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Genetic polymorphism in three species of tsetse flies (Diptera: Glossinidae) in Upper Volta

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Summary

Natural populations of *Glossina morsitans submorsitans* Newstead, *Glossina palpalis gambiensis* Vanderplank and *Glossina tachinoides* Westwood occurring within 150 km of Bobo-Dioulasso, Upper Volta were examined using polyacrylamide gel electrophoresis. No variation was found in the banding pattern for arginine phosphokinase (EC 2.7.3.3). *G. p. gambiensis* and *G. tachinoides* had three alleles for each of the thoracic enzymes octanol dehydrogenase (EC 1.1.1.73), malic dehydrogenase (EC 1.1.1.37) and alpha-glycerophosphate dehydrogenase (EC 1.1.1.8) and for midgut alkaline phosphatase (EC 3.1.3.1). The same situation was found with *G. m. submorsitans* except that only two alleles for alpha-glycerophosphate dehydrogenase and one for alkaline phosphatase were found. In each species, and for each of the enzymes, one allele was present at a frequency of 95% or greater. There was little or no variation between populations. Two laboratory colonies of *G. p. gambiensis* had less genetic variation than wild populations.

Key words: genetics; genetic polymorphism; population genetics; tsetse; *Glossina;* arginine phosphokinase; octanol dehydrogenase; alpha-glycerophosphate dehydrogenase; malic dehydrogenase; alkaline phosphatase.

Introduction

During the past 15 years use of electrophoretic techniques has greatly contributed to our understanding of the genetic diversity of laboratory and natural populations of many species. The techniques permit an estimation of the genetic diversity within a population by permiting determination of the

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proportion of randomly chosen loci which are polymorphic and an estimation of the extent of the polymorphism at each locus. Although these techniques have not been extensively applied to studies of tsetse flies, there is some information on laboratory populations. Of 26 loci studied in *Glossina morsitans morsitans* Westwood, 14 are polymorphic in one or more laboratory populations (van der Geest and Kawooya, 1975; van der Geest et al., 1978; Rolseth and Gooding, 1978; Gooding and Rolseth, 1978, 1979).

The primary objective of the present study was to measure the genetic variability of several natural populations of *Glossina morsitans submorsitans* Newstead, *Glossina palpalis gambiensis* Vanderplank and *Glossina tachinoides* Westwood in the vicinity of Bobo-Dioulasso, Republic of Upper Volta.

Throughout this paper the following convention is used: Enzymes are abbreviated using capital letters: ALKPH = alkaline phosphatase (EC 3.1.3.1), APK = arginine phosphokinase (EC 2.7.3.3), alpha-GPD = alpha-glycerophosphate dehydrogenase (EC 1.1.1.8), MDH = malic dehydrogenase (EC 1.1.1.37) and ODH = octanol dehydrogenase (EC 1.1.1.73); the loci for these enzymes are designated *Alkph*, *Apk*, *alpha-Gpd*, *Mdh* and *Odh* respectively.

Materials and methods

Tsetse flies (*G. m. submorsitans*, *G. p. gambiensis* and *G. tachinoides*), were collected between November, 1979 and March, 1980 near Bobo-Dioulasso, Upper-Volta, using biconical tsetse traps (Challier and Laveissière, 1973). The author collected flies at all localities mentioned below except at Komoé A and Komoé B (where flies were collected by D. Cuisance, H. Polizar and J. Fevrier) and Nda (where flies were collected by J. Fevrier). After flies were collected, they were maintained for from one to several days in the laboratory by feeding daily on guinea-pigs, then dissected, homogenized and electrophoresed. About 60% of the *G. p. gambiensis* examined were males while for the other species males only were examined. The electrophoretic apparatus and techniques used were described previously (Rolseth and Gooding, 1978; Gooding and Rolseth, 1978; 1979).

The enzymes studied were midgut ALKPH (for procedures see Gooding and Rolseth, 1978), and ODH, alpha-GPD, MDH, and APK from the thorax. For the thoracic enzymes the material was prepared and electrophoresed as described by Gooding and Rolseth (1979). Staining was done at room temperature (which varied from 25 to 35° C). ODH and APK were stained first (as described by Gooding and Rolseth, 1979), then the staining solution was removed from the gel and 20 to 25 mg DL-alpha-glycerophosphate (from Sigma Chemical Company) was dissolved in the staining solution for each gel and the staining continued until the alpha-GPD bands developed. Following this, 20 to 25 mg L-malic acid (from Sigma Chemical Company) was dissolved in 5–7 ml fresh electrode buffer and then added to the staining solution to stain for MDH. After each enzyme was stained the presence of the various bands was noted; the reactions were finally stopped by placing the gel in 7% acetic acid.

