive mitochondrial polymorphism, and in which the frequency of male-sterile individuals can be very high (up to 95%).

Ws7.E

ADAPTIVE SIGNIFICANCE OF CYTOPLASMIC GLUTAMATE-OXALOACETATE TRANSAMINASE POLYMORPHISM IN THE MOSQUITO *CULEX PIPIENS*

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Highly differentiated allele frequencies were found at the cytoplasmic glutamate-oxaloacetate transaminase locus (*Got-1*) in populations of the mosquito *Culex pipiens* from southern France (Pasteur, 1977), Italy (Bullini *et al*., 1981; Urbanelli *et al*., 1981; Bullini, 1985), Egypt and Israel (Bullini *et al*., 1985; Villani *et al*., 1986). In Europe, the *Got-1*^{100} allele shows frequencies from 0.95 to 1 in hypogeal populations, which are autogenous (not needing a blood meal for egg maturation) and breed in polluted waters; this allele is significantly less common (0.30 to 0.70) in anautogenous populations, breeding in epigeal sites. The consistent differences found in *Got-1* allele frequencies between autogenous and anautogenous populations, even if located very close to each other (e.g. less than 1 km) can not be accounted for only by the reduced gene flow evidenced between them by transplant experiments, but involves selective pressures at *Got-1* locus (Urbanelli *et al*., 1981; Bullini, 1982, 1983). It was proposed by Pasteur (1977), that *Got-1*^{100} is selected for in the autogenous, hypogeal populations; this allele would promote a more effective synthesis of acid aminoacids (aspartic and glutamic acid) necessary for the vitellum synthesis from larval reserves in the absence of a blood meal. However the finding of populations from Egypt and Israel, collected in polluted waters both hypogeal and epigeal, and showing a high frequency (from 0.95 to 1) of the *Got-1*^{100} allele (Bullini *et al*., 1985; Villani *et al*.,1986) requires further explanation. We suggest that *Got-1*^{100} allele could be selectively advantageous also to epigeal populations of *C. pipiens*, breeding in polluted waters, allowing them to mature eggs in waters rich in organic polluents and, at the same time, to reduce energy and time costs involved in the host search and blood meal.

Ws7.F ETHANOL STRESS VERSUS ADAPTATION TO ETHANOL IN *DROSOPHILA MELANOGASTER*

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Three inbred *Drosophila melanogaster* strains were exposed to exogenous ethanol in three different ways: (i) a one generation exposure to 5% ethanol (short term ethanol exposure); (ii) a 12 generation exposure to 5% ethanol (long term ethanol exposure); (iii) larvae exposed to 7.5% ethanol (ethanol shock). The influences of the different treatments on the activities of four enzymes (ADH, ODH, αGPDH and AOX) were compared in the three strains. The strains had different allelic combinations at the *Odh* and *Aldox* loci on their third chromosomes but they all contained the *AdhS-αGpdhF* allelic combination on the second chromosome. The results showed that the larval and adult metabolic responses to environmental ethanol were different. The activities of the allozymes common to all strains (ADH-S and αGPDH-F), showed strain-specific response differences which appeared to depend on the unique allelic combinations at the *Odh* and *Aldox* loci.

Ws7.G

GENETIC VARIATION AND LIFE CYCLE OF ENDOPARASITIC NEMATODES

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Allozyme studies carried out on 17 species of ascaridoid nematodes having different life-cycles have shown that their genetic variability is positively related to the degree of environmental heterogeneity they experience (Bullini et al., 1986). It was found that species whose life cycle is carried out on homeothermic hosts show a significantly lower genetic variability (mean H_e = 0.04) than do those needing both poikilothermic and homeothermic hosts (mean H_e = 0.15). A major role of natural selection in this phenomenon was suggested (Bullini et al., 1986). This hypothesis was criticized by Nadler (1987, 1990), mainly on a neutralistic basis.

In order to obtain a more complete picture, ten more ascaridoid species were analyzed, and compared with those previously studied. The general trend of a lower genetic variability in ascaridoid worms parasitizing homeothermic hosts than in those needing both poikilothermic and homeothermic hosts was confirmed (mean H_e=0.04 versus 0.12). However, some species of the latter group showed lower values of genetic variability than found in the previous study. Differences in population size, degree of inbreeding, bottleneck events, time and mode of speciation can account for the discrepancies found between some multiple-host ascaridoid species. Nevertheless, the overall picture confirms the major role of natural selection in determining different levels of genetic variability in this group of parasites. Interestingly, the average values of variability found in ascaridoid worms parasitizing only homeothermic vertebrates is similar to that of their hosts (H_e=0.04, from Nevo et al., 1984). On the other hand, the variability of ascaridoids parasitizing both poikilothermic and homeothermic species is similar to that found in their poikilothermic hosts (H_e = 0.12, from Nevo et al., 1984).

Ws7.H DOES SERPENTINE HAVE AN EFFECT ON THE POPULATION STRUCTURE OF *SILENE DIOICA (CARYOPHYLLACEAE)* ?

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Some plants are known to grow in most toxic environments, such as mines, smelter sites and natural ore and serpentine outcrops. Serpentine is a ferromagnesium-silicate mineral containing high concentrations of nickel and often also high concentrations of chromium and cobalt, in a form available for plants. These heavy metals, in particular nickel, are known to affect plant growth adversely. In addition to high concentrations of heavy metals, these soils are in general deficient in plant nutrients. They are also dry because of lack of organic material. Accordingly rather few species are adapted to grow on serpentine. The major serpentine areas of Sweden are located in the mountains of Västerbotten and Jämtland.

Most of the plants on serpentine are self-fertilizers or inbreeders. *Silene dioica (Caryophyllaceae)* is an exception. It is a perennial insect pollinated herb and as the name implies, it is dioecious and therefore obligatorily cross-fertilizing. *S. dioica* is one of the most characteristic plants on serpentine in Sweden. It grows at different altitudes, from the coniferous forest up to the low alpine region. Outside of serpentine it is abundant in subalpine tall herb meadows.

The aim of this work is to study the effect of long-time exposure to serpentine stress on the population structure of *S. dioica.* Both serpentine and adjacent non-serpentine meadow populations from four localities in Västerbotten and two localities in Jämtland have been studied by enzyme electrophoresis. Populations in Västerbotten, the northern part of the studied area, grow within an open pine or birch forest, while in the south, Jämtland, populations are surrounded by a continuous dense spruce forest. The distance between populations within a locality ranged from 100 m to 7 km.

Allele frequencies analyses showed that both serpentine and non-serpentine populations in Västerbotten and the non-serpentine populations in Jämtland are closely related to each other. This implies that serpentine does not exert a selection visible on the population structure. Evidently *S. dioica* has had the ability to colonize serpentine repeatedly. In Jämtland, however, the serpentine populations differ genetically from each other, as well as from the non-serpentine populations in Jämtland and all populations in Västerbotten. The allozyme divergence between serpentine and non-serpentine populations in Jämtland is evidently not due to direct selection on serpentine but rather represents the effects of isolation and drift. In Jämtland open patches of serpentine are surrounded by a dense spruce forest. This forest is inhospitable for *S. dioica* and seems to exclude the pollinators effectively and can, therefore, impose isolation.

Ws7.I

MIGRATORY BEHAVIOR AND ITS CONSEQUENCES FOR THE GENETIC STRUCTURE OF BLACKCAP (*SYLVIA ATRICAPILLA*) POPULATIONS

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The Old World warbler *Sylvia atricapilla* displays an array of different migration habits. Northern populations are long-distance migrants and completely migratory, Mediterranean populations are short-distance migrants and partially migratory and there is at least one population - on the Cape Verde Islands - which is sedentary.

Breeding experiments with birds of migratory and nonmigratory populations have revealed that migratory behavior has a substantial genetic basis in this species. The inheritance patterns suggest that migratory restlessness is a polygenic threshold character. Furthermore, two-way selection experiments have demonstrated that a partially migratory population can be selected to become entirely migratory or resident in three to six generations.

The effects of different migration habits on genetic population structure were studied in an electrophoretic survey of 39 protein loci in three natural and two laboratory populations representing all possible migration patterns. Genetic variability was highest in the migratory population and decreased with the proportion of migrants in the populations. Of the eight polymorphic loci found one enzyme polymorphism proved to be strongly associated with nonmigratory behavior. The "slow" allozymic variant of glycerol-3-phosphate dehydrogenase (G3PD) was exclusively found in sedentary populations. Moreover, this allele showed a strong response to artificial selection for nonmigration: its frequency increased significantly in three generations. We have circumstantial evidence for the assumption that G3PD is functionally linked to the display of migratory behavior. This entails that the allele frequency increase is attributed to selection rather than to genetic hitchhiking. Different selection-migration scenarios by which the distribution of the G3PD allozymes in natural populations could have evolved, and is currently maintained, are discussed in view of the prevailing theories on the origin of migratory behavior.

Ws7.J GENETIC STRUCTURE AND MICROEVOLUTION OF SOME EUROPEAN PLETHODONTID SALAMANDERS

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Ehrlich and Raven (1969) stated that gene flow would be less important in speciation than the neo-Darwinians thought. Larson *et al.* (1984) supported this point, observing that the species of plethodontid salamanders they studied generally do not comprise units connected by gene flow. In the present paper, data are given on the genetic structure and gene flow of the Italian plethodontids *Speleomantes* (formerly *Hydromantes*) *strinatii*, *S. ambrosii* and *S. italicus*. Evidence is provided of two secondary contact zones between contiguous species. In the case of *S. strinatii* and *S. ambrosii*, the two taxa are not presently hybridizing, but evidence of paleointrogression is given by the finding of *strinatii* alleles in *ambrosii* populations about 30 km apart. Much more widespread introgressive phenomena were detected between *S. ambrosii* and *S. italicus*. In this case, *ambrosii* alleles penetrate as far as 150 km in *italicus* genome. Our data (and others unpublished) indicate that plethodontid salamander species do comprise groups of populations connected by gene flow.

A second largely discussed point (Wake *et al.*, 1983; Larson *et al.*, 1984) concerns morphological stasis in these organisms, that would contrast with environmental and genetic changes they underwent during millions of years. The above mentioned Authors consider stabilizing selection as insufficient to explain phenotypic uniformity, suggesting a major role of genetic and epigenetic factors. Research carried out in our lab on a number of sibling species complexes, belonging to groups as different as plants, ascaridoid worms, mites, lacewings, mosquitoes, burnet and other moths, land salamanders, tree and green frogs, mole rats, etc., indicate that genetic and morphological differentiation can be largely independent. Morphological similarity can be due either to the techniques used, the number of characters studied and their adaptive significance, or to phenomena such as adaptive convergence, parallelism, selective maintenance of an unchanged phenotype (Ford, 1953; Bullini, 1976, 1983, 1985). These explanations seem sufficient and satisfactory for most of the cases studied so far; this would advice against formulating further hypotheses until the previous ones are fully tested.

Ws8.A GENETIC CHANGES IN NATURAL POPULATIONS UNDER ANTHROPOGENIC PRESSURES

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Genetic processes taking part in natural populations under various antropogenic pressures (fishing, artificial reproduction, transplantation) are discussed. The dynamics of these processes associated both with the increase and decrease of genic diversity estimated over a number of allozyme loci is shown to be equally deleterious for normal functioning of population systems.

A hypothesis is advanced according to which every population has an historically formed genetic optimum that determines its stable existence in time. Rational management of biological resourses is possible only by maintenance of such an optimum.

Ws8.B ON THE CONSEQUENCES OF GENETIC EROSION FOR POPULATION EXTINCTION

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One of the fundamental issues in conservation biology nowadays concerns the contribution of genetic erosion to the process of population/species extinction. Many plant and animal species presently face the problems of severe reduction in size and fragmentation of their natural habitat caused by human activities. As populations under these circumstances usually become small and isolated, they are expected to be subject to loss of genetic variation by genetic drift and inbreeding. This process of genetic erosion is often accompanied by a decrease in fitness (inbreeding depression).

Negative effects of genetic erosion have long been known from studies with domestic organisms but empirical support for its significance in natural populations is still scanty. We therefore are currently assessing the existence of deleterious effects of genetic erosion in natural populations of the plant species *Scabiosa columbaria* by comparing small and large populations for a number of aspects: (1) levels of genetic variation in relation to population size, (2) outcrossing rates and (3) fitness loss due to inbreeding. The data obtained so far reveal that smaller populations indeed show lower levels of genetic variation than larger ones. Furthermore, the species, under natural conditions largely outcrossing, appears very sensitive to inbreeding: offspring resulting from one generation of selfing showed a significantly lower viability than outcrossed offspring. However, the inbreeding effects did not correlate well with either differences in population size or with differences in gene diversity. Although the data mostly do not contradict the expectation, much more research is needed to ascertain the influence of genetic erosion under natural conditions.

Some general aspects of the above mentioned processes will be discussed.

Ws8.C

INBREEDING DEPRESSION AND POPULATION EXTINCTION: DOES CROSS FERTILIZATION OF DISCIPLINES LEAD TO VIABLE IDEAS?

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Within the framework of Conservation Biology increased genetic stochasticity in small populations is thought to enhance the extinction chance of the population. Inbreeding depression is a major phenomenon contributing to this expectation.

Although a large body of data exists concerning the role of inbreeding depression in the evolution of plant breeding systems, evidence for its influence on population extinction is virtually absent. Several problems which may alter expectations are discussed, including the relation between inbreeding depression on the one hand and selection, environmental variance and demography on the other. The issue of the relevance of genetic erosion as compared to demographic stochasticity is addressed.

Data on inbreeding depression in small and large populations of the perennial outcrosser *Salvia pratensis* are presented. Results from greenhouse experiments show considerable inbreeding depression in several life history stages. There is however much variance in expression between stages making general predictions about the contribution of inbreeding depression to population growth rate difficult. Furthermore inbreeding depression is varying between competition levels thereby making the contribution to population growth rate variable among environments as well as time.

These results demonstrate the difficulties of formulating adequate null-models for the tripartite relation between population size, inbreeding depression and extinction chance.

Ws6.D A POPULATION GENETICS APPROACH TO THE CONSERVATION OF GENE RESOURCES IN *PINUS LEUCODERMIS* ANT.

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Pinus leucodermis Ant. is a conifer with a discontinuous and restricted distribution in Italy, where it occurs in only four small groups of populations. Due to the restrictedness of its actual range and to the frequent occurrence of fires in these areas, it can be seen as a highly endangered species, whose genetic resources need to be analysed and conserved. We therefore undertook a comprehensive study of its population genetics, using isozyme markers. Our attention was mainly focused on the study of the mating system in natural populations and on the problem of the elimination of inbred seedlings in early developmental phases. Many studies have in fact shown that in conifers, which usually have very low levels of selfing and express severe inbreeding depression, positive fixation indices are observed in the seed stage, but not in the adult one. Selection against inbreds has been frequently invoked in order to explain this observation. Knowledge of the mating system parameters of the species and of the factors which can influence it, can be of major importance in order to minimize the effects of inbreeding depression, if artificial populations are to be established for dynamical gene conservation, whilst the problem of the elimination of inbreds during early life-cycle phases is of great concern, if nursery-grown seedlings have to be planted in order to create new populations. Seedlots from two natural populations were analysed at three different developmental phases. Mating system analysis was made by assaying dormant seeds and showed that the species is characterized by relevant levels of selfing, if compared with other conifers, and that this results in positive fixation indices in the embryo stage, but not in the adult trees. No significant variation in fixation indices nor any upward bias in the estimated outcrossing rates was observed in both stands, when germinated embryos were analysed. Directional selection was, however, observed at two loci in one population. When five years old nursery grown plantlets, which had experienced a high mortality, were analysed, an excess of heterozygotes similar to that of the parental trees was observed, thus showing that selection against inbreds acted after germination. These results will be compared with those obtained from the analysis of plantlets of the two stands grown in natural conditions.

Ws8.E

INBREEDING EFFECTS IN SMALL POPULATIONS : THE ROLE OF THE METAPOPULATION STRUCTURE.

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Small population size can result in an overall decrease in population fitness due to an increased expression of recessive deleterious genes which are maintained by recurrent mutations but may also purge the genome of these deleterious genes. The intensity of these effects will depend on the dynamics of the metapopulation the population belongs to.

Stochastic simulations were used to look at the influence of different factors, i.e. the number of founders of a population, their relatedness, and the population dynamics : growth rate, maximum size and life-span, as well as the direction of selection on the avoidance of inbreeding in the local populations of an overall metapopulation. The relevance of these results to published data will be discussed.

Ws8.F

MUTATIONAL MELT-DOWN: EXTINCTION OF SMALL POPULATIONS UNDER MUTATIONAL LOAD AND DEMOGRAPHIC STOCHASTICITY

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Genetic aspects are important in the evaluation of the risk of extinction for small populations. Using estimates of rate and effects of slightly deleterious mutations, we calculate the mean time to extinction under the joint action of mutation load and density-dependent stochastic population regulation. Accumulation of mutations diminish the individual survival probability, which leads to a reduction for population size before reproduction. This synergistic interaction has been called the mutational melt-down.

In asexual populations, the probability of extinction increases as the mutational effect increases and as actual population size decreases. As reference points for sexual populations, we present the expected extinction times without mutational load but with stochastic fecundity and sex-ratio under various types of population regulation. Selection and recombination does not prevent mutational melt-down in small sexual populations; slightly deleterious mutations reduce the mean time to extinction by several orders of magnitude. Stochastic fecundity is a minor direct source of extinction in sexual populations, but it leads to temporary reductions in effective population size, which increases the risk of extinction due to stochastic variations of the sex-ratio.

Ws8.G : Genetic and demographic variables in conservation

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Genetic variables of primary interest in the conservation decisions include inbreeding effects, losses of variation due to drift, and estimators of minimum viable size. Metapopulation dynamics is of common interest due to increased fragmentation of habitats and often we need measures of migration among subpopulations. Population geneticists have suggested certain guidelines for protecting and monitoring biodiversity as well as individual species. However, numerous factors affecting population growth, threshold territory, local reproductive success, etc.. require demographic information. Data from several rare plants and their community analyses will be reviewed to show how most decisions about in situ conservation or restoration are made without much or any genetic knowhow; the adaptive role of variation under rapidly deteriorating environments needs more critical research without which variation and genetic distance statistics provide rather little help. Population studies in Limnanthes, Orcuttia, Eucalyptus, and a few others will be discussed briefly to outline some critical research areas.

Ws8.H

Dynamic management of genetic resources : an experiment and some questions

J. David, J.P. Henry A. Gallais & P.H. Gouyon

In order to address the question of how to manage the diversity of a species under cultivation, an experiment and some models have been developed. The goal is to improve our understanding of the effect of local differentiation and partial migration on the genetic diversity of a species. Genetic diversity is understood here not only as the one which is usually measured using biochemical markers and modelled assessing neutrality. Rather, the goal of this study is to see if evolutionary biology can now provide answers to the questions asked by conservation programs i.e. how can we manage the diversity on *non neutral* polymorphisms.

The speed of divergence of isolated wheat populations issued from a common polymorphic population is studied on agro-morphological characters and other markers. The possibility of obtaining by this way phenotypes which were not present in the beginning is discussed and models tempting to predict the effect of diverse modes of genetic exchange between these populations (few each year, a lot every n years, metapopulation management...) are developed.

Ws9 MEASURING SELECTION IN HETEROGENEOUS ENVIRONMENTS.

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The workshop will take the form of a round table discussion.

In a model, we may describe a population that lives in a heterogeneous environment and we may make simulations of this population by drawing the survival and reproduction values from a different probability distribution for each segment of the environment. For each individual, survival is an all or none process. However, we are normally quite content with establishing differences in survival probability, especially if these can be related to properties of the organism-environment combination.

Basically, this is how I understand natural selection. I strongly suspect that in many, if not most, situations in which we would like to measure natural selection the heterogeneity in selection pressures (or the distributions from which survival or reproduction values should be drawn) is a) substantial and b) important in identifying the causal chain involved in the selection. It is obvious that there will often be a problem of discrimination power when we want to establish differences between the probability distributions for different phenotypes and different sub-environments, even if we limit ourselves to the major selection forces and simple linear functions or a two class characterisation of phenotype and environment.

In the field, I am often struck by the substantial number of individual birds that have severe handicaps, such as missing one eye, a foot, a broken bill, the feathers on half a wing eaten by lice etc. that apparently survive quite well and even raise offspring in a quantity and quality that is indistinguishable from normal. This leads to the idea that most properties are irrelevant for survival during most of the time. The selection coefficients that we measure are means that may result from a few extreme situations. (If this is really so, then there is an additional problem in the lack of independence of occurrences during a single extreme situation: e.g. if 20 % of the fledglings die in a severe thunder-storm after fledging, we may find a 20 % difference in survival if one area had one and the other area had two storms. For any systematic differences between the nestlings in these populations one might, if careless, conclude that there had been selection. This is a pseudo replication problem.

The problem of how to measure the heterogeneity in selection touches on our basic understanding of selection. At the same time there are no practical guidelines to reach reasonable compromises between the power of large numbers and the variation in selection pressures on a fine geographic and or temporal scale.

We will discuss the following questions:

1. In which or rather in what sort of research questions does this problem play a role ?

2. How do we allocate our research effort, how do we stratify our sampling to obtain the most information ?

3. In which sort of analyses of selection do we get any clues that there is important heterogeneity in the selection ?

4. How much is gained by understanding the mechanism of selection at a physiological level and direct measurement of the critical environmental parameter in the field ?

It seems to me that discussing these four questions may help us to derive some practical guidelines in dealing with this problem. I am curious to what extent there are general solutions and to what extent we have to revert to pragmatic system-specific solutions.

Ws10.A COSTS OF AVOIDANCE IN A PLANT-PATHOGEN SYSTEM: SILENE ALBA AND THE ANTHER SMUT FUNGUS USTILAGO VIOLACEA

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Polymorphisms for disease resistance seem to be rule rather than exception in natural plant populations. At least three hypotheses have been formulatied to explain the maintenance of such polymorphisms: (1) Cost of resistance, (2) Interactions of host genotype pathogen genotype and environment, and (3) Non equilibrium theories. The first hypothesis implies that in the present of the pathogen a resistant host should have a higher fitness than a susceptible host, but that the reverse should be true in the absence of the pathogen due to pleiotropic effects of resistance genes. Although such costs are frequently assumed in host pathogen models, experimental evidence is rather scarce.

Analogous to costs of resistance we will consider costs of disease avoidance that have a genetic basis but that have not necessarily been developed in response to pathogen pressure. We discuss such costs of avoidance in the dioecious host species white campion (Silene alba) to the anther smut fungus Ustilago violacea. The fungus effectively sterilizes both male and female hosts, transforming female hosts into sterile males, and producing its teliospores in the anthers. Hosts are most commonly infected in the adult, reproductive stage via spore deposition in the flowers by insects that serve the dual function of pollinators and vectors of the disease.

Experimental field studies showed that male hosts from late and shorter flowering half sib families had significantly lower infection rates than early flowering families due to (1) shorter exposure to spore transmission and/or lower transmission efficiency, and (2) higher 'physiological' resistance that shows a weak positive association with avoidance. In the absence of the pathogen, these host families had lower reproductive success indicating that there are indeed costs of avoidance in this system.

Ws10.B COADAPTIVE ASPECTS OF PARASITIC CASTRATION OF THE STICK INSECT CLONOPSIS GALLICA BY THE TACHINID FLY THRIXION HALIDAYANUM

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Data are presented on parasite-host relations between the tachinid fly *Thrixion halidayanum* and the stick insect *Clonopsis gallica*, an all-female species reproducing by thelytokous parthenogenesis. *T.halidayanum* does not affect mechanically the host tissues, feeding by suction. The host is not usually killed, but its development is delayed, the size of its fat body decreases, as well as its general activity. The most important consequence of parasitization consists in the inhibition of the development of the host ovaries in the larvae or in their involution and atrophisation in the adults, leading to a decrease or temporary inhibition of oviposition. After the parasites have left the host, egg production increases, although remaining lower than in unparasitized individuals. Parasitic castration by *Thrixion halidayanum* is of an "indirect" type and the secondary sexual characters of the host are not affected. Parasitic castration decreases the host "reproductive effort", (i.e. the total amount of resources utilized in a given period for reproductive purpose), enhancing indirectly the host survival. The coadaptive nature of this case of parasitic castration is also shown by the reversable effect of the parasite on the host ovaries, not determining its permanent sterility. This allows the host to survive and reproduce, and at the same time makes potential hosts available to the parasite progenies.

Ws10.C

AVOIDANCE OF SELF-SUPERPARASITISM BY THE PARASITOID *ANTROCEPHALUS PANDENS* WALKER

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Superparasitism is defined as the laying of a second clutch of eggs into a host that already contains conspecific parasitoid eggs. In the case of solitary parasitoids, the clutch consists of a single egg. Only one parasitoid can complete its development in each host, so in a superparasitized host there is competition between the larvae for possession of the host, after which only one remains alive. Two types of superparasitism can be distinguished; self-superparasitism, in which a female lays an egg in a host first parasitized by herself, and conspecific superparasitism, in which a wasp oviposits in a host first parasitized by a different individual. Self superparasitism adds no offspring to a female wasp's lifetime reproductive success, as it brings into conflict two offspring of the same mother, and it is therefore advantageous for wasps either to recognise hosts that they have parasitized or minimize the risk of self-superparasitism by their behaviour. This is especially important for wasps such as *Antrocephalus pandens*, a solitary pupal parasitoid of the rice moth *Corcyra cephalonica*, which has a limited egg supply and low lifetime fecundity. Conspecific superparasitism, on the other hand, can be an adaptive strategy when unparasitized hosts are scarce.

Three mechanisms have been proposed by which parasitoids could avoid self-superparasitism, each of which was tested with *A.pandens*. The first is possession of sensory abilities to distinguish hosts first parasitized by self and nonself. *Antrocephalus pandens* can distinguish between parasitized and unparasitized hosts, but cannot tell the difference between hosts parasitized by itself and a different individual.

Inexperienced wasps, which have never oviposited before, should be more willing than experienced wasps to superparasitize, because they can be sure that a parasitized host that they encounter was first parasitized by a different individual. Thus there is no risk of self-superparasitism. Experiments with *A.pandens* supported this hypothesis.

Wasps should avoid superparasitism strongly when they forage alone on a patch, as they would then be indulging in self-superparasitism. When they forage in the presence of competing conspecifics, however, they should cease to discriminate between parasitized and unparasitized hosts, for two reasons; firstly, there is a greater benefit to superparasitism when it is likely that it is conspecific rather than self superparasitism, and secondly, self-superparasitism can be advantageous when it is likely that a host will also have eggs laid in it by conspecifics. A wasp which has the most eggs in a host has the greatest chance of obtaining an offspring from that host. Experiments with *A. pandens* showed a change from strong avoidance of superparasitism when wasps were alone to a random distribution of eggs, indicating lack of selection between parasitized and unparasitized hosts, when wasps were in groups.

Ws10.D

HOW DOES THE HUMAN IMMUNE SYSTEM AFFECT COMPETITION BETWEEN MALARIA PARASITE GENOTYPES?

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It is known that malaria patients are frequently infected with mixtures of genetically distinct parasites. This implies that there should be 'direct' competition: different reproductive rates, different abilities to invade erythrocytes and differences in rates and/or timing of the transformation from asexual into sexual forms. How does this change if the human immune response is taken into account? The immune system, apart from its direct impact on the parasites, offers the additional opportunity to compete indirectly via differences in protection against the immunological attack, for example in the abilities to vary antigens and/or suppress the immune reaction. To get more insight into this situation models are developed for the erythrocytic cycles of two different parasite genotypes. They explicitly include erythrocytes, free merozoites, those erythrocytes infected by merozoites, those habouring gametocytes and finally T-lymphocytes as representatives of the cell-mediated immune attack. This makes it possible to study the dynamical behavior of this system and eventually determine an optimal strategy for the parasites in terms of the rate and timing of the production of gametocytes.

Ws10.E *ASOBARA TABIDA* VS *DROSOPHILA MELANOGASTER*: A COEVOLUTIONARY ARMS RACE ?

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The braconid *Asobara tabida* is one of the most important parasitoids of *Drosophila*-larvae in rotting fruits in Europe. In northern Europe the parasitoid mainly oviposits in *D. subobscura* whereas in the mediterranean *D. melanogaster* is the most important host species during a large part of the season. For the parasitoid, the main difference between these hosts is that *D. melanogaster* can defend itself against a parasitoid attack by encapsulating the parasitoid's egg, while *D. subobscura* does not possess this ability. In contrast to northern wasp populations mediterranean populations can prevent encapsulation to a certain degree. In addition, mediterranean *D. melanogaster* are stronger encapsulators than their northern conspecifics. This correlated geographic variation suggests that in the mediterranean parasitoid and host are engaged in a coevolutionary arms race. Both the mechanism by which mediterranean parasitoids prevent encapsulation as the way in which mediterranean *melanogaster*-larvae counter this mechanism are under investigation. However, other selection pressures may be responsible for the higher encapsulation capacity of mediterranean larvae: at first the eucoilid parasitoid *Leptopilina boulardi*, a specialist on larvae of the *melanogaster*-group, is common in the mediterranean; and secondly, melanin, a very important substance in the chain of events leading to encapsulation is also important during other parts of the host's life cycle. If selection pressures other than A. tabida are more important causes of the higher encapsulation capacity of mediterranean *melanogaster*-larvae the parasitoid is merely adapting to a changing environment, i.e. there is no coevolution in the strict sense.

Ws10.F

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In the enlightened view of parasite-host coevolution, selection will favor parasites that produce symptoms that result in the morbidity or mortality of their host when that 'virulence' is directly coupled with the capacity of the parasite to colonize and maintain a population within a host or be infectiously transmitted between hosts. But, is this all there is to the evolution of parasite virulence? Are there general reasons to anticipate a direct relationship between virulence and these features of a parasite's life cycle? What limits host evolution to counter the virulence of parasites, 'resistance'? Could the virulence of parasites be the result of coincidental evolution, byproducts of selection for other characters or perverse consequences of the host's response to infections? In this report I consider the answers to these questions provided by recent theoretical studies of the within-host population dynamics of microparasites and experimental studies of mechanisms of virulence in pathogenic bacteria.

Ws11.A

NEMATODE MOLECULAR PHYLOGENIES.

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Though *Caenorhabditis elegans* is well characterised individually, the genetic interrelationships among nematodes remains suprisingly little known. Several well characterised genes in *C. elegans*, both nuclear and mitochondrial, have been investigated to establish their usefulness in constructing phylogenies within *Caenorhabditis* and the Nematoda in general.

Among the Caenorhabditids the mitochondrial cytochrome oxidase II gene has proven inadequate at resolving a phylogeny within the group. Reasons for this may include idiosyncratic evolutionary features of the mitochondrial genome such as the large transition:transversion ratio, and the effects of extreme base compositional bias. Similarly the calmodulin-like single-copy nuclear gene did not resolve a *Caenorhabditis* phylogeny.

By contrast, the nuclear 26S ribosomal RNA gene has proved most informative in establishing a *Caenorhabditis* phylogeny. Regions have been identified that contain species specific variation (namely the eukaryote-specific 'expansion segments') which can be used in close species analyses. PCR primers have proved extremely successful at amplifying DNA from a wide range of nematode species and have provided valuable data for the identification of cryptic species. At least one pair of primers, that amplify the D3 'expansion segment' have worked successfully on all nematode DNA's so far examined. These could have much value in the rapid identification and characterisation of nematode species. So far members of free-living and parasitic genera have been examined, including; *Caenorhabditis, Heterorhabditis, Rhabditis, Cruznema, Coarctadera, Mesorhabditis, Steinernema, Ascaridia, Aspidodera, Paraspidodera* and *Heterakis.*

A comparative analysis of the 26S rRNA secondary structure amongst nematode species has revealed many compensatory base changes in classic stem regions of the molecule 'core' as well as within 'expansion segments'. Within the 'D3 expansion segment' extreme variation at the primary sequence level has been found though a conserved secondary structure is retained. All compensatory mutations lend support to the hypothetical eukaryote secondary structure model.

Very fast analysis of parts of the 26S gene (particularly D3) are now possible and the beginnings of a nematode sequence database established. By using PCR, individual nematodes and their larvae can be examined directly at the DNA level allowing traditional microscopical and molecular techniques to be combined in the identification of nematodes and their evolutionary relationships.

Ws11.B

THE GENOME OF CAENORHABDITIS ELEGANS

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The haploid genome of C. elegans contains about 100Mb of DNA, organised in six chromosomes. Most of the genome is covered by a map consisting of 17500 cosmids and 3500 YACs. 87Mb lie in 30 large contigs that have been assigned to chromosomal locations; most of the rest is represented by 43 smaller contigs. Assembly of the map involved detection of overlap between the cosmids by a restriction enzyme fingerprinting procedure, and then detection of overlap between YACs and cosmids by colony hybridisation. The contigs are now being linked by YAC-YAC walking.

The project is a community enterprise: anyone who works on C. elegans can send in clones for analysis, and in this way the physical map is progressively aligned with the genetic map. The map, which is transmitted electronically around the world, plays an important part in the molecular genetics of C. elegans. Apart from its direct use in molecular cloning, it serves as a vehicle for genomic communication between laboratories. Both information and clones are freely shared among all the research groups. The communication aspects are about to be further enhanced by means of a new database manager, acedb, which will incorporate not only the existing physical map but also the genetic map and all available DNA sequences, acedb is written in standard C, but in object oriented style; it runs under X windows and Unix, and readily expands to include new classes of object and any size of project.

The map is now being used as a basis for sequencing the genome. The sequence will provide a vast amount of biological information, and the project will serve as a technological pilot for still larger genomes, such as the human. We propose to set up an operation that will determine the sequence by the end of the decade. During a three year pilot project that has been initiated under the auspices of UK-MRC and US-NIH, we will sequence a contiguous region of 3Mb on chromosome III. By the end of the 1990s we hope to have accessed systematically all the genes of the organism. The sequence itself will be placed cosmid by cosmid in the public databases, as we go along, and will be a powerful resource in the molecular analysis of development.

Ws11.C

TIMING THE ORIGIN OF THE NEMATODES

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Accurately calibrated molecular clocks are useful tools for estimating divergence times both between and within the various metazoan taxa, even where fossil evidence is not available. Useful molecular clocks are either evolving proteins or DNA or RNA sequences. Their advantages and disadvantages will be briefly discussed. The choice of the appropriate clock(s) will also depend on the estimated timing for a particular evolutionary event i.e. rapidly evolving macromolecules are very useful for tracing back recent (on a paleontological time scale) evolutionary events, while very slowly evolving molecules e.g. cytochrome *c* may resolve events back to ca. 2 billion years.

The potentials and limits of this kind of approach will be dicussed and illustrated using the histone and cytochrome *c* sequences of *Caenorhabditis elegans* and *Ascaris suum*. Present data suggest that nematodes diverged from the evolutionary line leading to man about 1.1 ± 0.1 billion years ago. This is quite near the assumed divergence of plants and animals (1-1.2 billion years). The persistence of an operative glyoxylate cycle in nematodes and their capability of synthesizing polyunsaturated fatty acids *de novo*, which are typical properties of plants, strengthens the reliability of this estimation.

Ws11.D EVOLUTION IN HOPLOLAIMS (NEMATODA : TYLENCHIDA)

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Genera that show a transitional series are difficult to define : the series discussed is Rotylenchus - Scutellonema - Peltamigratus - Aorolaimus - Hoplolaimus. Two hypotheses are presented. First the evolutionary development of this series is associated with the theory of continental drift. Second the morphology of tylenchs is almost unchanged during the last 200-300 million years, explaining the large genetic variation found within some species.

Ws11.E

ANTI-OXYGENIC ENZYME ACTIVITIES AND LIFE SPAN IN *CAENORHABDITIS ELEGANS*

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The nematode *C. elegans* is a good model system for investigating the primary causes of longevity and ageing. Mutant alleles of *age-1* extend the mean and maximal life span of *C. elegans* in axenic culture by more than 100% and all of the increase of life expectancy is due to an increase in the length of postreproductive life. The *age-1* mutation also confers hyperresistance to hydrogen peroxide and to superoxide anions generated by Paraquat.

