some of the female of cross 1 carried the mMe^b allele, whereas her Z chromosome carried the mMe^a allele. Following meiosis, about 6% of the ova produced by that female carried a W or Z chromosome that had undergone crossing-over between the mMe locus and the locus (or region) controlling sex. Similarly, the female parent of cross 5 had a W chromosome carrying the mMe^c allele and a Z chromosome carrying the mMe^a allele; 5.3% of the offspring showed recombination between mMe alleles and the sex-determining genes.

The mode of inheritance of the sex-linked mMe locus in *Xenopus laevis* suggests that the dominant female-determining factors (W) and the recessive male-determining factors (Z) are carried on a pair of homologous chromosomes that behave like autosomes. This pattern of sex linkage is quite different from that found in mammals, in which the sex-linked genes are carried almost exclusively on the X chromosome, resulting in hemizygous male genotypes, and crossing-over between the X and Y is suppressed along much of their lengths[15]. It is consistent, however, with the mode of inheritance of sex-linked genes observed in other amphibians, i.e. *Pleurodeles waltlii*[16], *Rana clamitans*[1,2] and *Rana pipiens*[3,4]. Whether or not the mMe locus is sex-linked in these species has so far not been determined. However, comparison of genetic maps among North American *Rana* species suggests that the linkage relationship of sex-determining genes to other loci is evolutionarily unstable even within the same species group[2,4].

Cytogenetic and molecular evidence indicates that *Xenopus laevis* has a tetraploid origin. As a matter of fact, many of the protein loci tested in electrophoretic surveys show multiple banding patterns resulting from duplicate gene expression[11,17]. On the basis of electrophoretic phenotypes and segregation analysis, it appears that mitochondrial malic enzyme is encoded in a single locus in *X. laevis*. The second copy of the mMe locus has probably been silenced or lost as an effect of diploidization, as reported, for example, of the major histocompatibility complex[17]. Quite similarly, sex determination seems to conform to a model with two alleles (i.e. W and Z) segregating at a single locus. In support of this model, it has been shown that the presence of additional sex-determining genes in artificial *Xenopus* polyploids had the effect of disturbing the normal course of genetic sex determination[18].

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Comparative variation at four enzyme loci in ten Melanopline grasshoppers

W. Chapco[1]

Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2 (Canada)
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Summary. Previous investigations of the migratory grasshopper, *Melanoplus sanguinipes*, demonstrated geographical variation at visible loci but not at enzyme loci. Electrophoretic analysis of 3 other Melanoplines and an Oedipodinid also revealed uniform spacial distributions. Investigation of allelic patterns among these and 6 other Melanoplines suggests that selective rather than stochastic factors are operative.
Key words. Melanoplus sanguinipes; Camnula pellucida; grasshoppers; polymorphism; allozyme.

The migratory grasshopper, *Melanoplus sanguinipes*, is polymorphic for a number of heritable color and electrophoretic characters[2,3]. Visible traits display spacial variation, as exemplified by hind tibia color. In the province of Saskatchewan, there is a dramatic shift in red/blue frequency between parkland and prairie regions. For electrophoretic traits, however, frequencies are more or less the same between and within these areas. Geographical uniformity can result from 1) an interaction of genetic drift and migration; 2) some form of selection in which selection coefficients are independent of the external environment and migration effects are superfluous; or 3) homogenizing effects of gene flow that override local adaptive differences. This paper examines these hypotheses by looking at patterns of electrophoretic variation in several other Melanopline species and an Oedipodinid, *Camnula pellucida*, the clear-winged grasshopper. Since species are reproductively isolated, possible confounding effects of gene flow that may exist within species are obviated. Comparisons of allelic configurations between species should, therefore, be particularly illuminating[4].