Results

The localities at which flies were collected are shown in Fig. 1 and the electrophoretic banding patterns observed are shown in Fig. 2. Each fly has one or three bands of ODH, alpha-GPD and MDH. These banding patterns are interpreted as indicating that there is a single locus for each enzyme and that

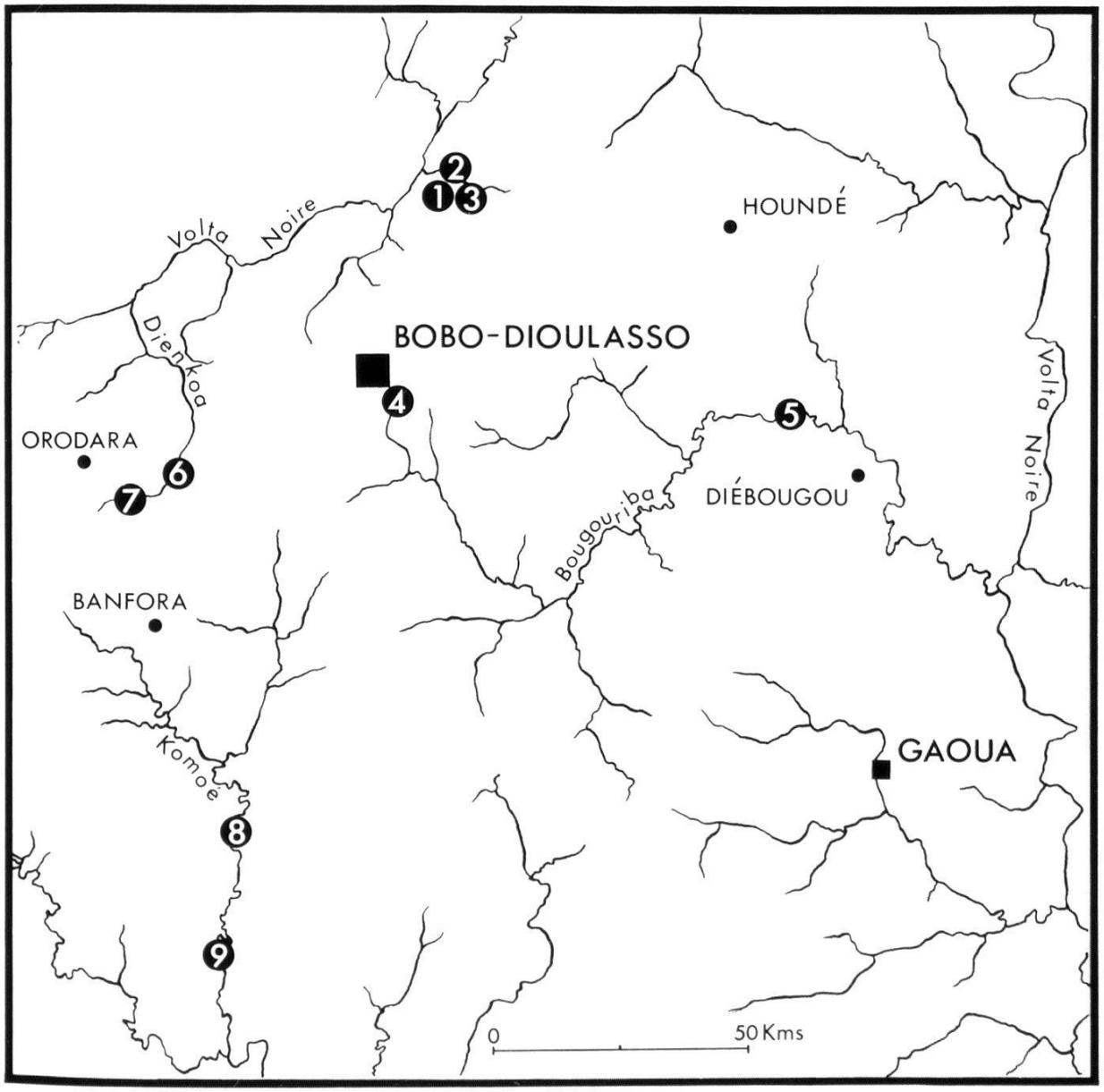

Fig. 1. The region in Upper Volta where tsetse flies were collected. Numbers on the map indicate the localities of: 1, Mare aux Hippopotames; 2, Lahissa river; 3, Sahagbeye, an intermittent stream; 4, San, an isolated spring and discontinuous stream near Koro; 5, Bougouriba river; 6 and 7, Topoko and Nda on the Dienkoa (Volta Noire) River; 8 and 9, Komoé A and Komoé B sites in savannah near the Komoé River.

