POPULATION BIOLOGY/GENETICS

Genetic Differentiation of *Anopheles claviger* s.s. in Europe

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ABSTRACT Two groups of *Anopheles claviger* sensu stricto Meigen (Diptera: Culicidae) were recently found in France, representing unclear genetic entities. To better understand this situation, sampling was extended to 13 European countries, and 47 samples were analyzed by investigating the polymorphism of 11 autosomal and 1 sex-linked allozyme loci. Genetic differentiation, as measured by F_{st}, between these two groups was confirmed, with no isolation by distance within each group. Among the twelve loci studied, none had diagnostic alleles. Group I is mainly located in western Europe (UK and south-west of France), and Group II covers eastern France and eastern and northern Europe. Intermediate populations, sampled at the overlapping range between them, do not display a heterozygote deficit, suggesting that these two groups are probably not genetically isolated. The origin of each group and its biological significance is discussed within the context of differentiation in refugia during recent glaciations.

KEY WORDS *Anopheles claviger,* allozymes, population genetics, sibling species, Europe

WITHIN THE CLAVIGER COMPLEX (Diptera: Culicidae), two morphological forms, designated *Anopheles claviger* (Meigen 1804) sensu stricto and *Anopheles petragnani* Del Vecchio, 1939, are classically recognized. These two forms are reproductively isolated (Coluzzi 1962), and can be distinguished morphologically by some characters of the immature stages (Coluzzi et al. 1965) and genetically at some enzymatic loci (Cianchi et al. 1980, Cianchi et al. 1981). This species complex is distributed abundantly in Europe, from the Atlantic coast to China and Central Siberia (93° East), and from Scandinavia (60° North) to North Africa (31° North) (Schaffner et al. 2001). The former medical importance of *An. claviger* s.l. as a vector of human malaria, especially around the eastern Mediterranean (Russell et al. 1963), has been superseded by its possible role in transmission of *Bunyaviridae* arboviruses (Pchelkina and Seledtsov 1978, Traavik et al. 1985), myxomatosis (Service 1971) and other pathogens such as *Anaplasma marginale* (Artemenko and Ponomarenko 1974), *Francisella tularensis* (Gutsevich et al. 1974), *Dirofilaria immitis* (Grassi & Noé in Séguy 1924), and *Setaria labiatopapillosa* (Cancrini et al. 1997).

Recently, two genetically differentiated groups of *An. claviger* s.s. were found in western and eastern France, respectively (Schaffner et al. 2000). These two groups seem to have a contact zone around the Rhone valley in eastern France, although the significance of these taxa is unclear, as no diagnostic locus was identified. It has been proposed that these taxa represent isolates from distinct refugia during the last glaciation that have expanded during the last warm phase, and come in contact recently (Schaffner et al. 2000).

The current study was undertaken to investigate the genetic variability and population structure of *An. claviger* s.s. on a broader scale (across Europe), in an attempt to interpret the significance of the two genetically differentiated groups. Sampling was also focused on the putative hybrid zone in eastern France, to better characterize the two genetic entities.

Materials and Methods

Mosquitoes. Larvae and pupae of *An. claviger* s.s. were collected during 1996–2000 from a total of 47 localities (Table 1), representing Austria (2), Belgium (1), Czech Republic (1), Denmark (1), France (32), Germany (2), Italy (2), Netherlands (1), Romania (1), Slovenia (1), Sweden (1), Switzerland (1), and the United Kingdom (1). After rearing to adulthood, the exuviae, head, wings, legs, and male genitalia were mounted on slides in Canada balsam for morphological examination. The morphological data will be presented elsewhere. From freshly killed sexed adults, the thorax and abdomen were stored in liquid nitrogen for allozyme analyses. The eighteen *An. claviger* s.s. samples previously published (Schaffner et al. 2000) were added to the present dataset for an overall analysis. For some populations presented in this previous study (I–C, I–E, I–F, I–H, I–J, II–F, II–M, II–Q, II–R, II–I), additional individuals were analyzed to increase the sample size.

Electrophoresis. Electrophoretic polymorphisms of the following nine enzymes were studied by starch gel electrophoresis (TM 7.4 buffer system) on adult mos-

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Table 1. Characteristics of the *Anopheles claviger* s.s. samples studied