The activities of catalase and superoxide dismutase in freshly made homogenates increase with the age of the worms. In addition, *age-1'* worms contain much higher levels of SOD-activity in the adult stage. Interestingly, glutathione peroxidase seems to be missing in *C. elegans*.

The level of superoxide anion production by the microsomal fraction decreases as the worms pass from the reproductive into the postreproductive stage. While superoxide anion production then continues to decrease as the worms age, this decrease levels off in *age-1* mutants.

Cu/Zn SOD has been purified from to homogeneity using ion exchange chromatography, copper chelate affinity chromatography and gel filtration, and its molecular properties have been studied. Much like Cu/Zn SOD from other organisms the native nematode enzyme is a dimer of approx. 40 kDa, which is stable to heat and SDS. Each monomer contains an intramolecular disulfide bridge, which mainitains the enzymatically active configuration. Unlike vertebrate Cu/Zn SOD the nematode enzyme is a basic protein, with isoforms focusing at pI 9.0, 8.1 (major isoform), 6.9 and 5.2 (minor isoforms). The pI 6.9 isoform is converted to the fraction focusing at pH 5.2 with increasing focusing time. However, small amounts of the isoforms with pI 6.9 and 5.2 are consistently seen after short electrophoresis of freshly made homogenates. No major differences were observed as a result of strain differences or of increasing age of the worms. A gene encoding for Cu/Zn SOD has recently been cloned and its molecular organization will be discussed briefly.

In conclusion, overexpression of catalase and superoxide dismutase increases life expectancy in *C. elegans*, though these enzymes may not detemine the onset of the ageing process by themselves. The multiple effects observed in *age-1'* worms suggest that *age-1* may encode a regulatory protein.

Ws11.F CONSTRAINTS, AND POSSIBILITIES, FOR EYE STRUCTURE AND LIGHT-SENSITIVE BEHAVIOR IN NEMATODES

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The relative simplicity of the nematode nervous system is illustrated by the eye structure. Whereas the retina of image-forming eyes of vertebrates has over 100 million photoreceptors (PRs), and the pigment-cup eye of planaria is lined with 200 PRs, the pigment-spot eyes of nematode species consist of a shadowing pigment structure and only one PR. Why don't nematodes have more complex eyes? The limitation appears to be the small body size, a minimum size of PRs for sufficient sensitivity, and a minimum pathlength through the pigment for sufficient shadowing.

What information can such a simple eye obtain about the environment? In a transparent organism, such as a nematode, a PR by itself can only measure the fluence of light at one point in space. However, if it is moved through space by locomotion, the spatial distribution of light intensity can be sampled sequentially, and this information can be used to guide a trial and error motion to brighter or darker areas. For example, *Caenorhabditis elegans* (which lacks an eyespot) reacts to increases in light intensity with a reversal bout. Repeated episodes as it crawls in a light gradient could result in a net migration to darker regions. With the addition to the eye of a shadowing structure, true phototaxis is possible and migration would be more efficient. The PR in this case measures the fluence of light coming from the region of space delimited by the shadowing structure. If the orientation of the eye is varied by a scanning motion, the directional distribution of light incident on the organism can be sampled sequentially. *Oncholaimus vesicarius* and *Mermis nigrescens* use this information to direct their motion away from or towards a light source, respectively.

How does the nervous system accomplish this? By manipulating the light stimulus we have shown with *Mermis* that the scanning motion of the head is essential. This motion, and the shadowing structure, would cause a variation of the PR signal, and the phase of this signal with respect to the bending of the head would provide the information needed for orienting the locomotion towards the light source. Proprioceptive signals indicating the bending of the head would be required.

To directly investigate how the nervous system processes this information, we have begun an investigation of electrophysiological signals of *Mermis* and have successfully recorded the PR signal. We also plan to identify the PR cells in tissues of *Mermis* and *C. elegans* using a probe for opsin expression derived from nematode opsin DNA (see our poster) and use the published neural map of *C. elegans* to interpret our observations in terms of the connectivity.

Ws12.A

ABSTRACT

WHAT IS SELECTED FOR WHEN FITNESS VARIES?

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Random and unpredictable changes over a wide range of temporal and spatial scales are typical of most natural habitats. The life history and behaviour of most organisms have evolved therefore in response to the selection regime characteristic of such randomly varying environments.

A distinction has to be made between random events to which individual organisms are exposed independently of each other, and random events which affect the whole population.

In the first case, selection maximises the arithmetic mean fitness averaged over all the individuals in the same generation. The mean fitness provides a complete description of the behaviour of the system except when population size is small enough so that stochastic processes at the individual level become important.

In the second case, selection maximises the long term growth rate, which can be expressed as the geometric mean or the expected logarithm of the per generation growth rate. The distinction between the two cases becomes less clear when populations are made of many small partly isolated subpopulations, or in perennial organisms with overlapping generations.

The establishment probability of a single new mutant depends on the mean and the variance of the individual fitness. When favourable new mutants occur very rarely, the mutants with the higher establishment probabilities are more likely to dominate the population. Eventually. however, the mutant with the highest mean fitness will take over.

The same processes determine the order of establishment of rare new colonizing species.

Ws12.B

THE EVOLUTION OF LIFE HISTORIES IN VARIABLE ENVIRONMENTS

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I will present recent work concerning the evolutionary consequences of spreading reproduction throughout life in different ways. In particular, the evolutionary consequences of varying degrees of iteroparity are analyzed with the aid of a model which incorporates 1) age structure, 2) random environmental variability, 3) life histories of arbitrary length, 4) age-specific variation and covariation of vital rates, and 5) explicit genetic determination of life history phenotypes. Analysis indicates that there is no general advantage to a more iteroparous life history in a variable environment. The evolutionary fate of a more iteroparous life history relative to a less iteroparous one will depend upon the magnitude of environmental variability as well as upon the correlation structure of vital rates. In addition, with *indifference* curves I will describe the potential for neutral differentiation of life histories, i.e., very distinct life histories with identical stochastic growth rates can coexist within a population. Finally, I will describe the dynamical connection between life history evolution within and between populations.

Ws12.C EFFECTS OF STOCHASTIC ENVIRONMENTS ON EXTINCTION OF PLANT POPULATIONS

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The role of environmental and demographic stochasticity on population dynamics and extinction of plants is explored through simulation modeling based on field-collected data. Data are organized into projection matrices summarizing survival, growth, and fecundity of individuals, and analyses were made based on 26 published data sets. Environmental stochasticity (ES) generates significant extinction risk, and sensitivity to ES is greatest for populations with low finite rates of increase. Moderate levels of ES imply minimum viable population sizes on the order of 10^3-10^5, greater than required to counter demographic stochasticity. Extinction risk is predicted for *Pedicularis furbishiae* based on observed variation in demographic parameters. Early successional environments on mesic or wet soils, if undisturbed, support viable *Pedicularis* populations. However, elasticity analysis suggests that in this nonequilibrial system, selection pressures on various life history traits vary temporally and spatially. *Pedicularis* metapopulations are characterized by extinction and recolonization of local populations, and are constrained to occupy habitat with intermediate disturbance frequencies.

Ws12.D

LIFE HISTORY EVOLUTION WITH FLUCTUATING DEMOGRAPHIC PARAMETERS

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Environmental fluctuation in life history parameters does alter the optimization problem which evolving life histories are supposed to solve. Under density regulation, annual growth rate is influenced by the direct effect of fluctuation as well as an indirect effect due to fluctuating population density. The 'best' strategy should maximize the geometric mean of its fluctuating annual growth rate by a compromise between optimizing the average performance and lowering the variability of annual growth rate.

Assuming arbitrary fluctuation around a given arithmetic mean growth rate, we explore the mechanisms causing difference between 'best' strategy in fluctuating vs. stable environments. If the annual growth rate is a linear function of the fluctuating parameter and the density, the 'best' strategy (e.g. the 'best' reproductive effort) may be shifted since

(i) it should diminish the fluctuation of annual growth rate
  - by lowering the direct effect of environmental fluctuation and
  - by lowering the indirect effect due to density fluctuation;

(ii) it should adapt to an altered population density since the fluctuation changes (usually decreases) the average density as well.

By looking for the maximum of geometric mean growth rate we can find the 'best' strategy only if the joint distribution of environmental and density fluctuation is given. Density fluctuation, however, depends on the life history of the established population. Therefore 'best' strategy can be defined only as the 'best in a given population'. If a strategy is the 'best' in its own established population, then it corresponds to an ESS - though it is not sure to invade an other population. Since a long term fitness depends on the established strategy, coexistence of strategies or disadvantage of rare type may result. Connection to the concept of effective resources (i.e., the different nonlinear averages of the fluctuating resource) introduced by Levins 1979 is discussed. These ideas are illustrated by two specific examples: the lottery model presented in the poster session (Kisdi & Meszéna: Contest competition in a stochastic environment), and a simple model elucidating the relationship between fluctuation-mediated coexistence and resource-competition models.

Levins, R. (1979): Coexistence in variable environment. Am. Nat. 114(6): 765-783.

Ws12.E RESPONSE TO RISK: A STOCHASTIC EVOLUTIONARY GAME

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The standard deterministic view of natural selection is the maximization of the expected reproductive success (or fitness) of an individual. There are two forms of indeterminacy in fitness: interactions (games) between individuals and environmental uncertainty. In the former case, fitness is conditional upon others and is dealt with by game theory (using the concept of ESS); in the latter fitness is probabilistic and analyzed by expected utility theory, dynamic programming, and other probabilistic methods. A stochastic evolutionary game is developed to analyze jointly both types of indeterminacy in fitness. Simulation modeling is used to analyze extinction risk in the evolutionary game.

For a stochastic game we consider risk-sensitive behavior of individuals with two morphs (strategies). The "conservative" morph employs a strategy that minimizes predation risk at the cost of low foraging success; the "risky" strategy faces higher predation risk in order to increase potential forage intake. The two morphs differ in the mean-variance trade-offs in environmental and/or demographic variability. Environmental variance is density-independent; demographic variance is density-dependent. Either strategy may be capable of invading the other. Under repeated mutation, or immigration from neighboring populations, the dominant morph may switch randomly between the risky and conservative types.

Our analysis suggests that any given population may display considerable individual variation in terms of risk sensitivity. There are two critical components of evolutionary stability: risk of extinction and possibility of initial invasion. Environmental variance is critical to the risk of extinction; while demographic variance is crucial to the invasion by a rare mutant/immigrant. With both environmental and demographic variances, switch-over between the two morphs becomes considerably frequent. Thus repeated invasion by the equivalent or inferior morphs may be most likely if both types of variability affect the population. Here the average degree of risk aversion displayed by individuals is lower than that which would be predicted by individual risk-sensitivity analyses, because of averaging the individual risks over the population. Thus the indeterminacy of both types may easily affect the process of natural selection and its outcome.

Ws12.F

QUANTIFYING ENVIRONMENTAL VARIABILITY, AND ITS RELATIONSHIP TO PARENTAL BEHAVIOR AND POPULATION VIABILITY.

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Understanding adaptation and selection under stochastically fluctuating environments requires that the nature of environmental variability be understood. In this presentation, I examine several techniques for quantifying environmental variability using climatic data and then relate measures of environmental variation to the parental care behavior, clutch size, and population viability of a hawk that feeds almost solely on freshwater snails and ranges from tropical Florida (USA) to Buenos Aires (Argentina).

Techniques to examine environmental variation for short- and long-term trends will be discussed using both continuous and categorical data. Time series techniques with continuous data provide measures of seasonality (short-term) and periodicity (long-term) of environments. Colwell's (1974) indices provide similar measures with categorical data.

Parental care behavior and demography of the Snail Kite (*Rostrhamus sociabilis*) is characterized by: (1) mate desertion by either sex when the young are still in the nest, if food is abundant or when brood size is small; (2) a low probability of successfully nesting, but a high probability of fledging all young after a mate deserts, if a nest reaches this point; (3) multiple brooding and nest initiations for up to 9 months a year in high water years, but few nests in drought years; and (4) high survivorship and a population that grows rapidly during high water years, but crashes due to high mortality and low recruitment during drought years.

Water levels in kite habitats fluctuate highly unpredictably, but have well delineated drought-flood (long-term) cycles. Seasonality (short-term cycles) of rainfall may be related to geographical trends in kite clutch size and desertion behavior. Deterministic and stochastic simulations based on different environmental states show how periodicity of long-term cycles (drought) strongly affects kite population viability.

Ws12.G MAINTENANCE OF PHENOTYPIC VARIATION IN A FLUCTUATING ENVIRONMENT

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Four possible population responses to fluctuating selection are: 1) evolution of a single genotype that produces a single phenotype that performs better on average than all other single phenotypes under the range of environmental conditions experienced, 2) evolution of a single genotype that gives rise to a mixture of phenotypes differentially suited to the various environments, 3) evolution of a single genotype that gives rise to phenotypes that are environmentally inducible, and 4) maintenance of multiple genotypes each selected by a different environmental condition. Each of these possibilities has been investigated for a population of freshwater planktonic copepods that experiences fluctuating selection in the form of interannual variation in the intensity of fish predation. Years with seasonally early and intense predation select for copepods that produce dormant eggs (capable of withstanding fish predation) early in spring. Years with late and mild predation select for copepods that produce dormant eggs late in the season.

The copepods exhibit ecologically significant variation in the timing of dormancy, thus response #1 above is ruled out. Field experiments show that egg dormancy in not induced by the presence or absence of fish, thus ruling out response #3. In the laboratory, egg dormancy is seen to be a genetically heritable trait. Thus multiple phenotypes from a single genotype is not the explanation for the observed variation in egg dormancy (response #2), while maintenance of genetic variation is supported (response #4).

A mechanism for the maintenance of genetic variation may lie in the joint action of fluctuating selection in combination with overlapping generations caused by long-term egg dormancy.

Ws12.H

A GENETIC MODEL FOR CONDITIONAL STRATEGIES: APPLICATIONS AND IMPLICATIONS

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Conditional strategies are phenotypically plastic traits that allow for the expression of discrete phenotypic variants (tactics) in response to environmental cues. Such traits are one way in which adaptation in a stochastic environment can be achieved. Well known examples include morphological, physiological and behavioral traits that have been variously labeled as environmentally cued polymorphisms, polyphenisms, developmental conversions or switchs, autoregulatory morphogenesis and conditional choices. We model the effects of natural selection on conditional strategies using conventional methods of quantitative genetics by assuming that such strategies are polygenic threshold traits. We apply the model to examples of conditional strategies taken from the literature, describing ways in which the model can be used to make quantitative predictions about how a conditional strategy will respond to natural selection. The implications of the model for what the concept of a stochastic environment entails for the adaptive evolution and maintenance of conditional strategies by natural selection are discussed.

Ws12.I

THE ESS OF SAMPLING AND LEARNING BY FORAGING BEES.

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I assume that in natural ecosystems, there is an approximately steady state turnover of species and locations of flowering plants, and of individuals and species of foraging bees. The optimal level of the searching and sampling effort of any one bee is an increasing function of the number of newly available unexploited flowers, and of the uncertainty for that bee of the expected net energy reward in different plant species or in different patches. A newly born solitary bee has to learn all the necessary information about the nectar distribution. Thus, the individual uncertainty, and the optimal search effort of the bees, decrease in older bees as they get more experience by searching and learning the distribution of nectar sources in the whole area. On the other hand, the number of unexploited patches or species is a decreasing function of the total search effort of the bee population, which depends on the average search effort per bee and the bee density.

I model an ESS distribution of the optimal searching and sampling effort of the bees, which has the property that it generates the nectar distribution to which it is optimal. Several consequences of this model are discussed, i.e. the effects of the relative densities of different species of bees and flowers, and of the turnover rates of the bees and the flowers.

Ws12.J

ADAPTATION UNDER UNCERTAIN FLUCTUATIONS

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Natural selection is commonly viewed as the maximization of the expected (mean) reproductive success (fitness) of an individual. In a stochastic environment, however, the optimization criterion (principle) of natural selection is different from that in a constant environment. Under uncertainty, mean fitness is not a sole indicator of natural selection; the variance (or actually the distribution) of fitness becomes also the critical factor of selection.

We have two aspects of adaptation in a in a stochastic setting: (1) the imperfection of adaptation due to the unpredictability of the environment, and (2) the adaptive response to cope with stochasticity. The latter includes bet-hedging life history traits such as iteroparity and risk-spreading dispersal, phenotypic and developmental plasticity, adaptive behavioral responses such as learning. The former indicates that the general view of adaptation in a stochastic environment should be quite different from that considered without stochasticity. We focus on this generality of adaptation *in* a stochastic environment.

Stochasticity appears in different levels and forms in the environment: each component affects adaptation differently. We review two distinctive forms of stochasticity and their corresponding adaptation: phenotypic variances and environmental variances. Phenotypic variances include trait variance and quality variance, and environmental variances include short-term individual variance and long-term populational variance.

Adaptation is the evolutionary response of an organism against the environment: Environmental stasis yields the perfection of adaptation. In contrast, environmental stochasticity produces the variability and/or flexibility of adaptation, at the sake of imperfection. Thus environmental stochasticity could be one of the most creative factors in adaptive evolution.

Ws12.K A LIFE HISTORY TRADE OFF IN *DROSOPHILA* AND ITS IMPLICATIONS FOR COEXISTENCE.

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Developmental rate is one of the most important aspects of the competitive ability of *Drosophila* larvae. Fast growing larvae have a better chance to reach the critical mass for pupation in a competitive situation. Adult survival, however, may be negatively correlated with developmental rate like in many groups of related species. Superior larval competitors (species with a high developmental rate), may not survive long enough as adults to reach an oviposition site (a fermenting fruit), when these sites are scarce. In environments where the availability of fruits varies in space and time, inferior competitors (species with a low developmental rate) may be able to coexist with superior competitors by taking advantage of times when fruits are scarce.

This hypothesis was investigated in a guild of frugivorous *Drosophila* species from a rain forest in Panama. The trade off between developmental rate and adult survival could be demonstrated. An age structured population model indicated that coexistence of species having different strategies with respect to this trade off, is enhanced by fluctuations in food availability. The interval at which food was provided, influenced the outcome of competition between two species in a population cage experiment as predicted. Further support was provided by a full year of field data: species with a low developmental rate had a higher relative abundance when fruits were scarce.

We conclude that the differences in life history strategy enhance coexistence, alongside with resource partitioning and aggregation over patches.

Ws13.A GENETIC BACKGROUND OF PLASTICITY IN WING PATTERN OF A TROPICAL BUTTERFLY.

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In Bicyclus anynana a dry season form (dsf) and a wet season form (wsf) occur. The dsf is a pale brown butterfly, while the wsf has prominent eyespots and a white median band. In the laboratory a continuous range of forms can be obtained by raising larvae at different temperatures. In this research heritabilities were determined at a dsf-temperature of 17°C, a wsf-temperature of 28°C and two intermediate temperatures, 20°C and 23°C, which are rarely observed in the field. At the extreme (natural) temperatures h^2 was generally high, at the intermediate (unnatural) temperatures generally low. This is contrary to the expectation that h^2 would be low where canalization has occurred (17° and 28°), and high where it has not (20° and 23°). Possible causes for this result are discussed.

Ws13.B ANALYSING GENETICS OF REACTION NORMS IN *DAPHNIA MAGNA*.

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The interpretation of differences among reaction norms still bears many conceptual and statistical problems. Observing the phenotypes of cloned organisms like *Daphnia* over a range of different environments is the easiest way to visualize the concept of reaction norm. We studied the reaction norms of 21 life-history traits of *Daphnia magna* in 2 food levels.

A comparison of three methods of quantifying plasticity showed that the heritabilities of trait differences across environments and the portion of variation accounted for by the interaction term in a two-way ANOVA were consistent with each other, but cross environment genetic correlations gave qualitatively different results. Within trait groups the heritabilities of differences were positively correlated with the mean broad sense heritabilities of the two environments. We recommend using the difference between environments or the slopes of reaction norms across environments as a measure of plasticity.

Ws13.C STABLE PHENOTIPIC STRUCTURES AND MODELS OF POPULATION ADAPTATION

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Evolutionary models of self-interacting population under constant environment are considered. Various types of inheritance of phenotypes correspond to essentially different stable phenotypic structures. For the wide class of the types including the replicator dynamics, stable structures correspond to such optimality concepts as Nash equilibrium, ESS and dominance solution (Maynard Smith, 1984, Taylor and Jonker, 1978, Vasin, 1989, Nachbar, 1990). But some other types lack such a correspondence.

In order to justify this correspondence for natural populations I consider a model, where the population is divided into self-replicated subpopulations with different types of the inheritance. I prove that the mentioned criteria of optimality determine stable phenotipic structures of the whole population,if the initial set of the types is broad enough.

Evolutionary models of a population interacting with environment ,whose parameters change through a large number of generations, are also considered. The ability for adaptation to such changes is investigated for different types of inheritance. I ascertain, what types guarantee the mean population fitness to be close to maximum under any environment.

Ws13.D EXPERIMENTAL STUDY OF GENOTYPE ⋆ ENVIRONMENT INTERACTIONS IN *DAPHNIA MAGNA*.

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Are the reaction norms of *Daphnia* clones parallel, or, in other words, are there genotype-by-environment interactions in life-history traits? If yes, do the reaction norms cross over a wide environment gradient? In which environments, rich or poor, are the interclonal differences higher?

15 clones of *Daphnia magna* were kept during 2 generations under 6 different food levels from 6 to 200 thousand cells of *Ankistrodesmus* per ml. In the second generation length at birth, length and age at maturity, length and number of offspring in the first 5 clutches were measured. The interactions were detected by means of 2-way mixed model ANOVAs and by estimating the heterogeneity of reaction norm slopes within and between clones. The later method provided the heritability of slopes. Genetic correlations between the same traits under marginal food levels were used to test for the crossing of reaction norms.

Strong interactions were detected for neonate length in both early and late clutches. Genetical heterogeneity of reaction norm slopes was found also for length at maturity and fecundity for which the interaction term in 2-way ANOVA was marginally or not significant. Up to 53% of variation in slopes was caused by genetical rather then by random factors. Low cross-environment correlations suggested that many of the reaction norms were crossing. This does not hold for the neonate length in the late clutches. The genetic variation of length at maturity and fecundity was higher in the best environments then in the poorest. The same was shown for the first principle component calculated from all the traits.

Ws13.E

THE MAINTENANCE OF POLYGENIC VARIABILITY: ARBITRARY STRENGTH OF SELECTION

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The equations describing multilocus dynamics with account of selection and recombination are very complex and cannot be investigated without simplifying assumptions. To simplify the analysis one usually assumes that the genetic system is in linkage equilibrium. Linkage equilibrium holds approximately if selection is much weaker than recombination. It is quite probable that the selection in natural population is, in general, weak. At the same time, new experimental data (Endler, 1986) give evidence that a stronger selection is not just an exotic exception. In this context it is important to analyze the behavior of multilocus systems when selection is not weak.

The problem considered here can be formulated as follows. Let the assumption about linkage equilibrium is used to prove the maintenance of polygenic variability in a quantitative genetic model and to predict allele or gamete frequencies, genic or genotypic variances, mean heterozygosity or the mean fitness of the population. Would these qualitative and quantitative results be valid if selection is not really weak?

To answer this question I consider a class of viability models that generalizes the standard additive model for the case of pairwise additive by additive epistatic interactions. Conditions for existence and stability of steady states in this model are determined. Using regular perturbation techniques, the case when selection is weaker than recombination and the case when selection is stronger than recombination are investigated. The results obtained are used to make conclusions on the dependence of the population characteristics on the relation between the strength of selection and the recombination rate. I argue that significant changes in steady population characteristics can be observed under reasonably strong selection.

Ws14.A AGE AND SIZE AT MATURITY IN A PATCHY ENVIRONMENT: MAXIMIZATION OF FITNESS MEASURE VERSUS EVOLUTIONARY STABILITY

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The evolution of age at maturity defined as the age at switching between allocating resources to growth and to reproduction is modelled in a patchy environment. Two approaches are compared: the simple optimization approach in which mean fitness (lifetime energy allocation to reproduction) is maximized while ignoring individual differences in strategies, and the ESS approach. The predictions of these two approaches differ: when two or more individuals compete in a patch the ESS is to mature later and at larger size than the strategy maximizing the fitness measure. This discrepancy results from frequency-dependence brought about by considering the resources and their exploitation explicitly. Once the ESS is established, the proportion of resources converted to offspring is smaller than the maximum possible, and hence the lifetime offspring production is decreased. The results suggest that an adaptive plastic response to the presence of competitors may aggravate the depression of fecundity resulting from competitive resource depletion.

Ws14.B

The evolution of life histories in spatially heterogeneous environments: Optimal reaction norms revisited

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Of several ways to model the evolution of optimal reaction norms, only some have been explored in detail. Here a generalization of the Euler-Lotka equation is derived that defines fitness in a spatially heterogeneous environment. In this case, maximizing fitness (the rate of increase over all habitats) is equivalent to maximizing the reproductive value of newborn in each habitat but not to maximizing the rate of increase that would result if individuals in each habitat were an isolated population. The equation can be used to find optimal reaction norms for life history traits, and some examples of optimal reaction norms for age at maturity are calculated. In contrast to previous results, the optimal strategy for an individual in one microhabitat is not independent of the conditions encountered by individuals in other microhabitats. Both the frequency and the quality of the microhabitats influence the rate of approach to the optimal reaction norm and its position. Microhabitat variation primarily in fecundity schedules leads to quite different reaction norms than does microhabitat variation primarily in mortality schedules. The equation is also used to calculate the sensitivity of fitness to departures of a trait in a particular habitat from the optimal reaction norm. Selection pressure is positively correlated with the quality and the frequency of the habitat in wich the trait is expressed. A formula for the relative importance of these two factors allows predictions of the habitat in which the variance in phenotypes about the optimal reaction norm should be smallest.

Ws14.C

NEGATIVE CORRELATION = TRADE-OFF? MODELLING INDIVIDUAL OPTIMIZATION

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Individual optimization is often invoked to explain the positive correlations found between life history parameters instead of negative ones which would correspond to trade-offs in life history theory. A common view is that better quality should increase the optimal fecundity as well as survivals related to the optimal fecundity yielding positive correlations between parameters even if they are traded off. On the other hand, a negative correlation is considered as an evidence for the existence of a trade-off. This view is criticized by a simple analytic model of individual optimization.

External and internal factors influencing the optimal strategy are included into a "quality" parameter in the model. Different qualities may embrace differences in microhabitats, territory, food availability, developmental influences etc.; moreover, non-additive genetic differences. Better quality of a parent may increase its own survival, juvenile survival of its offsprings, or both. On the other hand, increasing fecundity may reduce juvenile and/or parental survival as a cost of reproduction. According to their quality, parents can adjust their fecundity to maximize the reproductive value.

If better quality does increase the optimal fecundity and overcompensates the cost of increased fecundity then individual optimization truly leads to positive correlations. If better quality increases fecundity but cannot compensate for the cost, there is a negative relationship between fecundity and survival. Juvenile and parental survival may be negatively related without a trade-off between them if the cost of increased fecundity is overcompensated by better quality for one of them, but not for the other.

In opposite to the common view better quality may decrease the optimal fecundity: increasing parental survival may make the parent not to risk its own good survival by a high reproductive effort. Here a negative correlation between juvenile survival and fecundity may emerge even if they are not traded-off. Assume that juvenile survival is increased by better quality but it is not traded-off with fecundity. In this case better quality reducing fecundity and increasing juvenile survival creates a negative relationship between them despite of the lack of a trade-off. Thus we can conclude that neither a positive correlation excludes, nor a negative correlation alone proves the existence of a trade-off under individual optimization.

Ws14.D OPTIMAL ALLOCATION OF ENERGY TO GROWTH AND REPRODUCTION AN ASEASONAL ENVIRONMENT: A NULL MODEL FOR STUDYING THE EFFECT OF SEASONALITY.

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Seasonality is among the strongest selection forces in life history evolution. This may be a reason that the models of optimal energy allocation for annual organisms were published before the models for aseasonal environments. Environments with constant conditions are rare in nature if they exist at all. Such environments can be treated, however, as idealizations. Development of both physical sciences and population biology proved usefulness of nonexistent idealizations.

In my opinion, the best way to study the effect of seasonality is to start from the models for aseasonal situation. The predictions from these models can be considered a null hypothesis for the effect of seasonality. Seasonality should be incorporated into the models in two steps. First, the year should be split into two parts, i.e., breeding and nonbreeding seasons, each of them being uniform. Predictions from the models of this kind can be considered a null hypothesis for the effect of nonuniform conditions, during the breeding seasons. For example it is always optimal in uniform breeding season to grow than to allocate energy to reproduction that should be completed just at the end of the season. If conditions for offspring survival are much better early in the season, reproduction may precede growth. Comparing predictions from the models for uniform and nonuniform seasons allows to calculate how much such a shift of reproduction costs in the sense of offspring number. Similarly, it can be checked whether smaller size of male individuals in dioecious plants can be explained by their pik allocation of energy to reproduction earlier in the season in comparison to females.

Ws14.E

Remarks on density-dependent optimization

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What is maximized?

I present a generalization of the well-known equivalence of maximizing population density and maximizing per capita rate of increase. In a population limited by only one resource selection tends to maximize an effective density corresponding to the exploitation of the resource. Two examples are discussed. If individuals in different age or phenotypic groups load the environment to different extent, these differences have to be accounted for when the effective density is calculated. In lottery models inverse of the settling probability of juveniles plays the role of the effective density.

How does a change in environment modify a density-dependent multivariate optimum?

In a density-dependent population any change of the environment modify the evolutionary optimum directly, as well as due to the change of the equilibrium density, indirectly. Assuming, that the considered change in the environment is infinitesimally small, it can be shown that the change of the optimum of a trait can be calculated as the spread of the direct environmental and the density effect via a number of chains of traits. Contributions of these causality chains can be guessed qualitatively. An example with two independent variable (fertility and parental care) and connection to age-dependent selection is discussed.

Ws14.F MODELS FOR OPTIMAL GROWTH AND REPRODUCTION OF *DAPHNIA*

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We constructed a discrete-time model with overlapping generations for growth and reproduction of the cladoceran *Daphnia* and solved it numerically for resource allocation patterns to maximize the intrinsic rate of increase r under various environmental conditions. Conditions modelled include different functional forms for the size-dependencies of predation risk and net production. Growth after maturity can maximize r when net production and survivorship increase with body size. The optimal period for growth after maturity increases with the reproductive life span, but the life span need not be long to favor growth. The shape of the net production curve influences the extent to which body size is increased by delaying maturity or by growing after maturity. When net production increases with body size, but survivorship does not, growth after maturity is not optimal. However, simultaneous allocation to growth and reproduction can occur in the instar (time step) preceding maturity.

We also solved the model for resource allocation patterns to maximize the geometric mean number of resting eggs produced, which measures fitness when the season favorable to growth has a limited and variable duration. These optimal allocation patterns differ quantitatively and qualitatively from those that maximize r. For the corresponding predation risk and net production models, reproduction generally occurs earlier and more growth occurs after maturity in the optimal strategy for the variable environment. Growth after maturity occurs with all predation risk models. Increasing the mean or variance of season length causes convergence toward the life history that maximizes r.

Ws15.A GEOMETRICAL SYMMETRIES OF BIOLOGICAL FORMS

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Symmetry is a widely used concept in biology in the global description of organisms. Our goal is to give a rigorous mathematical treatment of geometrical symmetries, including continuous Killing and conformal Killing symmetries as well as discrete ones. We show that, due to the structure of 3 dimensional Euclidean space the maximal possible conformal Killing symmetry is a 10 parameter geometrical transformation, of which 6 parameters give the usual E(3) group keeping all the distances, while the 4 further parameters generate very special similarity rescalings. Since the E(3) group has a very limited set of possible hierarchies of subgroups, the possible steps from total E(3) of Haeckel's hypothetic *Moraea* to bilateral symmetry of higher animals (and beyond) can be classified into a very few evolutionary pathways. Some candidates (as e.g. radially symmetric *Coelenteratae* or axially symmetric (?) *Nematodae*) are mentioned for intermediate steps of symmetry breaking.

Ws15.B

EVOLUTIONARY CONSERVATION OF A MORPHOGENETIC MECHANISM

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Many properties of the organisms and their parts can be represented by hierarchical infolding of shell/membrane systems organizing into tubes, vesicles etc. We study this problem on the basis of a simple mechanical model and mechanochemically. The basic problem solved by the model is to find shapes for closed surfaces of given area and enclosed volume, for which the bending energy density of a bilayer shell/membrane is minimal (Verhas, Liquid Cristals 3: 1183-1190, 1988 ; Lipowsky, Nature, 349: 475-481,1991). The evolutionary pathways of shape transformations simulated by the model include self-reproduction by vesicle fission, variations of gastrulation, generation of spatially periodic shapes etc. From this observation we infer that the evolutionary variation of bending elasticity in molecular and cellular layers seems to be conserved in the 'tinkering' of novel shape variation. An approach will be suggested to interpret the dynamic couplings of information, mechanical deformation and historical contingencies related to the model.

Ws15.C

SPATIOTEMPORAL RECONSTRUCTION OF C. ELEGANS CELL LINEAGE BY COMPUTER AND ITS EVOLUTIONARY IMPLICATIONS

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The spatiotemporal unfolding of the cell lineage of *Caenorhabditis elegans* (Sulston et al. Dev. Biol. **100**: 64-119. 1983) has been reconstructed by computer. Real parameters of the *C. elegans* development have been estimated and analyzed mathematically in a theoretical framework. This reconstruction can throw light on the origin of form, symmetry and topology of a 'star worm'. The analysis of the worm suggests possible constraints for an explanation of the evolutionary invariance of its developmental design.

Ws15.D SYMMETRY AND TOPOLOGY IN CELLULAR AUTOMATA TRANSFORMATIONS I.: A TOPOLOGIC MODEL OF THE FIBONACCI PLANT STRUCTURES

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The basic concepts and principles in this model of Fibonacci plant structures have been based on a new approach of symmetry: symmetry by cellular automata. This approach defines a recast of laws used in morphogenetic construction of Fibonacci structure development. Known characteristics of such structures have been divided to initial and border conditions on one side, and to cellular automata operations on the other side. This distinction is both sensitive and suitable to separate the topological aspects in the transformation processes of the Fibonacci structure. The two conditions preserve the symmetry in the structure of Fibonacci plants in two forms: in the initial conditions and in the existence of enantiomorphous pairs /Bérczi, 1976, 1989/, while the operations by cellular automata work as local, weak topological transformators which rearrange the neighbours of "cells".

The new cast of conditions and operation in my model shows, that the sequence of Fibonacci plant structures can be ordered into a model which emphsizes the topologic character of both the locally homogeneous transformations and the whole Fibonacci structure family, too. Morover, the generalization of the operation has been made possible to introduce a classification of lattices on the cylinder /Bérczi, 1990/.

Ws15.E SYMMETRY AND TOPOLOGY IN CELLULAR AUTOMATA TRANSFORMATIONS I.: A TOPOLOGIC MODEL OF THE FIBONACCI PLANT STRUCTURES

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Ws15.F SYMMETRY AND ASYMMETRY IN THE EVOLUTION OF VERTEBRATES

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Since their first emergence (500 million years ago) Vertebrates have a bilateral symmetry.There is an appearent symmetry between the two sides of the body along a plane might be placed across the sagittal direction. This corresponds to the vertebral column and from phylogenetical point of view this is the most ancient symmetry. The symmetric position of the motorial system and also of certain internal organs is the consequence of this vertebrate column symmetry. In the more evolved groups of Vertebrates in addition to the sagittal-vertebral symmetry other secondary symmetry planes appear on the extremities. Unicellular bodies participating in the inner building of the body (like e.g. blood) show a radial symmetry while the elementary parts of solid materials have symmetry relations according to the system of crystallization characteristic of their own.