each active enzyme molecule is a dimer, thus homozygous flies have one band and heterozygotes have three. Flies have one or two bands of ALKPH indicating that the active enzyme in probably a monomer. Since heterozygous males and females were found, it is concluded that the loci *Odh*, *alpha-Gpd*, *Mdh*, and *Alkph* are located on the autosomes. For each of these four loci, three alleles were found in *G. p. gambiensis* and *G. tachinoides*. For *Odh* and *Mdh* the same situation exists in *G. m. submorsitans* but only two alleles for *alpha-Gpd* and one for *Alkph* were found. In all three species, a single APK band was found indicating the existence of one locus with a single allele. The lack of variation prevents

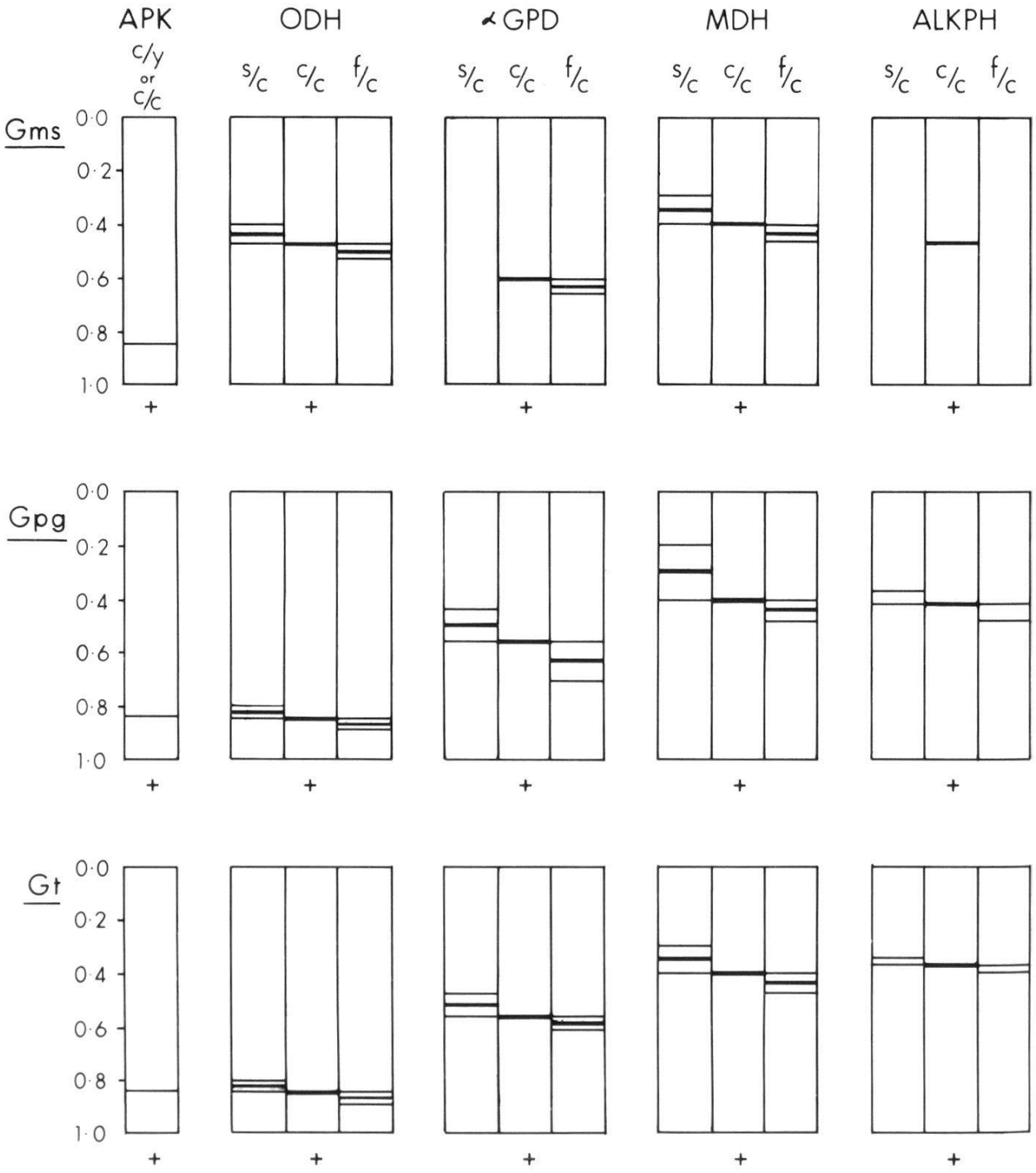

Fig. 2. Diagrams of the banding patterns seen on polyacrylamide gel electrophoresis. Migration was from the top toward the bottom (anode, +) of the gel. Numbers on the left are migration distances relative to the bromophenol blue marker. Abbreviations: *Gms, Glossina morsitans submorsitans; Gpg, Glossina palpalis gambiensis; Gt, Glossina tachinoides;* AKP, arginine phosphokinase; ODH, octanol dehydrogenase; alpha-GPD, alpha-glycerophosphate dehydrogenase; MDH, malic dehydrogenase; ALKPH, alkaline phosphatase. In designating the phenotypes, c, s and f refer to the common, slow and fast alleles; and Y refers to the Y-chromosome.

any interpretation of the location of *Apk* in the species studied, although in the closely related *G. m. morsitans* it is located on the X-chromosome (Gooding and Rolseth, 1979).

Table 1. Interspecific comparison of electrophoretic mobility of enzymes and allele frequencies for five enzymes in *Glossina morsitans submorsitans*, *Glossina palpalis gambiensis*, and *Glossina tachinoides*. The data are from all localities at which flies were collected in western Upper Volta. Average heterozygosity per locus (H) and its standard deviation (S.D.) were calculated using equations 6.5 and 6.6 from Nei (1975)