Code	Sample identity	Sample size	Longitude	Latitude	Locality (administrative area, country)	Sample date	Breeding site
I-A	F-01-Dombes	30	4° 59′ E	46° 04′ N	Sandrans (Ain, France)	09/1995	Ditch, meadow
I-B	F-12-Lapanouse	36	3° 02′ E	44° 20′ N	Lapanouse (Aveyron, France)	04/1995	Ditch, meadow
I-C	F-19-Millevaches	29	2° 12′ E	45° 40′ N	Sornac (Corrèze, France)	12/1994	Peat pool
I-D	F-21-Auxois	18	4° 23′ E	47° 05′ N	Voudenay (Côte d'Or, France)	09/1995	Spring, pasture pool
I-E	F-36-Brenne	29	1° 10′ E	46° 48′ N	St-Michel-en-Brenne (Indre, France)	11/1994	Ditch, forest
I-F	F-36-Vendœuvres	18	1° 22′ E	48° 48′ N	Vendœuvres (Indre, France)	11/1994	Ditch, marsh
I-G	F-42-Loire	36	4° 08′ E	45° 46′ N	Sainte-Foy-Saint-Sulpice (Loire, France)	12/1994	Ditch, meadow
I-H	F-44-Erdre	28	1° 24′ W	47° 22′ N	St-Mars-du-Désert (Loire-Atlantique, France)	11/1994	Pasture pool
I-J	F-49-Layon	30	0° 30′ W	47° 14′ N	Faveraye-Mâchelles (Maine-et-Loire, France)	11/1994	Pasture ditch
I-K	UK-SC-Strathclyde	21	3° 40′ W	55° 58′ N	Newton (Strathclyde, Ecosse, United Kingdom)	08/1998	Pool
II-A	AU-K-Karawanken	30	14° 35′ E	46° 35′ N	Lanzendorf (Kärnten, Austria)	03/1999	Spring, dock
II-B	AU-S-Salzburg	30	12° 54′ E	47° 58′ N	Oberndorf (Salzburg, Austria)	03/1999	Dirt track ruts
II-C	B-L-Rossignol	20	5° 20′ E	49° 41′ N	Tintigny (Luxembourg, Belgium)	03/1996	Ditch, forest
II-D	CH-V-Poutafontana	54	7° 25′ E	46° 15′ N	Pramagnon (Valais, Suisse)	09/1994	Marsh, forest
II-E	CZ-Bohemia	31	12° 45′ E	49° 32′ N	Čečin (Bohemia, Czech Republic)	09/1995	Spring, pool
II-F	D-BW-Schwarzwald	194	8° 06′ E	47° 52′ N	Lenzkirch (Bade-Würtemberg, Germany)	11/1993	Peat bog
II-G	DK-Himmerland	30	9° 52′ E	56° 47′ N	Rebild (Himmerland, Denmark)	05/1995	Ditch, meadow
II-H	D-MV-Mecklenburg	31	11° 05′ E	53° 41′ N	Gadebusch (Mecklenburg-Vorpommern, Germany)	04/1995	Ditch, meadow
II-J	F-01-Lavours	47	5° 44′ E	45° 52′ N	Talissieu (Ain, France)	03/1994	Peat spring
II-K	F-02-Thiérache	29	3° 51′ E	49° 54′ N	Autreppes (Aisne, France)	03/1996	Ditch, meadow
II-L	F-10-Orient	30	4° 28′ E	48° 14′ N	Vendeuvre-sur-Barse (Aube, France)	03/1996	Ditch, pool, forest
II-M	F-25-Chapelle	30	6° 07′ E	46° 36′ N	Chapelle-des-Bois (Doubs, France)	11/1995	Peat pool
II-N	F-52-Bassigny	31	5° 45′ E	47° 57′ N	Bourbonne-les-Bains (Haute-Marne, France)	09/1995	Covered washing-place
II-O	F-54-Boucq	30	5° 46′ E	48° 45′ N	Boucq (Meurthe-et-Moselle, France)	09/1994	Spring, forest
II-P	F-57-Saulnois	30	6° 38′ E	48° 49′ N	St-Médard (Moselle, France)	04/1995	Ditch, meadow
II-Q	F-63-Allier	31	3° 13′ E	45° 54′ N	Ennezat (Puy-de-Dôme, France)	12/1994	Ditch, garden
II-R	F-67-Hasslach	19	7° 24′ E	48° 33′ N	Still (Bas-Rhin, France)	03/1995	Pond border
II-S	F-67-Niederlauterbach	28	8° 06′ E	48° 58′ N	Niederlauterbach (Bas-Rhin, France)	11/1994	Ditch, forest
II-T	F-68-Amélie	57	7° 14′ E	47° 48′ N	Wittelsheim (Haut-Rhin, France)	02/1994	Brook (Joncus)
II-U	F-68-MarieLouise	37	7° 15′ E	47° 50′ N	Feldkirch (Haut-Rhin, France)	03/1994	Pool, forest
II-V	F-68-Mollau	22	6° 58′ E	47° 52′ N	Mollau (Haut-Rhin, France)	04/1994	Marsh (Carex)
II-W	F-70-Saône	31	5° 57′ E	47° 29′ N	Fretigney-et-Velloreille (Haute-Saône, France)	11/1995	Pasture pool
II-X	F-71-Bresse	30	5° 10′ E	46° 46′ N	Devrouze (Saône-et-Loire, France)	09/1995	Ditch, meadow
II-Y	F-74-MontBlanc	26	6° 52′ E	45° 55′ N	Chamonix-Mont-Blanc (Haute-Savoie, France)	03/1998	Brook, marsh (Phragmites)
II-Z	F-83-Argensl	10	5° 57′ E	43° 32′ N	Brue-Auriac-St-Estève (Var, France)	01/1996	Spring, ditch
II-ZA	F-88-Bussang	19	6° 51′ E	47° 53′ N	Bussang (Vosges, France)	09/1994	Tank, spring
II-ZB	I-FVG-Veneto	32	12° 50′ E	45° 47′ N	Portogruaro (Friuli-Venezia-Giulia, Italy)	04/1997	Ditch, forest
II-ZC	I-P-AstiPiemonte	23	8° 17′ E	45° 03′ N	Casorzo (Piemonte, Italy)	03/1998	Ditch, forest
II-ZD	NL-NB-Brabant	19	4° 47′ E	51° 30′ N	Meersel-Dreef (Noord-Brabant, Netherlands)	12/1996	Backwater
II-ZE	S-Öland	30	16° 37′ E	56° 39′ N	Södra-Bäck (Öland, Sweden)	04/1995	Marsh border
II-ZF	F-04-Volonne	10	6° 01′ E	44° 06′ N	Château-Arnoux-St-Auban (Alpes-de-Haute-Provence, France)	01/1996	Spring, pool
II-ZG	F-13-LaCraul	43	4° 49′ E	43° 38′ N	St-Martin-de-Crau (Bouches-du-Rhône, France)	01/1997	Ditch, forest
II-ZH	F-51-Possesse	30	4° 48′ E	48° 53′ N	Possesse (Marne, France)	04/1995	Brook, forest
II-ZJ	F-60-Oise	30	2° 12′ E	49° 26′ N	Laversines (Oise, France)	07/1998	Spring, washing-place, brook
II-ZK	SLO-Karst	24	14° 16′ E	45° 51′ N	Planida (Slovenia, Slovenia)	03/1999	Ditch, meadow
II-ZL	RO-M-Comana	8	26° 09′ E	44° 10′ N	Comana (Muntenia, Romania)	08/1999	Spring, well
X-A	F-71-Charollais	30	4° 34′ E	46° 37′ N	Joncy (Saône-et-Loire, France)	12/1994	Pasture pool

Longitudes and latitudes refer to the ED50 coordinates. Samples previously studied are in bold.

quito homogenates (Pasteur et al. 1988), providing 12 individual loci: α-glycerophosphate dehydrogenase (EC 1.1.1.8), locus *Gpd*, esterases (EC 3.1.1.1/2), loci *Est-2* and *Est-3*, glutamate-oxaloacetate transaminase (EC 2.6.1.1), loci *Got-1* and *Got-2*, hexokinase (EC 2.7.1.1), locus *Hk*-1, isocitrate dehydrogenase (EC 1.1.1.42), loci *Idh-1* and *Idh-2*, malic enzyme (EC 1.1.1.40), locus *Me-1*, mannose-phosphate isomerase (EC 5.3.1.8), locus *Mpi*, phosphogluco-isomerase (EC 5.3.1.9), locus *Pgi*, and phosphoglucomutase (EC 2.7.5.1), locus *Pgm*. Arbitrarily, the German sample II-F from Schwarzwald was used as reference standard. For each enzyme, the predominant electromorph band (putatively the commonest allele at each locus) was designated "100" and other electromorphs (alleles) were numbered according to their relative electrophoretic mobility, i.e., 110, 120, etc., for faster bands; 90, 80, etc., for slower bands. Because it was previously found that the locus *Mpi* is found only on the X chromosome (Schaffner et al. 2000), males were coded as hemizygotes for this locus.