Adult grasshoppers of *Melanoplus sanguinipes, M. dawsoni, M. packardii, M. bivitattus* and *Camnula pellucida* were collected during the summers of 1986 and 1987 in locations situated in the prairie parkland and prairies of Saskatchewan. Samples of *M. angustipennis, M. confusus, M. femurrubrum, M. infantilis,* and *M. gladstoni* were caught in prairie locations only; *M. bruneri* was obtained in parkland. Collections were made using a sweep net, usually along roadsides and/or adjacent fields.

Allozyme patterns were ascertained by vertical polyacrylamide slab gel electrophoresis (Protean™ II Slab Cell from Bio-Rad). Tissue preparation, buffers, running conditions and staining procedures were essentially the same as those previously described[3]. Variation at the following loci was ascertained: Ldh (lactate dehydrogenase), Mdh (malate dehydrogenase), Gpdh-1 and Gpdh-2 (glycerophosphate dehydrogenase). In previous investigations of *M. sanguinipes,* the frequency of the most common Ldh allele was between 0.8 and 0.9; Mdh and Gpdh-2 were somewhat less polymorphic with frequencies of the most common alleles between 0.9 and 1.0. Gpdh-1 was monomorphic. These loci were chosen for the present study partly because of these contrasting distributions and partly because their genetics is known[6, 7].

Allelic frequencies were estimated by gene counting. Locations within species were compared by applying χ^2 tests to 2 (common allele versus 'other' alleles pooled) $\times 2$ (prairie versus parkland locations) contingency tables.

Allelic frequencies are set out in the table for each locus and species. For the most part, results parallel those obtained previously for *M. sanguinipes:* Differentiation between prairie and parkland populations of *M. bivittatus, M. packardii, M. sanguinipes* and *C. pellucida* is negligible; and in most cases, each locus is characterized by a single predominant allele present in high frequency (table). At one locus (Ldh) in *M. dawsoni,* prairie and parkland frequencies differ at the 0.05 level of significance. Unless information on migration is available, however, no resolution of the 3 hypotheses presented in the introduction is possible, irrespective of how many species display uniform geographic allelic profiles. Reports of migration and outbreaks are legend for *M. sanguinipes*[3], whereas information on the other 4 species is patchy, conflicting or nonexistent[5, 8–11]. Of particular interest is the response of the normally brachypterous *M. dawsoni*[5] for which some interlocational differentiation might be expected, as, for example, in *Chorthippus bruneus*[12]. Still, exchange of even a small number of migrants each generation between subpopulations might be sufficient to prevent divergence[13].

Species, however, experience no genetic exchange, and a comparative examination of allelic profiles might help resolve the 'drift versus selection' issue. To this author's knowledge, the species presently investigated are reproductively isolated; interspecific couplings have never been observed in the wild or in laboratory trials involving *M. sanguinipes.* Of the 4 loci, Ldh is the most variable within and between species. Common alleles are Ldh^b for *packardii* and *angustipennis,* Ldh^c for *confusus, dawsoni, infantilis* and *gladstoni,* Ldh^d for *sanguinipes, bruneri* and *femurrubrum,* Ldh^e for *bivittatus* and Ldh^g for *C. pellucida.* With respect to Mdh, all Melanopline species are monomorphic for, or have high frequencies of, the allele, Mdh^b. *C. pellucida* is also monomorphic at this locus, but the predominant allele is Mdh^d. *C. pellucida* and all Melanopline species, except *M. infantilis* and *M. bivittatus,* are monomorphic for Gpdh-1^c; this allele is the most common one in *M. bivittatus. M. infantilis* is homoallelic also, but for allele Gpdh-1^a. For the second Gpdh locus, allele Gpdh-2^b is predominant, and occurs at very high frequencies in all species except *M. bivittatus, M. infantilis* and *C. pellucida.* In these species, Gpdh-2^a is the leading allele. It is difficult to envisage how these similarities (e.g. virtual identity with respect to Mdh) and differences (e.g. divergence with respect to Ldh but with species clustering for specific alleles) could be explained by stochastic factors. Insufficiency of time since divergence might arguably explain these patterns and in the absence of a fossil record, this is a possibility. Mathews[14] citing his work with