At the same time there are also symmetric parts within the body of Vertebrates, like e.g. heart, lung, digestive organs or the cellular structure of tissues.

Among Vertebrates either the development of an asymmetry within one individual (individual variations) can be observed or a functional evolutionary distortion. A frequent variant of the latter is adaptation while a special case of it is the development of the characteristic right-left side dominances during the hominization process. The lecture hints at also the questions related to cranial symmetry in certain Hominoid finds.

Ws15.G MORPHOLOGICAL HETEROCHRONISM IN HUMAN EVOLUTION

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In the hominoid and hominid phases of hominization, during the last 30 million years each morphological characteristics generally considered to be as morphologically diagnostic went through a development process at a different speed of their own, in a heterochronous manner. The aim of this lecture is to demonstrate the different evolutionary patterns and paces of morphological alterations of the facial part and of the neurocranium as well as of the dentition, based on the results of recent studies. In addition the lecture enumerates the questions referring to the heterochronous appearence of certain hominid specifics, like e.g. erect posture, tool-making, the use of fire or articulated speech. The knowledge and investigation of heterochronism may provide a chance to indentify, at least hypothetically, the phylogenetically missing links especially between African and Eurasian Hominoids.

Ws15.H

LATERALIZATION OF HUMAN BRAIN AS SPONTANEOUS SYMMETRY BREAKING

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A model calculation is shown for the lateralization of the early hominid brain. The toy model uses the following crude assumptions: i) a single gene controls the asymmetry; ii) the asymmetric brain results in a higher fitness; iii) the gene has 3 alleles as "symmetric", "right handed" and "left handed".

The numerical results are as follows: i) symmetric initial conditions lead to symmetric states, but above a critical value of increased fitness the symmetric state is composed from substantial amounts of left- and right-handed individuals; ii) below the critical fitness moderate initial asymmetries die out; iii) above the critical point any initial asymmetry results in total final asymmetry; iv) having this asymmetry been once established, any backcross to the wild symmetric population means an asymmetric initial condition, so again the process ends in total asymmetry in the original direction.

POSTERS

Ws16 Mathematical problems of the theory of evolution

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At the workshop the following problems will be discussed:

1. Nature of the constraints on the set of evolutionary trajectories.
2. Non-linear phenomena in evolving biological systems.
   - What kinds of interesting dynamical behaviour can be generated by non-linearities specific for biological systems?
   - What sort of biological non-linearities are sufficient for the appearance of dissipative structures?
3. The different meanings of stability and the concept of hierarchical stability.
4. The structure and canonization of the mathematical theory of biological evolution. What are the criterias for modelling selection?

PoA	GENOME EVOLUTION
PoB	EVOLUTIONARY CYTOGENETICS
PoBI	Karyotype evolution
PoBII	Other evolutionary cytogenetic studies
PoC	PHENOTYPIC AND GENETIC VARIABILITY WITHIN SPECIES
PoCI	Ecological aspects
PoCII	Human population genetics
PoCIII	Morphological traits
PoD	MATING SYSTEMS AND LIFE-HISTORY STRATEGIES IN PLANTS
PoE	ANIMAL MATING PATTERNS AND PARTHENOGENESIS
PoF	ANIMAL LIFE-HISTORY EVOLUTION
PoG	HYBRID ZONES AND SPECIATION
PoH	MOLECULAR PHYLOGENETICS
PoHI	Use of mtDNA
PoHII	Other studies in molecular phylogenetics
PoI	EVOLUTIONARY MORPHOMETRY
PoJ	MODELLING EVOLUTIONARY PROCESSES
PoJI	Evolution in structured populations
PoJII	Other models on evolution
PoK	ECOLOGICAL STUDIES AND EVOLUTION
PoL	IDEAS ON EVOLUTION

PoA.1 MULTIGENIC FAMILIES: RELAY-RACE COEVOLUTION AND RECAPITULATION

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Multigenic families (MF) represent the most promissing level of genome organization in studying the molecular bases of both developmental and evolutionary processes (Bodmer, 1981). Haldane's dilemma permits MFs to coevolve progressively towards complication by their structure in a relay-race mode (Rodin, 1985) through sequential duplication of ancestral genes. Each MF is in turn noted by a definite ontogenetic order of its gene expression. If any earlier expressed gene resembles the ancestral gene rather than its later expressed homolog, this could be considered as *a molecular recapitulation* (Zuckerkandl, 1968). However, the first comparison of human complete γ (fetal) and β (adult) chains that Zuckerkandl made in relation to α chain revealed no evidence in favour of the phenomenon. In contrast, we show here that molecular recapitulation does exist in MFs provided it is sites involved into selectively important functional bonds that are compared and K-selection control runs evolving species. For example, the number of non-synonymous substitutions in the codons of the functional centers of human globins increases considerably from the lowest value for embrionic (ε) genes towards the highest one for adult (α,β,δ) genes, while the total (for the whole sequence) number of mutations detected by means of the evolutionary tree construction is almost constant. A similar tendency have been found in globin genes of *Capra hircus* and *Xenopus laevis*, in Ig genes, in chorion protein genes, in the homeoboxes of segmentation genes of *D. melanogaster*, *etc*.

The relay-race principle and the gene recapitulation phenomenon are very instrumental in explaining some regularities and paradoxes of onto- and phylogeneses, namely: the dichotomic switches of gene expression during the development, allelic and isotypic constraints in the functioning of Ig genes, the clonal-selective mode of the immune response, the possible role of extra- and intragenome parasites (HIV-like viruses, Alu-like retroposons *etc*) during progressive molecular coevolution.

PoA.2 PUTATIVE ORIGIN AND FUNCTION OF THE COI-COII INTERGENIC REGION OF *APIS MELLIFERA* L. MITOCHONDRIAL DNA

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The mitochondrial genome of honeybees is characterized by the presence of a long intergenic sequence located between the COI and COII genes. In addition, the length of this sequence varies between and within subspecies. Four length categories (200bp, 250bp, 450bp and 650bp) have been found in 61 sampled colonies. Analysis of the sequence of the largest type reveal the existence of two units: P (54bp, 100% A+T) and Q (196bp, 93.4% A+T). The lengths encountered in the sample are explained by the following structural combinations: Q, PQ, PQQ and PQQQ. According to similarities in primary and secondary structures, the sequence Q has been divided into three parts : Q_1 (similar to the 3' end of the COI gene), Q_2 (similar to the neighbouring $tRNA^{leu}$ gene) and Q_3 (highly similar to the P sequence). These relationships led us to hypothesize that these sequences, which do not have any counterpart in *Drosophila yakuba* mtDNA, arose by tandem duplication. The successive molecular events have been inferred from the analysis of the other species of the genus *Apis*. The usual location of length variations in mtDNA control regions prompted us to examine the hypothesis that this COI-COII intergenic region might contain an origin of replication. High A+T content, stability profile, hairpin and clover-leaf putative secondary structures are all in favor of this hypothesis.

PoA.3 RETROVIRAL LIKE-FEATURES IN THE MONOMER OF THE MAJOR SATELLITE DNA FROM THE SOUTH AMERICAN RODENTS OF THE GENUS CTENOMYS

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A major satellite DNA from the South American rodents of the genus Ctenomys was recently described by us (Rossi et al. 1990. Mol. Biol.Evol.7:340-350). The satellite momomer termed RPCS (Repetitive PvuII Ctenomys sequence) is 337 bp long and 42% C+G. Here, we present data suggesting that RPCS arose by integration /deletion of retroviral DNA.

Retrovirus have transcriptional regulatory elements within the U3 region of their long terminal repeats (LTR) which flank the provirus. A polypurine (pp) region involved in the initiation of the DNA plus-strand synthesis marks the beginning of this U3 region. A pp region similar to the one observed in retroviral genomes is present in RPCS. Following the pp track most retroviruses also possess a short sequence which usually is AATG. The tetranucleotide CATG follows the pp track present in RPCS. Enhancers elements are located mainly within the U3 region of retroviral LTR. A concensus core sequence GTGGA/TA/TA/T is found in many viral and eukaryotic enhancers. Similar sequences are present in RPCS.

Nuclear factors involved in viral replication, transcription, pathogenesis and tissue-tropism interact with sequences within the enhancer region. We notice the presence in RPCS of two sequences which are similar to the concensus binding motif of nuclear factor 1 (NF1), implicated in the regulation of DNA replication and transcription. Another enhancer binding is the C/EBP protein, which binds the CCAAT sequence. A CCAAT sequence and a variation of this box, are also present in RPCS. Another set of concensus sequences that C/EBP protein binds are also present in RPCS. TATA box signals are present in the U3 region of retroviral LTRs. In RPCS a TATA box is also present. The signal of polyadenilation (AATAAA) downstream from the transcription start of retroviruses. For several eucaryotic genes and retroviruses, the dinucleotide CA is located at the polyA addition site about 20 bp downstream the polyadenilation signal. According to its position, the AAGAAA hexanucleotide and the CA dinucleotide, present in RPCS, ressemble retroviral polyadenilation signals.

Taken together, our analyses strongly suggest that the monomer of the major satellite DNA from the South American caviomorph rodents of the genus Ctenomys, was acquired from the U3-R region of the LTR of a retroviral genome. This raises a number of intresting questions about the role that this sequence may have played in shaping the host genome throughout evolution.

PoA.4 THE EVOLUTION OF COMPENSATORY SUBSTITUTIONS IN *DROSOPHILA* RIBOSOMAL RNA

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It has often been suggested that the frequently observed A-U <-> G-C compensatory substitutions in helices of RNA occur through slightly deleterious G.U. The involvement of mutation mechanisms specific to compensatory base changes has also been proposed by some authors. We have tested the hypothesis that compensatory susbtitutions evolve through slightly deleterious intermediate states. We have determined the sequence and secondary structure of two rapidly evolving domains of the large subunit ribosomal RNA for Brachycerous Diptera (about 550 nucleotides), and have scored substitutions in these two domains for a set of 82 related species of *Drosophila*. We have evaluated the rate of evolution of compensatory substitutions and the nature of intermediate states. The results of this analysis are compared to expectations of simple models of slightly deleterious substitutions. These results suggest several hypotheses about longer term evolution.

PoA.5 EVOLUTION OF SATELLITE DNA IN *DOLICHOPODA* CAVE CRICKETS

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Highly repetitive satellite DNA sequences from the genome of the cave cricket Dolichopoda schiavazzii (Tuscany,Italy) have been cloned in the pUC plasmid and 20 clones containing monomers, dimers and trimers of the basic unit were sequenced. The basic sequence has a length of 102 bp and hybridizes with filterbound genomic DNA of D.schiavazzii producing hybridization bands at fragment lengths in multiples of 102bp. A similar, although much weaker, pattern of hybridization was found in other related Italian species, D.geniculata, D.laetitiae, D.baccettii, D.aegilion, indicating the occurrence of the same sequence also tandemly repeated. In these species the sequence is present with low copy number while it is species specifically amplificated only in D.Schiavazzii, where the highly repetitive sequences contribute 30-60% of the entire genome.

The results of the sequencing show that here is only a low sequence variability, 5 to 10%, among all members of this satellite DNA. The "neighbor" repeats of dimers and trimers show the same variability as in randomly chosen repeats. This seems to indicate that a homogenizing process has the same efficiency among all copies indipendently where they are located in the genome.

The evolutionary relationships among the various Dolichopoda species here considered were formerly investigated on morphological, allozymic and scDNA hybridization grounds.

On the basis of allozyme genetic distance data, D.schiavazzii appears to have diverged from its closest relative D.aegilion roughly since 2 Myr. Since D.aegilion and its sister species D.baccettii showed a much lower amount of the same repeated sequences, our results suggest that the high repetitivity of the 102bp satellite DNA has probably evolved within the Pleistocene.

PoA.6 COEVOLUTION BETWEEN GENOME AND GENOME PARASITES AS A WAY TOWARDS THE GENOMES COMPLICATION

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The processes of concerted variability which actually result from the co-operation of such entities as on the one hand various mobile elements (a kind of "genome parasite"-GP) and on the other the genome itself ("host"), have been studied in this work.

Several systems of differential equations have been created and studied as well in order to model the following situations: 1) The GP is insertable in the vacant sites only, its free state (outside the "host" but inside the cell) being not durable; 2) The GP is insertable in the vacant sites only, its free state being durable; 3) The GP is insertable in both vacant and occupied sites ("molecular memory"), its free state being not durable (mammalian *Alu*-like repeats taken as its prototype); 4) The GP is insertable in both vacant and occupied sites; able to exist "on its own" (retroviruses taken as its prototype). At that we admitted that the genome is tolerant to the "selfish" proliferation of GP until the share of the occupied sites exceeds the limit 1/K. Our analysis revealed that the coevolutionary complication of GP - from the simplest, which is only able to be inserted in vacant sites; through further acquirement of tail repeats ("molecular memory") and to quite complexes with an extragenomial lifesyle - is accompanied with an interchange of selective coevolutionary restrictions on the genome size: upper limit - no limit - lower limit. Thus, genetically mobile elements may be regarded as an inner factor of progressive, coevolutionarily motivated complication of genomes.

PoA.7 EVOLUTION OF PROCARIOTES AND EUCARIOTES

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The evolutionary transition from an old to a new related species demands that new functionally sensible fragments of the genom be constructed, consisting of a certain sequence of nucleotide pairs or fragments of the old genom. Any given single mutation (including both single point and macromutations) only have a probability of 10^{-10} per one nucleotide site per division. Two concrete simultaneous single mutations may occur at a probability of about unit in a population including 10^{20} individuals, and three such mutations – in a population of 10^{30} individuals. Such numbers are not reached by any multicellular species. However procariote species generate up to 10^{30} individuals over several hundred years. Procariotes are capable of constructing new functionally sensible fragments of a genom. Such fragments may then be propagated among the eucariotes via horizontal transfer, thus stimulating their evolution. In the absence of horizontal transfer of the genetic material from procariotes the eucariotes become only capable of keeping up their specific stability and would not evolve.

As compared to the process of relaxation of the decay genotypes to the old normal genotype by means of single reverse mutations a probabilistic barrier is encountered in the process of transition from old to new related species. The existence of such a barrier explains the observed stability of the genom of each species, its capability to stabilize the optimal environmental conditions, and also the lack of transitory forms between separate species. The latter feature follows the ergodicity principle and is observed both in space, for any related contemporary species, and in time – for any related species down the paleontological chronicle.

PoA.8

DISTRIBUTION OF INSERTION SEQUENCES (IS) ON THE CHROMOSOME OF *E.COLI*: EVOLUTION OVER 20 YEARS.

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Most studies on frequencies and mechanisms of spontaneous mutagenesis are based on particular genes which are often chosen because they allow for easy screening for the incurring mutants. Such studies may be biased by the relatively small target offered to mutations, since at least some processes bringing about the alteration of genetic information are known not to occur fully at random along DNA molecules. Therefore we decided to concentrate on a screening for bacterial subclones having DNA rearrangements. Since IS transposition is expected to contribute in essential way to chromosomal DNA rearrangements, we started this approach by using as hybridization probes internal fragments of various IS elements after a restriction fragment length polymorphism (RFLP) analysis of the *E.coli* chromosome. The strain 3110 has been kept as stab cultures for up to 20 years in our lab and stabs of different ages were compared for their genetic variability. For the elder stabs, an impressive variety in the location of hybridizing DNA fragments was detected from independent colonies grown from one inoculum, ie. 60% of the subclones had different patterns. Moreover some individuals were shown to have several transpositions of different IS elements. These results reflect a high degree of genetic plasticity under the physiological conditions of stab cultures which do not allow for extensive propagation of the bacteria. Such a large amount of genetic variability accumulated in a clone derived from one single cell 20 years ago is currently analysed with multivariate statistical methods to search for the patterns of differentition among different IS elements.

PoBI.1

KARYOTYPE EVOLUTION IN SOME GROUPS OF THE PENTATOMOMORPHAN BUGS (INSECTA, HETEROPTERA)

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The karyotypes of 46 species from the relative primitive Pentatomomorphan families (Aradidae, Piesmatidae, Berytidae, Lygaeidae, Pyrrhocoridae) have been investigated. The male diploid chromosome numbers have been found to vary from 10 to 42, the numbers 14 (12+XY) and 16 (14+XY) being the most common. The last two chromosome numbers may considered not only as modal but also as the initial ones for the families enumerated and for the infraorder Pentatomomorpha as a whole. The chromosomes are of a holokinetic type in all cases.

The sex chromosomes mechanisms are fairly variable in the family investigated. In Aradidae, 1 species have $X_1X_2X_3Y$, 6 species – X_1X_2Y, 6 species - XY, and in one species subspecies with both X_1X_2Y and XY occur. In Piesmatidae and Berytidae all 17 species studied have XY in males. In Lygaeidae (altogether, including literature data near 330 species were investigated) XY (rarely X_nY and XY_n) have been found in 300 species and XO - in 30 species (nearly all in Rhyparochrominae). The Pyrrhocoridae have XO or X_1X_2O in all 16 species examined. Apparently XX:XY system may be considered as a modal one in the primitive families and in the infraorder as a whole. The idea of Ueshima (1979) that the XX:XO system is secondary in Pentatomomorpha is confirmed.

The problem of m-chromosomes in bugs is discussed and their origin from sex chromosomes is supposed.

In the evolution of the primitive Pentatomomorphan families the fragmentations of chromosomes occured more often than fusions.

PoBI.2 CHROMOSOME SETS OF TREMATODES: THEIR EVOLUTION, PHYLOGENY, RELATIONSHIPS WITH FIRST INTERMEDIATE HOSTS

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The intensive karyological studies of trematodes from the different groups allow to state the following: 1. There are 4 main phyletic lines of trematodes: Echinostomatoidea, Strigeoidea, Opisthorchoidea and Plagiorchoidea. It is being postulated that the first line developed from 22 single-armed chromosome sets. Ancestral karyotype of Strigeoidea line may be consistent of 20, Opisthorchoidea -18, Plagiorchoidea - 24 one-armed genome units.

2. Pericentric inversions, accumulation of DNA repetitive sequences are the driving forces in the early stages of the karyotype evolution. The next stages are marked by robertsonian translocations, reduction in chromosome numbers and symmetrization of karyotypes.

3. The rate of karyological evolution of trematodes is relatively low. Diploid number of chromosomes change from 12 to 28. Chromosome sets with 20 and 22 elements predominate.

4. Formation of huge gene linkage groups, containing up to 35-38% of the total length of haploid sets.

5. In comparison with the first intermediate hosts the chromosome sets of trematodes are very stable and there are no evidences of cytogetical effects of pollutants.

6. In some genera of Echinostomatoidea were determine correlation between level of their karyological divergence and phylogenetic relationships of snails.

PoBI.3

HETEROCHROMATIN AND SPECIATION IN MICROTUS SAVII (RODENTIA-ARVICOLIDAE)

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The role of heterochromatin in speciation is still not fully understood (see Sharma et al. 1990). However cytogenetic studies of Microtus savii (Rodentia Arvicolidae) could provide data to shed new light on this problem.

This species is present in the Italian peninsula and in Sicily and hence has an allopatric distribution. From a morphological and karyological point of view the specimens from Sicily do not differ from those of North and Central Italy (Krapp and Winking 1976). Hovewer in Calabria (Southern Italy) there is a different subspecies: Microtus savii brachycercus Lehmann, 1961, which differs both morphologically and karyologically. Its sex chromosomes show large blocks of heterochromatin. F1 crosses were obtained whithout any reduction of fertility, but the F2 was absent because of male total sterility.

Finally a third chromosome form is present in Southern Italy, but in this case the X chromosome differ from that of M. savii savii for a pericentric inversion with no additional heterochromatin. This form does not morphologically differ from other M. savii savii (Brunet Lecomte 1988).

We conclude that speciation is under way between the subspecies of M. savii. This speciation appears to be directly related to differences in sex chromosome heterochromatin.

PoBI.4

SPERMATOGENESIS IN TRIPLOID HYBRIDOGENETIC FROGS (*RANA ESCULENTA*).

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Hybridogenetic *Rana esculenta*, the common frog of Europe, is a hybrid between *R. ridibunda* and *R. lessonae*.

In the Lower Hungarian Plain we found mixed populations of male and female *R. ridibunda* syntopic with male *R. esculenta*. Karyological and electrophoretic studies revealed that all male *R. esculenta* were triploid (two *lessonae* genomes combined with one *ridibunda*, LLR-genotype). Cross breeding experiments involving triploid males with both *R.ridibunda* and diploid *R.esculenta* females produced exclusively triploid male offspring with the LLR-genotype. Spermatogenesis of triploids proceeds as follows:

--proliferation of LLR-spermatogonia
--premeiotic degeneration of the R-genome
--proliferation of LL-spermatogonia
--circumvention of the reduction division step
leading to LL-spermia

The presence of a marker band in the short arm of chromosome 7 of only one of the two L-genomes in some individuals indicated divergent origins of the two L -chromosome sets represented in some triploids: one from a *lessonae* male the other from an *esculenta* female that produced diploid LR-ova.

PoBI.5

ECOLOGICAL MECHANISMS OF THE POLYPLOIDY, ANEUPLOIDY AND HETEROPLOIDY DISPLAY BY THE GROUND VERTEBRATES OF TIEN-SHAN

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In this address it will be present the information about the display mechanisms such phenomena as a polyploidy,aneuploidy and heteroploidy by the Tien-Shan ground vertebrates. It is determined by us,that the mountain populations Bufo viridis were found to be polyploid. The beginnings of this phenomenon is bound up with the glacier approach in Tien-Shan.

The phenomenon of the polyploidy which was revealed amongst vertebrates (Bufo danatensis,Natrix tessellata,Crocidura suaveolens, Ellobius talpinus,Citellus relictus) has a local nature and is bound up with the high radiation bachground of radon waters.

By the individuals of the private populations:Rattus turkestanicus, Mus musculus,Meriones tamariscinus, Citellus re - lictus and by some others vertebrates species was revealed a high percentage of the meeting of various ploidity and diverse karyotype structure cells. Thus, for example, by R.turkestanicus was revealed a great number of the metaphases, which contain instead of the usual diploid set ($2n=42$) the cells with $4n=84$ and even $8n=168$. This phenomenon , as we see it, could be called the heteroploidy.

The heteroploidy phenomenon was determined by us in the regions of the deep hearts of the earthquakes with the force of high numbers and the great intensivity. Such mechanisms of the genetic changes display point to one of the ways of the species formation in process of the animals evolution.

PoBI.6

CYTOGENETIC ASPECT OF THE SPECIES VARIETY OF TIEN-SHAN FISHES

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It is determined in the Tien-Shan conditions, that the high variability of the karyotypes structure of the aboriginal fishes species, in particular, of species Diptychus and Schizothorax is correlated with the hightened morphological variability. It could be evidence of that, that the present species are found still in the state of the forming and the differentiation and the happening chromosomes rebuildings are playing a defined part in their evolution. The actively proceeding processes of the species formation confirme the unsteady karyotypes nature of the fishes species Schizothorax , Diptychus and some others ones.

According to the canalizated model of the karyotypes evolution (Bickham,Baker,1979) we have an opportunity to observe on the vast karyological material a great number of the chromosomes versions, which commonly are preceding the fixation of the optimum karyotypes for the present adaptive zone and the next morphological evolution. In connection with that, it could be believed, that the species variety of the Tien-Shan ichthyofauna is reached at the expense of the intensive chromosomes species formation.

It is not excepted, that the observing by Schizothoracinae variation of the number of the morphological different chromosomes, is caused by wide ecological adaptations,which are inevitable in the extreme conditions of the Tien-Shan mountain system. Seemingly, the karyotypes evolution of the alpine regions fishes is proceeding on the basis of the pericentric inversions, which are usually accompanying the species formation processes, and the others non-robertsonian reconstructions too. The evidence of that is a variability of the morphological different chromosomes number and a wide variation of the subtelocentric chromosomes.

PoBI.7 SPECIATION IN THE FAM. CHIRONOMIDAE, DIPTERA. CYTOGENETICS EVIDENCE

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Different pathways of speciation (allopatric, sympatric, stasipatric and introgression) have been found in fam. Chironomidae. The significance of the complex methodological approach for discovering of these types of speciation has been discussed.

It was given an example for "traditional" or "ordinary" pathway of speciation, which is associated with the gradual multiplication of interpopulation differences and which is culminates in the development of reproductive isolation. The so called "genetic" pathway starts with the development of reproductive isolation as a consequence of chromosomal rearrangements and culminates in divergence of chromosome structure and in ecological differences. Chromosomal speciation takes place by means of changes in the possibility of gene flow between forms with the same gene pool but different chromosomal complements.

It was underlined that sympatric species display more complicated chromosomal rearrangements then allopatric species.

The role of postmating and premating reproductive isolating mechanisms have been considered.

Some species from different localities have specific features of polytene chromosomes. On the basis of various polytene chromosome rearrangements they are considered as sympatrically differentiated interpopulation groups. Introgressive hybridization with a subsequent crossing-over is of particular important to the production of various recombinations.

PoBI.8 THE NEO-XY SEX DETERMINATION IN PAMPHAGID GRASSHOPPERS.

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It is generally accepted, that the properties of chromosome number of grasshoppers family Pamphagidae are characterized by their high degree of conservatism (2n♂=19,XO; NF=19) (White, 1973;Camacho et al.,1981; Santos et al.,1983).

But the data suggested in this article, dispel the mentioned opinion, as we have found the transformated karyotypes due to the fusion of large autosome and sex chromosome, resulting to the formation of metacentric neo-X chromosome and acrocentric neo-Y chromosome in 5 of 11 studied pamphagid species from the Middle Asia, Kazakhstan and the Caucasus. Thus, the sex determination is based on neo-XY♂/neo-XX♀ (2n♂=18;NF=19). The comparative analysis of C-heterochromatin localization in standart 19 and 18 described chromosome karyotypes suggests centromere - centromere fusion in Atrichotmethis semenovi, Asiotmethis heptapotamicus, Asiotmethis zacharyini (subfamily Akicerinae) while in Paranocaracris rubripes and Nocaracris cyanipes (subfamily Pamphaginae) it appears to be centromere - telomere association whith paracentromeric C-heterochromatic block of the original X-chromosome to be in the telomeric region of neo-X chromosome, thus responsible for the marking of the position of the latent or lost centromere. The neo-Y chromosome in different species are characterized by different, up to the whole heterochromatinization level.

PoBI.9

EVOLUTION OF DIPLOID CHROMOSOME NUMBERS IS ACCOMPANIED BY DUPLICATIONS/DELETIONS

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There are three main routes for evolutionary increase or decrease of diploid chromosome numbers. All are connected with duplications or deletions of chromosome segments:

1) Robertsonian interchanges *sensu strictu*

- Fusion of telocentric mouse chromosomes yielding Robertsonian metacentrics is accompanied by reduction of the redundancy of telomeric sequences at sites of the original centric termini (Fig.1).
- Fission of a metacentric *Vicia faba* chromosome gives rise to two telocentrics with telomeric sequences at their centric termini which were not resolvable in the primary constriction of the original metacentric (Fig.2).

2) Meiotic mis-segregation in individuals heterozygous for two symmetric reciprocal translocations involving three chromosomes

The crucial translocations may involve

a) one metacentric and two acrocentric chromosome pairs (Fig.3) (experimentally confirmed for the broad bean by Schubert and Rieger 1985, Fig.4);

b) two pairs of acrocentrics (Fig.5);

c) two pairs of metacentrics (Fig.6); b) and c) not yet confirmed. For all three variants increase and decrease in chromosome number may occur simultaneously if the accompanying duplications/deletions are tolerated. If deletions are lethal, a biased increase of chromosome number has first to provide sufficient redundancy to tolerate later on deletions accompanying the decrease of chromosome number.

3) Breakage-fusion-bridge-cycles of metadicentrics which result from asymmetric reciprocal translocations between homologous metacentrics may yield acrocentrics replacing the original metacentric chromosomes (observed for *Tradescantia* by Östergren and Östergren 1983). Duplications in this case result from BFB-cycles (Fig.7), the source of the additional telomeres is not yet clear.

PoBI.10

ALLOPLOID NATURE OF CETERACH AUREUM (CAV.) BUCH

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Two cytogenetically and morphologically distinct *Ceterach* taxa exist in the Canary Islands as follows: *Ceterach aureum* (Cav.) Buch - tetraploid- bearing large fronds and *Ceterach aureum var. parvifolium* Benl and Kunkel -octoploid-bearing small fronds.

The autoploid or alloploid nature of *Ceterach aureum* had not been stated. In order to clarify this question it was crossed with another diploid *Ceterach* species; *Ceterach officinarum ssp. bivalens.*

Analyses of chromosome pairing in numerous spore mother cells of the synthetic hybrid *Ceterach aureum x Ceterach officinarum ssp. bivalens* gave only a few (approximately 10) bivalents and a large number (more than 80) univalents. This indicates a) the alloploid origin of *Ceterach aureum* and, b) that *Ceterach officinarum ssp. bivalens* is not involved in the origin of *Ceterach aureum.*

PoBII.1 IS ASPLENIUM RUTA-MURARIA L. SSP. RUTA-MURARIA (ASPLENIACEAE; PTERIDOPHYTA) AUTOPOLYPLOID?

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Experiments and observations by earlier investigators such as Vida (1970) and Bouharmont (1972) indicated that *Asplenium ruta-muraria* L. ssp. *ruta-muraria* is an autotetraploid of the diploid *A. ruta-muraria* subsp. *dolomiticum* Lovis et Reichstein. Most of the plants of *A. ruta-muraria* ssp. *ruta-muraria* have regular meiosis with 72 chromosome pairs. In some natural populations Vida noticed irregular chromosome pairing with up to 16 quadrivalents, with trivalents, pairs, and univalents. In the present investigation plants from two populations showing regular meiosis were chosen. When one assumes that an autotetraploid plant has four homologue sets of chromosmes and that there is random pairing with a (genetically regulated) mechanism preventing the formation of quadrivalents, then tetrasomic inheritance should be expected. Electrophoretic investigation of the allozyme phosphoglucoisomerase (PGI) revealed that plants show fixed heterozygosity and behave like allotetraploids. Offspring of plants with the allelic constitution of AABB and with an enzyme phenotype of three bands (dimer) always showed the AB phenotype. A plant with the allels AABC gave offspring with phenotypes AC, AB and ABC. This indicates that it is always the same chromosomes that form pairs and that pairing may be connected with some recognition mechanism: perhaps the consequence of small allelic differences between segments. Once more, it is apparent that the terms auto- or allopolyploidy signify only extremes. This investigation is a further example illustrating that the interpretation of meiotic behaviour is difficult and the regulation of chromosome pairing is still not fully understood.

Bouharmont, J. 1972. Origine de la polyploidie chez *Asplenium ruta-muraria* L. Bull. Jard. Bot. Nat. Belg. 42: 375-383.

Vida, G. 1970. The nature of polyploidy in *Asplenium ruta-muraria* L. and *A. lepidum* C. Presl. Caryologia 23: 525-547.

PoBII.2 ISOZYMES AND THEIR IMPORTANCE FOR BREEDING TETRAPLOID CORN

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Polyploidy is one of the most powerful means of evaluation, because it evenly increases the genom and hence the information capacity of an organism /Vida, G./. Some natural polyploids, both wild and domesticated like alfalfa, potato, sweet potato and bread wheat are very succesful. With the 1937 discovery of the "colchicine technique" for inducing polyploidy, breeders have started using plyploid methods on many crops. Among these sugar beet, red clolver, perennial ryegrass, annual flowers are valuable polyploids. However, maize, rye, barley and rice are not very succesful as tetraploids because of their low seedset. They have mainly theoretical importance.

The first tetraploid maize was obtained by L.F. Randolph in 1932. He found that autotetraploid maize had broader and thicker leaves, sturdier stalks, larger tassels, larger ears and kernels than diploid plants of similar genotype. Randolph also found that seed set was generally lower in autotetraploids than is diploids.

The success of plant breeding depends considerably upon the genetic variability of basic material. The avaiable germ plasm sources of tetraploid corn are limited. Furthermore there are a lots of problems, such as unequal distribution of quadrivalents, complicated segregation of genes, high number of heterozygotes and the long time in developing new inbred lines, which make the breeding of tetraploid corn more difficult than diploid corn breeding.

Utopia for plant breeders would probably include some relatively simple, accurate laboratory procedures for evaluation of breeding materials in juvenile stages that would eliminate much of the costly, time-consuming field testing. Electrophoretic separation of isozymes has been extensively used to characterize breeding stocks and inbred lines. Investigation of genetic diversity and inbreeding process by isozyme marker loci makes the selection easier at the tetraploid level.

Alcohol-dehydrogenase-1 and esterase isozymes were extracted from embryos of tetraploid corn seed and separated by PAGE.

Biochemical data have revealed the genetic variability of our tetraploid synthetic corn population. Meiotic segregation of chromosomes could be detected on molecular level. Due to the selectional superiority of Adh1-F allele or/and random process during the inbreeding the frequency of the Adh1-S allele gradually decreased. Of the nine possible patterns, only four groups of esterase isozymes with different electrophoretic mobility could be observed on the gel slabs of some S_3 families.

PoXI.3 GENETICS OF THE PARASITIC PSR CHROMOSOME IN NASONIA VITRIPENNIS

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Paternal sex ratio (psr) is a supernumerary chromosome in the parasitoid wasp *Nasonia vitripennis*. It is transmitted via the sperm of male carriers and causes supercondensation and subsequent loss of the paternal chromosomes after fertilization of an egg. The effect is to change the zygote from diploid (=female) to haploid (=male), carrying the psr chromosome, in this haplodiploid sex determination system.

Three basic questions concerning psr action are 1) how does PSR recognize the paternal chromosome set in the fertilized egg, 2) how does it destroy this, and 3) how is it protected against its own action? Molecular analysis of psr revealed several families of tandomly repeated DNA sequences. Low homology is observed between the psr specific families, except for two highly conserved regions of approximately 15 bp each, that are palindromes. Two structures are hypothesized as the functional domains of PSR: 1) the repeats themselves, or 2) one or more unique genes. Some possible mechanisms of PSR action include synthesis of a product that affects chromatin condensation, or binding of a factor required for proper replication, either directly to the repeats or to a gene product.

To test whether the repeats are necessary for PSR function, deletions in the psr chromosome were induced by radiation. Deletions of 5 different PSR repeats were determined using DNA hybridization techniques. No specific repeats were found to be associated with psr function. To test whether PSR action depends on the number (dosage) of repeats, genetic complementation experiments with non-functional PSR chromosomes were carried out. Loss of function in deleted PSR chromosomes could possibly be restored by pairing two identical non-functional PSR chromosomes.

The relationship between PSR action and its protection was investigated by pairing functional with non-functional PSR chromosomes in males. Transmission of non-functionals was not reduced by the presence of a functional PSR chromosome, even if the non-functional had been maintained separately for five generations. This indicates that PSR DNA is genetically immune against PSR action.

PoBII.4 ESTABLISHING HOMOLOGY BETWEEN HUMAN AND PRIMATE CHROMOSOMES BY *IN SITU* SUPPRESSION HYBRIDIZATION.

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Knowledge of chromosomal homology is essential for determining the origin of human chromosomes, for phylogenetic reconstruction, for understanding the mode of chromosomal evolution and clarifying the role of chromosomes in speciation. However, for many species in which gene mapping data is absence or contradictory, homology has been suggested only by subjectively matching banding patterns. We established the homologies between all chromosomes in the human, great ape, gibbon, and macaque karyotypes by chromosomal *in situ* suppression (CISS) hybridization of chromosome specific DNA libraries. In contrast to single gene mapping, CISS hybridization covers the whole chromosome of the target species and therefore allows a refined analysis of inter-chromosomal rearrangements. These are the first complete, chromosomal homology data sets that have been provided between man and other species.
In the great apes our results confirmed already suggested chromosome homologies, but resolved some still open questions concerning particular interchromosomal rearrangements: the apomorphic reciprocal translocation in the gorilla between chromosomes homologous to human 5 and 17 was confirmed. Three whole chromosome translocation were found in the macaque karyotype, but, except for chromosome 2 all human genes may have been linked for more than 20 million years. Whereas human, great ape and macaque chromosomes are highly conserved the gibbon karyotype has experienced massive reorganization. The 22 autosomal human chromosomes have been divided into 52 elements to compose the 20 gibbon autosomes. Only five human chromosomes have not been involved in interchromosomal rearrangements. These data support the hypothesis that gibbon chromosomes are characterized by an extremely high evolutionary rate Molecular cytogenetics and in particular CISS hybridization promises to bring new power to comparative cytogenetics.