Data Analysis. Conformity with Hardy-Weinberg (HW) expectations was tested for the proportions of genotypes at each locus, using the exact U-score test in presence of the alternative hypothesis of heterozygote deficiency (Rousset and Raymond 1995). A global test across samples and/or loci was also performed (Rousset and Raymond 1995). Genotypic associations between each pair of loci in each population were tested using the probability test described by (Raymond and Rousset 1995a). For each locus pair, global tests (Fisher method) were performed across all populations (Manly 1985). Departure from HW was measured using the F_{is} estimator proposed by Weir and Cockerham (1984). Genotypic differentiation between populations was tested by computing an unbiased estimate of the *P* value of a log-likelihood (G) based exact test (Goudet et al. 1996). Population differentiation was measured using the F_{st} estimator (Weir and Cockerham 1984). Isolation by distance was analyzed as described by Rousset (1997), i.e., computing the relationship between pairwise estimates of $\hat{F}_{st}/1 - \hat{F}_{st}$ and logarithm of geographic distance. A possible positive relationships was tested with a Mantel test, using the Spearman rank correlation coefficient statistic. Geographical distances between localities were taken as the shortest measurement on a map. Computations were performed by Genepop version 3.1d (Raymond and Rousset 1995b) and multiple testing used the Bonferroni method (Hochberg 1988). A graphical representation of the genetic proximity among samples was performed as follows. Pairwise Nei genetic distances (Nei 1972) were computed, and were organized in an unrooted tree using the neighbor-joining algorithm (Saitou and Nei 1987). One hundred bootstrap trees were generated, from which a consensus tree was obtained. Groups were displayed in the consensus tree if they were present in at least 72.5% of the bootstrapped trees. All these computations were performed using Phylip version 3.6(alpha3) (Felsenstein 2002). Because data for eight samples were missing, this procedure was performed on subsets of the whole data set, to locate these eight samples in the consensus tree (all of them fall within the multifurcation of Group II, see below).

Results

Description of Polymorphism. All 12 loci have multiple alleles. Frequencies of each allele in each sample are presented in the Appendix. Genotypic differentiation was first tested between the samples from the same locality, and none was rejected ($P > 0.38$). The samples were then pooled for further analysis.

Genotypic associations were tested at each pair of loci in each locality. Random association was rejected ($P < 0.05$) in 31/822 tests (or 3.8%), although none remained significant when taking into account multiple tests. A global test across populations for each locus pair revealed no pairs with significant values ($P > 0.07$).

Significant departure from HW equilibrium, because of heterozygote deficiency, was observed in 6/247 cases (Appendix). None was significant when the number of tests performed was taken into account. For all loci and localities, no significant ($P > 0.5$) heterozygote deficiency was found, suggesting that null alleles are at a low frequency or absent. However, a significant heterozygote excess was present for *Est-2* and *Pgi* across samples ($P < 10^{-3}$), suggesting that selection is present. Selection acting at electrophoretic loci such as *Est* and *Pgi* is not uncommon (e.g., Koehn et al. 1983, Watt et al. 1983), and they should be removed from population genetic analyses concerned primarily by inferences on population structures based on neutral markers. These two loci were then removed for further analyses (and the significant heterozygote excess disappeared, $P > 0.10$).

Genetic Differentiation Among Samples of *Anopheles claviger* s.s.

Genotypic differentiation among *An. claviger* s.s. was highly significant (considering all loci: $\hat{F}_{st} = 0.052$, $P < 10^{-5}$), consistent with the previous description of two genetic groups (Schaffner et al. 2000). To formally identify these groups, a tree describing the genetic proximity between samples was constructed, and a consensus tree was built from 100 bootstrap replicates. Two groups were apparent (Fig. 1), one characterized by a single multifurcation—previously described as Group II—and the remaining tree corresponding to Group I. Examination of pairwise $\hat{F}_{st}$ values (Fig. 2) confirmed globally the grouping, with the exception of X-A which does not belong clearly to either of the two groups, and has also an intermediate position in the tree. Two other populations (II–ZL and II–ZJ) are included in Group II only on the basis of the tree, because their differentiation with Group I is lower than the other samples of Group II. Groups are thus characterized by large between-group values (91% of pairwise F_{st} values >0.05) and low intragroup values (Group I: 64% of pairwise F_{st} values <0.03; Group II: 87%). Group I represented localities in western and southwestern France, whereas Group II represented localities in eastern France, Italy, and northeastern Europe (Fig. 3). The X–A population, not belonging clearly to Group I or II, is located in central France, within the overlapping range of both groups. The two populations classified in Group II only on the basis of the tree (II–ZJ and II–ZL) are from northern France and Romania, respectively (Fig. 3). Within each group, genotypic differentiation among populations was low but significant (Group I: $\hat{F}_{st} = 0.021$, $P < 10^{-5}$; Group II: $\hat{F}_{st} = 0.010$, $P < 10^{-5}$)

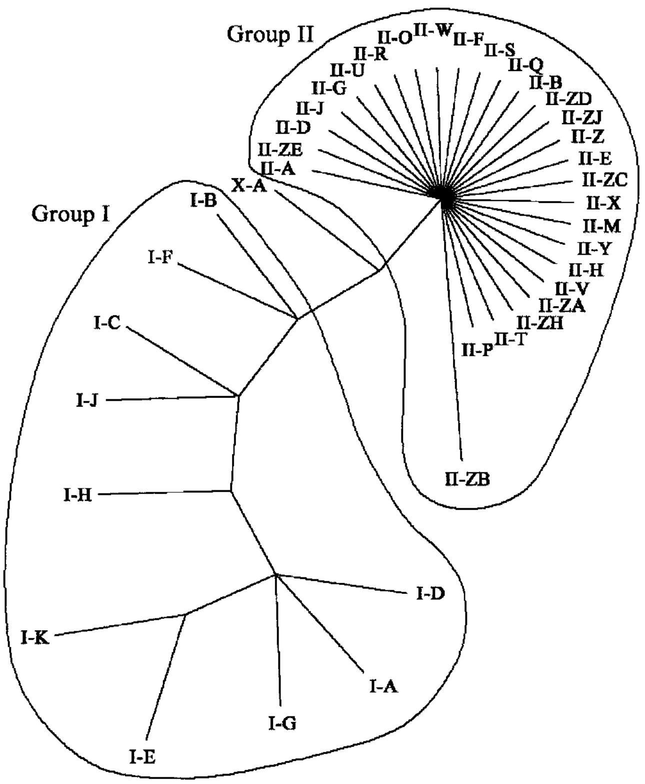

Fig. 1. Graphical representation of the genetic proximity among samples. A consensus unrooted tree is constructed from 100 bootstrap replicates. Samples not depicted are all located within the multifurcation of Group II. See text for details.