Allele frequencies for 4 electrophoretic loci in 11 grasshopper species

Locus	Allele	Sang south	Sang park	Daws south	Daws park	Pac south	Pac park	Biv south	Biv park	Conf	Fem	Inf	Glad	Ang	Brun	CPel south	CPel park
Ldh	a	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.222	0.000	0.000	0.000
	b	0.008	0.000	0.000	0.000	0.806	0.875	0.026	0.000	0.182	0.000	0.000	0.000	0.556	0.000	0.000	0.000
	c	0.000	0.036	0.734	0.524	0.177	0.114	0.105	0.179	0.500	0.000	0.690	1.000	0.222	0.000	0.000	0.000
	d	0.817	0.771	0.118	0.214	0.000	0.011	0.000	0.000	0.000	0.929	0.300	0.000	0.000	1.000	0.000	0.000
	e	0.000	0.000	0.088	0.095	0.000	0.000	0.868	0.821	0.273	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	f	0.175	0.193	0.059	0.167	0.000	0.000	0.000	0.000	0.023	0.071	0.010	0.000	0.000	0.000	0.147	0.135
	g	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.853	0.865
	N	63	70	34	21	31	44	38	14	22	28	50	15	9	6	75	63
	χ^2		0.86		5.14*		1.32		0.37								0.08
Mdh	a	0.000	0.017	0.021	0.000	0.095	0.061	0.000	0.000	0.000	0.020	0.010	0.000	0.000	0.000	0.000	0.000
	b	0.960	0.958	0.958	1.000	0.892	0.939	0.986	1.000	0.926	0.963	0.959	1.000	1.000	1.000	0.000	0.000
	c	0.040	0.025	0.021	0.000	0.014	0.000	0.014	0.000	0.074	0.019	0.031	0.000	0.000	0.000	0.000	0.062
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.957	0.918
	e	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.021
	N	50	60	24	25	37	49	36	15	34	27	49	18	9	7	70	73
	χ^2		< 0.01		2.13		1.24		0.42								0.94
Gpdh-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	0.873	0.850	1.000	1.000	0.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.127	0.150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	N	55	59	37	23	26	33	59	10	30	18	31	5	5	9	26	30
	χ^2		–		–		–		0.08								–
Gpdh-2	a	0.009	0.008	0.015	0.000	0.000	0.000	0.689	0.545	0.028	0.000	1.000	0.000	0.000	0.056	0.981	0.984
	b	0.991	0.983	0.956	0.955	1.000	1.000	0.311	0.455	0.972	1.000	0.000	1.000	1.000	0.944	0.019	0.016
	c	0.000	0.008	0.029	0.045	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	N	53	60	34	22	34	35	66	11	36	20	31	14	5	9	80	64
	χ^2		0.24		< 0.01		–		1.76								0.04

N = sample size; each χ^2 value (1 df) compares prairie (south) and parkland (park) areas; * $p < 0.05$.

Coleoptera fossils speculates that most of the North American insect fauna evolved prior to the Pleistocene. Moreover, Vickery[15] firmly believes that the Melanopline species are even phylogenetically older than that – perhaps as old as the North–South American split. This view is based on the existence of a rather close affinity between the Nearctic *Melanoplus* and the Neotropical sister genus, *Dichroplus* and the fact that the amount of radiation, speciation and distribution within each group is very extensive. Vickery also notes that the fossil record that exists for other insect groups supports the claim that most of the existing North American insect fauna evolved early. Therefore, a reasonable interpretation of the allozyme data is that commonalities of allelic distributions stem from purifying selection in the case of the Mdh and Gpdh loci and some form of balancing selection in the case of the Ldh locus. Furthermore, for species exhibiting similar patterns, it is proposed that the selection constraints, whatever their nature, are identical. It is entirely possible, of course, that the patterns stem from selection acting on closely linked loci rather than on the enzyme loci themselves. While it does seem implausible that linkage disequilibrium between the studied loci and fitness loci would be identical in separate lineages for such a long time, in the absence of map data, a hitchhiking effect cannot be ruled out. Returning to the main objective of the paper, it would have to be concluded by extrapolating from the interspecific findings that the uniform allelic distributions between populations in prairie and parkland locations (despite differences in soil, food and so on) are best explained by hypothesis 2.