Gene Locus	Species	Number examined	Number of alleles	Electrophoretic mobility Rf			Allele frequency			Heterozygotes		
				s	c	f	s	c	f	No. observed	No. expected*	Obs. frequency
Apk	G.m.s.	138	1	–	0.84	–	–	1.0000	–	0	0	0.0000
	G.p.g.	546	1	–	0.84	–	–	1.0000	–	0	0	0.0000
	G.t.	603	1	–	0.84	–	–	1.0000	–	0	0	0.0000
Odh	G.m.s.	138	3	0.40	0.47	0.53	0.0216	0.9460	0.0324	15	14.29	0.1087
	G.p.g.	546	3	0.79	0.84	0.89	0.0092	0.9625	0.0284	41	39.70	0.0751
	G.t.	601	3	0.80	0.85	0.91	0.0025	0.9867	0.0108	14	15.81	0.0233
αGpd	G.m.s.	63	2	–	0.60	0.66	–	0.9921	0.0079	1	0.99	0.0159
	G.p.g.	426	3	0.44	0.56	0.71	0.0023	0.9941	0.0035	5	5.01	0.0117
	G.t.	459	3	0.48	0.56	0.61	0.0011	0.9815	0.0174	17	16.69	0.0370
Mdh	G.m.s.	71	3	0.29	0.39	0.46	0.0141	0.9718	0.0141	4	3.92	0.0563
	G.p.g.	424	3	0.20	0.40	0.49	0.0012	0.9894	0.0094	9	8.90	0.0212
	G.t.	468	3	0.30	0.40	0.47	0.0021	0.9936	0.0043	6	5.96	0.0128
Alkph	G.m.s.	26	1	–	0.47	–	–	1.0000	–	0	0.00	0.0000
	G.p.g.	175	3	0.37	0.42	0.48	0.0029	0.9914	0.0057	3	2.99	0.0171
	G.t.	289	3	0.34	0.37	0.40	0.0069	0.9792	0.0138	10	11.83	0.0343

Average frequency of heterozygous individuals per locus (H) ± S.D.
G.m.s. = 0.0349 ± 0.0200
G.p.g. = 0.0245 ± 0.0126
G.t. = 0.0233 ± 0.0076

* No. heterozygotes expected = Number of flies examined $[1-((\text{freq s})^2+(\text{freq c})^2+(\text{freq f})^2)]$

Table 2. Allele frequencies and heterozygosity in four natural populations of *Glossina tachinoides* in western Upper Volta, and in a laboratory colony maintained at I.E.M.V.T., Maisons-Alfort, France, and in two natural populations of *Glossina morsitans submorsitans* in western Upper Volta. For calculation of heterozygosity at each locus (h), average heterozygosity per locus (H), and the standard deviation of H, see Nei (1975, p. 131)