PoBII.5 A VARIANT OF RIBOSOMAL GENES IS CLUSTERED ON THE SEX CHROMOSOME OF ASELLUS AQUATICUS(CRUST.ISOP.) MALES

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The karyotype of the isopod crustacean Asellus (Asellus) aquaticus (L.) Racovitza (2n=16) is as a rule formed by eight homomorphic chromosome pairs. A number of males from a population collected in the Sarno river near Naples has a heteromorphic chromosome pair (Rocchi et al, 1984).This heteromorphism is due to the presence of two heterochromatic areas on a metacentric chromosome. The heterochromosome is inherited only through the male line. This situation suggests that we are dealing with the morphological differentiation of one sex chromosome. The heterochromatic areas of A. aquaticus karyotype are normally telomeric, associated with the nucleolar organizers. All heterochromatic areas, including those of the heterochromosome, fluoresce brightly after staining with GC-specific dye chromomycin A_3.
In the present work we used a probe containing 18S, 5.8S and 28S ribosomal sequences to probe males and females from the Sarno population of A.aquaticus by using Southern blotting and in situ hybridization. Our results show the presence of a ribosomal gene variant in male DNA and the occurrence of ribosomal sequences associated with the two heterochromatic areas of the heterochromosome.

Rocchi,A.,Prantera,G.,Lanza,V., Di Castro,M.,-Chromosoma,89, 193,1984.

PoBII.6

TRIPLOIDY INDUCTION: A NOVEL TOOL FOR INVESTIGATING HETEROSIS IN *MYTILUS EDULIS*

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The concept of ploidy manipulation and its uses both in commerce and research is introduced, with particular emphasis on the potential use of triploid *Mytilus edulis* to investigate the phenomenon of heterosis. Possible genotypes and percentage heterozygosity of cohorts of diploids or triploids obtained by targetting meiosis I or meiosis II are illustrated and the manner in which electrophoresis of such animals could be used to investigate the link between heterozygosity and growth explained.

PoCI.1 DISTURBANCE, COMPETITION, AND THE MAINTENANCE OF CLONAL DIVERSITY IN OBLIGATELY PARTHENOGENETIC DAPHNIA PULEX

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Laboratory microcosm experiments tested the intermediate disturbance hypothesis, and examined the effects of disturbance on the maintenance of clonal diversity (i.e. clonal richness) and competitive interactions among obligately parthenogenetic clones of the freshwater cladoceran Daphnia pulex. No significant effect of disturbance size (i.e. dilution volume) on clonal richness was noted. However, frequency of disturbance had a pronounced effect on clonal richness, with the greatest number of clones maintained at an intermediate disturbance frequency. Competitive hierarchies among clones were quite deterministic within a given experiment. Generally, one or two clones dominated, with several less-abundant clones persisting throughout an experiment. Results suggest that intermediate disturbance could be an important mechanism that can maintain genetic variation in natural populations (i.e. via pre-emption of competitive exclusion between genotypes). This could have a direct bearing on the maintenance of both intra- and interspecific diversity.

PoCI.2 ADVANCES IN THE GENETIC STRUCTURE OF *TAPES* CLAMS.

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Nine stocks of the clam *Tapes philippinarum* and ten samples of natural populations of *Tapes decussatus* from various Mediterranean localities have been characterized by means of electrophoretic analysis at 17 allozyme loci and multivariate analysis of 17 morphometric measurements.

The study confirmed the existence of high genetic differentiation and morphometric differences between *T. philippinarum* and *T. decussatus* and revealed the absence of any introgression in a sample from the Po delta supposed to be hybrid on the basis of some phenotypic traits.

Both species showed high levels of genetic variability within populations and high values of the fixation index at some loci. These results are comparable to those already reported for other molluscs.

In *T. philippinarum*, age was found to be positively correlated to average individual heterozygosity, and negatively related to the average fixation index.

A comparison of three samples of the same age, deriving from the same broodstocks, reared for about 18 months at different conditions, revealed notable genotypic and phenotypic differences. In particular, besides to changes in the genotypic distribution a sample seeded in the Lake Sabaudia (Tyrrhenian Sea) differed from those grown in the artificial ponds of Goro (Adriatic Sea) because it showed a positive relationship between individual heterozygosity and growth rate. These changes wich occurred between samples genetically homogeneous at the moment of the seed seem to represent a response to environmental changes, rather than the outcome of genetic drift.

Results from this study suggest a way to experimentally approach the largely debated relationship between heterozygosity and growth rate.

PoCI.3 ELECTROPHORETIC INVESTIGATIONS OF BLACK SEA FISHES AND THEIR PERSPECTIVES.

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A research of fish population structure by utilizing Biochemical Genetics metods began in the Black Sea at last two decades of the our century.We couldn't to say that they become common for years past,but researches have been doing constantly in some Scientific Centres.

A most studing fish of the region is Black Sea Anchovy.The population structure of the this species are known well.Population Genetics techniques be used Sprat,Horse Mackerel,mullets.Many species never have been investigated.

We examined a enzyme polymorphism of some Black Sea fishes. Have been taken following objects:

-Whiting(Merlangus merlangius euxinus,Nordmann);

-Horse Mackerel(Trachurus mediterraneus ponticus,Aleev).

Nineteen enzymes were studied by utilizing the Method(horizontal electrophoresis in polyacrylamide gel).Six of them were polymorphic in white muscles of Horse Mackerel(Esterase, Lactate dehydrogenase,Phosphoglucomutase,Malate dehydrogenase NADP$^+$,α-Glycerophosphate dehydrogenase,Asparagenase).Polymorphisms of LDH,Est enzymes was found by Dobrovolov(1977,1978), but last four polymorphic enzymes have been found in a first time.

Also four enzymes of Whiting are found to be polymorphic (Est,Malate dehydrogenase,Isocytrate dehydrogenase,Glucose 6-phosphate dehydrogenase).

All these polymorphic enzymes can be utilized in future population researches.

PoCI.4

GENETIC DIVERSITY AND ORIENTATION BEHAVIOUR IN NATURAL POPULATIONS OF THE SANDHOPPER TALITRUS SALTATOR

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Talitrid amphipods are currently the object of extensive research aimed at elucidating their orientation behaviour and genetic structure.

Natural populations of the sandhopper Talitrus saltator living on differently oriented Italian shores were shown to be behaviourally adapted to their original shoreline: both expert and laboratory-born individuals (without any experience of their natural situation) orient significantly seawards, if dehydrated, with only the sun visible. This genetically determined directional tendency can be corrected by learning in the course of individual life, in the event of dislocation and/or changes in the shoreline.

Comparisons of geographically different populations showed differences in the relative role of genetic determinism and plasticity: some populations behaved more as genetically determined and others more plastically.

Results from analysis of allelic variation at nineteen enzyme loci revealed high levels of genetic divergence between the Tyrrhenian and the Adriatic populations (Nei's genetic distance = 0.40). The average degree of genetic variability differs among the populations examined and a positive correlation has been found between the degree of heterozygosity and the degree of genetic determinism in orientational behaviour.

Both parameters (heterozygosity and behavioural orientation) show a significant relation to the "stability" of the shorelines. The results may be interpreted in terms of "genetic homeostasis"

Individual multilocus genotypes and single orientation behaviours have been also considered and preliminary results are shown.

PoCI.5 THE EFFECT OF RIVERS ON THE DIFFERENTIATION OF SALAMANDER POPULATIONS

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The Central European Rhenish Slate Mountains are fragmentated by three rivers (Rhine, Moselle and Lahn) into four distinct ridges: Eifel, Hunsrück, Taunus and Westerwald. Thus they provide a suitable subject for the study of the influence of rivers on the genetic differentiation of populations. Rather immobile terrestrial species like the fire salamander, *Salamandra salamandra* L. 1758 (Amphibia, Salamandridae), which can be expected to be unable to cross such rivers on any considerable amount, are of special interest.

Larvae of *S.salamandra* were collected from 17 brooks and brook systems within the Rhenish Slate Mountains. 14 presumptive enzyme loci were studied by means of horizontal starch gele electrophoresis (CK-s, CK-f, GDH, GPI, IDH, LDH-s, LDH-f, MDH-s, MDH-s, ME, Pep-s, Pep-f, PGM, PK).

The spatial distribution of two alleles of the locus CK-s that are diagnostic for the two Central European subspecies *S.s.salamandra* and *S.s.terrestris* (see Veith 1991) show a river dependant pattern: The River Rhine between Westerwald and Eifel and the River Moselle between Eifel and Hunsrück completely restrain the gene flow between adjacent mountain ranges.

A significant influence of the number of separating rivers on the pairwise calculated 'Nei's average genetic distance (D_N)' was proved by several tests: The correlation coefficient of the linear regression model, a multiple regression analysis and a one-way analysis of variance. Nei's D_N was also calculated per kilometer of direct geographic distance (D_{GL}) as well as for the geographic distance along the water courses (D_{GW}). Student's t-tests for three groups of pairs of populations (0, 1 and 2 rivers between two populations) again proved the influence of rivers on the genetic differentiation of populations.

PoCI.6

GENETIC STRUCTURE OF POPULATIONS OF *ACHILLEA NOBILIS L.* AND *ACHILLEA OCHROLEUCA EHRH.* IN HUNGARY

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The genus Achillea is a taxon rich in species with 12 representatives in Hungary. Some of them are distinct botanical species with good characteristic traits, while others, in the millefolium-complex are hardly identifyable with many taxonomical and genetical problems (A. collina, A. millefolium, respectively). A. nobilis is spread over Eurasia, the territory of A. ochroleuca is localized in the Pannonian-Pontian region. Both of them are well established botanical species. The time of appearing of these species in the Carpathian basin is unknown. Probably, they could be naturalized in their recent habitats after the last glacial period. It is open to question whether this and their characteristic life-history traits, perennial lifespan and polycormonic vegetative reproduction are reflected in the structure of the populations. Further question we have tried to answer is as follows: are there any correlation between the ecological conditions (basic rock, microclimate, soil, cenosis, geographical localization) and the genetic diversity, genetic distance of populations, as well.

We analized isoenzyme polymorphism data of 7 populations of A. nobilis and that of 9 populations of A. ochroleuca by FELSENSTEIN's PHYLIP Version 3.1 programs on the basis of allelic frequencies (CONTML), furthermore on the basis of Nei's and Hedrick's genetic distances (FITCH).

Genetic distances of populations of both species proved to be relatively great with high G_{ST} values and allelic frequencies apart from the equlibrium state. Predominance of some genotypes in certain populations was observed without positive correlations with the geographical position, genetic distances or ecological parameters of the populations, respectively.

It would seem from the dendrograms that polycormonic reproduction, chance and human effects played the main role in shaping the structures of these populations with active microevolutionary processes even nowadays working.

PoCI.7

ALLOZYME VARIATION IN *PODARCIS FILFOLENSIS*: BIOGEOGRAPHIC INFERENCES FROM ELECTROPHORETIC DATA

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Podarcis filfolensis is a lacertid lizard inhabiting the Maltese Archipelago and the Pelagie Islands (Linosa and Lampione)(Bischoff, 1986). It has historically been considered closely related to *P. wagleriana*, a species occurring in Sicily and in some minor Sicilian islands (Aegadian and Aeolian Islands)(Lanza and Cei, 1977).

In the present paper allozyme variation in *Podarcis filfolensis* was analyzed by horizontal starch electrophoresis at 26 loci. For interspecific comparisons some samples of the related species *P. wagleriana* and *P. sicula* were also investigated. The amount of genetic divergence between populations was evaluated using Nei's (1978) unbiased genetic distance.

The populations from Malta, Gozo and Comino (*P. f. maltensis*) and Filfola (*P. f. filfolensis*) are genetically very similar to each other (Nei's average $D = 0.032$), while the population from Linosa (*P. f. laurentiimuelleri*) is genetically relatively differentiated from those inhabiting the Maltese Archipelago (Nei's average $D = 0.095$). These data indicate that geographic isolation is quite recent in the case of the *P. filfolensis* populations occurring in the Maltese islands. On the other hand, the *P. filfolensis* population from Linosa - an island far apart from the Maltese Archipelago - has remained geographically isolated for a considerable time from the Maltese mainstock (400.000-500.000 years according to Nei's formula).

Podarcis filfolensis, though morphologically similar to *P. wagleriana*, is genetically well differentiated from the latter (Nei's average $D = 0.483$), while being relatively more close to *P. sicula* (Nei's average $D = 0.287$). This testifies to a closer relationship between *P. filfolensis* and *P. sicula* than between the former and *P. wagleriana*, and - in contrast to the hypothesis provided by Lanza and Cei (1977) - indicates in fact that *P. wagleriana* and *P. filfolensis* did not arise from a common Sicilian stock.

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PoCI.8 GENETIC STRUCTURE OF POPULATIONS IN FRAGMENTED HABITATS: CAVE CRICKETS IN ETRUSCAN TOMBS.

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The Etruscan necropolis "La Banditaccia" at Cerveteri, near Rome, consists of a few hundred tombs excavated in the tufa rock, varying in size, morphology, abiotic factors and community patterns, a large number of them being inhabited by the cave cricket *Dolichopoda laetitiae*.

Such habitat heterogeneity and fragmentation led us to investigate the possible occurence of genetic subdivision in the cave cricket population.

In a previous step, lasted around three years, we have individually marked 2900 cave crickets and characterized 130 tombs in a multidimensional space by mean of several physic and biotic parameters.

The mark-recapture network allowed to establish the potential distribution of cave crickets throughout the whole necropolis and to determine the area of preferential utilization.

A preliminary genetic analysis, based on 22 allozyme loci, pointed out a heterogeneous genotypic distribution (average F_{ST} = 0.045) in tombs assigned to 5 groups according to their ecological descriptors and topography.

The same methodology has been repeated in a new experiment where a larger sample of individually marked and recaptured crickets was submitted to genotypic analysis.

The relationship between genetic structure and spatial and ecological heterogeneity is discussed utilizing different explanatory models.

PoCI.9 EVOLUTIONARY RELATIONSHIPS AMONG CAVE AND SURFACE CRAYFISH FROM CHIAPAS (MEXICO)

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The cave fauna of Chiapas (Mexico) has received particular attention by biospeleologists in the last two decades. Because of its geographic location at the boundary between the Nearctic and Neotropic regions, its high biome heterogeneity and its complex orographic situation associated with a prevailing limestone geological nature, this area provided unusual opportunities for cave colonization and evolution by a variety of taxa.

Procambarus crayfish are frequent colonizers of caves and groundwaters in this region. Besides the already known cave dwelling populations of more or less troglophilic (i.e.: facultative cavernicoles) species represented by *P.mirandai*, *P.sbordonii* and *P.pilosimanus* (Hobbs, 1989), several new cave populations and species have recently been discovered. Some of these populations show high degrees of adaptation to cave life as indicated by high development of troglomorphic characters, including microphtalmy or complete blindness and depigmentation.

In a previous study we analized a complex situation discovered at the Cueva de los Camarones, in the Municipality of Cintalapa, where two species showing different degrees of cave specialization coexist sympatrically with some amount of asymmetric gene flow between them (Sbordoni et al., 1988; Cesaroni et al., submitted).

This study raised several questions concerning the role of factors shaping the genetic structure of cave populations in respect of their surface ancestors, and their evolutionary distance relationships in respect of the geography of drainage systems.

In the present paper we extend the analysis to additional samples of crayfish from both subterranean and surface waters, collected in four geographically distinct areas throughout Chiapas.

The main results of the allozyme electrophoretic analysis and the morphometric study of these samples are presented and discussed.

PoCI.10

GENETIC DIVERSITY AND WIDTH OF HOST PLANT SPECTRUM OF PHYTOPHAGOUS INSECTS

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In general. it seems that total genetic diversity H is positively correlated with the width of the host plant spectrum of phytophagous insects expressed in a number of plant genera. The results support the heterozygous generalist hypothesis that predicts positive correlation between genetic diversity and a varying environment. The results are higly significant. The Sperman nonparametric coefficient ensuing from a comparison of 54 phytophagous insects of 5 insect orders with the numbers of their host plant genera, is $r_s=0.471$, $P>0.005$. This result has been supported by test of the samples of species characterised by different widths of their host plant spectra. In the case of Wilcoxon two samples test were made comparing species feeding on only one plant genus (23 species) and species that feed on more plants (31 species). These samples were very different too ($t_s=3.78$, $P>0.001$) and the results support hypothesis that there is a significant difference between specialists and generalists. Three samples of phytophagous insects were compared by a third test: the first sample were the same species as in the case of the first group in the previous test (23 species), the second sample consisted of species feeding on more than one plant generus within one family (16 species), in the third group were species feeding on more plant genera of more families (15 species). The results of Crustal-Wallis test were higly significant too ($H_{sk}=19.088$, $P>0.001$). We cannot reject the hypothesis that these selected groups of phytophagous insects are different at the level of genetic diversity.

A positive correlation between the host plant spectrum of phytophagous insects and genetic diversity exists. Our result support the niche width variation hypothesis that predicts a positive correlation between the width of the ecological niche and genetic diversity.

PoCI.11 ISOLATION BY DISTANCE AS POSSIBLE CAUSE FOR GEOGRAPHIC VARIATION IN BIRDS?

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Birds are highly vagile and frequently have large breeding ranges. Their potential to overcome natural barriers, and consequently to freely disperse lends them to study the effects of gene flow on the genetic structure of populations. Wright's isolation by distance model predicts that continuously distributed species should differentiate if dispersal per generation is small compared to the total range of the species. The question to be addressed is whether avian populations diverge due to the paucity of genetic exchange imposed by geographic distance alone. This is done by comparing predictions from isolation by distance models with actual values of genetic differentiation as determined by the geographic variation of allozyme distributions and taxonomic subdivision. Taking Palearctic passerines as an example, I will try to evaluate the importance of those demographic parameters which largely determine neighbourhood size (e.g. dispersal, population density, life expectancy) for the genetic divergence within avian species.

In the species studied the degree of genetic differentiation among populations, as revealed by allozymes, is low and agrees with isolation by distance expectations: The more limited the dispersal of a species, the greater the genetic divergence between populations and the larger its number of geographic races. However, most subspecies are separated by physical barriers rather than distance *per se*. Furthermore, variation in ecological and/or morphological characters, on which classic taxonomic classification is based, is, as a rule, not correlated with allozymic variation. The implications of these findings for the significance of gene flow as a "dedifferentiating evolutionary force" are discussed.

PoCI.12

AN UNUSUAL MUTANT OF CAENORHABDITIS BRIGGSAE (G16).

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The founder animal of strain vg-182 was isolated as a Large Roller progeny of an EMS treated C. briggsae (G16) hermaphrodite. It has segregated only a few offsprings including Lons and animals of variable phenotypes. Lon hermaphrodites were singled and self-fertilized through subsequent generations and then crossed out several times. During this process 7 of 8 fertile lines segregated Lon males, Large Dpy hermaphrodites, Small Dumpies and Large Rollers. At the end, loci represented by one X-linked dominant lon, one autosomal recessive dpy and one independent, autosomal squat allele, respectively, could be identified and named temporarily as lon-2, dpy-2 and sqt-1. lon-2(d) proved a dominant epistatic gene over dpy-2 and a semidominant epistatic one over sqt-1., which means, that a male of lon-2(-)/0; dpy-2/dpy-2; sqt-1/sqt-1 genotypes is phenotypivally Lon. (Worms of sqt-1; +/+; lon-2 genotype exhibited Large Roller phenotype while those of sqt-1/+; lon-2/0 genotype were large, Non-Roller males.) The male segregating (Him) phenotype could not be separated from lon-2(d). The lon-2 hermaphrodites kept in liquid nitrogene still keep their "him" phenotype, those which were kept in laboratory conditions lost their male-segregating abilityt. The possibilities of getting a mutator strain of C. briggsae are discussed.

PoCII.1 RELATIONSHIP BETWEEN HETEROZYGOSITY AND VARIATION OF ANTHROPOMETRIC TRAITS IN HUMAN POPULATIONS.

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There is a growing body of literature suggesting that relationship between morphological variability and genic heterozygosity, as revealed by electrophoretically detected loci, across individuals in natural populations demonstrates evidence for adaptive significance of protein polymorphism. The relevance of these data with respect to theoretical and applied studies in human genetics is discussed. The relationships between variability of several polygenic traits and multiple-locus heterozygosity (9 polymorphic protein loci and 5 blood group loci) were examined in the adult population from Moscow. This study demonstrates that individuals with average level of heterozygosity are characterized by maximal fitness. It is concluded that an average level of individual heterozygosity is optimal for human populations.

PoCII.2 VNTR LOCI AND HUMAN MICROEVOLUTION

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A possible approach for estimating N_e (the effective population size) in natural populations may be based on loci with a very large number of selectively neutral alternative alleles, because their frequency distribution in populations depends on the product N_e times μ (the mutation rate of the locus) only, a parameter usually indicated by the symbol θ. If we arrive at an estimate of θ for a population of interest, and we know the value of μ of the locus, then we have a very reliable estimate of N_e.

A class of loci which show the above characteristics are the VNTR's (Variable Number of Tandem Repeats), which are currently under investigation in many human populations, generally for purposes of forensic medicine. They segregate for tens of alleles in relatively small population samples, and may be thought of to be selectively neutral, because they are not translated and differ only by small length. Although the methodological problem of exactly distinguishing very similar alleles is still open, causing at present the impossibility to deepen the analysis beyond certain limits, we have shown that a statistical analysis based on the probability of recurrence of specific genotypes and of a given value of the experimental error may afford the more likely genetic composition of a sample. Thus, we may estimate the allele frequency distribution of populations within given confidence limits.

By applying the sampling theory of neutral alleles for both the infinite and the k-allele models we arrived at an estimate of the value of θ from the best fit of the theoretical curves to the observed frequency distributions in some examples. We found that the two models produced very similar θ values. Since the mutation rate at these loci has been proven to be very high in some cases, it seems not unreasonable to assume that it should be relatively easy to determine for a locus of interest; once its estimate will be obtained, the effective size of all populations for which θ has been evaluated, is automatically known. In conclusion, it is suggested that VNTR loci may be extremely informative about the values of relevant microevolutionary parameters in human populations.

PoCII.3 GENETIC STRUCTURE OF 12 HUNGARIAN ETHNIC GROUPS

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Homozygozity index and different genetic distances were calculated on the basis of gene frequencies of 26 genetic markers in 12 Hungarian ethnic groups including 1514 persons. Cluster and principal coordinate analyses were performed to describe similarity in genetic structure of these populations. The inbreeding coefficient and fixation index were calculated. Genetic drift was detected in two ethnic groups (in 'Székely' and 'csángó'). Two ethnic groups 'Matyó' and 'Palóc' have similar genetic origin.

The Gypsies and Jews were different from the others. Our results confirm the North-Indian origin of the Gypsies.

5 groups were detected by a combination of cluster analyses and principal coordinate analysis on the basis of Nei's genetic distance. The most dissimilar were the 'Gypsy' and the 'Csángó' ethnic group. The ancient Hungarian population was also relatively different from the others. The first of the other groups comprises the following populations: Matyó, Kiskun, Nagykun, mixed Hungarian; and the second one consists of: Palóc, Jász, Székely.

PoCIII.1 TRANSPOSABLE ELEMENT-INDUCED VARIABILITY AND RESPONSE TO ENVIRONMENTAL SELECTION IN *D. MELANOGASTER* QUANTITATIVE TRAITS.

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Relationships between environmental and genetic variability in quantitative characters have been dealt with in a study on the effects of cyclic selection for ethanol tolerance on wing size in *Drosophila melanogaster*. Moreover, as it is known that transposition of P elements may contribute to mutational variance in quantitative traits, replicated cage populations were started from reciprocal crosses between an Oregon (M cytotype) and a π2 S (P cytotype) strain to study the evolution of P-induced genetic polymorphisms. The effects of P transposition on phenotypic and additive genetic variance were controlled during several generations before the selection experiment was started. The effects of the temporally variable environment was first verified after one year.

Here we present the main results obtained analysing L3 vein length.

- Populations derived from MxP dysgenic crosses show an increase in the additive genetic variance when compared with PxM offspring, suggesting a mutational component due to mobilization of P elements. This phenomenon persists in the absence of selective pressures.
- The cyclic selective regime reduces the additive genetic variance in all populations, but its effects are stronger in PxM than in MxP populations, as if in the offspring of the dysgenic crosses mutational variance were either continuously produced, or controlled by some balancing selection mechanism.

PoCIII.2 DROSOPHILA POPULATION RESPONSE TO ARTIFICIAL SELECTION FOR MORPHOSIS FREQUENCY

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There are presented investigation data of Drosophila population response to artificial selection for morphosis frequency change. It is shown that information of environment influences on ontogenesis through the feedback channels is realized at the population level and results in changing phenetic and genetic population structure including regulation of reproductive functions and development processes. The results of the model experiments can be applied, apparently, when considering data obtained during studying natural drosophila populations inhabiting the territories with increased radiation background.

PoCIII.3

QUANTITATIVE TRAITS IN SERIALLY BOTTLENECKED FLIES.

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Since 1985 we have been maintaining several lines of *Drosophila pseudoobscura* under a cyclic bottleneck-flush-competition crash protocol. This protocol reflects, under laboratory conditions, the requirements proposed by H. Carson for his "founder-flush" speciation theory. Bottleneck sizes vary from 1 to 9 couples and there are two different original populations with distinct genetic architectures (presence or absence of inversions in chromosome 3).

Along this general protocol, several experiments have been carried out, such as tests for pre- and postzygotic isolation between derived and ancestral populations, analysis of the evolution of competititve ability and evolution of quantitative traits.

In this communication, we will present data on a set of ten morphometric traits, evaluated for parents and 4 offspring in 10 derived lines and both ancestral populations at different times along the general experiment.

The analysis of phenotypic and additive variance-covariance matrices will allow an extension of Bryant's results with *Musca domestica* and a test of Lande's model of evolution for quantitative traits.

PoCIII.4

THE STUDY OF CORRELATIONS BETWEEN THE MORPHOLOGICAL VARIATION COMPONENTS WITH ALLOZIME HETEROZYGOSITY IN EUROPEAN ANCHOVY.

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We considered three components of morphological variation: 1)within sample (WS) component, 2)between-sample (BS) component and 3)correlation between different plastic traits (C). In order to consider as many factors which may influence the relations in question, an original algorithm of the data management and analysis is suggested. Multivariate methods were used.

The study was based on the data from two population systems of anchovy (Asov and Black sea), different in population structure, characterized by 4 polymorphic loci. The relation between allozyme loci heterozygosity (H) and variation components was found in both populations. The relation between C and H was identical in both populations and both sexes. The relation between the WS variation component and H is somewhat different in the two populations and the relation between the BS component and H had different signs in males and females in the more heterogeneous Black sea population. We also found the effects of individual loci on the observed relations.

PoCIII.5

MORPHOLOGICAL VARIABILITY IN **JUGLANS REGIA** L.

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We have studied samples of Juglans regia L. coming from 25 different locations in central Italy. All the available plants for each provenience have been collected. Five leaves and five fruits for each sample have been measured. The aim of the work is to compare the morphological variability of two sets of characters (leaves and fruits) at two levels: among different provenances and within each area. The preliminary results here reported have been obtained using analysis of variance.

Both leaves and fruits characters are significantly different among provenances, the only exception is the stalk width because of its high variability within each plant. Also the variability in each sampled geographic area is high, pointing out that even if the different origins are recognizable (especialy for those groups of plants far from each other), there could be a genetic differentiation within each sampled area that must be confirmed by the genetic analysis. A possible enviromental source of variation is unlikely because of the very restricted area within sites.

The degree of morphological variability for fruits and for leaves characters is the same. This results contrasts with our expectations, since the two sets of traits reflect quite different biological functions. As matter of fact we could expect much more selection, and hence much less genetic variability, for highly fitness correlated traits, like fruit characters.

PoCIII.6

MORPHOLOGICAL AND GENETIC VARIATION IN CASTANEA SATIVA Mill. FROM TURKEY.

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A high degree of genetic variability and differentiation between populations of Castanea sativa Mill. from Turkey has been previously observed on the basis of isozyme analysis (Villani et al., 1991). Preliminary investigations showed that such differentiation could be also detected at some morphological fruit traits (Villani et al., 1990). In order to find further evidences of genotype-phenotype correlations, variability at leaf level has been explored.

Two years old seedlings obtained by sowing 80 half-seeds from six localities of Western, Central and Eastern part of Turkey, were examined for a number of leaf characters. Five leaves per plant were analysed for 10 quantitative traits by means of a image analyzer. Electrophoretic analysis, based on 18 isozyme loci was carried out on the remaining half-seeds of the same plants. The results of such morphological and genetic analyses were compared and correlated with those previously obtained on the same seeds and based on 13 morphometric fruit traits.

All data were processed by uni- and multivariate statistical analysis. The results confirmed a consistent degree of variability and diversity, both at genetic and morphological (seeds and leaves) level, among the turkish populations of Castanea sativa Mill.

PoCIII.7

SUBSPECIES IN THE WEEVIL *RHINOCYLLUS CONICUS*: CONCORDANCE OF ELECTROPHORETIC AND MORPHOMETRIC DATA

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Rhinocyllus conicus Frölich (*Col.; Curculionidae*) is an oligophagous weevil whose larvae are developing in thistles (*Asteraceae*; subtribe *Carduineae*). As the weevil is used as a biocontrol agent and the existence of biotypes is discussed, the presented study aims to present a survey of potential differentiations in different regions of its natural distribution area.

About 2000 specimens originating from Spain, France, Germany, Italy, Greece and Israel pooled into fourteen regions were examined by means of horizontal starch gele electrophoresis and exoskeleton morphometrics.

Nine loci (six of them polymorphic) were used to characterize weevils genetically. The UPGMA-dendrogram constructed of Nei's genetic distances shows two distinct groups. Mean genetic distance between members of different groups is 0.073 (SD 0.025) and between members of the same group 0.023 (SD 0.015) and 0.021 (SD 0.020) respectively.

Eleven morphometric parameters were used in a discriminant function analysis which also divided the fourteen regions into two groups. Between these two groups there is no significant difference in the body length of weevils but in the ratio of body length to body width: weevils of the one group being broader than the others. In a classification test more than 93 % of all individuals are reclassified into the correct group.

Both, electrophoretic and morphometric analysis reveal the division into two concordant groups. One group contains all weevils from mediterranean regions, the other group contains weevils originating from temperate regions. The amount of genetic and morphologic differentiation allows the recognition of a mediterranean subspecies in *Rhinocyllus conicus*, which perhaps may be identical to the formerly described species *Rhinocyllus oblongus* Capiomont.

PoCIII.8

DEVELOPMENTAL STABILITY IN F1 TO F39 HYBRIDS OF ISOLATED HOUSEFLY POPULATIONS

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To study the effect of hybridization on the developmental stability of houseflies two distant strains of *Musca domestica* L. have been hybridized. Hybrids were followed for 39 generation, F1 to F39. When percent survivals of parents and hybrids were studied, among the reciprocal hybrids, one type showed high survivals for all generations and both types of hybrids exhibited fluctuations in their survivals. This contrasting behaviour of reciprocal hybrids and subsequent generations within the reciprocal hybrids provided an interesting system to study the relationship between genomic incompatibilites, coadaptibility and their reflections on the developmental stability.

As the measure of developmental stability fluctuating asymmetry was utilized. To calculate asymmetries six different methods were used.

PoCIII.9 EXPERIMENTAL INDUCTION OF A DARWINIAN GRADUAL EVOLUTIONARY VARIATION IN ARABIDOPSIS THALIANA

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After many years of research work, a gene-duplication-inducing chemical agent - GDI - was found, which cannot induce other mutation types. Using this GDI, recurrently reiterated treatments and selection for larger leaves was applied on growing plants of a homozygous laboratory strain of A. thaliana, during seven treated and ten non-treated generations.

The resulted gradual increase of the size of the leaves from one generation to another, i.e. the evident positive reaction to selection in the series of trated generations suggested,that the expressivity of the quantitative characters controlling polygenes can be increased by induced additional gene-copies. It was conspicuous, that the fertility of plants remained normal in all generations.

In the final hybrid analysis, in the F_2 generation a similar transgressive segregation appeared, as by the crosses between the geographical races of the wild plant species. Based on th these results, the following hypothesis was formulated:

The phenotype of the largest $7M_3$ plant is controlled by an antagonistic system of positive and negative polygenes, in which the positive polygene loci contain an increased number of gene-copies. Consequently,under the conditions of natural selection, in the microevolution of clines,the gradual change of the size of plant organs could resulted rather by additional polygene-duplications, than by series of allelic-mutations, as was supposed by others.

The finding of a pure gene-duplication-inducing chemical compound opens the way toward a man-directed evolutionary change of the polygenic systems of the eukaryotic genomes.

PoCIII.10 MODIFICATIONAL VARIABILITY OF HAEMOPOETIC CELLS OF AMPHIBIA,REPTILIA AND AVES UNDER RADIATION EXPOSURE

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The increase of radiation level accelerates the mutational process and affects nonstochastically stimulating modificational variability. Investigation of these tendencies is important for evolution processes understanding and is of great practical value.

The morphofunctional characteristics of haemopoetic cells were investigated on representatives of Amphibia (R. arvalis,B.bombina), Reptilia (L.agilis,E.orbicularis,N.natrix) and Aves (10 species) inhabited in conditions of increased radiation level in 10km zone around Chernobyl atomic station.

In comparison with control animals from noncontaminated areas hypertrophy of haemopoetic cells, decreas of specific granules contained in eosinophilic and basophilic granulocytes were detected in Amphibia and Reptilia blood. Neutrophil nuclei hypersegmentation and micronuclei appearence (apart from the nucleus) were frequently distinguished. For erythrocytes number of double nuclear cells and micronuclei increase as well as cytoplasm vacuolisation. For Reptilia the variability of haemopoetic cells was more expressed in L.agilis than in E.orbicularis or N.natrix.

Observed phenotypic changes may be indused by radiation influence because the similar alterations have been determined after experimental gamma exposure (1.5Gy) of R.ridibunda. On the whole changes were more expressed in Amphibia than in Reptilia that corresponds with the idea of different radiosensitivity of these animal groups.

Basophilia and eosinophilia were peculiar to Aves blood. Fragmentated nuclei, cytoplasm vacuolisation and changes in granularity character were revealed in pseudoeosinophils. Red marrow has been characterized by increased number of pseudoeosinophils and basophils with higher hypertrophy.

Morphological analysis of blood cells and haemopoetic organs of vertebrate animals reveals the similar way of cell modification variability in conditions of radioactive contamination.

PoD.1

SEX ALLOCATION IN HERMAPHRODITE INDIVIDUALS IN GYNODIOECIOUS SPECIES:

Intra and inter-specific comparisons in the genus *Thymus*.

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Angiosperms are generally hermaphroditic, and individuals theoretically allocate their reproductive resources so that they produce half of their progeny via ovules (i.e. female function) and half via pollen (i.e. male function). In contrast, gynodioecious species contain female (i.e. male sterile) individuals that only reproduce by seeds. The maintenance and frequency of these females, within populations and/or species, depends on two factors: i) their ability to reallocate unused male resources to seeds and ii) the population genetics of the nuclear and cytoplasmic genes responsible for male-sterility in the context of colonisation and extinction of natural populations. In such species, sexual resources allocation in ermaphrodite individuals (i.e. the share of investment in male function) depends on female frequency since there is a selective pressure favoring male (versus female) function in hermaphrodites when females are abundant (versus rare).