Isolation by Distance. To better understand the forces controlling genetic exchange among *An. claviger* s.s. populations, we examined variation between $\hat{F}_{st}/1 - \hat{F}_{st}$ and the log of geographic distance (Rousset 1997) within each group. This analysis considered only females at the *Mpi* locus, but combined both sexes for the other autosomal loci. Values of $\hat{F}_{st}/1 - \hat{F}_{st}$ increased significantly (one-tailed Mantel test, $P < 0.03$) with geographical distance, indicating relative isolation by distance (not shown). Within each group, no isolation by distance was found (Group I: slope = 0.0042, Mantel test, $P = 0.23$; Group II: slope = 0.0007, Mantel test, $P > 0.50$).

Discussion

Our study confirms the existence of two genetically divergent groups of *An. claviger* s.s. that were suspected in France (Schaffner et al. 2000). The present large sample across Europe allows us to better define the geographical range of both groups. Group I (10 localities) is mainly located in western Europe (United Kingdom and the southwest of France), and Group II (36 localities) covers eastern France and eastern and northern Europe (Fig. 3). Within each group, there was no trend of isolation by distance over the geographical range surveyed, i.e., each group was relatively homogeneous among samples studied from several sites. Among the ten loci studied, none had diagnostic alleles, indicating that Groups I and II are either not genetically isolated, or that their geographic isolation may be too recent for diagnostic genetic loci to have evolved. Populations sampled near the overlapping range between them do not display any heterozygote deficit, suggesting that these two groups are probably not genetically isolated. This suggests the existence of free mixing when both groups meet, with no inviability of hybrids. Further characterization of the zone, with the possibility of hybrid sterility, requires additional studies.

It has been proposed that Groups I and II of *An. claviger* s.s. represent two members of a species complex, resulting from their allopatric divergence in southern refugia during (at least) the last glaciation period (Schaffner et al. 2000). During a warm phase, the invasion of northern territories from all refugia results in a hybrid zone wherever both genetic entities meet. This scenario has been repeatedly proposed for various plants and animals (for a review, see Hewitt 1996, Hewitt 1999). The current study suggests Group I most likely originates from the Iberian peninsula, where it is still present, although not common. The origin of Group II is not settled. Two samples from northern Italy belong to Group II, and one sample from Romania is not clearly classified. Thus, it cannot be excluded that a third group exists in eastern Europe, corresponding to the Balkanic refugium (Hewitt 2001). Under this scenario, Group II probably origi-

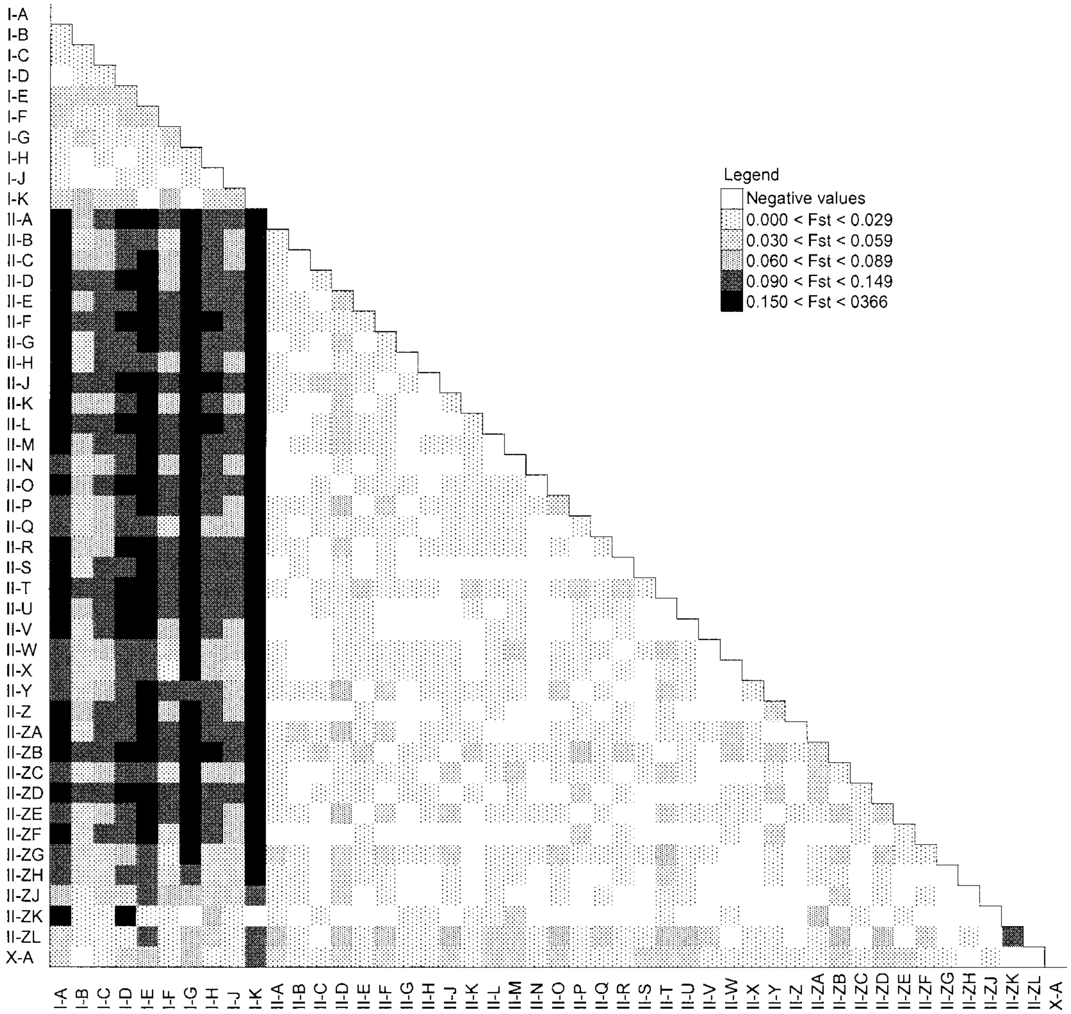

Fig. 2. F_{st} estimates observed between pairs of *An. claviger* s.s. samples. Samples are ranked according to their group (I, II, and X). Darker intensities of gray correspond to higher F_{st} estimates, as indicated in the legend. The large overall dark rectangle on the left represents the inter Group I and II comparison.

nates from the Italian refugium. It is noteworthy that the contact zone, located in eastern France in a place with no substantial topographic barriers, is characteristic of a suture zone between populations coming from the Iberic and Balkanic (or another easternmost) refugia (Taberlet et al. 1998, Hewitt 1999, Hewitt 2000). However, it is unclear whether or not the Alps represent a physical barrier for *An. claviger* s.s. from Italy.