		G. tachinoides					*G. m. submorsitans*	
		Localities				I.E.M.V.T. colony	Localities	
Gene locus	Alleles	Koro	Bougouriba	Komoé A	Komoé B	Animal fed*	Komoé A	Komoé B
Apk	c	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	h	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	no. examined	13	253	164	169	158	54	84
Odh	s	0.0000	0.0000	0.0061	0.0030	0.0918	0.0185	0.0238
	c	1.0000	1.0000	0.9726	0.9790	0.9082	0.9630	0.9345
	f	0.0000	0.0000	0.0213	0.0180	0.0000	0.0185	0.0417
	h	0.0000	0.0000	0.0536	0.0412	0.1667	0.0719	0.1244
	no. examined	13	253	164	167	158	54	84
αGpd	s	0.0000	0.0000	0.0030	0.0000	0.0000	0.0000	0.0000
	c	1.0000	0.9565	0.9970	1.0000	1.0000	0.9891	1.0000
	f	0.0000	0.0435	0.0000	0.0000	0.0000	0.0109	0.0000
	h	0.0000	0.0832	0.0060	0.0000	0.0000	0.0216	0.0000
	no. examined	13	184	164	94	158	46	16
Mdh	s	0.0000	0.0026	0.0000	0.0000	0.0000	0.0185	0.0000
	c	1.0000	0.9896	1.0000	0.9947	1.0000	0.9722	0.9688
	f	0.0000	0.0078	0.0000	0.0053	0.0000	0.0093	0.0312
	h	0.0000	0.0206	0.0000	0.0105	0.0000	0.0544	0.0605
	no. examined	13	193	164	94	158	54	16
Alkph	s	0.0000	0.0000	0.0225	0.0000	0.0032	0.0000	0.0000
	c	1.0000	1.0000	0.9607	0.9728	0.9968	1.0000	1.0000
	f	0.0000	0.0000	0.0169	0.0272	0.0000	0.0000	0.0000
	h	0.0000	0.0000	0.0763	0.0529	0.0064	0.0000	0.0000
	no. examined	3	104	90	94	158	9	16
	H ± S.D.	0.0000	0.0208 ± 0.0161	0.0272 ± 0.0159	0.0209 ± 0.0110	0.0346 ± 0.0330	0.0296 ± 0.0145	0.0370 ± 0.0248

* The bands had the same migration rate as those found in wild flies, except the bands produced by Odh^s migrated much slower (Rf = 0.71) than those produced by the Odh^s in the wild type flies.

It must also be pointed out that when gels are stained for alpha-GPD, several bands may appear depending upon the duration of the staining. The first to appear, and the most prominent, is the band shown in Fig. 2; three other bands migrate slightly slower (and occasionally a slightly faster band is seen) but variation in these bands has not been noted. It is not known whether these fainter bands are controlled by other loci or whether they are artifacts produced from the alpha-GPD studied here.

For each of the enzymes one allele is present at a very high frequency (greater than 0.94) and this allele is designated allele c (= common) (Table 1). For most enzymes there were two other alleles, one responsible for a band with slower migration (s) and the other responsible for a fast migrating band (f) (Table 1). The frequency of the rare alleles is always less than 0.0325 (Table 1). All the heterozygotes observed involved the common allele and there was good agreement between the number of heterozygotes observed and the number expected (Table 1). The average frequency of heterozygous individuals per locus ranged from 2.33% to 3.49% (Table 1). Data on *Apk*, *Odh*, *alpha-Gpd*, and *Mdh* are available for each of 63 *G. m. submorsitans* (9 of which were heterozygous at one locus), 466 *G. tachinoides* (32 of which were heterozygous at one locus) and 428 *G. p. gambiensis* (42 of which were heterozygous at 1 locus and 1 fly was heterozygous at *Odh* and *alpha-Gpd*). Because of the low frequency of the rare alleles, the paucity of individuals heterozygous at two loci was to be expected.

Those natural populations of tsetse flies where more than 12 individuals were examined are compared with respect to allele frequency and heterozygosity (H) (see Dobzhansky et al., 1977, p. 51) in Tables 2 and 3. All populations show the same pattern: for each enzyme the same allele is common in all populations and it is present at a very high frequency while other alleles, if present, exist at low frequencies; the heterozygosity at each locus is low, as is the mean heterozygosity (H, Tables 2 and 3). *G. p. gambiensis* from the animal-fed colony at C.R.T.A., Bobo-Dioulasso was compared with each of the wild populations with respect to H. The greatest differences were with the two populations on the Dienkoa river: Topoko, mean diff. = 0.0242, t diff. = 2.7887, 6 d.f., $p < 0.05$; Nda, mean diff. = 0.0228, t diff. = 1.7057, 8 d.f., $p < 0.10$. A small sample of flies from the C.R.T.A. membrane-fed colony indicated that this colony was homozygous at the four loci examined (Table 3). Data on *G. tachinoides* from the colony at I.E.M.V.T. are included in Table 2 for comparison with wild flies. These flies show as much heterozygosity as wild flies. Although the colony flies are descendants of pupae collected near N'Djamena, Chad, the electrophoretic mobility of the enzymes, except the band produced by the slow allele of *Odh*, was the same as the mobility of the enzymes from the wild flies collected near Bobo.