The neutralist position is also untenable from another consideration. It is possible that what are called alleles in this article are, in fact, electrophoretic mobility classes comprising several alleles that correspond to polypeptides with the same electrophoretic mobilities. But as Lewontin[4] has pointed out, if a large number of alleles do comprise each mobility class, then by the law of large numbers, one would expect independently evolving populations (or species) to have the same frequency distribution of classes. An examination of the table clearly shows that this is not the case.

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Catalase in sulfide- and methane-dependent macrofauna from petroleum seeps[1]

E. N. Powell, A. C. Morrill and R. R. Bidigare

Department of Oceanography, Texas A & M University, College Station (Texas 77843, USA)
Received 8 August 1988; accepted 4 November 1988

Summary. Vesicomyid and lucinid clams and tubeworms from Gulf of Mexico petroleum seeps, all of which bear symbiotic sulfide-oxidizing bacteria, have much lower catalase activities than shallow-water species lacking symbionts. A petroleum seep mussel bearing methane-oxidizing bacteria is unusual in having catalase activities as high as shallow-water bivalves. Unlike sulfide-dependent meiofauna from shallow-water marine sands, catalase from all petroleum seep species was inhibited by 3-amino-1,2,4-triazole.
Key words. Catalase; sulfide; methane; oxygen; petroleum seep; bivalve; vestimentiferan.

Two types of sulfide-dependent metazoans are known. 1) Sulfide-dependent meiofauna, thiobios, are found in most shallow-water marine sediments where an oxic surface layer is separated from a sulfidic deeper layer by a chemocline[2, 3]. Thiobiotic meiofauna inhabit subsurface sediments below the oxygenated upper layer of marine sands, the sulfide system of Fenchel and Riedl[4]. The sulfide system constitutes a rigorous environment, toxic to most animals, and organisms living there have developed unusual strategies for survival. These include mechanisms for sulfide detoxification[5, 6], and the modification of some normally sulfide-sensitive pathways, aerobic respiration for example[7], to be sulfide-insensitive. 2) The second group of sulfide-dependent animals are macrofauna primarily associated with hydrothermal vents, cold water sulfide seeps and petroleum seeps. Unlike thiobiotic meiofauna, which generally lack bacterial symbionts, many of these macrofauna contain sulfur-oxidizing bacteria[8 – 10]. Their survival appears to be heavily dependent upon sulfide detoxification[11, 12] and sulfide control (e.g. sulfide-binding proteins)[13 – 15]. Consequently, those sulfide-insensitive metabolic pathways of the meiofauna have remained sulfide-sensitive in these macrofauna, as they are in most animals.

Oxygen, like sulfide, can be toxic. Oxygen toxicity is produced primarily by superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($OH\cdot$) which are produced by a variety of oxygen-dependent enzymatic reactions associated with electron transport systems, some immune responses, and a variety of oxidases[16 – 18]. The oxidation of inorganic sulfide[19], pathways of sulfide detoxification[20] and photochemical reactions of sunlight and water[21, 22] may also be important in oxygen radical formation.

Morrill et al.[23] examined the enzyme catalase which catalyzes the detoxification of H_2O_2:

$$2\,H_2O_2 \rightarrow 2\,H_2O + O_2$$

These investigators suspected that thiobiotic meiofauna should have little catalase because thiobios live under contin-