Many species in the genus *Thymus* (Labiatae) have high frequencies of females. Three study species - *Thymus zygis*, *T. vulgaris* and *T. mastichina* - contain average female frequencies of 50, 60 and 72% respectivelly, always with a high variation among populations. Relationships between the female frequency and i) the female advantage in seed production and ii) the sex allocation of hermaphrodites, are observed among populations within each species and among species. Different results are obtained at these two levels of comparison.

PoD.2

INTRA-POPULATION GENDER VARIATION IN *PLANTAGO CORONOPUS*

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In sex-allocation theory a negative relationship between the amount of resources spent on female- and male function is often assumed. Also the often observed diferences in seedweight between hermaphrodites and male-steriles in gynodioecious species is explained by stating that male-steriles don't have to form anthers, and in this way save resources for their female function, which leads to heavier seeds. However, there are few empirical studies in support of this idea. Research carried out on the gynodioecious *Plantago coronopus* showed 1) male-steriles have on average a 20% higher seedweight compared to hermaphrodites 2) within the group of hermaphrodites there are large differences between individuals in pollen production. These results will be discussed in relation to sex-allocation theory.

PoD.3

EFFECTS OF INBREEDING IN LYCHNIS FLOS-CUCULI (CARYOPHYLLACEAE): TWO GENERATIONS OF SELFING.

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In an ongoing experiment, lines of L. flos-cuculi are selfed for several generations and inbreeding depression is evaluated, to get an understanding of the dynamics of inbreeding depression in relation to degree of inbreeding. Additionally this design makes possible to differentiate between parental and offspring inbreeding effects. Results from the first 2 generations are presented here. Plants were grown in the green house from either selfed or outcrossed seeds. Each plant was pollinated with self pollen, pollen from full siblings, and unrelated pollen in different flowers. Seed abortion, seed weight, germination speed and germination rate was measured (additionally survival and fruitset of offspring will be obtained).
Parental plants grown from selfed seeds gave rise to seeds that had a lower and slower germination than seeds sired by outcrossed parents. Selfed flowers from both parental groups had a significantly higher seed abortion rate, and developed lighter seeds with a lower and slower germination compared to unrelated and sibling crosses. Significant interaction was found in germination speed between pollen treatment and parental origin, showing a greater inbreeding depression in progeny from selfed parents. In a canonical discriminant analysis based on all characters, it was possible to discriminate between both parental origin and pollen treatments, with sibling crosses placed intermediate between self and outcrossed. These results show, that inbreeding depression in L. flos-cuculi is expressed by both parental and offspring effects, and that inbreeding depression is increasing with increased levels of inbreeding.

PoD.4

PARTIAL SELFING AS AN OPTIMAL STRATEGY.

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In a deterministic population genetic it is shown, that partial selfing can be an optimal strategy. The only necessary assumption is that inbreeding depression in consecutive generations of selfing can be described as a constant decreasing exponential function. The model gives an estimate of the expected selfing rate in a population with mixed mating and a known inbreeding depression function. Validity of the model was tested using data from rape seed, beans and alfalfa.

PoD.5 PATTERNS OF RESOURCE ALLOCATION IN RUMEX ACETOSA AND R. ACETOSELLA

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The sorrels _Rumex acetosa_ and _R. acetosella_ (Polygonaceae) are perennial dioecious weeds which occur naturally in a variety of habitats and exhibit a very plastic above-ground morphology. When the patterns of resource allocation were investigated, males were found to allocate more to reproduction during the time of flower production than did females, whereas females invested considerably more in reproduction during seed production. Altogether, females allocated both a higher total amount and a higher proportion of energy to reproduction than did males. By using regression analysis, the influence of plant size on reproductive effort was examined separately for males and females. The results indicated that reproductive effort is usually independent of the size distribution of the plants. Thus spatial and temporal comparisons of allocation patterns in populations and sexes with different size distributions were justified. An analysis of variance was conducted to investigate the effects of population, season, sex and their interactions on the resource allocation patterns and plant size. In both _Rumex_ species, different interaction effects were found to be most important.

PoD.6 POPULATION SIZE AS THRESHOLD FOR INFECTION OF SEEDS OF *SALVIA PRATENSIS*

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Considering the dynamics of pathogens and/or herbivores small size of the host - plant population may have two consequences.

If resistance has a genetic basis the increased levels of inbreeding in the small host population may result in increased levels of susceptibility among individuals. On the other hand if the population growth rate of the pathogen or herbivore is influenced by the size of the host population there may exist a critical population size below which pathogen or herbivore is absent.

Evidence for such a threshold effect is presented for seed infection of *Salvia pratensis*. These seeds are infected by the cynipid wasp *Aylax salviae*. Infection may be as high as 80 % but is only present in populations with more than about 300 individuals. There is no correlation between infection rate and geographical distribution nor is there any relation with the biotic and abiotic characteristics of the populations.

As infected seeds develop into galls these seeds are lost for the reproductive output of the individual. Therefore infection has a large negative effect on fitness.

While small population size is generally associated with reduced viability, these results demonstrate the existence of an advantage for the small populations.

PoD.7 AVAILABILITY OF LIGHT AND SPACE AFFECTS GROWTH AND REPRODUCTION IN *RUBUS SAXATILIS* L.

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Genetically identical plantlets of *Rubus saxatilis* differed in size and reproductive output when grown for three growing seasons free of interference from other plants except that from 0, 2, or 4 artificial plants. Plantlets free of artificial plant neighbours had significantly higher growth rates, produced significantly higher numbers of flowers and vegetative descendants than those interferred by the plastic plant imitations. Plants with two artificial neighbours differed similarly from those with four neighbours. Flowering was not reduced by vegetative growth nor vice versa. As there was no competition of soil resources, and the genetic component of variation was eliminated, it can be concluded that the observed variation in growth and reproduction of *Rubus* plantlets was determined merely by the availability of light and space to them.

PoD.8 EFFECTS OF VIABILITY ON FLOWERING, IT´S TIMING AND REPRODUCTIVE SUCCESS IN TWO MARSH-ORCHIDS.

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The viability of plants has been shown to appear in the size of an individual. Importance of the leaf-area, able to provide energy resources for the individual, is essential. On nectarless Marsh-Orchids (*Dactylorhiza* spp.) viability is connected to reproductive success in a more complicated way than in nectariferous and insect-pollinated plant families. So far quite a little attention has been paid to the viability as a component of fitness in these species. Our aim in this study is to show the effect of viability on reproduction with special request to the deceptive pollination system occuring in *Dactylorhiza incarnata* and *D. traunsteineri*. We also attempt to show the affect of leaf-area (viability) on the initiation of flowering. These studies were carried out during May-August 1989 and 1990 in Central-Finland. Our results suggest that those plants with large leaves, high inflorescenses and many flowers produced the most ovules. Since the timing of flowering was also depending on the plant's viability, those *D. incarnata* flowering earlier produced more ovules. Viability in terms of leaf-area clearly had an affect on the plants reproductive success. Moreover, many-flowered and tall Marsh-Orchids were more attractive and had a higher fitness in terms of fruit set. Our result that those Orchids with the highest viability started their flowering earliest might benefit from flowering simultanously with species containing nectar like *Menyanthes trifoliata* and *Andromeda polifolia*.

PoD.9

LIFE HISTORY AND NICHE DIFFERENTIATION BETWEEN TWO CYTOTYPES ($2n = 4x = 40$, $2n = 6x = 60$) OF *POLYGONUM AVICULARE* IN A FALLOW FIELD

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Polygonum aviculare is a complex of annual weeds colonizing various kinds of disturbed habitats. Subsp. *aequale* ($4x = 40$) is restricted to trampled soils while subsp. *aviculare*, in which two cytotypes have been reported ($4x = 40$, $6x = 60$), is usually found in cultivated fields. In a first-year fallow-field, both cytotypes of subsp. *aviculare* were found growing together in a mixed population. There was evidence, however, for temporal niche differentiation between them. The tetraploïd type completed its life cycle early in the summer, when the plant cover was still scarce. On the contrary, the hexaploïd one, developing a higher vegetative biomass, was able to compete with a denser vegetation and to persist later in the year. Cultivation in uniform conditions revealed that these differences in life history had a genotypic basis although both cytotypes germinated at the same time.

	4x	6x	$F_{1,18}$
Flowering date (days)	48	70	$p < 0.001$
Biomass allocation to seeds (%)	40	20	$p < 0.001$
Life span (weeks)	21	27	$p < 0.001$
Number of seeds	1394	3328	$p < 0.001$
% seeds before 20th week	90	33	Not tested
Total biomass (g)	7.8	31.2	$p < 0.001$

The 4x and 6x cytotypes show r-selected and K-selected traits, respectively. The latter are typical of the ruderal - competitive strategy as defined by Grime (1977). Phenotypic plasticity was investigated along a soil fertility gradient. Although both cytotypes showed a typical opportunistic response (300-fold variation in seed yield), the 4x, owing to its shorter life span, consistently produced 2 to 3 times less seed as the 6x under fertile conditions. Thus, it is only in short-lived sites subject to unpredictable disturbance such as weeding, that late flowering types would be at a disadvantage. In conclusion, although as in most weeds, phenotypic plasticity obviously plays an important role in the adaptability of the genotypes, niche specialisation between cytotypes may partly account for the high colonizing success of subspecies *aviculare* in the early stages of secondary succession.

PoE.1

GENETICS OF MATE CHOICE IN DROSOPHILA

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Genetic basis of mate choice and mating preference of allopatric sibling species Drosophila virilis and D. lummei was studied in a copulation cage both by multiple choice and no choice methods. Different kinds of isolation indexes were estimated. Mate choice was not random either between the pure species, or between the F_1's, or between the species and F_1. Visible recessive markers on the chromosomes of D. virilis were used in the analysis of genetic basis of mate choice and mating preference: 16 combinations of either homozygous or heterozygous D. virilis autosomes are recognizable. The effect of autosomes was estimated by using factorial experiments. The effect of homozygous D. lummei autosomes on prezygotic isolation between D. virilis and D. lummei remains unclear because of the lack of suitable D. lummei markers. The effect of the X chromosome in each generation was estimated on the basis of reciprocal crosses.

The only D. lummei marker available was white on the X chromosome. We had a white-eyed mutant stock from both species, and visual stimuli seem to be important especially for D. lummei: white-eyed D. lummei males did not find any mates during the observation period, 30 minutes. Within half an hour, 70 % of D. virilis and 47 % of D. lummei wild type flies copulate with conspecific mates.

Genetic basis of mate choice and mating preference is complicated and autosomal, unlike the incompatibility systems of postzygotic isolation mechanisms between D. virilis and D. lummei. The fifth chromosome most affected mate choice and mating preference in both sexes.

PoE.2

ADULT SELECTON ON INVERSION POLYMORPHISM IN A NATURAL POPULATION OF *Drosophila buzzatii*

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The mating pattern and sexual selection associated with the inversion polymorphism have been investigated in a natural population of *Drosophila buzzatii*. Two independent samples of adult flies were collected: non-mating individuals (base population) and mating pairs. All individuals were karyotyped at the second and fourth chromosomes by crossing them to an homokaryotypic stock and analyzing the salivary gland chromosomes of their progeny. A sequence of models with increasing simplicity (decreasing number of independent parameters) was fitted to the data. Each model was tested using the G-statistics or likelihood ratio test. Null hypotheses of no selection and random union of gametes and karyotypes were tested comparing the fitting of consecutive models. The main results were: (1) no deviations from random mating were found; (2) inversion and karyotype frequencies did not differ between sexes; (3) karyotype frequencies did not depart from the Hardy-Weinberg expectations; and (4) sexual selection was non significant in both sexes. These results are discussed in the light of complementary evidence obtained in the same species.

PoE.3

RANDOM MATING IN A STRUCTURED NATURAL POPULATION OF *Drosophila buzzatii*.

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The cactophilic fly *Drosophila buzzatii* feeds and breeds upon the microorganisms associated with the decaying *Opuntia* (prickly pear) tissues which constitute an ephemeral and patchy resource. There are founder effects associated with the colonization of these substrates and the number of parents breeding on a single rotting cladode is approximately ten. It has been suggested that inbreeding may be relatively common in nature because newly emerging flies from a breeding site, which are more closely related than flies taken at random from the whole population, are more likely to mate with each other.
Using allozymes as the genetic probe, we were able to show that wild *D. buzzatii* females and males engaged in copulation are mating at random; i.e., female-male genotype combinations were not statistically different to their expectations based on marginal frequencies. Hence, putative inbreeding due to local random mating of genetically related flies was not detected. It is concluded that individuals raised from a niche disperse and mate at random with other members of the population, so only one round of drift is taking place.

PoE.4 ASTONISHING HIGH RATE OF MULTIPLE PATERNITY IN A NATURAL POPULATION OF *Drosophila melanogaster*.

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Captured wild females of *Drosophila melanogaster* were permitted to lay eggs in standard food vials, during seven consecutive days. Then genotyped at two loci on the second chromosome (*Adh* and *α-Gpdh*) and two loci on the third chromosome (*Est-C* and *Pgm*).

A sample of the progenies of homozygous females for the second and/or third chromosome, were examined electrophoretically for the same loci that their mothers. Those containing more than two different genotypes were considered to stem from more than one father, there being no crossing over in the males.

The observed frequency of multiple mating represents only a part of the true frequency. Using the appropriate statistical probabilities, the actual frequency can be inferred.

Our data shown up that multiple insemination is present in almost 100% of the cases.

The results are discussed in relation with the high density of the population and the fitness and sexual selection of *Drosophila melanogaster* females.

PoE.5 DNA-FINGERPRINTING IN MARMOT POPULATIONS

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A variety of social organization systems can be found among marmot species, including asocial, polygynous, monogamous and probably also polyandrous forms. Field observations suggest a correlation between environmental constraints and circannual rhythmicity on the one hand and sociality on the other. However, exact data on the genetic relatedness within the group and the reproductive success of the individuals are not yet available. We have therefore used DNA-fingerprinting techniques to analyse the mating system of the alpine marmot (*Marmota marmota*). Surprisingly, we found very low polymorphism with convential DNA-fingerprinting techniques, which may be due to the small population size of this species in the Berchtesgaden region (Bavarian alps). A related species with a similar social system, *Marmota caudata*, which lives in the Himalaya region, shows indeed a somewhat higher level of polymorphism using the same techniques.

For a further analysis of the well studied Berchtesgaden population, we are now developing alternative techniques, including SSLP's and the molecular analysis of MHC polymorphisms.

PoE.6

POPULATION STRUCTURE AND MATING SYSTEM OF THE PILOT WHALE *GLOBICEPHALA MELAS*

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We have analysed DNA-samples from the long finned pilot whale (*Globicephala melas*), which were collected as part of an international collaboration sponsored by the Faeroese government, by means of DNA-fingerprinting. This whale species is hunted at the Faeroe islands by driving whole swimming pods on the beach. This allows a complete sampling of all individuals in a pot, including the foetuses from pregnant females. We have used multi-locus mini-satellite probes and simple sequence length polymorphisms (SSLP) to analyse the population structure, as well as the mating system of this species. Our results indicate a matriline structure of the pods, with related females staying together. Interestingly, it appears that none of the males swimming with the pods is the father of any of the pubs.

In an extension of the study, we have used the primer set developed for *Globicephala* also on other whale species and found that they recognize the homologous loci in all of them and partly even in land-living ungulates. Cloning and sequencing of the loci revealed an unusual high conservation of the sequences flanking the simple sequence stretches.

PoE7 THE ORIGIN AND EVOLUTION OF THELYTOKOUS PARTHENOGENESIS: SPONTANEOUS VERSUS HYBRID THEORY

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Most authors consider tychoparthenogenesis (i.e.the occasional spontaneous development of unfertilized eggs), as the starting point for all thelytokous parthenogenesis (e.g., Vandel,1931;Suomalainen,1950). This hypothesis (the so-called spontaneus theory) is supported by:a) the observation in many animal groups of self-perpetuating all-female lines spontaneously produced by unfertilized eggs of bisexual species; b) the finding that artificial selection often greatly increases low spontaneus rates of parthenogenesis, indicating a genetic control of this way of reproduction. The high levels of genetic heterozygosity found in many parthenogenetic organisms is explained by this theory as resulting from a buildup over time of mutations, up to the loss of diploidy.

A contrasting hypothesis for the origin of thelytokous parthenogenesis (the so-called hybrid theory) considers interspecific hybridization as causing a tendency towards parthenogenetic development and reproduction; accordingly, meiosis of diploid hybrids would be so upset as to produce unreduced eggs (e.g., Uzzell and Goldblatt, 1967).

Neither of these two theories seems satisfactory in giving a general explanation of the origin and evolution of thelytokous parthenogenesis. The spontaneous theory accounts for the origin of thelytoky, but does not explain the widespread fixed heterozygosity found in many parthenogenetic forms. On the other hand, the hybrid theory accounts for the latter phenomenon, but not for the transmission of the hybrid genome to the next generation. It should be noted that these theories have been mainly supported by authorities working respectively on invertebrate and vertebrate parthenogenesis.

In our opinion, the most likely hypothesis for the origin of many thelytokous forms is that hybrid eggs, produced in areas of extensive interspecific crosses, may develop by thychoparthenogenesis. Among self-perpetuating all-female lines that arose this way, those allowing transmission of the hybrid genome are expected to be selected for. Accordingly, hybridization would not itself cause changes in the maturation divisions (which are genetically controlled), but only favour their selection through heterosis (Bullini and Nascetti, 1990). In groups where egg activation is needed, as vertebrates, interspecific hybridization can make it available several hybrid developing eggs, from among which mutants for thelytokous parthenogenesis can be selected for.

PoE8

GENETIC VARIATION IN HYBRID AND NON-HYBRID PARTHENOGENETIC STICK-INSECTS (INSECTA, PHASMATODEA)

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Among stick insects, thelytokous parthenogenesis appears to be a widespread phenomenon, either as the only way of reproduction (parthenogenetic taxa), or associated with bisexual reproduction (geographic parthenogenesis). Parthenogenesis in this group is under genetic control, as shown by selection experiments (Bergerard, 1958; Bullini, 1965), and can be achieved through various mechanisms, leading to strong differences in genetic variability.

A number of cases are presented: a) geographic parthenogenesis in *Bacillus rossius*, where the diploid number is restored in early embryonic development after a normal meiosis, and complete homozygosity is attained; b) obligatory parthenogenesis in the hybrid species *Bacillus whitei*, *B. atticus*, *B. lynceorum* and *Clonopsis gallica*, associated with permanent heterozygosity at several loci and different degrees of clonal variation. The short- and long-term evolutionary success of the different parthenogenetic strategies found in stick insects is discussed, with particular emphasis: 1) on the so called "demographic advantage", 2) on the "heterotic advantage", and 3) on the success in exploiting disturbed habitats. Finally, the two contrasting hypotheses on the origin and evolution of thelytokous parthenogenesis ("spontaneous" versus "hybrid" theory) are examined.

PoE9

FROM HYBRIDOGENESIS TO PARTHENOGENESIS IN THE GENUS BACILLUS (INSECTA PHASMATODEA)

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Among Vertebrates hybridogenetic reproduction has been so far demonstrated in the Poeciliopsis and Rana esculenta complexes. In the former, the involvment of diploid hybridogens in the origin of triploid gynogens from fertilized unreduced eggs has been suggested (Schultz, 1989, in S.K. Meffe and F.F Snelson (eds), Ecology and Evolution of Livebearing Fishes, Prentice Hall, pp. 69-87).

Among invertebrates the first hybridogen to be discovered was the Northwestern Sicilian hybrid Bacillus rossius-grandii benazzii. Allozymic marker analysis of the offspring of B. rossius-g. benazzii females X B. grandii or B. rossius males showed the hemiclonal transmission of the maternal rossius genome in the great majority of the descendants, the discarded g. benazzii set being replaced by the genome of the fathering male (Mantovani and Scali, 1990, Inv. Rep. & Dev., 18 (3): 185-188).

From inseminated eggs apparently unable to transmit any maternal genetic material the production of abundant (5-18%) all paternal descendants of both sexes has been recorded. This natural androgenetic reproduction, even if genetically and embriologically very interesting and also unexpectedly enriching hybridogen-host species relationships, does not appear of long term evolutionary importance. On the other hand, the observed rare gynogenetic individuals certainly appear more relevant for the evolution of parthenogenesis. In addition, we observed a rudimentary but very widespread parthenogenesis in B. rossius-g. benazzii eggs: i.e. the haploid rossius nucleus starts dividing and some cells also diploidize, but further embryogenesis is prevented (Mantovani and Scali, submitted for press). Both cytological and allozyme-marker findings evidentiate important pre-requisites to clonal transmission of the female genome and therefore the possible evolution of parthenogenetic morphs from hybridogenetic ones is here strongly suggested.

Moreover, in the Southeastern Sicilian hybrid B. whitei (B. rossius/g. grandii), among true thelytokòus clones the existence of females experiencing hybridogenetic, androgenetic and gyno-parthenogenetic reproduction, similarly to B. rossius-g. benazzii, has been evidenced (Scali et al., 1991, Frustula entomologica, 12:103-108). All this supports that hybrid thelytokous taxa could derive from an initial hybridogenetic complex.

PoFI.1

LIFE HISTORIES AND FIELD OBSERVATIONS OF CO-EXISTING *DAPHNIA* SPECIES AND THEIR HYBRIDS

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A population consisting of *Daphnia* species of the *Daphnia longispina* group was studied in a shallow eutrophic lake. This population consists of *D. galeata, D. cucullata* and their hybrids.

The genetic composition of the population was studied using three allozyme markers: GOT, PGI and PGM. Both species were fixed for different GOT alleles, which means that the hybrids could be distinguished as heterozygotes.

The clonal composition of the population was analyzed every two weeks during two years. The seasonal abundance of the parental species and their hybrids differed during the year, but within these groups the same genotypes are found during the year. Genotypic variation was the highest for *D. cucullata* and the lowest for *D. galeata, D.galeata x D. cucullata* was intermediate.

Life history variation was examined among and within the two species and their hybrids. This was done in an culturing experiment with 15 GOT-PGI-PGM genotypes, (every genotype represented by 3 clones) at three temperatures (12.5, 17.5 and 22.5 ^{o}C) and two food concentrations (0.38 and 1.13 mg C l^{-1}). For several life-history characters (offspring size, size at maturity, newborn size and age at maturity) a significant species (i.e. *D. galeata, D. galeata x D. cucullata, D. cucullata*) effect was found.

Generaly, hybrid clones showed intermediate life-history traits when compared with the parental species. When comparisons were made among PGI-PGM genotypes within a given species a significant genotype effect was found in an ANOVA for some life-history characters.

PoFI.2

BODY SIZE AND REPRODUCTIVE EFFORT IN MALE FLESH FLIES

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The number of sperm contained in virgin male flesh flies (*Neobellieria* (= *Sarcophaga*) *bullata*) is strongly influenced by their size and age, furthermore the number of sperm transferred to females during copulation is positively correlatated with male body weight. Sperm number in male flies is related to size by the equation Ln Sperm Number = 9.24 + 0.675 Ln Male weight (mg). Virgin male flies held without access to females continue to produce sperm at a linear rate during the first 16 days of their lives. On average males produce 19,637 sperm per day, however, larger flies produce sperm at a greater rate than smaller flies; males ranging in size from 15 to 36 mg produced 17,800 ± 1,899 sperm per day whereas males ranging in size from 50 to 76 mg produce 27,036 ± 2,803 sperm per day. Males transfer an average of 6,965 ± 712 sperm in copulations lasting 165 ± 15 minutes. The number of sperm transferred was significantly correlated with body size whereas mating duration was not. These results clearly document the relationship between body size and male reproductive effort and complement a large body of work relating body size to reproductive effort in females.

PoFI.3 GENETIC VARIATIONS IN RETENTION DURATION AND OVARIAN ACTIVITY KINETICS IN VIRGIN *D. MELANOGASTER* FEMALES.

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In *D. melanogaster* virgin females, absence of insemination induces a preoviposition period the duration of which is genetically determined by genes (or groups of genes) distributed on the three major chromosomes.

Opposite genotypes obtained by artificial selection differ not only in their retention capacity but also in their ovarian activity. In the short retention genotype (m = 1.5 days) substantial daily fecundity is supported by constant ovarian activity only slightly reduced in comparison to mated flies's productivity. In contrast, in the long retention genotype (m =14.7 days) ovarian activity starts identically to that of the opposite strain but is characterized by an arrest 24h after emergence. Vitellogenesis drops, egg retention and oocyte resorption occur and the emission of follicules by the germarium ceases for several days. This 1st wave of vitellogenesis leads to the formation of a batch of mature eggs that are kept in retention in the ovaries, in consequence of the delay of ovulation.

As oogenesis regulation depend on brain and CC-CA controls and ovulation onset depends on a myotropic brain hormone, it is hypothesized that the genetic detreminants of retention capacity are involved in some control over the kinetics of brain activity.

This retention capacity is subject to natural selection. In natural populations, the relative frequency of each genotype present clinal and seasonal variations supposed of adaptive value, in which the long retention phenotypes are favored in lower environmental temperature.

PoFI.4 TWO WAYS FOR GEOGRAPHICAL EXPANSION.

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Drosophila melanogaster and *Drosophila simulans* are sibling species that expanded from tropical Africa to temperate regions where both colonized similar environments and similar resources.

In spite of parallel evolution, each species presents its own adaptive pattern especially in the management of their reproductive effort.

The occurence of a cold season entails a non-reproductive period and leads to drastic reduction in population size and to frequent depletion of food supply.

To surmount these difficulties, *D. melanogaster* deploys progressive genetic modifications. The number of ovarioles increases along a latitudinal cline and allows a higher potential fecundity for temperate flies. Moreover, their capacity to control egg deposition in reaction to unfavorable environment by means of an oviposition blocking process slightly increases with latitude. In reaction to the lack of sexual partner that often occures when population size is reduced (after the bottle-neck of overwintering or after a drought period) virgin females present a longer preoviposition period than tropical flies. In natural populations, this retention capacity increases along a latitudinal cline by the increasing frequency of long retention genotypes which are rare in African populations. This variation is correlated with an increased reactivity to insemination for the temperate flies . Both characteristics avoid loss of material and allow rapid colonization of available food.

In contrast, *D. simulans* presents reduced variations. The number of ovarioles slightly increases with latitude and the potential fecundity remains low. The capacity to stop egg deposition appears high in tropical populations but decreases with latitude. In tropical areas, the retention capacity of virgin *D. simulans* females is shorter than that of *D.melanogaster* and it remains identical whatever the latitude. Correlatively, the reactivity to insemination stimuli is low and stable. Despite these apparently lower adaptive characteristics, *D.simulans* and *D.melanogaster* present similar expansion in tropical and European regions with differences, however, in population sizes.

PoFI.5

MULTIPLE MATING AND REPRODUCTIVE SUCCESS IN THE SIMULTANEOUSLY HERMAPHRODITIC LAND SNAIL *ARIANTA ARBUSTORUM*

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The effect of multiple mating on reproductive success was investigated in the land snail *Arianta arbustorum* under laboratory conditions. *A. arbustorum* is a simultaneous hermaphrodite which can store sperm after reciprocal copulation. In the field, individuals mate 1-4 times each reproductive season. Virgin snails were randomly assigned to one of four different treatments: individuals received 1) many copulations, 2) one copulation per year, 3) one copulation in two years and 4) no copulation. Animals with multiple mating produced more eggs than those copulated only once, while the control animals with no copulation produced very few, unfertilized eggs in the first year. The difference in reproductive output between multiple-mated and single-mated snails increased in the second reproductive season. This result suggests that multiple mating increases the lifetime reproductive success in *A. arbustorum*.

PoFI.6 HABITAT PREDICTABILITY AND LIFECYCLE STRATEGIES IN THE GENUS *LIPARA* (DIPTERA; CHLOROPIDAE).

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The flies of the genus *Lipara* are strict monophagous parasites of the common reed, *Phragmites australis* (Poaceae). Due to feeding activities and/or metabolic products, the newly formed internodes of the shoot are strongly shortened and a typical cigar- or spike like gall is formed.

Reed is a perennial rhizomatous grass that produces fresh shoots every year during spring. Because these shoots dry up and die at the end of the summer, they can only serve as a source of food for the herbivore during a short time of the year. Former studies have revealed there exists a high between-plant and between-year variation in plant quality caused by several interacting factors as there are the genetic differences between reedclones, water and nutrient contents of the soil and interspecific competition with other plants. Besides this, the annual bud emergence and growth of the reed is strongly influenced by climatic (e.g. temperature) factors.

During the course of evolution two main solutions have evolved to overcome higher mentioned problems within the genus *Lipara*.

a.- the *L.pullitarsis* strategy: The female fly emerge early in the season; they deposit a high amount of eggs, randomly distributed among the reedshoots; there is a high mortality rate of larvae before gall-formation can take place.

a.- the *L.lucens* strategy: The female fly emerges later when the young reedshoots are already well developed; they carefully select a suitable place to deposit a restricted number of eggs; there is a rather low mortality rate of larvae before gall formation.

Preliminary studies on the habitat selection of *Lipara* species revealed clear intra-specific differences between separate reedbeds due to local conditions.

PoFI.7

THE CLONAL ECOLOGY OF HETEROCYPRIS INCONGRUENS (OSTRACODA)

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We have previously described a seasonal succession of eletrophoretic clones of *Heterocypris incongruens* (Crustacea, Ostracoda) in an obligate parthenogenetic population in a rice field located in the Po plain (Northern Italy).

A multilocus genotype (clone) dominant in the summer (clone S) was substituited by a different one (clone W) in the winter. We have also identified a third electrophoretic clone (clone I) which is rare all through the year.

Laboratory experiments confirmed differences in thermal ecology among genotypes (clones).

Here we report the results of life table experiments at 24 °C and 16:8 and 12:12 light-dark periods supporting the role of photoperiod on the biological cycle of different clones. In summer-like light conditions (16:8 L:D) the summer clone (clone S) shows a decrease in mean age at first deposition and an increase in egg production and hatching while the winter clone (clone W) produces fewer eggs and almost all of resting type. On the other hand, in winter-like light conditions (12:12 L:D) clone S shows a decrease in egg production and an increase in resting egg percentage while clone W shows, a decrease in age at first deposition and an increase in egg deposition and hatching. Clone I (rare in the rice field and fastest growing in the laboratory at 24°C and 12:12 L:D) doesn't show a clear pattern in reaction norms in response to seasonal changing factors such as temperature and photoperiod. The only clear feature is an almost non existent production of resting eggs in any condition.

Temperature and photoperiod seem the environmental factors that drive the mechanism of clonal succession of W and S clones observed in the rice field. W and S clones seem to maximize their fitness in winter and summer respectively: in short run, increasing egg and offspring production while securing their persistence, in the long run, by the deposition of resting eggs that hatch in respons to specific environmental cues.

PoFI.8

FRESHWATER CLAM *ANODONTA PISCINALIS* (NILSS.) USES CHEMICAL CUES TO RECOGNIZE THE HOST

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The release of the parasitic larvae, or the glochidia, of Unionidae takes place in spring and is believed to be passive. Because the mortality of released glochidia is high (>90%), adaptations that improve the survival of glochidia could be expected to evolve. Such an adaptation would be the recognition of the host fish by reproductive females. We conducted two experiments to examine weather such adaptations exist.

Both experiments were run in 96 aerated (8 litre) aquaria filled with lake water (17 °C ± 2 °C) using sieved (1 mm) sand as a bottom material.

For **the first experiment** we exposed mature female clams from four populations to (1) control, (2) roach (*Rutilus rutilus*) and (3) perch (*Perce fluviatilis*) treatments. The experiment was designed to answer the question: **"Do female clams recognize the host fish and respond by releasing larvae?"**. In fish treatments a small fish was added to aquarium. After six days, we mixed the water and sieved it to calculate the number of released glochidia.

72 clams were left for the analysis after the exclusion of the cases where the water was spoiled by dead fish. 51 of these clams (70.8%) released glochidia. More clams reproduced in fish treatments (80.6 %) than in control treatment (58.1 %)(X^2 = 4.30, df = 2, p = 0.038). More glochidia were released in fish treatments than in control (medians for treatments 1, 2, and 3 were 2, 128 and 65 respectively)(ANOVA, effect = treatment, F(2,39) = 12.02, p < 0.002). **These results indicate that female clams recognize the host fish and respond by releasing larvae.**

In the second experiment we asked the question: "By what mechanism do clams recognize the host fish?". Clams of two populations were exposed to six treatments: (1) control, (2) smell of fish, (3) smell of glochidia, (4) movement of fish, (5) shadow and (6) contact with fish. Treatments 2 and 3 were set up by adding 200 ml of water from the fish tank or water that had contained glochidia. Movement of fish was simulated by dragging a small spoon-bait 20 strokes across aquaria. Contact was achieved by touching the valves of the clam with an aquarell brush. Shade was cast with a cardboard box. Treatments 4, 5 and 6 were replicated six times per day, treatments 2 and 3 three times per day, for six days.

We excluded clams that started reproduction already at the acclimation phase. 76 of the remaining 78 clams released glochidia (97.4 %). More glochidia was released in chemical treatments (2 and 3) than in other treatments (medians for treatments 1 - 6 were 159, 1020, 1059, 142, 109 and 131 respectively)(*a priori* contrasts, treatm. 2 and 3 vs control, F(1,64) = 4.69, p = 0.03; 2 and 3 vs other, (F(1,64) = 8.62, p = 0.005; 4, 5 and 6 vs control, F(1,64) = 0.08, p = 0.78). **This indicates that female clams use chemical cues in the regulation of the release of glochidia.**

Our results indicate that all possible fitness components should be considered if the reproductive performance of individuals is evaluated. Our results also support the view that in some life history types different kinds of recognition mechanism, in this case host-finding mechanisms, are of essential importance, and maybe more important than for example the absolute number of offspring produced.

PoFI.9

RESPONSE OF OVIPOSITING WATER-LILY BEETLE FEMALES ON EGG LAYING BY OTHER FEMALES

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For many plant-feeding insects, the selection of the oviposition site is a critical stage for the survival of their offspring. We have studied oviposition behaviour of water-lily beetle (*Galerucella nymphaeae* L.). Females lay their eggs in clutches on the floating leaves of the yellow-water-lily (*Nuphar lutea*) and after hatching the larvae feed on leaves. The food supply of a single leaf is limited and only a certain number of beetles can survive on each leaf. Our question is if females avoid intraspecific competition and avoid laying eggs on leaves with conspecific eggs and larvae? We studied the preference of egg laying experimentally in small aquaria. Females were allowed to choose sites between empty leaves and leaves with larvae or eggs. Females clearly preferred leaves without larvae, but they did not avoid leaves with conspecific eggs. While it is particularly important to avoid leaves with larvae, it would also be benefitical to avoid leaves with eggs. Partly imperfect female behaviour might be due to constraint in evolution.

PoFII.1 KINSHIP EFFECT ON SOCIAL BEHAVIOUR AND POPULATION GROWTH IN BANK VOLES *CLETRIONOMYS CLAREOLUS*

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We examined the effect of relatedness on social behaviour and population growth in bank vole *Clethrionomys glareolus*; a species with strict territoriality among breeding females. We used four experimental populations in large enclosers: two founded by females of close kin ("Friends") and two founded by mutual unrelated females ("Strangers"). Founder males were mutual related or otherwise familiar in "Friends" populations and unrelated in "Strangers" populations. Number of matured females and litters did not differ between experimental populations during the experiment. In spite of that "Friends" populations grew twice as faster as "Strangers". This was caused by higher recruitment and survival of the young among "Friends", which might be a consequence of agonistic behaviour of matured individuals towards juveniles. This is suggested by lower trappability and smaller-sized home ranges of juveniles among "Strangers". Home ranges of the "Strangers" young were at a greater distance from home ranges of mature strange females, which may also indicate that they try avoid mature individuals. Space sharing among mature females seems differ between experimental populations, too. Mature females home range centers were more closely one another among "Friends". Anyway there was no evidence of altruistic space sharing between mature females and their related young females which may help young females to occupy an exclusive home range. Related young females are only allowed to settle in mature females home range but their are not allowed to reproduce.