The data from the natural populations are summarized in Table 4 with regard to the frequency of polymorphism. Populations were designated as

Table 3. Allele frequencies and heterozygosity in two laboratory populations and seven natural populations of *Glossina palpalis gambiensis* in western Upper Volta. For calculation of heterozygosity at each locus (h), average heterozygosity per locus (H), and the standard deviation of H, see Nei (1975, p. 131)

Gene locus	Alleles	Localities							Colonies	
		Mare aux Hippo.	Lahissa	Sahag-beye	Koro	Bougour-iba	Topoko	Nda	Animal fed	Membrane fed
Apk	c	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	h	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	no. examined	53	136	25	93	75	69	93	469	40
Odh	s	0.0094	0.0037	0.0000	0.0000	0.0267	0.0072	0.0161	0.0000	0.0000
	c	0.9623	0.9596	0.9400	0.9355	0.9667	0.9855	0.9785	0.9984	1.0000
	f	0.0283	0.0368	0.0600	0.0645	0.0067	0.0072	0.0054	0.0016	0.0000
	h	0.0731	0.0778	0.1128	0.1207	0.0647	0.0287	0.0422	0.0032	0.0000
	no. examined	53	136	25	93	75	69	93	315	40
αGpd	s	0.0000	0.0000	N.D.	0.0000	0.0000	0.0000	0.0133	0.0000	0.0000
	c	1.0000	1.0000	N.D.	1.0000	1.0000	0.9855	0.9800	1.0000	1.0000
	f	0.0000	0.0000	N.D.	0.0000	0.0000	0.0145	0.0067	0.0000	0.0000
	h	0.0000	0.0000	N.D.	0.0000	0.0000	0.0286	0.0394	0.0000	0.0000
	no. examined	53	59	0	93	75	69	75	198	40
Mdh	s	0.0000	0.0000	N.D.	0.0000	0.0000	0.0000	0.0067	0.0000	0.0000
	c	1.0000	1.0000	N.D.	1.0000	0.9932	0.9783	0.9667	1.0000	1.0000
	f	0.0000	0.0000	N.D.	0.0000	0.0068	0.0217	0.0267	0.0000	0.0000
	h	0.0000	0.0000	N.D.	0.0000	0.0135	0.0425	0.0647	0.0000	0.0000
	no. examined	53	59	0	93	73	69	75	155	40
Alkph	s	0.0000	0.0000	N.D.	0.0000	N.D.	N.D.	0.0000	0.0147	N.D.
	c	1.0000	1.0000	N.D.	0.9500	N.D.	N.D.	1.0000	0.9853	N.D.
	f	0.0000	0.0000	N.D.	0.0500	N.D.	N.D.	0.0000	0.0000	N.D.
	h	0.0000	0.0000	N.D.	0.0950	N.D.	N.D.	0.0000	0.0290	N.D.
	no. examined	52	66	0	20	0	0	31	102	0
	H ± S.D.	0.0146 ±0.0146	0.0156 ±0.0156	0.0564 ±0.0564	0.0431 ±0.0277	0.0196 ±0.0154	0.0250 ±0.0089	0.0293 ±0.0127	0.0064 ±0.0057	0.0000

Table 4. Frequency of polymorphism in natural populations of tsetse flies in western Upper Volta. Data are from the same populations documented in Tables 2 to 4

Gene locus	*G.m.s.*		*G.p.g.*		*G.t.*	
	1*	2*	1	2	1	2
Apk	0.00	0.00	0.00	0.00	0.00	0.00
	(2)**	(2)	(7)	(7)	(4)	(4)
Odh	0.50	1.00	0.28	1.00	0.00	0.50
	(2)	(2)	(7)	(7)	(4)	(4)
αGpd	0.00	0.50	0.00	0.33	0.00	0.25
	(2)	(2)	(6)	(6)	(4)	(4)
Mdh	0.00	1.00	0.00	0.33	0.00	0.25
	(2)	(2)	(6)	(6)	(4)	(4)
Alkph	0.00	0.00	0.25	0.25	0.25	0.50
	(2)	(2)	(4)	(4)	(4)	(4)
Avg. frequency of polymorphic pop. per locus ± S.E.	0.10	0.50	0.11	0.38	0.05	0.30
	±0.10	±0.22	±0.06	±0.16	±0.05	±0.09

* Populations are designated as polymorphic using two criteria: Criterion 1, the frequency of the common allele is less than or equal to 0.9500; criterion 2, the frequency of the common allele is less than or equal to 0.9900.