Anopheles claviger s.s. prefers breeding sites with cold water (see p. 140 in Bates 1949), and is now distributed in northern Europe and southern Scandinavia (Natvig 1948, Utrio 1975, Mehl 1996), corresponding approximately to the northern distribution limit of the oak *Quercus robur* (Ferris et al. 1998). Interestingly, the white oak located in the Italian peninsula has invaded western and northern Europe after crossing the Alps at the start of the Holocene, when the temperatures were warmer than they are now, because of an increase of solar radiation received by the earth's atmosphere (Petit et al. 2002). Nowadays, *An. claviger* s.s. is rather common in the Alps below an altitude of ≈1,100 m, and its maximum altitude is at 1,600 m (Léger and Mouriquand 1918), leaving very few opportunities to cross the Alps from South to North. However, as for the white oak, crossing was probably possible at the start of the Holocene. A thorough sampling in Italy and the Balkans is required to evaluate this possibility.

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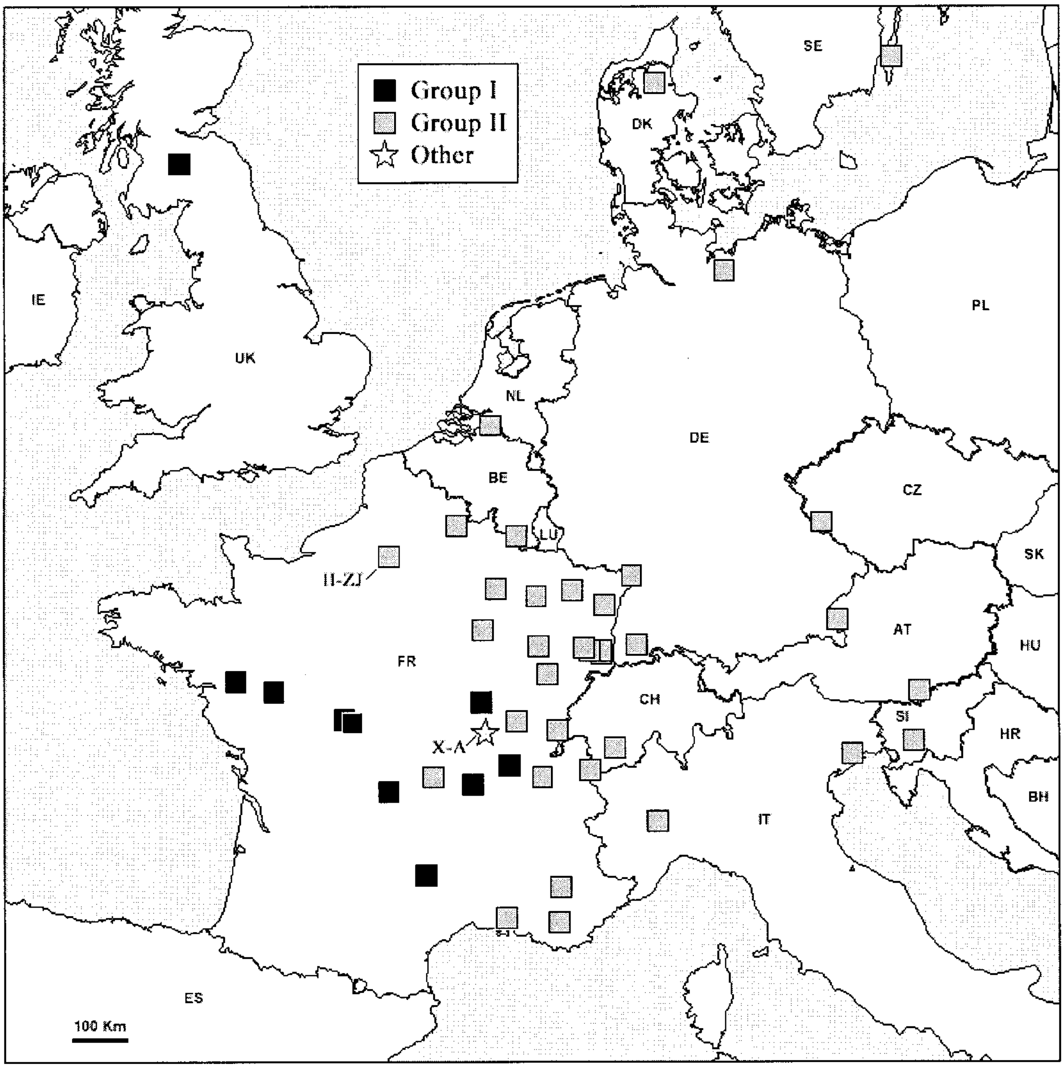

Fig. 3. Sampling localities for the *An. claviger* s.s. (see Table 1 for details). Black and gray squares represent samples attributed to Group I and Group II, respectively. Star represents one sample (X–A) from a nonclassifiable locality. Samples II–ZJ and II–ZL (the latter from Romania is located further east) are included in Group II only on the basis of the tree (see text). Country borders are outlined.

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Appendix. Allelic frequencies observed at 12 putative allozyme loci, for *An. claviger s.s.* from 47 localities. Number of mosquito(es) analysed at each locus in parenthesis. Fis estimates are underlined when there is a significant ($P < 0.05$) departure from HW due to heterozygote deficiency; none remain significant when taking into account multiple tests (see text for explanation)