PoFII.2 PHENOTYPIC PLASTICITY IN SPACING BEHAVIOUR AND ADAPTATION OF REPRODUCTION TO CHANGING CONDITIONS IN FIELD VOLE (*MICROTUS AGRESTIS*)

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Populations of *Microtus agrestis* were studied by live trapping in Konnevesi, Central Finland in field and forest. The spacing behaviour of reproductive females varied between cohorts, habitats and in time. The home range overlap in field fluctuated greatly during the summer. Excluding aggregative behaviour in early summer, the overwintered females were mutually territorial. Their home range size and overlap reacted basicly to their own numbers. The maturation of young females was not regulated by territoriality. The young females, which formed the majority of reproductive females since midsummer, reacted more on total population density. Increasing density seemed to induce aggregation. In addition to density the overlapping was correlated with the number of litters. The females in the less favourable forest overlapped less and had greater home ranges than females in the field.

The reproductive success of females in the field was inversely density-dependent as was the maturation rate and survival of young reproductive females too. The dispersal of young reproductive females started when the reproductive success in field decreased to the level found in suboptimal forest surroundings. I conclude that the females try to compensate the suggested disfavourable effects of density by spacing behaviour. There exist age-dependent differences: the old females react by mutual territoriality. They enlarge their home ranges possibly to family home ranges where the resources of habitat can be maximally converted to reproducing young. The density sensitive young females first react by enlargening home ranges and eventually by shifting their reproduction to space and time where the possibilities to succeed are the best. These flexible behavioural tactics allows the field vole to successfully inhabit seasonally changing habitats.

PoFII.3 SHORT TERM CHANGES IN AGE STRUCTURE OF CAVE CRICKET POPULATIONS.

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Previous studies on several *Dolichopoda* cave cricket populations showed the existence of contrasting patterns in age structure related to different ecological and historical characteristics of the cricket habitats.

An aseasonal age structure pattern characterized by the absence of a synchronic life cycle, was revealed in populations inhabiting caves with high energy input and relatively stable high temperature. A seasonal pattern showing synchronization among individuals in growth and reproduction time, occurs in caves characterized by scarcity of trophic resources and recent origin (i.e. man made caves).

Two colonization experiments carried out by transplanting *Dolichopoda* population samples into previously unexploited caves, provided the opportunity to test whether short term changes occurred in demography and genetic structure. These experiments, performed some years ago by researchers of the Laboratoire Souterrain, were originally aimed at studying acclimatization of cave organisms.

One of the two transplanted population revealed a definite change in age structure from an aseasonal pattern, as in the original population, to a seasonal pattern. This change occured after only ten years, roughly corresponding to five generations, because of the semivoltine life cycle of *Dolichopoda*.

In the other experiment, where the original population showed a seasonal age pattern, no substantial change in age structure has been observed even if the time span since colonization was longer (16 years).

The comparative analysis of results from these experiments confirms the existence of a relationship between age structure and availability of food resources. Furthermore, these results provide hints to discuss the role of selection, genetic drift and phenotypic plasticity in the expression of factors, directly affecting the age structure, such as embryonic or nymphal diapause and duration of the oviposition period.

PoFII.4

INDIVIDUAL OPTIMIZATION OF CLUTCH SIZE IN THE GREAT TIT (Parus major).

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In bird studies there is evidence that individual birds maximize their fitness by adjusting the clutch size to their environment and or their individual 'quality'. In the Great tit the picture emerges that the reproductive value of clutch and parents is positively associated to natural variation in clutch size, while artificial variation in clutch size lowers their reproductive value (Pettifor 1989, Tinbergen & Daan 1990). This supports individual optimisation of clutch size. Contradicting evidence indicates clutch size to be non-adaptive, at least on the individual level (Dhondt et al 1991).
Here we discuss an experiment designed to test specifically whether individual optimization in Great tits can be shown to occur. Clutch size was taken as a quality indication of the birds in their environment. Birds with different clutch sizes that hatched the same day were given the same number of young on day two. Nestling mortality and growth was measured, as well as the fate of the parents as a function of the original clutch size the parents laid.

PoFII.5

Seasonal variation of clutch size in blackbirds (Turdus merula): a new explanation

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Similarly to other open-nesting passerines clutch size of blackbirds has a seasonal maximum. Lack and Snow attributed this seasonal pattern to the amount of food carried to the nestlings, which depends on the food abundance and daylength. According to this hypothesis partial losses in larger clutches should be the least in the nestling periods of nests laid at the time when the average clutch size was maximal.

However, our data - collected in a 13 ha urban park in four successive breeding seasons from 1986 to 1989 - do not support this explanation. The averages of hatching-, fledging- and breeding successes of nests which fledged at least one offspring in 15-day overlapping periods have minimum values in those periods where the average clutch sizes were the greatest. The seasonal patterns of all these partial successes correspond well with the pattern of average daily amount of precipitation of periods 10-12 days preceding egg-laying. It is well-known, that the availability of the main food type of blackbirds, that is of earthworms has a good correlation with precipitation, consequently the amount of rainfall is a good indicator of food-abundance in this species. It was shown in other species that the food shortage during egg-laying has an effect on the quality of eggs, which can lead to developmental problems causing hatching failures or spread hatching which causing great weight-asymmetries among siblings leads to brood reduction even if the food-supply is satisfactory during the nestling period.

If the seasonal patterns of the two most common clutch sizes are examined separately, the partial hatching success of clutch size 5 is found to be much lower than that of clutch size 4 at the beginning and at the end of the breeding season. On the other hand the patterns of fledging success do not differ very much. The patterns of partial breeding success suggest that females laying 5 eggs react more strongly and earlier to the drier period preceding egg-laying than females laying only 4 eggs. The different sensitivity of the two clutch sizes to the food-shortage during laying leads to that more nestlings fledge from clutch size 4 than clutch size 5 at the beginning and at the end of the breeding season, while in the middle of the season the two clutch sizes fledge about the same amount of offsprings.

PoFII.6 AUTOMATIC OBSERVING OF HOLE-NESTING BIRDS DURING THE PARENTAL CARE PERIOD

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Studying reproductive strategies one of the main problems is the measurement of costs of reproduction. Measuring the efficiency of parent birds requires a method which collects field data continuously to answer the following questions:

- How does the feeding activity of the two sexes differ?
- How do parents' weights change during incubation and feeding?
- How much is the weight of the loads (food for nestlings per visit)?

These questions were difficult or even impossible to answer by the earlier methods. We have tried to solve the problem by setting up an on-line data-recording system consisting of a (portable) PC, 1-4 portable electronic balances (Mettler PM4600) and a power supply. Using the balances we observe continuously the weight of the nestboxes. A special software was developed, which can handle (select and record) data coming from 1-4 balances simultaneously. The output database contains the following data about each visit: sex and weight of the visiting parent, weight of the load, exact time of entering and that of leaving (time passed since the last visit of the parent and duration of the visit). The system was tested during two breeding seasons with Collared Flycatchers, Blue and Great Tits breeding in artificial nestboxes.

PoFII.7

Density-dependent success in large, natural broods of the Collared Flycatcher (Ficedulla albicollis) in bad years

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The problem: Several brood size manipulation studies have revealed trade-offs between brood size and fledging success while recent studies of natural broods of hole-nesting birds seldom indicate the presence of such relationship. However, individual optimization cannot be perfect. One may expect heavier loss of nestlings in large, natural broods under poor feeding conditions. Thus bad years with low recruitment rate or plots with high population density leading to low level of food availability should be tested for phenotypic selection against high fertility.

Data: Breeding data collected in 4 colonies of the Collared Flycatcher, *Ficedula albicollis* between 1982 and 1990 were used. Population density was extremely high (10-20 pairs/ha) at one plot where the number of nest-boxes were doubled in 1982. Years with high avegare number of fledged young were called "good years", (82,83,86) years with low number of fledged young were considered as "bad years" (84,85,89,90).

Methods: A series of hierarchical loglinear models with three categorical variables (**brood size**: small and large; **fledging success**: lower or higher than a given threshold; **years** (good, bad) or **density** (low, high)) were tested for three-factor interactions. Density-dependence of fledging success was also tested with the method of first differences.

Results:

1. In bad years a significant 3-factor interaction exists between brood size, fledging success and density. Difference between the fledging success of the large broods at the high and small density plots is significantly larger than the difference between the success of the small broods.
2. At the high density plot bad years reduced the success of the large broods in a greater extent than that of the small ones.
3. The year to year change in fledging success is significantly correlated with the year the year to year change in population density at the high density plot.

PoFII.8 REVERSED SEXUAL SIZE DIMORPHISM IN TENGMALM'S OWL: IS SMALL MALE SIZE ADAPTIVE?

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Selection pressure on male and female size and reversed sexual size dimorphism (RSD, males smaller than females) of Tengmalm's Owls was studied during 1981 - 1990 under fluctuating food conditions in western Finland. Dimorphism indices of 379 breeding pairs were calculated for body mass, wing, tail and beak lengths. Breeding success of pairs was approximated by the number of eggs and fledglings produced. The degree of RSD within pairs was not of great importance to the breeding success. No clear evidence for the starvation, female reproductive effort, female dominance and sexual selection hypotheses was found. The selective pressure on male size varied depending on the phase of vole cycle. Light and long-tailed males were most successful in their breeding attempts in low vole years, whereas heavy and short-tailed males were most successful in high vole years. Morphological characters of females did not have obvious effects on breeding success. The results for males also held when young (1-2 -year old) and old (>3 -year old) males were treated separately. There seems to be a selective pressure which results in males to be economical hunters in poor vole years, when they spend much more energy in hunting than in good vole years. These high energy costs in low vole years are partly compensated by lightness of male, which improves flight performance. Thus, light males breeding in poor and good vole years may increase their lifetime breeding success in comparison to heavy males that can breed only in good vole years. In addition, stabilizing selection may exist because of varying selection pressure on male size depending on the phase of vole cycle.

PoFII.9 - DEMOGRAPHY AND STOCHASTIC EXTINCTION IN PALEARTIC GEESE POPULATIONS

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Age-specific survival rates and fecundities have been estimated from population sensusses in nine populations of geese overwintering in western Europe. These data have been used to simulate the population dynamics of the populations in a varying environment and to assess their extinction risk over the next 100 years.

PoG.1 EVIDENCE OF GENE FLOW WITHIN THREE SPECIES OF THE *EREBIA TYNDARUS*-GROUP (LEPIDOPTERA: SATYRIDAE).

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The *tyndarus*-group of the genus *Erebia* (Lepidoptera: Satyridae) is represented in the Alps by three species, *E. tyndarus* (Esper, 1781), *E. cassioides* (Reiner & Hohenwarth, 1792), and *E. nivalis* (Lorkovic & De Lesse, 1954), respectively. The distribution of *E. tyndarus* and *E. cassioides* is basically allopatric, but several zones of contact have been reported. *Erebia nivalis* has its main distribution together with *E. cassioides* in the Eastern Alps, disjunct populations, however, are found in Switzerland.

Contact zones of these taxa exist in the Swiss Alps near Grindelwald and Mürren. We have analysed population samples from both localities by enzyme electrophoresis (vertical starch gels, 15 loci) and we have evaluated levels of genetic identity (NEI-Index) and gene flow (Nm); (*E. tyndarus*: 3 samples from Grindelwald; *E. nivalis*: 2 samples from Grindelwald, 1 sample from Mürren; *E. cassioides*: 2 samples from Grindelwald, 1 sample from Mürren).

Estimates of genetic identity found in interspecific comparisons ranged from I = 0.97 ($nivalis_2$ and $cassioides_1$; both from Grindelwald) to I = 0.60 ($nivalis_1$ and $tyndarus_1$; both from Grindelwald). Clustering of coefficients of genetic identity (WPGMA-method) did not result in seperate clusters of the *nivalis*- and *cassioides*-samples.

Levels of gene flow (Nm) found in interspecific comparisons were in the range which indicates actual or very recent gene flow. They were as high as Nm = 3.3 in the comparison of *nivalis* and *cassioides* from Grindelwald, the comparison of *nivalis* and *tyndarus* from Grindelwald gave Nm = 1.4 , Nm = 1.1 was found in the comparison of *nivalis* and *cassioides* from Mürren. All levels found are well above Nm = 0.5 which would indicate near complete interruption of gene flow.

The results of the electrophoretic survey suggest actual or very recent gene flow among the three *Erebia* taxa in our area of study.

PoG.2

SELECTION AND RECOMBINATION IN A MOUSE HYBRID ZONE: INTROGRESSION PATTERNS OF X CHROMOSOME GENES

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The study of gene flow across a hybrid zone between two differentiated populations provides insight into the genetic basis of speciation. The width of the cline for a given locus reflects the selective pressure it is submitted to in the hybrid genome. As selection acts on correlated sets of loci rather than on individual loci the form of the clines will depend to a large extent on the ratio between selection which eliminates the foreign alleles and recombination, which allows those that are more or less selectively neutral to introgress into the other genetic background (Barton 1983). The hybrid zone between *M. m. domesticus* and *M. m. musculus* provides a particularly good system to study selection and recombination as a large number of markers with known chromosomal assignments are available. Earlier we showed that the Y chromosome introgresses less than the autosomal markers and proposed that the introduction of a foreign Y chromosome perturbs specific co-adapted gene combinations that have evolved in each sub-species. As the Y chromosome is known to interact with the X chromosome in sex determination and differentiation, one might expect that some genes on the latter will also come under the same negative selection pressure in the hybrid genomes. To investigate this possibility we studied the introgression patterns of three markers on a 50cM segment of the X chromosome across a Danish transect of the zone. The centre of this segment does not introgress at all which suggests that it contains genes that are unable to function properly in the foreign genetic background. The flanking X chromosome markers show asymmetric introgression patterns with *musculus* alleles penetrating into the *domesticus* genome but not the reverse. As the introgression of the Y chromosome shows a similar asymmetry, our results are consistent with the idea that genes on the sex chromosomes interact in differentiated coadapted system(s).

PoG.3

TWO HYBRID ZONES BETWEEN *PODARCIS SICULA* AND *P. WAGLERIANA* (REPTILIA: LACERTIDAE): PATTERN AND DIFFERENCES

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Podarcis sicula and *P. wagleriana* are two lacertid lizards which occur sympatrically in Sicily, Aegadian and Aeolian islands (Böhme, 1986; Henle and Klaver, 1986; Capula et al., 1990). At the morphological level identification of the two species in the localities where they coexist may be difficult; on the other hand, the detection of four loci (*Gapd, Got-1, Gp-1, Gp-2*) found to be diagnostic between allopatric populations of *P. sicula* and *P. wagleriana* allows a correct identification of all individuals (Capula et al., 1990).

Studying allozyme variation by means of starch gel electrophoresis in a number of populations of both species from Sicily, Aegadian and Aeolian islands it was possible to detect natural hybridization at Vulcano Island (Aeolian Archipelago) and Marettimo Island (Aegadian Archipelago). At Vulcano Island pure *P. sicula* and *P. wagleriana* specimens together with F_1 hybrids were found, and the rate of hybridization was particularly high (relative frequency of hybrids = 0.148). At Marettimo Island pure specimens of *P. sicula* and *P. wagleriana*, F_1 hybrids, and backcrossed individuals were observed, and the rate of hybridization was lower than that detected at Vulcano (relative frequency of hybrids = 0.087).

In both islands F_1 hybrids and backcrossed individuals were found in biotopes recently modified by man, and this indicates that habitat alteration could affect the premating isolating mechanisms, possibly raising the mating success of heterospecific pairs. Although *P. sicula* is genetically well differentiated from *P. wagleriana* (Nei's average unbiased genetic distance = 0.388)(Capula et al., 1990) and natural hybridization between these species was not observed in Sicily, the high rate of hybridization detected at Vulcano Island as well as the backcrossed specimens found at Marettimo Island suggest that introgression is possible.

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PoG.4 GENETIC EVIDENCE FOR HYBRID SPECIATION OF *Pinus densata*

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Species' hybridization is often regarded as important factor in plant evolution. The occurrence of several crossable, sympatric *Pinus* species from subsection *Sylvestres* in Asia has led to suggestions that hybridization has played significant role in the evolution of the genus *Pinus* on this continent.

Pinus densata was previously suggested to represent a Tertiary hybrid between *P. tabulaeformis* and *P. yunnanensis*. In order to provide genetic evidence for this suggestion we analyzed chloroplast (*cp*) DNA and allozyme variation in these three taxa. The developed *cp*DNA markers could easily distinguish between *P. tabulaeformis* and *P. yunnanensis* and were subsequently used to determine the parentage of *P. densata*. The analysis demonstrated that *P. densata* populations accommodate nearly equal proportions of *cp* genomes of *P. tabulaeformis* and *P. yunnanensis* which strongly supports earlier suggestion of hybrid origin of this species. The aforementioned finding was further supported by results from analysis of allozyme variation. *P. tabulaeformis* differed markedly from *P. yunnanensis* with respect to allozyme frequencies while populations of *P. densata* were intermediate between the two putative parents. In addition, *P. densata* possesses a combination of morphological characters of the putative parental taxa and has adapted to new ecological habitat at high mountain elevations. We thus conclude that *P. densata* represents a stabilized natural hybrid that has become adapted to a unique environment where neither of the parental species can normally grow.

PoG.5 GENETIC POPULATION STRUCTURE IN THE GENUS *RHYMOGONA* (DIPLOPODA: CRASPEDOSOMATIDAE): ENZYME ELECTROPHORETIC DATA.

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Rhymogona is a small genus of the Diplopoda family Craspedosomatidae which comprises seven nominal species. These taxa are distinguished by subtle differences in morphology of genitalia. The genus has a very restricted distribution, which extends north of the Swiss Alps to the Black Forest in the northeast and is limited from northwest to southwest by the Vosges, Côte d'Or and the Savoie. Several of the nominal species are known from one or a few localities only. We have attempted to study the distribution in detail and to include genetic studies on allozyme variation based on starch gel electrophoresis.

Our data suggest that we are dealing with a ring species distributed basically around the Swiss and French Jura. The electrophoretic analysis reveals six distinct groups of genetically differentiated populations. Adjacent groups of populations differ by allele substitution in one out of twelve enzyme loci surveyed. Populations at the extremes are nominal *R. cervina* and *R. montivaga*, which differ by allele substitution in four out of twelve enzyme loci surveyed.These taxa come in contact in the Swiss Jura and in the Swiss Alps, where they form very narrow hybrid zones.

PoG.6

ENZYME ELECTROPHORETIC COMPARISON OF PARAPATRIC *BOMBUS ARGILLACEUS* AND *B. RUDERATUS* (HYMENOPTERA: APIDAE), WITH SPECIAL REFERENCE TO POPULATIONS FROM CONTACT ZONES.

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Among the European bumble bees *Bombus* (*Megabombus*)*argillaceus* Scopoli and *B.* (*Megabombus*)*ruderatus* Fabricius show a remarkable vicariance. *B. ruderatus* is widespread in western and southern Europe, *B. argillaceus* is found in northern Italy and in the southeastern European countries. Specific distinctiveness of these taxa is not accepted by all authors, some regard them as subspecifically distinct. A contact zone of *B. ruderatus* and *B. argillaceus* is known in the southeast of France. We have found another contact zone in the Apennines. Hybridization does occur, but hybrids are very rare. Among more than 100 queens collected in the contact zones, we have found one hybrid only.

Electrophoretic studies (20 enzyme loci scored) revealed variation at the Got-2 locus, which involved two alleles, Got-2^{109} and Got-2^{104} respectively. Allele Got-2^{109} appears to be the ancestral form, since it was found fixed in all other European *Megabombus* species and in the Japanese *B. (Megabombus)yezoensis* as well. The distribution of these alleles in *B. argillaceus* und *B. ruderatus* populations was as follows: *B. argillaceus* queens invariably were homozygous Got-2$^{109/109}$ (including 18 specimens from the contact zone in the Apennines and 35 specimens from the contact zone in southeastern France); *B. ruderatus* queens from Italy (ssp. *atrocorbiculosus*) and those from Sardinia (ssp. *sardiniensis*) and Corsica (ssp. *perezi*) were invariably homozygous Got-2$^{104/104}$ (including 3 queens from the contact zone in the Apennines); in contrast, French populations of *B. ruderatus* (ssp. *eurynotus*) were polymorphic and this polymorphism is widespread in France. However, the frequency of allele Got-2^{109} increased towards the *B. ruderatus* / *B. argillaceus* contact zone. This suggests that the Got-2-polymorphism is due to introgression.

PoG.7 ALLOZYME POLYMORPHISM AND REPRODUCTIIVE INTERECTIONS OF ASOV AND BLACK SEA RACES OF EUROPEAN ANCHOVY.

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Two races of anchovy have been studied for 4 years with respect of allozyme polymorphism at 4 loci (Idh, Ldh, Aat and unspecific esterase). There were now differences between the races in Ldh and Aat. In Idh and Est considerable differences in allele frequencies were found. Among the methods of analysis the most effective turned out to be the consideration of the 127 samples in the parametric space of the frequencies of major Idh and Est loci. A intergroup linear correlation was found between the allelic frequencies of the two loci. This relation is explained by the hybridization occurring between the races. The hybridization is caused by the increasing of salinity of Asov sea, based on anthropogenic influence. The survey of morphological traits and blood groups also supported the presence of hybridization.

Using the 4 polymorphic loci the population structure of Asov and Black sea population was studied. The Black sea population was found to be heterogenic in its race composition. The hybridization occurs in this population. We analysed the temporal changes of race composition in the Black sea population. In Asov sea population only the local race was found. There was a correlation found between the Est alleles frequency and water salinity. This correlation may reflect the process of adaptation in Asov population.

PoG.8

LARVAL ECOLOGY AND SPECIATION OF MARINE PROSOBRANCHS (MOLLUSCA, GASTROPODA)

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The marine prosobranchs have adopted several developmental modalities, that can be interpreted as reproductive (JABLONSKI & LUTZ, 1980, 1983), as well as adaptive (STRATHMAN, 1978a, 1978b, 1985) strategies. Presence of either larvae with a long pelagic life, or a short or absent pelagic larval phase, exert a remarkable influence on life history of the species, expecially with regard to their dispersal capability, the possibility and the extent of gene flow between populations, and the extinction rate of the species (MILEIKOVSKY, 1971; SCHELTEMA, 1972, 1977; SHUTO, 1974; VALENTINE & JABLONSKI, 1986). Generally, developmental types can fall into two fundamental categories: 1) planktotrophic development, with larvae feeding on plankton, spending a relatively long time in the pelagic stage; usually the interpopulation variability is not greater than the intrapopulation one; 2) non-planktotrophic development: mostly lecithotrophic, it includes also direct development, brooding etc.; larvae, if present (lecithotrophic), have at their disposal more or less large yolk supply, reach metamorphosis without feeding on plankton and usually spend lesser time or no time at all in the plankton; due to the relative isolation of the demes, intrapopulation variability is greater than the intrapopulation one. Speciation mechanisms related in some way to larval ecology were previously classified in one of the two following categories: a) Speciation within group with planktotrophic development : here speciation events are usually suggested to occur at the edges of the ancestral species' areal (HANSEN, 1978; SHUTO, 1974); b) Speciation within group with non-planktotrophic development : the alleged poor dispersal capability is usually considered the ground of the reduced or even absent gene flow between populations. A classic allopatric model explains well this case: many examples show that in some conditions radiation may be favoured. Among the mediterranean prosobranchs there are many pairs of sibling species that differ in the presence/absence of a planktotrophic larval phase during their development. It is suggested (OLIVERIO, 1991) that they are the products of as many events of speciation, involving loss of planktotrophy as the main factor, thus indicating the existance of a third kind of speciation: c) Speciation associated to the loss of planktotrophy: the mechanism of speciation would involve the very modification of the type of larval development; we may think that environment can act on the species switching off the pelagic larval phase in specifical conditions, for example when selecting against planktotrophs. Restricted areals, higher predation rate, poor food availability, etc., can be considered as main selecting factors (STRATHMANN, 1978b). The finer mechanisms migth be still delineated, nevertheless the model here presented is intended just as a working hypothesis. It must be noted that analogous pairs of species are known from other areas (Baltic Sea, Red Sea) and at least from another phylum (Annelida). Consequently, this model needs to be carefully tested, through a multidisciplinary approach, since its eventual importance in the evolutive history of prosobranch can be greater than it is currently suggested.

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PoG.9

INTROGRESSIVE ORIGIN OF RADIATE GROUNDSEL: AAT-3 EVIDENCE

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Although gene exchange between species via introgressive hybridization is a well known phenomenon among plants, there is little evidence of stabilised introgressants having evolved into new taxa distributed beyond the zone of active hybridization. One possibe example of an introgressive origin of a new plant taxon in the British flora is that of the radiate groundsel, *Senecio vulgaris* var. *hibernicus* (2n=40), following hybridization between the introduced radiate species *S. squalidus* (2n=20) and the native non-radiate groundsel, *S. vulgaris* var. *vulgaris* (2n=40). Evidence in support has emerged from a survey of allelic variation at a locus (*Aat-3*) encoding aspartate amino transferase. The *Aat-3c* allele was found to be present at high frequency in British populations of *S. squalidus* and was also common in radiate *S. vulgaris* var. *hibernicus*, but was rare among individuals of non-radiate var. *vulgaris* which co-occurred with var. *hibernicus* and was absent from British, Irish and mainland European populations monomorphic for var. *vulgaris*.

Radiate Groundsel exhibits a significantly greater outcrossing rate than the non-radiate variant and consequently is subject to the 'cost of outcrossing' in populations polymorphic for radiate and non-radiate type. Despite this disadvantage, the new variant has spread widely in Britain since its origin in the 19th Century.

PoHI.1

Poster, Third Congress of European Society for Evolutionary Biology, Debrecen, Hungary, 1991

LAGOMORPH MITOCHONDRIAL DNA EVOLUTION

Systematic heteroplasmy in Leporid family

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We characterized mitochondrial DNA (mtDNA) molecules extracted individually from 180 European wild and domestic rabbits (*Oryctolagus cuniculus*), 13 European hares (*Lepus europeaus*), and one Eastern cottontail (*Sylvilagus floridanus*). This study took into account restriction site polymorphisms and length variation of noncoding region. Nucleotide divergence data indicate that mtDNAs from the three species diverged at nearly the same time. The ancestor molecule can be estimated 6-8 million years (MY) old if the rate of divergence: 2% per MY determined for other mammalian species also holds true for Leporids (paleontological data on Leporids seem consistent with this rate).

Every animal regardless of species was heteroplasmic carrying a set of molecules with various lengths of the noncoding region, as well as a variable number of repeated sequences which contribute to them. Preliminary data on mtDNA from an *Ochotona rufescens* (a member of the other family of the Lagomorph order) does not reveal any intra-individual length variation. Since it is not present in near relatives (rodents, primates) we suggest that this systematic heteroplasmy, probably generated by a rate of localized mtDNA rearrangements high enough to counterbalance cellular segregation of rearranged molecules, is a shared derived character of Leporids.

The origin of European rabbits and the organization of their diversity in Western Europe will be documented.

PoHI.2

EVOLUTION OF THE MITOCHONDRIAL RIBOSOMAL RNA IN THE ORIENTAL SPECIES SUBGROUPS OF DROSOPHILA

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The usefulness of using the mitochondrial DNA for systematic studies has been pointed out numerous time.
One of the advantages is the existence of highly conserved regions as well as rapidly evolving highly variable regions.
The choice of the region to be analyzed can be modulated on the basis of the relatedness of the species under analysis and on the kind of issues to be addressed.
Conserved regions can be used to construct universal PCR primers for estimating the evolutionary rates in distantly related species.
To understand the evolution of the molecule it is important to compare a range of divergence levels and to take into considerations also the structural and functional aspects.
The sequences analysis of the subunits of the ribosomal RNA can be very valuable either because of the different evolutionary rates of the different domains and also because allows the estimate of the influences of the secondary structure on the rate and patterns of nucleotide substitutions.
We used universal primers to amplify and direct sequence a segment of the mitochondrial small ribosomal subunit (12s) and a segment of the large ribosomal subunit (16s) in different species of Drosophila belonging to different subgroups of the melanogaster group with progressively increasing time of divergence .
Tha data are discussed either on the context of the proposed phylogenetic relationships among the species analyzed and on the proposed model of secondary structure.

PoHI.3

SPECIATION AND PARAPHYLETISM IN HARES: mtDNA EVIDENCE.

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Mitochondrial DNA (mtDNA) from specimens of the African hare *Lepus capensis* (*L.cp*), the Iberian hares *L. castroviejoi* (*L.cv.*) and *L. granatensis* (*L.g.*) and the European hare *L. europaeus* (*L.e.*) was analysed for restriction site variation with seven endonucleases. Fourteen different variants were found among the 34 animals studied. Restriction maps were constructed and the phylogeny of the variants inferred from estimates of pairwise nucleotide divergences. MtDNA of *L.c.* was found to be the most divergent from that of all other species, consistent with an African origin of the genus. We estimated that mtDNA in hares diverges at a rate of 1.0-1.8% per MY assuming that the European and African populations separated 5-6 MYBP. Maximum intraspecies nucleotide divergences were 1.3% in *L.cp*, 2.6% in *L.cv*, 2.7% in *L.g.* and 13.0% in *L.e.* The latter species contains two mtDNA lineages, one on the branch leading to *L.cv.*, the other on that leading to *L.g.* The separation of these two lineages from those of either *L.cv.* or *L.g.* appears much older than the first paleontological record of *L.e.* in the Iberic peninsula. This suggests that the apparent polyphyletism of *L.e.* is not due to secondary introgression but to the retention of ancestral polymorphism in *L.e.*, to which *L.cv.* and *L.g.* are thus paraphyletic for mtDNA. The results suggest that *L. e.* has evolved as a very large population for a long time or has been fractionated. As far as mtDNA is concerned, *L. e.* appears as the common phylogenetic trunk which has divesified during dispersion over the European continent and from which *L. cv* and*L. g.* speciated locally in the Iberic peninsula.

PoHI.4

POLYMORPHISMS IN MITOCHONDRIAL DNA OF PARASITIC WASPS USED AS BIOLOGICAL CONTROL AGENTS

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More than one hundred species of parasitic wasps belonging to the genus *Trichogramma* (Hymenoptera: Chalcidoidea) have been morphometrically described. Previous protein electrophoretic analysis of some species revealed that alleles at esterase loci were species-discriminant. Those egg parasitoid species that are involved in biological control programs against Lepidopteran pests, are of course the best described. However, little is known about the level of genetic variation both between and within species.

This paper reports preliminary results of an mtDNA RFLP analysis. MtDNA was isolated from isofemale lineages of six *Trichogramma* species unambiguously characterized by morphology and isoenzymes. Some restriction enzymes cleaving 6-bp sites reveal polymorphisms that are potentially useful for the identification of parasitic wasps. The level of variation in both the length and the restriction site maps of *Trichogramma* mtDNA molecules are within the range of those found in other animal species. Genetic distances between the six *Trichogramma* species at the mitochondrial level are compared to distances obtained from morphology and isozyme previous investigations.

PoHI.5 VARIATION IN mtDNA IN INTRODUCED CHAMOIS POPULATIONS

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We investigated genetic variation in chamois (*Rupicapra rupicapra*) populations in order to differentiate between introduced lineages and indigenous populations. Alpine chamois (*R. r. rupicapra*) live throughout the European Alps. They have been introduced in areas outside the Alps, e.g. into the Chartreuse region in France., where there is also a different subspecies *R. r. cartusiana* to be found in small populations. Alpine chamois show high levels of biochemical variation, but genetic relationships among populations could not be clarified unambiguously by enzyme electrophoresis. Alpine chamois were sampled from different populations throughout the Alps. In the Chartreuse Mountains we analyzed samples from chamois of supposedly introduced origin and from populations furthest away from the original introduction sites. Mitochondrial DNA, a small, extra-nuclear and maternally inherited molecule, was chosen to trace back population lineages in time and space. With the Polymerase Chain Reaction (PCR) we amplified a 359 bp region of the Cytochrome b gene and sequenced it.Alpine populations showed variation in their Cytb-sequences. Chamois taken from the area of introduction in the Chartreuse region show the same genotypes as found in their ancestral population in the French Alps. The endemic Chartreuse chamois carry a monomorphic mtDNA Cytb-genotype which is unique to this population and could not be found in any of the Alpine populations. The status of the subspecies *R. r. cartusiana* is thus corrobotated. This study also shows the application of mtDNA sequences in identifying relationships between chamois populations and their evolutionary implications.

PoHI.6 DNA AMPLIFICATION AND MICROEVOLUTION OF FAM. CHIRONOMIDAE, DIPTERA

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Besides chromosome rearrangements changes in the heterochromatin content between homologous chromosomes of related species of fam. Chironomidae have accompanied the evolutionary process. In light of this the amount of heterochromatin, its localization of different species have been studied.

The appearance of centromere heterochromatin of Chironomus plumosus L. in several European populations (Bulgaria, Hungary, Finland and Switzerland) is traced. Swiss and Finland populations are characterized by large dark centromeric heterochromatin. Compared to the other European populations these populations have diverged considerably with regard to the amount of heterochromatin. The importance of amplification in this process is pointed out. However, this different centromere heterochromatin amount hasn't any isolated effect which was proved by hybridization test.

The amount of DNA content in centromere heterochromatin of sibling species of genus Glyptotendipes and their hybrid was measured, using a scanning microspectrophotometer. Significant differences were found in the amount of centromere heterochromatin of Ist, IInd and IIIrd chromosomes between sibling species as well as in their hybrid. Differences were found not only in the amount of heterochromatin but also in quality of heterochromatin. The reasons for these differences were discussed.

PoHI.7

Workshop on The subdivision of Species, Third Congress of European Society for Evolutionary Biology, Debrecen, Hungary , 1991

ORGANIZATION OF DIVERSITY IN EUROPEAN RABBITS

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Originating in Spain, *Oryctolagus cuniculus* (European rabbit) its now largely distributed in Western Europe, a consequence of both the multiplication of wild animals and the beginning of domestication by man.

An insight into rabbit history is given from examination of mitochondrial DNA (mtDNA) diversity in wild rabbit populations from Spain, France a Tunisian island and in domestic stocks. First, the mtDNA types detected (22 over 180 rabbits studied) can be assigned to two clear cut lineages (A and B, 4% nucleotide divergence) well separated geographically (Southern Spain for A, all the other places for B). A noticeable polymorphism characterizes each population sampled in Southern Spain, mtDNA diversity being detected also at the family level, while populations in Southern-East France and on the Tunisian Island are quasi monomorph. The low level of diversity found on the Tunisian Island is in agreement with an introduction of rabbits by man more than 2 000 years ago. The absence of variability in Southern France is quite surprising : this region was believed to have been, at the time of glaciations, a refuge for rabbits which have given rise to the present European rabbits. It seems more plausible, from mtDNA results, that rabbits took refuge in Northern Spain (where the highest diversity is found) while the situation in Southern France can be explained by a founding effect due either to climate changes, pathologies, predation or to man's actions. The level of diversity in Southern as well as in Northern Spain reveals that these populations did not undergo recently a drastic population size reduction in spite of known recurrent pathologies (myxomatosis, haemolytic virus)

The two domestic races studied: Fauve de Bourgogne and New Zealand, exhibit the same mtDNA type (named Fb) with only one variant. The presence of Fb type in rabbits domesticated during the last century and in a population known to have been created in the XV century as well as the close relatedness of Fb type to the type found on the Tunisia Island let us think that man probably sampled several times in the same pool during the last thousand years.

PoHII.1

THE HAEMOGLOBIN OF *ASCARIS SUUM*.

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The origin of plant haemoglobins (Hbs) may be explained by horizontal or vertical evolution [1,2,3]. Since insects and nematodes are strongly interacting with plants, they are potential candidates for the introduction of globin genes into the plant kingdom.

In contrast with the legHb genes, the *Chironomus* globin genes are characterized by the absence of introns, excluding the insects as potential candidates for gene transfer.