** The numbers in parentheses are the number of populations studied.

polymporphic on the basis of the frequency of the most common allele. Regardless of the criterion used (frequency of common allele less than or equal to 0.95, or less than or equal to 0.99) the average frequency of polymorphic populations per locus is small, being 10% or less by the most restrictive criterion and 50% or less by the least restrictive criterion.

Discussion

The enzymes studied were chosen after some preliminary work with *G. p. gambiensis* from the laboratory colony at C.R.T.A., Bobo-Dioulasso and with some wild-caught flies. The thoracic enzymes were chosen because four enzymes could be stained on a single gel and the midgut enzyme was used later in the study when it was found that the guts could be stored frozen before use. Thus, in the latter part of the study, a single fly was used for assessing five enzyme systems. Because wild-caught females of *G. m. submorsitans* and *G. tachinoides* were needed for other projects at C.R.T.A., none were available for the present study.

Time limitations and the low frequency of the rare alleles prevented me

from performing transmission experiments to confirm that the electrophoretic variations observed were, in fact, genetically controlled. However in *G. m. morsitans*, the appropriate genetic experiments have demonstrated genetic control of the banding patterns for ALKPH (Gooding and Rolseth, 1978) APK and ODH (Gooding and Rolseth, 1979). Recently, electrophoretic variants of MDH and alpha-GPD have been found in *G. m. morsitans* in our laboratory and experiments now in progress indicate that these variants are under genetic control.

The electrophoretic data permit a limited assessment of the taxonomic relationships between the three taxa studied. Using the data in Table 1, and assuming that any two alleles giving bands whose calculated Rf values differ by no more than 0.01 are identical, Nei's mean genetic identity (I) has been calculated (Nei, 1972). The mean genetic identity of the pairs of species are as follows: I (*G.m.s./G.p.g.*) = 0.4055; I (*G.m.s./G.t.*) = 0.4085 and I (*G.p.g./G.t.*) = 0.8014. These results are consistent with the generally accepted view (see for example Potts, 1973; Jordan, 1977) that *G. p. gambiensis* and *G. tachinoides* (subgenus *Nemorhina*) are more closely related to each other than either species is to *G. m. submorsitans* (which is in the subgenus *Glossina*). Within each species, each population has been compared to all other populations by use of Nei's mean genetic identity and the lowest value found was 0.9986.

The general picture which emerges from this study is that there is little genetic variation in *G. p. gambiensis*, *G. tachinoides* and *G. m. submorsitans* collected within 150 km of Bobo-Dioulasso, Upper Volta. Within each species there were no interpopulation differences using either Nei's mean genetic identity (I) or mean heterozygosity (H) as criteria. The genetic variation in laboratory populations of *G. p. gambiensis* is even lower than in natural populations. This no doubt reflects the history of the colonies which began with 125 wild females (wild-caught flies or emerged from field collected pupae) collected near Bobo-Dioulasso in 1972 and allowed to expand to a colony of approximately 4000 females maintained at I.E.M.V.T., Maisons-Alfort, France. (Itard, pers. commun., see also Itard, 1976.) From this material the animal-fed C.R.T.A. colony was established in 1975 at Bobo-Dioulasso and maintained as a closed colony except for the introduction during 1978 and 1979 of a few pupae whose fathers were trapped within 100 km of Bobo-Dioulasso. Offspring of wild-caught males accounted for 0.24% and 0.88% of the pupae retained in the C.R.T.A. colony during 1978 and 1979 respectively (data from E. Sellin, pers. commun.). No laboratory colony of *G. tachinoides*, established from material collected in Upper Volta, was available for comparison with the wild flies. However, a colony of *G. tachinoides*, established from 732 males and 931 females, collected as pupae near N'Djamena, Chad, during 1965 and 1966 has been established at I.E.M.V.T., Maisons-Alfort, France (Itard, pers. commun., see also Itard and Maillot, 1966; Itard et al., 1968) and 200 pupae from this colony were sent to my laboratory at U of A and examined electrophoretically.

Adults emerging from these pupae showed as much heterozygosity as did wild caught *G. tachinoides* (Table 2), although fewer of the enzymes were polymorphic. With the exception of the band produced by the slow allele of *Odh*, the electrophoretic mobilities of the enzymes from the colonized flies were the same as those from the wild flies collected near Bobo. The band produced by the slow allele of *Odh* migrated much slower (Rf = 0.71) than the slow band found in wild flies.