	Populations											
	I-A	I-B	I-C	I-D	I-E	I-F	I-G	I-H	I-J	I-K	II-A	II-B
Locus												
aGpd	(30)	(36)	(29)	(16)	(29)	(18)	(36)	(28)	(30)	(21)	(9)	(30)
140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983
80	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
Fis	-	-	-	-	-	-	-	-	-	-	-	0.0000
Est-2	(30)	(35)	(27)	(18)	(26)	(13)	(28)	(23)	(26)	(15)	(8)	(30)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.043	0.019	0.000	0.000	0.033
100	0.833	0.957	0.907	0.944	0.846	0.808	0.946	0.848	0.808	0.800	0.875	0.967
90	0.000	0.043	0.074	0.028	0.058	0.192	0.054	0.087	0.135	0.100	0.000	0.000
80	0.167	0.000	0.019	0.028	0.077	0.000	0.000	0.022	0.038	0.100	0.125	0.000
Fis	−0.1837	−0.0303	−0.0656	−0.0149	−0.1019	−0.2000	−0.0385	−0.1000	−0.1547	−0.1429	−0.0769	−0.0175
Est-3	(30)	(33)	(27)	(17)	(27)	(16)	(23)	(25)	(27)	(20)	(29)	(30)
120	0.050	0.000	0.000	0.059	0.000	0.063	0.000	0.000	0.019	0.025	0.017	0.000
110	0.017	0.091	0.130	0.118	0.185	0.125	0.087	0.180	0.167	0.050	0.017	0.033
100	0.817	0.758	0.815	0.765	0.685	0.688	0.804	0.720	0.741	0.775	0.776	0.783
90	0.050	0.061	0.037	0.029	0.074	0.094	0.087	0.080	0.037	0.150	0.121	0.150
80	0.067	0.091	0.019	0.029	0.056	0.031	0.000	0.000	0.037	0.000	0.069	0.033
70	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.020	0.000	0.000	0.000	0.000
Fis	−0.0140	−0.1047	0.0857	−0.1584	0.0315	−0.2245	−0.1379	0.2954	0.1376	−0.1793	−0.1685	0.0031
Got-1	(1)	(35)	(7)	(6)	(5)	(11)	(9)	(4)	(8)	(19)	(30)	(29)
120	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.052
100	1.000	0.971	1.000	0.917	1.000	1.000	0.944	1.000	1.000	1.000	0.983	0.931
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.083	0.000	0.000	0.056	0.000	0.000	0.000	0.000	0.017
Fis	-	−0.0149	-	0.0000	-	-	0.0000	-	-	-	0.0000	−0.0419
Got-2	(10)	(36)	(8)	(7)	(13)	(9)	(7)	(8)	(15)	(11)	(30)	(29)
120	0.050	0.028	0.063	0.071	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
100	0.950	0.917	0.938	0.929	0.962	1.000	1.000	1.000	1.000	0.955	1.000	0.931
80	0.000	0.056	0.000	0.000	0.038	0.000	0.000	0.000	0.000	0.045	0.000	0.052
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	0.0000	−0.0553	0.0000	0.0000	0.0000	-	-	-	-	0.0000	-	−0.0419
Hk-1	(6)	(36)	(28)	(6)	(26)	(18)	(35)	(28)	(30)	(21)	(30)	(30)
120	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000
110	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.024	0.000	0.000
100	1.000	1.000	0.982	1.000	0.981	0.972	1.000	1.000	1.000	0.976	1.000	1.000
80	0.000	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	-	-	0.0000	-	0.0000	0.0000	-	-	-	0.0000	-	-
Idh-1	(12)	(33)	(14)	(5)	(10)	(6)	(19)	(10)	(12)	(0)	(27)	(21)
110	0.000	0.015	0.000	0.000	0.000	0.083	0.132	0.000	0.083	-	0.000	0.024
100	1.000	0.985	1.000	1.000	1.000	0.917	0.842	1.000	0.917	-	1.000	0.952
90	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.000	0.000	-	0.000	0.024
Fis	-	0.0000	-	-	-	0.0000	−0.1309	-	−0.0476	-	-	−0.0127
Idh-2	(0)	(30)	(4)	(0)	(0)	(1)	(10)	(0)	(2)	(0)	(13)	(0)
120	-	0.017	0.000	-	-	0.000	0.000	-	0.000	-	0.000	-
100	-	0.983	1.000	-	-	1.000	1.000	-	1.000	-	1.000	-
80	-	0.000	0.000	-	-	0.000	0.000	-	0.000	-	0.000	-
Fis												
Me-1	(27)	(36)	(21)	(16)	(16)	(10)	(26)	(16)	(18)	(20)	(29)	(30)
110	0.000	0.000	0.000	0.000	0.000	0.000	0.038	0.000	0.000	0.000	0.000	0.000
100	1.000	1.000	0.952	1.000	1.000	1.000	0.962	1.000	1.000	1.000	1.000	1.000
90	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(90 = 80 in Schaffner et al., 2000)												
Fis	-	-	−0.0256	-	-	-	−0.0204	-	-	-	-	-
Mpi	(3)	(28)	(19)	(4)	(13)	(17)	(23)	(11)	(17)	(5)	(28)	(28)
120	0.000	0.186	0.000	0.143	0.000	0.000	0.069	0.000	0.000	0.000	0.310	0.064
100	0.600	0.721	0.889	0.429	0.870	0.964	0.690	0.750	0.815	1.000	0.643	0.872
90	0.400	0.093	0.111	0.286	0.130	0.036	0.241	0.250	0.148	0.000	0.000	0.000
80	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.037	0.000	0.048	0.064
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	−1.0000	0.0200	0.0000	0.2727	−0.0588	0.0000	0.6429	0.6000	−0.1429	-	−0.1751	0.3571
Pgi	(28)	(36)	(29)	(16)	(29)	(13)	(35)	(28)	(29)	(21)	(9)	(30)
110	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
100	0.661	0.681	0.655	0.844	0.672	0.692	0.529	0.750	0.552	0.548	1.000	0.817
90	0.196	0.292	0.293	0.125	0.293	0.308	0.429	0.214	0.397	0.310	0.000	0.167
80	0.143	0.014	0.052	0.031	0.034	0.000	0.043	0.036	0.052	0.143	0.000	0.017
60	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	−0.3290	−0.2794	−0.2711	−0.1194	−0.4074	−0.4118	0.0000	−0.2642	0.1161	0.0457	-	0.0333
Pgm	(28)	(35)	(25)	(16)	(19)	(18)	(33)	(20)	(22)	(20)	(29)	(30)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.034	0.000
110	0.000	0.029	0.040	0.031	0.000	0.000	0.015	0.000	0.068	0.025	0.034	0.067
100	0.518	0.614	0.540	0.500	0.368	0.667	0.364	0.600	0.568	0.325	0.897	0.867
90	0.482	0.343	0.340	0.438	0.605	0.333	0.545	0.400	0.364	0.625	0.000	0.050
80	0.000	0.014	0.080	0.031	0.026	0.000	0.076	0.000	0.000	0.000	0.034	0.017
Fis	0.0883	0.1639	−0.2118	0.3548	−0.1379	−0.2230	0.0487	−0.0160	0.1813	−0.1692	−0.0566	−0.0867
Fis All loci	**−0.1435**	**−0.0897**	**−0.1840**	**0.0369**	**−0.1580**	**−0.2306**	**−0.1111**	**−0.0259**	**0.0090**	**−0.1418**	**−0.1890**	**−0.0047**