Nematode Hbs are characterized by high to extremely high oxygen affinities. The oxygen affinity of *Ascaris suum* haemoglobin is the highest ever observed (P50 = 0,001 mm Hg). This high affinity must have a structural base. In an attempt to reconstruct the haem surrounding the amino acid sequence was elucidated at the protein level [4].

The extracellular Hb (M_r = 328.000) of *Ascaris suum* is built up from eight identical subunits with M_r 38.500 each carrying a single haem group [5].

The globin chain consist of 312 amino acid residues forming two very similar (62 %) covalently bound domains, of 147 residues each and a carboxyterminal extension of 18 residues. Alignment of both domains with known globins clearly shows that the determinants defining the globin fold, such as a CD1 (Phe), F8 (His) and C2 (Pro), are all present. The major discrepancies with classic globin sequences occur in the E and G helix. Molecular modelling will be necessary to analyze wether this discrepancies can be the structural base for the observed high oxygen affinity.

Protein sequencing can't reveal the presence or absence of introns. However the splicing sites common for all globins seems to be kept conservatively. The elucidation of the primary structure of *Ascaris suum* Hb will now allow the isolation of its genes.

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2. Appleby, C.A. et al. (1990) Aust. Syst Bot 3, 81-89
3. Lewin, R. (1984) Science 226, 328
4. De Baere, I. et al. (1991) Embo J. "In preparation"
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PoHII.2 A MOLECULAR CONTRIBUTION TO FISH PHYLOGENY

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The phylogeny of Teleostean fishes raises still much discussion. The order Anguilliformes represents a homogeneous group within the infradivision Elopomorpha, one of the four of Teleostei.

Globins represent a good system for molecular phylogeny of Vertebrates. All globin sequences determined among Teleostei so far belong to species from the infradivision Euteleostei. The European eel, Anguilla anguilla (L.), seems to have the simplest hemoglobinic system, with an acidic and a basic component.

We have determined a preliminary sequence of the alpha polypeptide of the basic hemoglobin of A. anguilla in order to investigate the relationship between Elopomorpha and Euteleostei.

Moreover, the oxygen affinity of the basic component of A. anguilla is not pH-dependent, like the components of a few species belonging to Euteleostei, such as Salmo irideus and Catostomus clarkii. These basic pH-insensitive components can either have the same origin or be appeared independently in the two infradivisions. The sequence comparison between our polipeptide and the other ones could be of value in solving this problem.

PoHII.3

Poster abstract

S. PELGER: The evolution of the hordein gene family

The composition of the major storage protein, hordein, in wild barley species has been studied by using SDS-PAGE, Coomassie staining, and immunoblot assay with monoclonal antibodies. The reaction of antibodies makes a useful complement to gene sequencing in the search for homologies among proteins. Monoclonal antibodies have been raised against hordeins from the barley variety 'Bomi' (ULLRICH et al. 1986). We have earlier shown that it is possible to obtain cross-reaction outside the cultivated barley (PELGER and HØYER-HANSEN 1989). These antibodies have now been used to investigate the hordein composition in all species of the *Hordeum* genus.

The antibody reactions, together with the banding patterns after Coomassie staining, showed that polypeptides similar to the two major hordein groups of cultivated barley, the B- and C-hordeins, are produced in all wild *Hordeum* species. The varying distribution patterns of the recognized epitopes indicate that there are both similarities and differences between the two hordein groups. The similarities show that the coding genes have been derived from a common evolutionary origin. Since there is a general distinction between B- and C-hordeins in the entire genus, it is clear that the divergence of their coding genes preceded the divergence of the *Hordeum* species.

The presence of the same antigenic site in two different species indicates that they are evolutionarily related. Among the wild species two rarely occurring sites were exclusively found in *H. vulgare* ssp. *spontaneum* and *H. bulbosum*, which confirms that they are the cultivated barley's closest relatives. This could also be seen in the distribution of the more common epitopes, which were present in many polypeptides of these species.

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ULLRICH, S.E., RASMUSSEN, U., HØYER-HANSEN, G. and BRANDT, A. 1986. Monoclonal antibodies to hordein polypeptides. -Carlsberg Res. Commun. 51: 381-399

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PoHII.4

MOLECULAR SYSTEMATICS IN MAMMALS: A COMPARISON OF ISOZYME ELECTROPHORESIS AND DNA HYBRIDIZATION DATA FOR RECONSTRUCTING THE PHYLOGENY OF THE GENUS MUS (MURIDAE: RODENTIA).

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The mice of the genus Mus sensu lato are small murine rodents distantly related to the wood mice (Apodemus) and rats (Rattus), and they comprise, for Eurasia alone, about 20 species and many more subspecific taxa. Marshall (1977) presented a synopsis of the taxonomy and morphological variation (mainly cranial) in Asian Mus, and his key to the ca. 17 species and three subgenera of mice was a sound working hypothesis for further molecular systematics experiments.

Isozymes electrophoresis at 28 structural loci yields pairwise genetic distances which indicate a succession of four successive adaptive radiations marked by quasi-simultaneous speciation events. The relationships within each level cannot be fully resolved without ambiguity, and conflicting results are obtained when one takes various numbers of loci into account, or when different outgroups are used.

DNA hybridization estimates the numbers of nucleotide substitutions in pairwise comparisons of the single-copy nuclear fractions of the genomes under scrutiny. DNA distances, which exhibit the properties of a metric, appear to behave in a clock-like manner (relative rate tests), and a calibration of the scnDNA clock has been based on the Rattus / Mus dichotomy, an event dated at ca. 10 Millions Years Ago by the fossil record. The resolving power of DNA hybridization can also discriminate between the other murine genera related to Mus, and it appears that the true mice are more closely related to the African Praomys than to any other Ethiopian or Oriental murine genus so far tested.

Furthermore, the molecular time scale allows us to discuss the historical biogeography of some taxa in the genus Mus, taking into account the paleontological data which depict the fossil history of these rodents: this will be illustrated by the case of the probable origin of the African Nannomys pigmy mice.

PoHII.5 A MULTIDIMENSIONAL APPROACH TO THE SYSTEMATICS OF *HIPPARCHIA* BUTTERFLIES

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The butterflies of the genus *Hipparchia* (subgenus *Parahipparchia*) are widely distributed from Europe, across Northern Africa and Turkey to Turkmenistan. Several species represent insular endemisms both in the Mediterranean Sea and the Atlantic Ocean.

This genus was recently object of systematic reviews, but difficult and controversial attribution of populations to species or subspecies rank, based on traditional taxonomic approaches, gave us the opportunity to apply a quantitative, multidimensional approach to clarify systematic and evolutionary relationships within this subgenus.

Multivariate analyses were employed to study independently three character sets: allozyme data, morphometric profiles of male genitalia, and quantitative descriptors of wing patterns and shape. 18 populations from the Mediterranean area belonging to 9 presumptive species or subspecies were analyzed at 25 allozyme loci, 11 genitalic morphometric measurements and several descriptors of wing patterns. Morphometric data were also obtained for additional samples from museum or private collections belonging to other 7 different species or subspecies.

Generally, electrophoretic analysis of enzymatic polymorphisms showed high levels of genetic variability within populations and low levels of genetic differentiation between populations.

The comparisons of the ordination patterns from principal component analyses and the branching patters from cluster analyses for the three character sets allowed us to outline a satisfactory, though complex, systematic arrangement. In addition, discriminant analyses provided essential indication on the most reliable taxonomic characters to be considered for current systematic work. Evolutionary relationships among the *Hipparchia* populations are also discussed with reference to historical factors. Results from this study show that the colour and wing patterns may be subjected to fast evolutionary rates because their adaptive significance. Therefore such descriptors cannot be considered as reliable taxonomic characters at the specie level.

PoHII.6 GENETIC vs MORPHOLOGICAL DIVERGENCE OF ITALIAN *MARMORANA* SNAILS (MOLLUSCA, PULMONATA, HELICIDAE)

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Generally, land snails display distributions of considerable interest in biogeography. Snail species are often related to specific substrates and tend to have narrow and discontinuous ranges with a resulting distributional pattern of insular type. The land snail subgenus *Marmorana* (*Ambigua*) is distributed in Italy from the 43rd parallel N southward to the Peloritan Mountains in Sicily. Twentyone populations, representatives of the entire distribution area, were studied in order to assess their taxonomic status, and to trace some biogeographical and phylogenetic hypotheses. A preliminary morphological analysis was carried out on 126 specimens from all but one of the populations: biometrics (by means of uni- and multivariate analysis) on 15 characters of the genital apparatus revealed statistical differences at both population and species level, though we were unsuccessful in finding good diagnostic characters. Starch gel electrophoresis was employed to study the genetic variability and divergence. The examen, at 27 allozymic loci, of the genetic structures revealed the existence of three groups of populations genetically isolated, possibly corresponding to three different species (Fig.): *M.* (*A.*) *signata* (Frrussac, 1821), distributed from the Val Nerina, southward to the Matese area; *M.* (*A.*) *fuscolabiata* (Rossmassler, 1842) of Cape Circeo and the Appennines from Benevento province to the Apulia, Calabria, and Sicily (Peloritan Mountains); *M.* (*A.*) *argentarolae* (Paulucci, 1986) in the Argentario area (including Aegilion Island), Uccellina Mountains and Mount Amiata. The three species are characterized by sets of diagnostic alleles. All data are discussed in the perspective of some possible phylogenetic and biogeographical hypotheses. An ancient connection with the Sardinian species of the subgenus *M.* (*Tyrrheniberus*) seems to be witnessed by the electrophoretic pattern of a population of *M.* (*T.*) *ridens*, assayed together with the *M.* (*Ambigua*) ones (Fig.): it showed a greater genetic affinity with the tuscan species *M.* (*A.*) *argentarolae* than with the other two species (*signata* and *fuscolabiata*). Phylogenetically informative alleles were cladistically analyzed by the PAUP package (Swofford), using the maximum parsimony method; this analysis provided a phylogenetic hypothesis, in the form of a cladogram (Fig.). An original Apenninic distribution of the ancestor could have been fractioned by paleoclimatic events, giving rise to the present, somehow contradictory pattern, after several speciation and recolonization events. A more exhaustive and detailed definition of the biogeography and phylogeny of this group will probably arise from a wider study of the whole genus *Marmorana*.

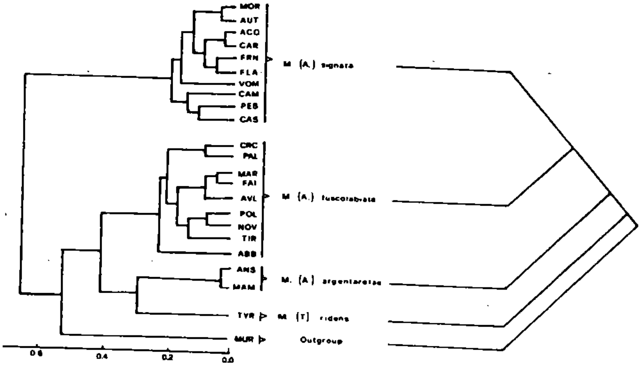

Fig. UPGMA (Nei's D) tree (left) and Parsimony cladogram (right) of Italian *Marmorana*.

PoHII.7

GENETIC DIVERGENCE, PHYLOGENY AND BIOGEOGRAPHY OF SEVERAL SPECIES OF MEDITERRANEAN PLECOPTERA

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Stoneflies are suitable objects for biogeographical studies due to their antiquity, their ecology, their sedentary habits and the good knowledge of their phylogenetic system (Zwick, 1980). The stonefly-fauna of the lands facing the Mediterranean basin is highly heterogeneous because of the various origins and for the evolutionary history characterizing every group of organisms. One of the most interesting group is the *Protonemura corsicana* complex of species which shows a Circummediterranean-Caucasian distribution with several relict or insular species. The study of the phylogenetic relationships within the group can aid in the comprehension of the biogeographical events occurred in this area and the ecological, geological, and evolutionary factors which have caused the present distribution. Fourteen populations belonging to five species of this group were studied. Electrophoresis was performed on horizontal starch-gel; samples were screened for variation at 17 presumptive loci and genetic divergence between populations was calculated using Nei's (Nei, 1978) and Rogers' (Rogers, 1972) distance indices. Phenograms were drawn using UPGMA (Sneath and Sokal, 1973) and the Distance Wagner procedure (Farris, 1972). Allozymic data were also used to derive a cladistic interpretation using a maximum parsimony method (PAUP 3.0; Swofford, 1989). Phenetic treating of allozymic data does not seem to support the theory of a Miocenic colonization of the Mediterrranean basin (Nicolai, 1985). *P. ichnusae* (from Sardinia) results to be connected with *P. helenae* (from Sicily), then following *P. corsicana* (from Corsica). The time of divergence calculated following Nei (1975) and Sarich (1977) are not in agreement with the geological detachment of the microplates (27 m. y.) which should have caused the present distribution according to the vicariance hypothesis. A more recent colonization by means of dispersal should be supposed, as also hypothesized for the mayflies (Zurwerra et al., 1987). On the contrary cladistic analysis is not congruent with phenetic methods. Infact through a cladistic approach *P. ichnusae* results to be more closely related to *P. corsicana*; this phylogenetic reconstruction would be indeed in agreement with the Miocenic vicariance hypothesis. The different systematic arrangement could be explained as a result of a random fixation of different alleles during bottleneck events in a highly polymorphic Corso- Sardinian ancestor. In this case the low genetic distance observed has to be explained and, mantaining the constancy of molecular evolutionary rate, we should suppose a low rate of mutation in stoneflies. Further researches are needed in order to build a more detailed theory on the biogeography of this group, especially through the study of the genetic structure of the North-African species.

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PoHII.8 EVOLUTIONARY DISTANCES BETWEEN tRNA ISOACCEPTORS DETERMINATED BY BOOLEAN ALGEBRAIC METHOD

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In comparative sequence analysis distance is considered to be a measure of temporal evolutionary separation with assumption that substitution probabilities are uniform and time invariant at all positions. As it is well known, these assumptions in many cases are not realistic. For a set of n sequences which have been separated from a common ancestral precursor sequence there were considered three separation distances: of individual sequences from the precursor, the distance between the master or consensus sequence and the precursor and the average distance between individual pairs of sequences. The main difficulty in this approach in applying it to evaluation of experimental date is that the average distance from the ancestral sequence is not known.

In the proposed method the "precursor sequence" is constructed on the basis of structural invariants, determined from primary structure of tRNA-s by Boolean algebraic method, called Iterative Canonical Decomposition or ICD. We have tested the method on the results of other laboratories changing experimentally tRNA identities by point mutations. Our results are in good agreement with the experimental data revealing the structural-functional equality or differences in some cases even contrary to the sequence homologies. We will report the application of the ICD method to answer of further problems of similar nature, and will compare the results with those obtained by more conventional means.

PoHII.9 MODELLING OF THE INITIAL PHOTOBIOLOGICAL SYSTEMS BASED ON PROTOPORPHYRIN IX

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It is suggested that intermediate compounds in biosynthetic pathway of Chl could play functional role at the early stages of evolution of photosynthesis. Protoporphyrin IX (PPIX) is kye compound among these precursors. We carried out investigation on spectral properties of PPIX in different environment, including organised media (proteinoid, protein, micelles, reversed mecelles, liposomes). The spectral parameters have been detected to indicate the interactions of PPIX molecules in such systems. Two tipes of PPIX aggregates are probably formed in water: non fluorescence clusters corresponding to the absorption peak at 642-648nm and the fluorescence friable dimers (or monomers, weakly linked with clusters) with strong solute-solvent interactions corresponding to the absorption peak at 610-612nm. When PPIX interacted with basic proteinoid and human serum albumin, two different mechanismus of tying are observed. Some changes in the physico-chemical properties of PPIX in different microenvironment have been detected by changes in fluorescence and fluorescence exitation spectra. The increase quantum yields resulting from the formation of PPIX complex with HSA or proteinoid correlates with the increasing of their photochemical activity. Solubilazation of PPIX by the charged micelles (SDS, CTAB) is strongly influenced by electro static interactions sensitive to ionic strength. In the case of non-charged Triton X-100 particles a smoll part of the clusters remains also aggregated in the crown of micelle. The properties of PPIX in liposomes and reversed micelles (AOT) are analogous with these in uncharged micelles. The results are dissussed in terms of the possible role of PPIX in the primitive photosynthesis.

PoHII.10

A rRNA BASED MOLECULAR PHYLOGENY OF LOWER VERTEBRATES : CONFRONTATION WITH MORPHOLOGICALLY BASED CLADOGRAMS

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About 500 nucleotides from domains D8, D2 and the 5'-end region of the LSU rRNA from 33 species of Vertebrates (Chondrichthyans, Choanates, and Actinopterygians) were sequenced and used to study the phylogeny of these corresponding species. Different methods of treatment were used for calculating distance matrices and for constructing phylogenetic trees (Neighbor-joining, Fitch and Margoliash , Maximum Parsimony with the bootstrap checking). The effects of changing the outgroups, modifying the species sample under analysis and modifying the techniques of tree construction were systematically analyzed. This allowed an empirical but detailed evaluation of the robustness of the dendograms and the results were similar if not more informative than those obtained through the bootstrap. The major points emerging from our study are: a) The molecular dendrogram shows many points of congruence and a few contradictions with the generally accepted morphologically based cladogram, and certains areas of indetermination ("multifurcations"), b) The monophyly of Actinopterygians on one hand and Chondrichthyans on the other hand is well supported, c) Three major multifurcation points identified correspond to Chondrichthyans-Sarcopterygians-Actinopterygians divergences, Ginglymods-Halecomorphs-Osteoglossomorphs-Elopomorphs divergences, and Rajiforms-Galeiforms-Hexanchiforms divergences, d) In contrast with cladistic phylogeny, the monophyly of Choanates, of Tetrapods, and even of Lissamphibians was not supported. It appears that the divergence of branches in these groups took place very early, nearly concomitantly.

The discussion will focuss on the multifurcation points to understand whether they are due to a lack of information or to the "simultaneous" emergence of the corresponding lineages

POHII.11 IMPLICATIONS OF EYE FEATURES AND OPSIN SEQUENCES FOR THE EVOLUTION OF NEMATODES

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Can a comparison of the morphological features of nematode eyes indicate relationships between nematode taxa? Of the eyes described at the level of electron microscopy, those of *Enoplus anisospiculus*, *Deontostoma californica* and *Chromadorina bioculata* are the most similar. The melanin granules are concentrated in a projection of a marginal cell of the pharynx which forms a depression in which the photoreceptor (PR) lies. This structure is best developed in the cup-shaped shadowing pigment of *D. californica*. The eye of *Oncholaimus vesicarius* appears to be more distantly related, with the melanin granules concentrated in the anterior of a pharyngeal muscle cell, and with the PR lying in a gap between this cell and the large buccal cavity. That of *Diplolaimella* sp. is also formed of melanin granules, however the cup-shaped pigment structure, as well as a tiny lens, appears to be formed in a sheath cell. The eye of *Mermis nigrescens* is very different, with crystalline hemoglobin deposited in evaginated hypodermal cells. The PR is probably located within the hollow cylinder of pigmentation so formed.

The relationships predicted from these features resemble those constructed from classical taxonomic criteria with one exception. Two of the 3 genera with the most similar eyes, *Enoplus* and *Deontostoma*, have been placed in the same suborder, *Oncholaimus* has been placed in a different suborder of the same order, and *Diplolaimella* and *Mermis* have been put in other orders. *Chromadorina*, however, is thought to be more distantly related than indicated by this comparison of eye features. It is possible that the eyes of *Diplolaimella* and *Mermis* have arisen independently.

Comparison of the amino acid sequences of opsins, derived from DNA sequences of various animals, has revealed that the photosensitive rhodopsin molecules of vertebrate, arthropod and moluscan eyes must have an early common ancestor. Could comparisons of opsin sequences of the lower metazoa be useful in clarifying evolutionary relationships between the lower phyla or within phyla? Work begun in our lab may eventually answer this question. We have cloned 5 unique DNA fragments from a *C. elegans* genomic library which hybridize with the *Drosophila ninaE* opsin gene (This is one of four opsin genes expressed in *Drosophila* eyes). Interestingly, hybridization occurs at moderate stringency levels. This indicates a greater sequence homology between the *ninaE* and *C. elegans* opsin genes than between *ninaE* and many other opsin genes for which lower stringency levels are necessary for cross-hybridization. This will be confirmed by sequence comparisons. We have begun to sequence one of the five *C. elegans* genes and may be able to report a partial amino acid sequence and a comparison with known opsin sequences at the meeting. Future plans include obtaining opsin sequences from the nematode species compared above.

PoI.1 STUDIES ON THE MORPHOLOGY AND MICROEVOLUTION OF LOWER PLEISTOCENE BATS (CHIROPTERA) IN HUNGARY.

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Beremend Nos. 16 and 17 are the first known localities with extensive and thus, very important fossil bat populations in southern Hungary. Mandibular remains of about eight hundred individuals belonging to some 20 species were studied, and statistical analyses were made with the help of the Systat Inc.'s statistical and graphical computer programmes.

The age of these faunas is clearly of the Betfian substage of the Lower Pleistocene with the significant rodent species *Allophaiomys pliocaenicus* Kormos,1932.

Bones of young subadult individuals were seldom encountered and if so in a very small number. These did not come from a nursery but from hibernating populations.

The bat remains suggest that the climate was milder than today. This is strongly supported by the relatively great abundance of *Rhinolophus mehelyi* Matchie,1901, the Mediterranean horseshoe bat, in the deeper parts of the locality (Loc.No.16). Nowadays, the species is with an almost strict distribution in the Mediterranean.

The Mediterranean horseshoe bat at Beremend seemed to fully agree with the population described from Malta Island as *Rhinolophus mehelyi birzebbugensis* Storch,1974 also from the Lower Pleistocene. Statistical analyses indicated close alliance with the recent North African population and a relative distance from the Southeast European and West Asian (Iraqi) animals.

The sympatric occurrence of *Myotis schaubi* Kormos,1934 and *Myotis* cf.*nattereri* (Kuhl,1818) -although it also appeared much earlier already during the Upper Pliocene at Villány Loc.No.3- clearly supports the latest ideas that the fossil species *M.schaubi* was not ancestral to *M.nattereri*, and even that these were probably not close relatives as it was thought to be earlier.

The present analyses revealed *M.schaubi* to be apparently an immediate descendant of the *Myotis kormosi-rapax* Heller,1936 complex of Gundersheim, with no continuity in the recent European faunas.

Microevolutionary problems of other species as of *Myotis blythi*(Tomes,1857), *M.emarginatus* (Geoffroy,1806), *M.bechsteini* (Kuhl,1818), the extinct *Plecotus (Corynorhinus) crassidens* (Kormos,1930) and *Myotis steiningeri* Kormos,1934 were also analysed.

PoI.2 MULTIVARIATE ANALYSIS OF MORPHOMETRIC VARIATION OF TWO SUBSPECIES OF THE WATERSTRIDER *GERRIS COSTAE* (HETEROPTERA: GERRIDAE) IN THE ALPS AND THE APENNINES.

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Geographic variation of the two subspecies *G.c.costae* Herrich-Schaeffer and *G.c.fieberi* Stichel in the Alps and the Apennines was studied by means of multivariate morphometric methods. 14 metric characters were measured using an image analysis system.

I used canonical variate analysis to allocate samples of different regions to one of the two subspecies. Samples with scores intermediate between the two subspecies were found from the Maritime to the Western Alps. I found two geographic trends in morphometric variation within this area. First, a North-South trend and second, a trend depending on the altitude of my sampling locations. From North to South and from high to low elevation samples tended to show a morphometric variation closer to *G.c.fieberi*-samples.

Canonical trend surface analysis revealed similar geographic trends of the morphometric variation. High correlation cofficients (0.93 males; 0.88 females) between the canonical variates of the two separate analysis suggest that they show identical geographic trends.

Comparisons of the pattern of morphometric variation of laboratory-reared offspring with the pattern of their parents sampled from natural populations show that geographic variation is mostly determined genetically. Intermediate individuals from field populations could be identified as natural hybrids between the two subspecies since laboratory-reared hybrids scored intermediate compared to the offspring of pure strains.

PoI.3

ALLOMETRY AND MORPHOLOGICAL INTEGRATION IN THE SKULL OF RODENTS

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Skull shape and size are of primary importance for studying the systematics and evolution of mammals. The link between multivariate generalization of allometry and morphological integration is explored in data sets representing linear measurements of the skull of several rodent species.

Covariance structures indicative of functional and/or genetic unit will also be reflected in joint patterns of allometris scaling, and the general allometric size component may subsequently be partinioned into subunits.

Examples are given from selected rodent and carnivore taxa.

PoI.4

MORPHOMETRIC ANALYSES WITH SAMPLES OF EIGHT SUBSPECIES OF STRIPED FIELD MICE, *Apodemus agrarius* PALLAS (RODENTIA, MAMMALIA), IN ASIA.

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In order to determine the taxonomic status of *Apodemus agrarius chejuensis* from Cheju island in Korea, three hundred and eleven samples of eight subspecies of striped field mice (subspecies *agrarius*, *ningpoensis*, *pallidior*, *chevrieri*, *insulaemus*, *manchuricus*, *coreae*, and *chejuensis* of *A. agrarius* Pallas) from Turkey, China, Taiwan, Manchuria, and Korea in Asia were used.

Four external and 27 cranial characters were measured and their measurements were utilized for multivariate anayses such as cluster, principal component, and discriminant analyses.

Four forms were revealed. A largest-size form was *chejuensis*, whereas a large-size form was *chevrieri*, which was also reported as a species by Wang (1985).

A medium-size form and a small-size form were *coreae* and other five subspecies (*agrarius*, *ningpoensis*, *pallidior*, *insulaemus*, and *manchuricus*), respectively, although their difference is clinal.

A discontinuous gap was revealed between *chejuensis* (a largest-size form) and six subspecies (a medium-size form and a small-size form). The subspecies *chejuensis* appeared to be a distinct species, but it is concluded that molecular analyses are necessary before it is reported as a new species.

PoI.5

MULTIVARIATE DETERMINATION OF THE SPECIFIC AND SUBSPECIFIC STATUS OF *MUS* FOSSILS

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Abstract: The extensive research dealing with the genus *Mus*, has rendered this complex of species one of the emblematic models of multidisciplinary approaches to the study of evolution. Nevertheless, a very striking feature of this model is that evolutionary biological studies were performed much earlier than palaeontological ones. This was due to the extreme difficulty in identifying species by morphological criteria both in extant and fossil material. This problem was solved by morphologically studying the specimens after biochemical determination. In using this method, a clear morphological specific discrimination of all European taxa of *Mus* has been established using cranial and mandibular features (Guerassimov *et al.*, 1990).

Otherwise, a review of the occurrence of mice in palaeontological and archaeological remains have led to a good understanding of house mouse progression in Eurasia and around the Mediterranean Sea (Auffray *et al.*, 1990). It probably began with the arrival of the house mouse (*Mus musculus domesticus*) in the Levant, 10,000 bc (Auffray *et al.*, 1988) and finished with the colonization of North-Western Europe by the Iron Age (1st millenium bc). The hybrid zone between *M. m. musculus* and *M. m. domesticus* could therefore have been formed from the Neolithic in Eastern Europe to the Iron Age in Northern Europe. On the other hand, interpretations of molecular data based on mtDNA divergence, have suggested that the colonization of Europe and North Africa by the house mouse occurred between 30,000 and 180,000 years ago (Sage *et al.*, 1990). This discrepancy between palaeontological and molecular approaches means that it becomes critical to clearly establish the specific status of available fossil remains from this whole region.

The present study attempts to discriminate recent species and subspecies of *Mus* based on the most common fossil material, the teeth. Measurements taken on M/1 and M/2 only and treated by Discriminant Factorial Analysis (DFA) lead to a good discrimination between *M. m. domesticus* and *M. spretus* as well as between *M. m. musculus* and *M. m. domesticus*. Afterwards, using multivariate analogy with recent species, we analyze *Mus* fossil material dated at upper Pleistocene from Morocco and Iron Age from Denmark: *M. spretus* was the only species occurring in the Moroccan study site (c.30.000 bp), and astonishingly enough *M. m. domesticus* (1 specimen only) was determined in an Iron Age harbour in Denmark, in a place today inhabited by *M.m. musculus*. Beyong these punctual results, the main purpose of this study is to promote the wide-spread use of this kind of study with a view to improve our knowledge about mouse colonization of Europe and especially to allow the use of fossil data to calibrate biological evolutionary clocks for *Mus*.

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All the other references come from - (1990) *Biol. J. Linn. Soc.*, 41.

PoI.6

THE ARCTOIDS CARNIVORA : COMPARISON OF SOME PALEONTOLOGICAL AND MOLECULAR DATA

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The origin of order Carnivora is attested by fossils from early Cenozoic, but we must wait the Lower Oligocene to observe the forms which are considered as the ancestors (or near the ancestors) of the existing families. We are interesting here more particul arly by arctoids (Ursidae, Mustelidae, Procyonidae, and pinnipeds (seal, walrus, sealion)). Relationships between these different families have often been the subject of discussion. We are going to see from the paleontological and the molecular point of view how we can conceive the arctoids.

The paleontological study allows to propose that the ursoid lineage (Cephalogale) and the musteloid one (Mustelictis) diverge as early as the Upper Eocene in Asia from primitive arctoids like Amphicynodon. Within the musteloid group, the first representatives of Procyonidae (including the lesser panda) and of Mustelidae appear during the Miocene. The Musteloidea superfamily has already been proposed (Schmidt-Kittler 1981) to regroup Procyonidae and Mustelidae and the Oligocene forms. Several works based on molecular data agree with the paleontological observations (Miyamoto and Goodman 1986). But then appears a rank problem about Arctoidea : they can't stay at the superfamily level, but at the infraorder one. This last would embrace the superfamilies Ursoidea and Musteloidea. Concerning the pinnipeds, their mono or diphyletic origin isn't still cleared. It would be researched in the Upper Oligocene and some recent works (Berta 1990, Wyss 1989) based on morphological study on the fossils and on the extant forms conclude monophyletism and a relationship with Ursidae. The results obtained with the molecular approaches seem to indicate only one origin, but the position of presumed ancestor within arctoids stays doubtful (de Jong 1986) or nearer Mustelidae (Arnason and Widegren 1986). Finally, several molecular works have been undertaking about the primary structure of Hemoglobins of some ursids, mustelids, procyonids and pinnipeds. A synthesis of all these results will be soon realize in the poster.

PoJI.1

Analysis of transient genetic dynamics of metapopulations.

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The metapopulation is regarded as being a family of subpopulations, connected by migration processes. Each of subpopulations is characterized by frequencies of its alleles, type of mating and number of individuals. The population as a whole is characterized in addition by a graph and intensities of migrations. The analysis shows, that the type of mating may greatly influence on genetic dynamics. Besides the well-known model of random mating, bringing to a binomial distribution of alleles numbers, another models, bringing to other distributions are considered.

Two approaches are presented to investigate the genetic dynamics. The first one is based on the development of a computer simulation model. The second approach consists of the developing of a numerical-analytical method of investigation. Here the information about statistical moments of gene frequencies in the whole population, correlation coefficients of different subpopulation gene frequencies and heterozigocities are of main interest. Method for calculating these characteristics under the transition from one generation to another is given.

An iterative application of this method gives a possibility to investigate not only asymptotic behavior of the system, but also a transition period. This period is of great interest because in real biological metapopulations we have data only about this period of evolution. We show that the dynamics of gene frequencies in this period is of another type than asymptotic one and give its analytical estimates.

PoJI.2 GENETICAL DIVERGENCY AND POLYMORPHISM IN SUBDIVIDED POPULATION WITH SELF LIMITATION, COMPETITION AND A STABLE MIGRATION PATTERN.

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The pink salmon (Onchorhyncus gorbuscha), inhabiting the Pacific seaside of the USSR, have such characteristics as two-year life cycle, leading to occurrence of two isolated populations (lines) of even and odd years, large areal , homing and migrations, fluctuation of local sub population sizes, and competition between lines. There is a genetical difference among lines in the the same deme and among the demes in the line.

The one-locus two-allele population subdivided on N demes is considered. The fitnesses of genotypes AA, Aa and aa in i-deme are w , 1 and v .Within i-th deme the dynamics of size $x(n)$ and A-allele frequency $p(n)$ at n year are described by difference equations

$$x'(n) = a\ x(n-2) \exp(-b\ x(n-2) - c\ x(n-1))\ s\ (p(n-2))$$

$$p'(n) = (2\ w\ p^2(n-2) + p(n-2)\ (1-p(n-2))\ )\ /s\ (p\ (n-2))$$

where $s\ (p) = w\ p^2 + p\ (1-p) + v\ (1-p)^2$, The migration is defined by a constant matrix $M=[m_{ij}], i,j=1,..N$. Investigation was made for some migration patterns, equivalent for both lines. The fitnesses w and v , fertility a , parameters of self limitation b and competition between lines c were equivalent for lines in the same deme.

Numerical investigation showed that both stable polymorphism and allele fixation are possible. The most interesting is the fact that for constant "genetical" parameters w and v , the increase in "ecological" a, b and c leads to a bifurcation of stable manifolds of allele frequency trajectories. While genetical difference among demes depends on fitnesses v and w , the divergency of lines mainly depends on competition and fertility.,

PoJI.3 ESTABLISHMENT OF UNDERDOMINANT CHROMOSOME REARRANGEMENTS IN MULTIDEME SYSTEMS WITH INTERDEME MIGRATION AND LOCAL EXTINCTION AND RECOLONIZATION.

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The fixation probability of underdominant chromosome rearrangements in multideme models with interdeme migration (Slatkin, 1981) is equal to the ratio between the corresponding probability in a single deme (U) and the number of demes (n), i.e. U'=U/n, when migration rate is very low. This probability decreases as migration rate increases; some quantitative results were also obtained for higher migration rates using the method Monte Carlo.

The same result was obtained (U'=U/n) studying multideme models with local extinction and recolonization, without migration or with very low migration rates (Lande, 1979, 1985).

The aim of the present work is to estimate the fixation probability of underdominant chromosome rearrangements in multideme systems:

1) with colonization models different from those previously studied (Lande analyzed only the "propagule pool model");

2) with unnegligeable migration rates.

A very high number of simulations with the Monte Carlo method was carried out and the main results were the following:

1) fixation probability is generally low in models with appreciable migration rate; however when deme size is very small such a probability is not much lower than U/n, even if there is an unnegligeable migration rate;

2) the approximation U/n does not work well in some models; in particular it overestimates the real fixation probability if colonization is accomplished by several individuals coming from different demes;

3) fixation probability increases in models with interdeme migration if lacal extinction and recolonization are introduced, even if, for the few parameter values tested, this increase is not noticeable in some cases.

PoJI.4

MAINTENANCE OF SEX IN A HETEROGENEOUS ENVIRONMENT

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Previous theoretical models for the maintenance of sex though competitive interactions have not explicitly modelled for habitat heterogeneity. The purpose of this paper is to introduce habitat heterogeneity, using the same approach as that used by Storbeck (1), who investigated the conditions for the maintenance of polymorphism in a heterogeneous environment.

I explore the coexistence of sexual and asexual species in a multi-niched heterogeneous environment with a model assuming: (a) reproduction of sexual and asexual organisms occurs within each niche, subsequent to selection, (b) the *i-th* niche produces a proportion c_i of the total offspring, which are then randomly dispersed to all niches, where selection occurs, (c) the selection coefficients of sexual species and asexual clone in the *i-th* patch are W_i and V_i, respectively, and (d) the frequencies of sexual and asexual individuals in the *i-th* patch are p_i and $(1 - p_i)$, respectively. I express the functional forms of W_i and V_i as extensions of the Lotka-Volterra equations. The cost of sex, β, is assumed to affect the rate of increase of asexuals, r_a, as follows: $r_a = \beta b - d$; where b and d are the density-independent birth rate and death rate of the sexual species, respectively.