The low level of genetic variability in these three species is a little surprising considering the results obtained with laboratory populations of *G. m. morsitans*. In the natural populations, no variants of APK were found, but in *G. m. morsitans* two *Apk* alleles with frequencies of 0.980 and 0.020 were found in a relatively small laboratory colony (Gooding and Rolseth, 1979). The same colony had three *Odh* alleles with frequencies of 0.008, 0.664 and 0.348 (Gooding and Rolseth, 1979) and two *Alkph* alleles with frequencies of 0.438 and 0.562 (Gooding and Rolseth, 1978). All three enzymes in *G. m. morsitans* showed considerably more genetic variation than the corresponding enzymes in the natural populations reported upon in this paper.

When compared with other species, the wild tsetse flies had a rather low level of genetic variation. In the present study the mean heterozygosity (H) in the adequately sampled populations varied from 1.46% to 4.31% compared with H values of 13.4% in 57 species of invertebrates and 6.0% in 68 vertebrate species (summarized on p. 56 of Dobzhansky et al., 1977). It is interesting to note that the family Glossinidae consists of a single genus containing 30 taxa (species and subspecies) whose structure and mode of life are quite similar. Thus the evidence gathered on the tsetse flies, although rather tenuous, is consistant with the hypothesis that low levels of genetic variation within a species would provide little opportunity for selection and hence for speciation or divergence.

An ecological description of the sites at which flies were collected is beyond the scope of this paper. Suffice it to say that the sites had been studied by C.R.T.A. personnel and are considered typical for the species collected there (Cuisance, pers. commun.) with the exception of the following two sites. The site at Mare aux Hippopotames is a typical *G. tachinoides* habitat and few *G. p. gambiensis* were found there when the site was visited at the end of November 1979. However, between then and March 1980, *G. p. gambiensis* invaded this site and on March 20, 1980 only 12 *G. tachinoides* and 88 *G. p. gambiensis* were collected. (It is interesting to note that the *G. p. gambiensis* from Mare aux Hippopotames have only the alleles found in the population on the Lahissa which is a permanent tributary of the Mare.) At Koro there is a small and isolated spring with a *G. p. gambiensis* population but until our collection in mid-March no *G. tachinoides* had been recorded from this site. The *G. tachinoides* sample was small and only the common alleles were found.

The populations at Topoko and Nda were sampled because they are on the Dienkoa river and close to the site where the C.R.T.A. has successfully sup-

pressed or eradicated a population of *G. p. gambiensis* through release of sterilized males (D. Cuisance, H. Politzar, pers. commun.). As noted above these populations are genetically extremely similar to the laboratory population ($I > 0.9997$) but they are the only wild populations which were siginficantly more heterozygous than the animal-fed laboratory population. Assuming that the populations at Nda and Topoko were genetically the same as the (now eradicated) population at the sterile male release site, the workers on that program have the satisfaction of knowing that the program succeeded in a population which, although genetically very similar, was significantly more heterozygous. It would be very interesting to know how much genetic difference could exist between a natural population and a laboratory colony used to provide sterile males and still have a successful sterile male program. Although the data obtained in this study do not answer the question, electrophoretic techniques may prove useful in assessing the situation in other successful sterile male programs or in a program which fails to eradicate an adequately isolated natural population.

Genetic comparisons of populations or species ought to be based on a reasonably large number of randomly chosen loci (Nei 1975, p. 131). For a variety of reasons, this is not always possible and preliminary comparisons may be made using a less than ideal data set. In the present study, only five loci were examined and any interpretation of these results in terms of the total amount of genetic variation in tsetses must be tempered with the realization that this sample represents an extremely small portion of the total loci. However with this qualification, three findings are noteworthy: first, the genetic data obtained were consistant with the generally accepted taxonomic relationships among the species studied; second, there was little genetic variation in the natural populations of tsetses; and third, all three species showed the same pattern, in that all five enzymes had a common allele at a frequency greater than or equal to 95% and there were, at most, two rare alleles. A «neutralist» explanation of this pattern is hard to envision unless all three species had been recently decimated in western Upper Volta with the present allele frequencies reflecting a founder effect. On the other hand, tsetse flies are generally recognized to be well adapted to their environment, thus assuring their survival despite a very low reproductive rate. If the various electrophoretic forms of the enzymes studied have different effects upon fitness, it would be easy to imagine that for each enzyme one allele has been selected for and that the others are selected against and survive in the population at low levels in heterozygotes. What ever the mechanism producing the observed distribution of alleles, it appears to operate in all three species and any explanation must account for this.

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