Populations											
II-C	II-D	II-E	II-F	II-G	II-H	II-J	II-K	II-L	II-M	II-N	II-O
(10)	(54)	(29)	(194)	(30)	(31)	(47)	(11)	(10)	(30)	(31)	(30)
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.050	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.050	0.000	0.000	0.000
0.950	1.000	1.000	0.995	1.000	0.984	1.000	1.000	0.950	1.000	1.000	0.983
0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
0.0000	-	-	−0.0026	-	0.0000	-	-	0.0000	-	-	0.0000
(19)	(41)	(28)	(163)	(30)	(29)	(42)	(19)	(22)	(28)	(30)	(23)
0.000	0.012	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.012	0.036	0.049	0.033	0.034	0.012	0.000	0.000	0.000	0.033	0.043
0.947	0.939	0.929	0.920	0.933	0.897	0.988	1.000	0.932	0.946	0.933	0.935
0.026	0.037	0.036	0.003	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.022
0.026	0.000	0.000	0.028	0.033	0.052	0.000	0.000	0.045	0.054	0.033	0.000
−0.0141	−0.0336	−0.0385	−0.0606	−0.0357	−0.0599	0.0000	-	−0.0328	−0.0385	−0.0357	−0.0312
(18)	(42)	(31)	(166)	(30)	(29)	(46)	(22)	(27)	(29)	(31)	(25)
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	0.012	0.016	0.036	0.033	0.000	0.011	0.091	0.000	0.069	0.016	0.000
0.778	0.690	0.871	0.801	0.833	0.776	0.837	0.773	0.870	0.810	0.806	0.720
0.167	0.262	0.081	0.081	0.083	0.103	0.054	0.091	0.093	0.103	0.129	0.200
0.056	0.036	0.032	0.081	0.050	0.103	0.098	0.045	0.037	0.017	0.048	0.080
0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000
-0.0393	0.0139	−0.0884	−0.1544	0.0000	0.0096	0.0258	−0.1602	−0.0964	0.0701	−0.0577	−0.0827
(3)	(17)	(30)	(106)	(30)	(31)	(7)	(5)	(4)	(25)	(0)	(10)
0.000	0.029	0.017	0.005	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000
1.000	0.971	0.967	0.986	1.000	1.000	1.000	1.000	1.000	1.000	-	1.000
0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000
0.000	0.000	0.017	0.005	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000
-	0.0000	−0.0087	−0.0048	-	-	-	-	-	-	-	-
(1)	(11)	(31)	(93)	(30)	(30)	(2)	(0)	(0)	(24)	(6)	(8)
0.000	0.000	0.000	0.022	0.000	0.067	0.000	-	-	0.021	0.000	0.000
1.000	0.909	1.000	0.962	0.967	0.883	1.000	-	-	0.979	1.000	1.000
0.000	0.091	0.000	0.016	0.033	0.033	0.000	-	-	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.017	0.000	-	-	0.000	0.000	0.000
-	−0.0526	-	−0.0238	−0.0175	−0.0741	-	-	-	0.0000	-	-
(9)	(54)	(30)	(182)	(30)	(31)	(49)	(19)	(15)	(30)	(18)	(30)
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	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1.000	1.000	1.000	0.997	0.983	1.000	0.990	0.974	0.967	0.967	1.000	1.000
0.000	0.000	0.000	0.003	0.017	0.000	0.010	0.026	0.033	0.033	0.000	0.000
-	-	-	0.0000	0.0000	-	0.0000	0.0000	0.0000	−0.0175	-	-
(0)	(23)	(29)	(76)	(18)	(24)	(27)	(0)	(0)	(23)	(3)	(18)
-	0.043	0.000	0.033	0.028	0.042	0.056	-	-	0.022	0.000	0.028
-	0.957	1.000	0.967	0.972	0.938	0.944	-	-	0.978	1.000	0.972
-	0.000	0.000	0.000	0.000	0.021	0.000	-	-	0.000	0.000	0.000
-	−0.0233	-	−0.0274	0.0000	−0.0298	−0.0400	-	-	0.0000	-	0.0000
(0)	(18)	(27)	(39)	(12)	(16)	(17)	(0)	(0)	(15)	(0)	(13)
-	0.000	0.000	0.000	0.000	0.000	0.000	-	-	0.000	-	0.000
-	1.000	1.000	1.000	1.000	0.969	1.000	-	-	1.000	-	0.962
-	0.000	0.000	0.000	0.000	0.031	0.000	-	-	0.000	-	0.038
(13)	(32)	(31)	(153)	(30)	(31)	(23)	(20)	(19)	(30)	(20)	(22)
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1.000	0.984	1.000	0.993	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.977
0.000	0.016	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023
-	0.0000	-	−0.0033	-	-	-	-	-	-	-	0.0000
(0)	(42)	(26)	(93)	(23)	(24)	(42)	(0)	(0)	(22)	(16)	(19)
-	0.086	0.140	0.115	0.273	0.159	0.185	-	-	0.324	0.269	0.148
-	0.857	0.767	0.851	0.697	0.773	0.796	-	-	0.647	0.692	0.815
-	0.029	0.023	0.000	0.000	0.045	0.000	-	-	0.000	0.038	0.000
-	0.029	0.070	0.020	0.030	0.023	0.019	-	-	0.029	0.000	0.037
-	0.000	0.000	0.014	0.000	0.000	0.000	-	-	0.000	0.000	0.000
-	−0.0992	0.0588	−0.0969	0.1000	0.0732	−0.1702	-	-	−0.1324	0.5325	−0.2727
(20)	(53)	(29)	(155)	(30)	(31)	(38)	(26)	(28)	(26)	(31)	(30)
0.000	0.000	0.000	0.000	0.000	0.016	0.013	0.000	0.000	0.000	0.000	0.000
0.800	0.821	0.914	0.861	0.850	0.823	0.803	0.827	0.768	0.885	0.887	0.817
0.175	0.179	0.086	0.135	0.117	0.145	0.171	0.173	0.232	0.115	0.113	0.183
0.025	0.000	0.000	0.003	0.033	0.016	0.013	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	0.000	0.000	0.000
-0.1922	0.1756	−0.0769	−0.0998	0.1288	−0.1599	−0.1974	0.0789	−0.2857	−0.1111	−0.1111	0.0151
(19)	(51)	(32)	(169)	(30)	(31)	(44)	(29)	(30)	(30)	(28)	(29)
0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.034
0.158	0.039	0.141	0.056	0.133	0.113	0.057	0.155	0.083	0.017	0.036	0.034
0.789	0.902	0.781	0.914	0.817	0.855	0.932	0.793	0.883	0.900	0.839	0.897
0.026	0.059	0.000	0.015	0.017	0.016	0.011	0.034	0.017	0.067	0.054	0.017
0.026	0.000	0.078	0.015	0.017	0.016	0.000	0.017	0.017	0.017	0.071	0.017
−0.1755	0.1453	−0.1874	−0.0653	−0.1496	−0.1180	−0.0509	−0.1810	−0.0827	−0.0642	0.3919	−0.0533
−0.1745	**0.0145**	**−0.1020**	**−0.1582**	**−0.0941**	**−0.0547**	**−0.2576**	**−0.1259**	**−0.2334**	**−0.1181**	**0.0528**	**−0.1104**