I describe sufficient conditions for coexistence, in terms of carrying capacities, rates of increase, and competition coefficients. I also consider the circumstances under which sex can spread when it is rare or resist invasion when it is common. The two-fold advantage of asexuality is important only in the case of r-selected species, living in unstable habitats. Asexual species will exclude their sexual ancestors only if the resource distribution is narrow in the patches that contribute the most to population growth. Coexistence can be achieved through incomplete niche overlap, with the sexual species using a broad range of available resources and the asexual specializing in a subset of those resources.

1. Am. Nat. 108:152-156 (1974)

PoJI.5 CONTEST COMPETITION IN A STOCHASTIC ENVIRONMENT: DISADVANTAGE OF THE RARE TYPE

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Environmental stochasticity leading to variable annual growth rate lowers the long term fitness (geometric mean growth rate) compared to a stable growth rate with the same arithmetic mean. This well known effect may make the rare type be at a disadvantage in a lottery competitive model with fluctuating survival. Under lottery competition the established haplotype has a constant annual growth rate 1, while the growth rate of a rare type does fluctuate.

For the model assume that a "white noise" environmental process generates a fluctuation in adult survival such that percentage changes are the same for each haplotype. Juveniles produced in surplus occupy spaces become free by adult death; juveniles failed to find free space die. Since the number of spaces is given, the population size is stable (contest regulation). Different haplotypes have different fecundity and average adult survival, fecundity and adult survival are traded-off.

The haplotype which is optimal in stable environment corresponds to an ESS in fluctuating environment as well. By numerical methods we can seek for other ESS types and investigate which type can invade which one. We can conclude that

(i) in fluctuating environment there may be more alternative ESS types, which correspond to the local extrema of growth rate in an established stable environment population;

(ii) a strong fluctuation may lead to a rare disadvantage such that the ESS type cannot invade an established non-ESS population. In this case the population evolves through a number of types replacing each other toward to or away from the ESS type, depending on the nature of the extremum.

PoJI.6

POPULATION DYNAMICS OF THE PARASITIC PSR CHROMOSOME IN NASONIA VITRIPENNIS

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An assemblage of non-mendelian sex ratio elements occur in natural populations of the parasitoid wasp Nasonia vitripennis. These include MSR, a cytoplasmic element that causes production of nearly all-female families, and PSR, that causes production of all-male families. Paternal Sex Ratio (PSR) is a supernumerary (B) chromosome that is transmitted via sperm, but causes destruction of the paternal chromosomes (except itself) shortly after egg fertilization. Due to haplodiploidy, this results in the conversion of diploid (female) eggs into haploid (male) eggs. Because it eliminates the genetic contribution of PSR-bearing males, PSR can be considered an extreme selfish genetic element.

N. vitripennis has a highly subdivided population structure in nature, with mating occurring among progeny in temporary patches of host fly pupae (Protocalliphora).

A theoretical analysis showed that PSR can only invade panmictic populations if a female-biased sex ratio is produced. Subdivided population structure selects against PSR, whereas high fertilization proportion (such as produced by the MSR element) increases PSR frequency. PSR can not exist in subdivided populations (temporary mating demes lasting one generation) when foundress number is less than three. The equilibrium frequency of PSR depends strongly on fertilization proportion. In populations producing the Hamiltonian ESS ($x = [(N-1)(2N-1)/N(4N-1)]$) PSR never achieves frequencies over 3% for any deme size. In contrast, if the population produces a high fertilization proportion (i.e. greater than 90% as produced by MSR), then PSR can achieve frequencies over 90% when deme size is three or larger.

Population experiments using two deme sizes (3 and 12 foundress demes) and strains producing two fertilization proportions (standard (LabII) 57-67% and MSR (MI) 90-93%) confirm these predictions. PSR was not maintained in 3 foundress deme standard populations, whereas it achieved frequencies over 0.90 in 12 foundress deme MSR populations. At these frequencies PSR could potentially drive populations to extinction. Results also showed that PSR selects against the MSR cytotype in highly demic populations, resulting in polymorphic equilibria in both elements, which could regulate PSR frequency.

PoJI.7 THE EVOLUTION OF GENE FREQUENCIES IN AGE-STRUCTURED POPULATIONS UNDER WEAK SELECTION

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We consider one-locus multi-allele age-structured population. The dynamics of allele frequencies $p_i(t)$, i=1,...,n, and the density of newborns, S(t), are described by the system of equations

$$p_i(t)S(t) = \int_B^C p_i(t-x)\, S(t-x) \sum_j K_{ij}(x)\, p_j(t-x)\, dx \qquad (1a)$$

$$S(t) = \int_B^C S(t-x) \sum_{ij} K_{ij}(x)\, p_i(t-x)\, p_j(t-x)\, dx, \quad i,j=1,\dots,n. \qquad (1b)$$

where $K_{ij} = F_{ij}(x)\exp\left(-\int_0^x a_{ij}(\tau)d\tau\right)$, $[B,C]$ is the reproductive interval, F_{ij} and a_{ij} are the age-dependent fecundity and mortality for the genotype (i,j).

In the case of weak selection equation (1) can be transformed to the form

$$dp_i/dt = p_i\left(\frac{\int \omega_i dx - 1}{\int x\omega_i dx} - \frac{\int \omega dx - 1}{\int x\omega dx}\right), \quad i=1,\dots,n, \qquad (2)$$

where $\omega_i = \sum_j K_{ij}(x)\, p_j(t-x)$, $\omega(x, t-x) = \sum p_i(t-x)\,\omega_i$.

Eq.(2) can be considered as an equation with time-dependent delete for which Krasovsky's theorems (1956, 1959) hold true. One can show that $f(t) = f(p_1, \dots p_n) = (\int\omega dx - 1)/\int x\omega dx$ is a Ljapunov functional for Eq.(2) and that the conditions for stability of equilibria are written as

$$(-1)^i u_i > 0, \quad i = 1,\dots,n-1,$$

where u_i are the main minors of the matrix $\|u_{ij}\| = \|K_{ij} + K_{nn} - K_{in} - K_{nj}\|$ and $K_{ij} = \int_B^C K_{ij}(x)\, dx$.

PoJII.1

On the role of mutator genes in the evolution process.

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The process of spontaneous mutation in some cases is under control of genotype. For example, there are so-called mutator genes which determine the rate of mutation of the other genes. The mutator genes have no effect on the individual fitness and so can not evolve by direct effect of selection. The following questions arise:

1. *Is any trend in evolution of mutator genes or its evolution can be considered as a random drift?*
2. *How does natural selection effect on the evolution of mutator genes?*
3. *How does the evolution of mutator genes effect on the rate of population adaptation?*

A stochastic model is proposed to analyze some patterns of evolution of hereditary variability mechanisms similar to mutator genes. [1]. In a finite population, every individual genotype is identified by two continuous parameters x and x^*. "Mutator" x^* has no phenotypical expression and controls the mean value of x variation. Although the mutation are random and independent for both x and x^*, the evolution of the mutator x^* due to the indirect effect of selection exhibits a trend, which result in an acceleration of the population adaptation to the environment. It has been shown that the rate of adaptation due to mutator genes is exponential whereas without mutator genes only linear. Within the framework of Martingal theory, the convergence and convergence rate theorems were proved for the evolutionary process by constructing a stochastic Liapunov function what can be considered as the function maximum search for fitness f [2].

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PoJII.2 POPULATION MODELS WITH THE LARGE NUMBER OF LOCI

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The new method of studying dynamics of multilocus systems based on using stationary probabilistic measures on infinite sequences of finite symbols is proposed. The method is applied to multiplicative uniform case, when effects of alleles combinations don't depend on its chromosome locations. For example, we consider infinite diploid population with nonoverlaping generations and multiplicative fitness. It's supposed that all loci are on the only chromosome and have identical marginal fitness. In these circumstances dynamic of multilocus gametes in diploid populations can be described as evolution of stationary measures defined by matrix of conditional probabilities transitions from allele to allele along chromosome (transfer-matrix). We demonstrate, that calculation of mean population fitness reduced to evaluation of maximum eigenvalues of transfer-matrix. Recurrent equations described dynamics probabilistic measures in terms of transfer-matrixes are concluded. Our method gives the opportunity to obtain the exact analytical results for the models with infinite number of loci.

PoJII.3 ON SOME NON-RANDOM ENCOUNTER MODELS IN POPULATION BIOLOGY

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For mathematical models of selection in diploid random mating populations and ecological Volterra-type competition models there are some important features in common. That is the qualitative analysis of dynamics in such models is greatly facilitated due to existence of potential functions, i. e., functions that steadily increase along non-equilibrium model trajectories. The analysis shows that frequency form of ecological competition model corresponds to population genetics model of viability selection. Note that models meet the same principle of random encounter. That is the species in community and genes in diploid organism paired at random.

For these models the potential functions are well known. Potential function exists also for more general population genetics model, namely, for the model of selection in population with coefficient of inbreeding F. In the inbred population genotype frequencies no more satisfy random encounter (Hardy-Weinberg) principle. Potential function in this case nevertheless exists.

Now we try to introduce non-randomness of encounter in ecological model by separating intraspecies competition in a manner that is similar to one in the inbred population. The potential in this case may be found also. The situation be more general when model coefficients are density-dependent. Here we consider the model with a particular form of such a dependence when the model coefficients are the functions of corresponding encounter quantities. In this case the potential also may be written explicitly. Due to potential existence the dynamics of all the models considered be gradient-like .

PoJII.4

ENERGETICS, EXTREMUM PROPERTIES AND EVOLUTIONARY OPTIMALITY OF CHARACTER VALUES IN A CONSUMER-RESOURCE MODEL

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A model for consumer-resource dynamics which takes into account an energy budget of consumer is developed. The model is described by ordinary differential equations. The consumer population growth velocity is supposed to depend on consumer individual's weight (as a measure of energy balance) and character values of consumer also. Let several consumer populations compete with each other through renewable resource feeding. Because of limited resource availability the energetics of consumer populations with "bad" character values becomes unbalanced and these populations are eliminated. The character values of such a consumer population that wins competition with any invader are said to be evolutionary optimal. The most interesting problem consists of searching for the evolutionary optimal (stable) values of characters.

For the model the criterion of evolutionary stability is proved: any point of evolutionary optimal values of characters is a local maximum point of consumer growth velocity. Here the velocity is considered as being a function of consumer character values, c, and equilibrium weight of consumer individuals as a function in c (equilibrium value of resource density is regarded to be fixed). Besides, the maximum value of the growth velocity must be zero. An equivalent formulation of the criterion states that any point of evolutionary optimal values of consumer characters is a point of local minimum of equilibrium resource density regarded as a function in character values c. So, the problem of searching for evolutionary optimal values of consumer characters reduces to testing some function for extrema.

PoJII.5 COEVOLUTION IN TWO-SPECIES ECOSYSTEMS

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Models describing changes of evolutionary lag-load are presented. Analysis of the evolutionary behavior of species within simple two-species model ecosystems shows that it very strongly depends on the precise form of relationship between changes in the evolutionary lag loads of these species. Subtle differences in the form of this relationship, or in its parameters, cause the system to shift from Red Queen behavior to local stasis or extinction. The analysis further shows that Red Queen coevolution appears quite commonly in two-species competitive systems, provided that the interaction takes nonlinear form. In predator-prey situations, Red Queen evolution strictly speaking does not occur. Nonlinear interactions may result, however, in Red Queen coevolutionary fluctuations.

PoJII.6

COEVOLUTION IN FOOD WEBS

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Considerable attention has been paid to the population dynamics of species interacting in food webs, but this work has considered often only genetically uniform populations, with no consideration of the genetic variation present in natural populations, and the differences in fitness of individuals consequent upon that variation. We have constructed a mathematical model of food web assembly based on the Lotka-Volterra predator-prey equations, which includes different genetic variants within species. This model has been used in a computer simulation to investigate the effect that natural selection has on structuring trophic interactions. Further investigations are in progress directed towards understanding the effect of evolution upon the structure and stability of simple food webs. Analytical work based upon fitness functions of Lotka-Volterra form has been used to confirm results of the computer simulation. This work indicates that coevolution may not often, if at all, lead to coevolutionarily stable states in predator-prey interactions, since the predator and prey have diametrically opposed interests.

PoJII.7

THEORETICAL TESTS OF THE DNA REPAIR AND MUTATION THEORIES OF SEX

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We have tested two alternative hypotheses of the maintenance of sex in eukaryotes : the DNA repair hypotheses which says that recombination is necessary for the repair of double strand breaks and Kondrashov's mutation theory stating that sex provides advantage in getting rid of deleterious mutations with synergistic fitness effects. We have compared the sexual strategy with a hypothetical parthenogenetic one, the Prudent Reparator which can repair double strand breaks by gene conversion resulting only in a small amount of homozigosity. Our second test concerns the question whether one can define a Prudent Reparator (with an appropriate rate of gene conversion) so that its performance closely matches those of outcrossing sexuals under the assumption of synergistic fitness effects of deleterious recessives. It is shown also that a lower complementation ability of parthenogens is not an inpenetrable barrier to their succesful establishment, if the invaders genome is relatively uncontaminated by deleterious mutant alleles, and there are always such genotypes in the mutant distribution of the sexual population. We used multilocus computer simulation and worked up the dynamics of genotype classes.

Key references :

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PoJII.8 STABILITY OF SPECIES AND SEXUAL DIMORPHISM

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In many multicellular species the probability of decay (deleterious) mutations exceeds unit per genom per generation. That means that more than half of the newly-born individuals bear decay fragments in their genotypes, such fragments being absent in the parental genotypes. The genetic stability of a population may only be supported then via forceful exclusion of the decay individuals from the population. It may occur either via increasing their death rate, or via decreasing their birth rate.

When the population is divided into males, themselves incapable of reproduction, and females, which are capable of such reproduction, however following a sexual contact with a male only, a possibility opens to reduce the birth rate of decay individuals. A male may let a normal female reproduce and prevent a decay one from reproducing. Females with holding from copulation, and males competing among themselves strain together to exclude all the decay males from the reproductive process. In case of sexual dimorphism the regulation of the birth rate is only possible on the basis of polygyny. Polyandry is an implicit variant of polygyny, with the decay males being stimulated into raising the off-spring of the normal males via non-proclaimed excitation of females and via sexual gratification of such decay males by the females (similar to food gratification).

In case of hermaphroditism and monogamy, as well as that of parthenogenesis, only the death rate may be regulated in decay individuals. Regulating their birth rate becomes impossible. Both the hermaphroditic and the sexual monogamous mode of breeding accelerates the process of relaxation to normal genom in small populations, if the decay polymorphism in such populations has increased following a short-term perturbation of their ecological niches. In large populations (10^9 individuals) neither hermaphroditism nor monogamy offer any advantages as compared to parthenogenesis. No type of sexual reproduction has any advantages over parthenogenesis in the evolutionary process.

PoJII.9

MODELS FOR SOMA-GERM EVOLUTIONARY INTERACTIONS IN VOLVOX

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The origin, maintenance and transitions of the soma-germ relationships have been considered important evolutionary problems since Weismann. Weismann argued that the soma and the germ consist of different cell lineages, which display evolutionary sequestration. This sequestration is not universal. G. Bell (1985) (see Bell & Koufopanou, Phil.Trans. 1991, in press) has suggested a hypothesis that the soma and the germ line stem from an evolutionarily specialization as a source and a sink of metabolites. We find this hypothesis interesting, because evolutionary studies mainly emphasize the soma-germ separation, but rarely their dynamic couplings. We have constructed and analysed simple models for studying some consequences of Bell's hypothesis with the following assumptions:

1. The organisms of the genus Volvox can be represented by flow networks obeying selection rules for flows.
2. The repertoire of the flows is a characteristic property in Volvox.
3. There is at least tree different metabolic flows between soma and germ. We note that at least three classes of genes have been identified as candidates for the soma-germ symmetry breaking or division of labor (Kirk, Trends in Genetics, 4: 32-36, 1988).
4. There are metabolic pooles or stores.

The computations of simulated, evolutionarily changing flows display periodic motions, constrained oscillations with shifting, transient constraints, irregular behavior or else. The allometry of soma and germ can be derived from the variation of the flows.

PoK.1

COMMUNITY DYNAMICS vs. LIFE TRAIT PATTERN IN RESPONSE TO THE ENVIRONMENTAL FLUCTUATIONS.

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Based on an extensive fossil record, a reaction of the mammalian communities and changes in the life trait patterns in the populations consituting them have been examined in respect to the environmental fluctuations produced by the Quaternary glacial cycles.

Theoretically, two marginal alternatives have been available: either (a) to respond the fluctuations by changing its organisation pattern (composition of the community, foraging pattern, reproductive strategies etc.) or (b) to evolve the adaptations enabling to resist a disadvantageous phase of a fluctuation without changing own principal qualities (comp. phenomena of poikilothermy and homoiothermy as a metaphore to the (a) and (b) strategies respectively). While (b)-like reaction, i.e. a resistence upon the fluctuations appeared as an original strategy in all community types under study this has not been the case with life trait pattern in their members. Core species of these (b)-like communities reacted upon the respective fluctuations with the (a) strategy. A reveresed situation has appeared with the forms and the communities derived of the formers. The advanced state is thus characterized by complete alternation of different community types (and/or different chorological units) each being composed of the populations which, within certain limits, resist disturbance without changing essential aspects of their life trait patterns.

Both the strategies are further examined with aid of a probabilistic model (estimating the critical intensities and duration of disturbance disbalancing the system) and discussed in respect to the factors responsible for the above mentioned development.

PoK.2

WATER ODOUR PREFERENCE AND POPULATION ISOLATION IN NEWT.

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Site tenacity is an ethological component of population isolation. Fidelity for the breeding site has been shown to be relatively strong in the alpine newt (Triturus alpestris; Joly & Miaud 1989). Amongst the mechanisms of orientation towards the breeding site, chemical cues emanating from the pond play a major role (Joly & Miaud, unpub. data). Does the fidelity for a particular breeding site be supported by the odour of its water? In other words, do newts recognize and prefer water odour from their own breeding site?

Newts was given the choice between water from their own pond and water from another pond, also inhabited by a newt population. Several experiments have been carried out differing in the distance separating the two ponds of a pair.

When the distance between two ponds exceeded one km, a great majority of newts preferred water from their home pond. But when the pond are nearby (less than one km), the most often no significant preference was observed, even if the ecological communities of the two ponds were very different.

The wandering of adult newts around their breeding site is known not to exceed three or four hundred meters; so the experimental procedure did not reveal a preference for water from a particular pond situated inside of the home range. Such a result suggests that, on a little space scale, site fidelity is not supported by chemical cues exclusively emanating from the site. The preference observed when the distance between the sites increases suggests that the role of chemical cues acts more in the process of isolation of metapopulations rather than in that of isolation of local populations.

The question is now to determine the possible feed-back influence of the newts themselves on the water odour of a particular site.

PoK.3 HERBIVORY AFFECTS GROWTH, REPRODUCTION AND DEFENCE IN STINGING NETTLE

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Effects of herbivory on plant growth and reproduction seems to vary from negative through indifferent to even positive responses. Environment sets limits to plant's defensive mechanisms and possibilities to recovery; defensive reactions and total recovery from herbivory are more likely in a resource rich environment. We tested the overall effects of simulated herbivory on the recovering ability and reproductive output of the stinging nettle, Urtica dioica L. grown in two different densities.

We collected the rhizomes from different plants and cut them into 5 cm long pieces. These pieces were randomly planted to plastic pots to two different densities (1 or 3 pieces/pot) in an unheated greenhouse. The pots containing one or three stinging nettles were randomly assigned to seven damage treatments, consisting of small and larger scale leaf area removal and removal of plant apex.

The clipping of leaf blades affected positively the growth of the plants in both densities, while removal of the plant apex clearly decreased growth. Number of branches and dry weight of inflorescences in the main stem were lower in plants assigned to the apex removal treatment. However, the dry weight of inflorescences from the branches was higher (7-108- fold) in damaged than in control plants. Thus, the small scale damage treatments increased significantly the total reproductive output of the plants. This positive effect was even stronger in the high density. The stinging trichome number/cm^2 increased in plants that were assigned to the removal of 1/2 leaf in the lower density whereas in higher density these treatments decreased the trichome number. The removal of the apical bud increased trichome number by 26% and 39% compared to control (low and high density, respectively).

According to our results stinging nettle is able to compensate for the losses due to small scale (appr. 5% of biomass removed) leaf herbivory and destruction of apical dominance. Our results suggest that the stinging trichomes could act as an induced defence in resource rich situations when competition is absent. It would be energetically advantageous for the plant to be able to produce defensive structures only when subjected to herbivory. The new expanding leaves which responded by increasing their trichome number may also be more precious to the plant and more palatable to herbivores. Therefore the new leaves may be better defended.

PoK.4

INTERACTION BETWEEN THE PLANT *PLANTAGO LANCEOLATA*, THE FUNGUS *PHOMOPSIS SUBORDINARIA* AND THE WEEVIL *CEUTORHYNCHIDIUS TROGLODYTES*.

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The research is directed at the study of the ecology and genetics of a pathosystem, composed of a plant, a fungus and a weevil.
The fungus Phomopsis subordinaria causes a spike and scape disease on *Plantago lanceolata* and reduces the seed production. The weevil *Ceutorhynchidius troglodytes* lays her eggs in the spikes and the larvae feed on the maturing seeds. Both the weevil and the fungus are strictly tied to *P. lanceolata* as a host.
The weevil was shown in outdoor experiments to transmit the fungus to the spikes where infection usually starts.
Results from field studies showed that weevil eggs were laid early in the season while *P. subordinaria* progressively increased from July onwards reaching its maximum at the end of the season. Therefore, no role of importance in transmitting the disease could be attributed to the weevils in this phase.
Untill now, only quantitative resistance has been foud in the *Plantago-Phomopsis* interaction. If natural selection occurs in this pathosystem, selection caused by the fungus either acts through resistant genotypes or through earlier flowering genotypes (escaping the disease but favouring the number of weevil oviposition sites).

PoK.5 DORSAL LIGHT REFLEX IN BUMBLEBEES, AND ITS IMPORTANCE FOR BUMBLEBEE - PLANT COEVOLUTION

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Bumblebees of two species, Bombus lapidarius L. and B. muscorum L., were tested, one at a time, in a large transparent flight cage which could be illuminated either from above, or from below. When illuminated from above, bumblebees walked and flied normally. When illuminated from below, they were able to walk, but not to fly. When trying to fly, they kept to turn their dorsal side in the direction of the light, and, as a consequence, they kept falling down on the floor of the cage. Such a postural response to the direction of the light is known as the "dorsal light reflex".

As well known, foraging bumblebees prefer, as a rule, to move upwards than downwards between food sources. Numerous morphological and physiological features of bumblebee-pollinated plants arose probably as a direct adaptation to that behaviour of their pollinators. The present report identifies one of important causal factors of that behaviour, and, as a consequence, one of primary factors of evolution of some features of bumblebee-pollinated plants.

PoK.6

BIOGEOGRAPHIC PATTERNS OF SPECIATION IN SOME XEROMONTANE NOCTUIDAE (LEPIDOPTERA) GENERA

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Definition: Xeromontane is the faunal type connected with the core areas in the arid-semiarid Oreal (high-mountains)
Explanation: Xeromontane is the faunal type of arid oreal biomes (with prevailing physical weathering) as opposed to the alpine ones (with prevailing glacial and fluvioglacial relief formation). Xeromontane species are adapted in their life-history to arid-semiarid conditions (timing of larval diapause, terricolous caterpillars of "cutworm"-type etc.).

The poster displays selected examples for the following speciation/distribution patterns:

Sibling species by vicariance
Sibling species by peripatric isolation
Species group evolved by change of life history
Speciation and subspeciation with secondary expansions
    - from xeromontane to steppe biomes
    - from xeromontane to xeric arboreal
Speciation by a continental vs. W-Asiatic divergence of a genus
Supposed origin of the genus in the Monsoonic SE Asia: diversification by passing a "Xeromontane filter"
Supposed origin of the suprapecific group (group of monophyletic genera) in the Monsoonic SE Asia: diversification by passing.
    - a "Xeromontane filter"
    - a "Boreo-continental filter" (leading to Holarctic distribution)

PoK.7

EVOLUTION OF THE EYE SPOTS IN THE WING PATTERNS OF THE FAMILY SPHINGIDAE

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Eye spots from the species of the genera Smerinthus, Paonias and Pachysphinx (Sphingidae) were examined.The eye spots of various representatives of these genera were compared with the purpose to trace the progresse of evolution of these patterns from "normal" wing patterns. The probable course of development of the eye spots in the genus Smerinthus (from the original two parallel transverse lines and the dark wing margin in the distal part of the hindwing) was described and figured.The beginning of development passed,with the greatest probability,without the selective pressure of the predators (small birds). The aim,being the warning (or rather intimidative)function of the eye spots,could function only when they at least partially had acquired their final form.Not before the beginning of this development which must have been,as it were,the result of the "inner dynamics" of the living system the selective pressure of predators could begin and gave a reason to the perfection of the eye spot.

POK.8

FUNCTIONAL RESPONSE OF *PARDOSA HORTENSIS*: DO WOLF SPIDERS RESPOND TO CHANGES IN PREY DENSITY?

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The number of prey attacked by predators is often a function of prey density. Such response of predators to changes in prey density is called functional response. Functional responses were classified by Holling (1959) into three types, all of them having a specific effect on prey population dynamics.

Laboratory experiments were carried out to study the functional response of *Pardosa hortensis*, a common wolf spider species. Spiders were placed into Petri dishes containing different number of the prey items, *Drosophila melanogaster* fruit flies. The 6 different prey densities were hold constant by replacing every fly eaten. The exact behaviour of the spiders was monitored over the experiment by a behaviour registration programme, thus besides data on number of prey items eaten we were able to gain information on sequential handling times and time spent on other activities than eating.

The experiments revealed that the functional response of *Pardosa hortensis* is basically Holling II type. However, there is an unusual depression at medium prey densities in the course of the curve, which pattern has only been found in another spider functional response experiment (Smith and Wellington, 1983). Our tentative explanation for the phenomenon is (i) there is a natural increase and decline in the predation up to the medium densities; (ii) spiders seems to respond to high densities by multiple feeding and partial consumption of the prey, which behaviours result in a final fast increasing section of the functional response curve.

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PoK.9 NON-RANDOM LARVAL FEEDING BUT LACK OF HABITAT CHOICE IN THE CACTOPHILIC FLY DROSOPHILA BUZZATII

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Drosophila buzzatii is a colonizing species that feeds and breeds on decaying cactus tissues. The yeasts associated with the rotting process are the major source of food for both the larval and adult stages. We have studied the yeast community associated with the rotting Opuntia ficus-indica (prickly pear) cladodes in a natural population (Carboneras, southeastern Spain). A significant spatial (among-rots) as well as temporal (among-rotting stages) variation was detected for both the abundance and diversity of yeasts. We also studied quantitatively the yeast present in the guts of second and third instar larvae collected from the same Opuntia rots. It was found that the larvae do not contain a random sample of the yeast species present in the substrate. Pichia cactophila and Pichia kluyveri were more frequent in the larval guts than in the cladodes, whereas Candida sonorensis and Candida boidinii showed the opposite. A regression of the frequency of each yeast species in the larval gut against its frequency in the substrate indicated that D. buzzatii larvae exhibit a significant preference for P. cactophila, whereas C. sonorensis and C. boidinii are avoided. Furthermore, in a subsample of the same larvae we determined the karyotype at the second and fourth chromosomes which are polymorphic for paracentric inversions. No differences among the various karyotypes were observed in their preference for P. cactophila. Therefore, although the D. buzzatii larvae do not feed at random, no evidence for habitat choice at the karyotypic level was found.

PoK.10

Distribution of *D. subobscura* in North America and comparison with other *Drosophila* species

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Bimonthly collection of *Drosophila* species, during a 16 month period have been carried out in three localities in California (Eureka, Davis, Gilrey). Data shows that the colonizing species, *Drosophila subobscura*, is well established and has an annual cicle similar to the one in the Old World. The frequency peaks of the different species alternate in time.

The diversity of species is higher in Davis although the species are more equally distributed in Eureka, the index of evennes being higher in this population.

The difference between the three populations account for 25% of the total species diversity. For the pair Davis-Gilroy it is lower due to their similar environmental conditions. The seasonality accounts for 46% and 50% of the total species diversity in Davis and Gilroy respectively, and only for 39% in Eureka. In this population the climatic differences along the year are milder. The differences between years explain only a small percentage of the total species diversity.

A cluster analysis and principal component analysis within populations show the similarity between species according to their distribution trend.

PoK.11 ANTIOXIDANT ENZYMES IN ANTARCTIC MARINE ORGANISMS EXPOSED TO HIGH AND LOW PARTIAL PRESSURE OF OXYGEN.

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The concentration of antioxidant enzymes, superoxide dismutase (SOD) and catalase in tissues of aerobic organisms depends on the partial pressure of dissolved oxygen.

The Antarctic environment is an optimal model to study the presence and distribution of SOD and catalase because of its constant, low temperature and high partial pressure of oxygen, which involves adaptation processes for different marine organisms.

We have studied three species of Antarctic ciliates (*Euplotes rariseta, Euplotes focardii* and *Uronema marinum*) and two species of Antarctic fishes (*Pagothenia bernacchii* and *Chionodraco hamatus*).

Ciliates of Ross sea have an increased cellular concentration of SOD or catalase in comparison with the sub-Antarctic ones. In some species more developed type of SOD (Cu-SOD) have also been observed.

In white-blooded Antarctic fishes, which have a low partial pressure of oxygen in tissues, a remarkable reduction of SOD and catalase in comparison with the red-blooded fishes occurs.

Work supported by Programma Nazionale di Ricerche in Antartide.

PoK.12

SPECIES DISCRIMINATION BASED ON OLFACTION IN MALES OF RELATED MICE SPECIES

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It is well known, that odour based species discrimination occures in rodents. This study analyses intermale communication accompaniing territorial marking.

Reactions of males to species specific odours were examined using different methods including counter marking and behavioral preferences in familiar and non-familiar environment. Preference and counter marking were displaied only in case of contact with odour of the same species. Population specificity was not found. There were no signifficant differences between reactions to odourless objects and objects scented with odour of related species.

Absence of behavioural preference and counter marking reaction to male odour of related species could be result of simple divergence in the chemical communication canal caused by neutral evolution and subsequent loss of ability to recognize signal's information content. On the other hand possible influence of the selective pressure could not be excluded. Especially decision rules of recipient are theoretically susceptible to sympatry in the past and/or present.

PoL.1

THE ANALOGY BETWEEN THE EVOLUTION OF EUSEXUALITY IN EUCARYOTIC CELLS AND ANTHROPOGENESIS

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The bioevolution is canalized by systemic constraints resulting from ontogenetic processes. As a consequence, the general pattern of successive steps of increasing complexity in progressive evolution should be the same for both the unicellular and the multicellular level. It is demonstrated that the mechanisms of eusexuality in eucaryotic cells and the mental structures of human mind (the final results of the evolution on their levels) are analogues, because they iniciate a horizontal transport of information. The evolutionary pathway leading to them seems to follow the same general pattern of successive steps. A model is presented which describes a periodisation of evolution on both levels and indicates an isomorphic pattern of qualitatively defined steps. Basing on HEGELs principle of the negation of negation, it uses the opposite between temporal and spatial forms of complexity as parameter of periodisation.

PoL.2

ADAPTATION AND EVOLUTION

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It has been earlier considered that adequate character of adaptation is a reflektion of living nature expediency /Kant I., DeLamarck Y.B./ and that the evolution is the convergent /Berg L.S./ not diverget process /Darwin Ch./. The universal characteristics of organism's adaptability are the morpho-physiological progress, the increasing of population size and the development of new areas. A motive force of adaptation is the natural selection, and the way of its realization is the specialization of differentiated parts of organism. Besides the greater the number of specialized organs and systems the more independent of environmental factors the organisms. Through the processes of mutability, selection and fixation in genotype the morphological adaptations have the decisive significance for the evolution of living matter. The importance of modifications and behaviour for evolutionary process increases essentially when the level of development of animal's integrative systems /nervous and endocrine/ rises.

As to low organized organisms they to the more extent are under the influence of external for them mechanisms such as a natural selection. The process of adaptation in these organisms is basically realized at the expense of high degree of reproduction. When the inner integrative mechanisms have been developed, their significance in regulatory processes in animals more rises, and in this connection the survival of animals increases, but the reproductive ability decreases. The functioning of selection manifestes itself basically in initial and final periods of these animals ontogenesis, when the functional possibilities of their inner integrative systems are insufficient.

PoL.3

LOCAL ADAPTATION AND EVOLUTION

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Natural communities in the biota are capable of compensating adverse changes in their environment, sustaining it in a state, optimal for life. Every species in a community is not only adapted to that environment, but contributes to the stabilization of that environment and hence should not adapt to any environmental fluctuations. Both the adaptation and stabilization programs are written into the normal genotype, and are distorted during decay (deleterious) mutations. Under optimal conditions the normal genotype features the highest competitive capacity and frequency of occurrence. It is prescribed to the accuracy of neutral mutations which do not alter the competitive capacity.

When conditions deviate from the optimum, the competitive capacities in the normal and the decay individuals equalize, and the decay polymorphism in the population increases. When the conditions return to optimal, the maximum competitive capacity and the maximum numbers of the normal individuals are restored. Such a process is seen as random oscillations around the normal genotype without any forward microevolutionary shift. All the "switching" non-decay mutations which broaden the habitation areal of the species are also encoded in the normal genotype (e.g., the direction and the duration of migration for the migrating birds from various parts of their areal). Such switching mutations become senseless after parts of the genom encoding them decay.

In small populations the decay of the normal genom and its relaxation back to that norm occur via genetic recombination which accompanies sexual breeding, provided the decrease of the number of such decay mutations results in a monotonous increase of the competitive capacity. If some fragment of the normal genom is lost in every individual of the population, such a relaxation becomes only possible via inverse mutations, independent of the dominating mode (sexual or asexual) of breeding. No type of sexual reproduction has any advantages over parthenogenesis in the evolutionary process.

PoL.4 BIOLOGICAL EVOLUTION AS RESULT OF PROTECTIVE MECHANISM ACTION OF BIOSYSTEMS

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As a result of strict logical construction, the thermodynamic approach frequently permits, from more general positions, the essence of phenomena related to biosystems to be elucidated. The Thermodynamics of Accumulation Processes /TAP/ and the thermodynamics of irreversible processes are, nowadays, the two branches of the non-equilibrium thermodynamics, which studies the changes of systems' state using a measurable time. TAP deals with phenomena /processes and effects/ associated with the introduction, transformation and accumulation of mass, or energy, or both, in affected, non-isolated /open or closed/ systems, i.e., phenomena associated with an increase of the free thermodynamic potential, due to positive work done upon the systems by exogenous impacts /influences/. Since all biosystems are non-isolated systems exposed to external impacts, the TAP-approach in their investigation is the most appropriate one. TAP accepts a new evolution criterion: each evolution development degree of a living system /subsystem/ is proved and manifested by an acceleration of the total impact exercised by it upon other systems or environment in general. Six levels of protective mechanism /PM/ of the systems are distinguished in TAP and the Principle for preservation of the PM-level has been defined: each system integrated as subsystem in another, bigger or more general system, preserves its PM unaltered and manifests that PM in cases of immediate impacts acting upon it. From the Principle interpreted by TAP-regularities follows the postulate: each evolution degree of a system should decrease the surface densities /SD/ and moving forces of the impacts affecting the system, even when the impacts are provoked, e.g., by the biosystems which require influx of energy and substances for their existence. The Principle and postulate are exampled by the universal - counteraction - PM of cohesion-associated monocellular organism groups in the primary ocean after the origination of the life on the earth. Their PM - proliferation in order to decrease the impacts' SD - being provoked by impacts could result only in a "differentiation" and a development of multicellular organisms. Other example is the evolution of cancerous mechanism in the tissues of multicellular organisms.

Author Index

The author index contains the names of only those persons whose abstracts are included into this volume. In case of workshop contributions also presented as a poster the abstracts can be found among the posters and the workshop codes are in parentheses.

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