Appendix. Continued

	Populations											
	II-P	II-Q	II-R	II-S	II-T	II-U	II-V	II-W	II-X	II-Y	II-Z	II-ZA
Locus												
aGpd	(30)	(31)	(19)	(28)	(57)	(37)	(22)	(31)	(30)	(19)	(8)	(19)
140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
120	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
100	0.983	1.000	1.000	1.000	1.000	0.986	1.000	1.000	1.000	1.000	1.000	1.000
80	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000
Fis	0.0000	-	-	-	-	0.0000	-	-	-	-	-	-
Est-2	(30)	(26)	(15)	(26)	(56)	(38)	(21)	(29)	(28)	(5)	(8)	(17)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.033	0.058	0.033	0.058	0.054	0.039	0.000	0.000	0.000	0.000	0.000	0.029
100	0.950	0.923	0.900	0.904	0.920	0.921	0.976	0.879	0.911	1.000	1.000	0.941
90	0.017	0.019	0.033	0.000	0.018	0.000	0.024	0.034	0.018	0.000	0.000	0.029
80	0.000	0.000	0.033	0.038	0.009	0.039	0.000	0.086	0.071	0.000	0.000	0.000
Fis	−0.0235	−0.0471	−0.0370	−0.0593	−0.0554	−0.0496	0.0000	−0.0889	−0.0630	-	-	−0.0159
Est-3	(30)	(28)	(16)	(26)	(56)	(37)	(22)	(30)	(28)	(7)	(8)	(18)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.033	0.054	0.000	0.000	0.027	0.014	0.045	0.033	0.054	0.000	0.063	0.028
100	0.900	0.768	0.906	0.827	0.786	0.811	0.750	0.783	0.786	1.000	0.688	0.861
90	0.067	0.125	0.094	0.115	0.116	0.108	0.114	0.133	0.089	0.000	0.188	0.056
80	0.000	0.054	0.000	0.058	0.071	0.054	0.091	0.050	0.071	0.000	0.063	0.056
70	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000
Fis	−0.0675	−0.1759	−0.0714	−0.1364	−0.1707	−0.1416	−0.1846	−0.1708	−0.1510	-	0.2881	−0.0759
Got-1	(28)	(16)	(12)	(21)	(9)	(22)	(9)	(4)	(6)	(26)	(4)	(11)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000
100	1.000	1.000	1.000	1.000	0.889	1.000	1.000	1.000	1.000	0.981	1.000	1.000
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	-	-	-	-	−0.0667	-	-	-	-	0.0000	-	-
Got-2	(28)	(20)	(14)	(21)	(9)	(22)	(8)	(12)	(21)	(23)	(1)	(5)
120	0.000	0.000	0.000	0.000	0.056	0.000	0.000	0.000	0.000	0.000	0.000	0.000
100	1.000	0.975	1.000	0.976	0.944	1.000	1.000	1.000	1.000	1.000	1.000	1.000
80	0.000	0.025	0.000	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	-	0.0000	-	0.0000	0.0000	-	-	-	-	-	-	-
Hk-1	(30)	(31)	(16)	(28)	(57)	(38)	(22)	(12)	(14)	(25)	(5)	(19)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.000	0.000	0.000	0.018	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000
100	1.000	1.000	1.000	0.982	0.982	0.987	1.000	0.958	1.000	1.000	1.000	1.000
80	0.000	0.000	0.000	0.000	0.018	0.013	0.000	0.000	0.000	0.000	0.000	0.000
Fis	-	-	-	0.0000	−0.0090	0.0000	-	0.0000	-	-	-	-
Idh-1	(26)	(12)	(11)	(8)	(16)	(9)	(9)	(7)	(1)	(16)	(0)	(10)
110	0.077	0.042	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.000	-	0.100
100	0.923	0.958	1.000	0.938	0.969	1.000	1.000	1.000	1.000	0.969	-	0.900
90	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.031	-	0.000
Fis	−0.0638	0.0000	-	0.0000	0.0000	-	-	-	-	0.0000	-	−0.0588
Idh-2	(26)	(3)	(6)	(1)	(14)	(8)	(7)	(0)	(0)	(6)	(0)	(8)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	-	0.000	-	0.000
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	1.000	-	1.000
80	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	-	0.000	-	0.000
Fis												
Me-1	(30)	(26)	(19)	(27)	(14)	(29)	(21)	(25)	(28)	(25)	(7)	(16)
110	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(90 = 80 in Schaffner et al., 2000)												
Fis	-	-	-	-	-	-	-	-	-	-	-	-
Mpi	(26)	(25)	(11)	(24)	(39)	(37)	(20)	(7)	(6)	(9)	(1)	(13)
120	0.281	0.118	0.133	0.190	0.163	0.172	0.161	0.000	0.111	0.231	0.000	0.318
100	0.625	0.794	0.867	0.714	0.837	0.828	0.839	1.000	0.889	0.769	1.000	0.682
90	0.000	0.088	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
80	0.094	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	0.7059	−0.1429	0.0000	0.2067	−0.1250	−0.2121	0.4286	-	-	1.0000	-	−0.6000
Pgi	(30)	(31)	(19)	(28)	(43)	(36)	(19)	(29)	(26)	(7)	(9)	(18)
110	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.071	0.000	0.000
100	0.883	0.806	0.895	0.875	0.802	0.875	0.921	0.810	0.885	0.786	0.889	0.889
90	0.117	0.177	0.105	0.125	0.174	0.125	0.053	0.172	0.096	0.071	0.111	0.111
80	0.000	0.016	0.000	0.000	0.012	0.000	0.026	0.017	0.019	0.071	0.000	0.000
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fis	−0.1154	−0.2020	−0.0909	−0.1250	−0.0597	−0.1290	−0.0385	−0.1938	−0.0909	−0.0909	−0.0667	−0.0968
Pgm	(30)	(28)	(18)	(28)	(40)	(37)	(22)	(28)	(24)	(7)	(10)	(18)
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.028
110	0.183	0.018	0.139	0.089	0.013	0.068	0.114	0.161	0.042	0.214	0.100	0.028
100	0.750	0.839	0.778	0.857	0.962	0.905	0.864	0.768	0.813	0.786	0.850	0.861
90	0.050	0.071	0.000	0.018	0.025	0.027	0.023	0.054	0.104	0.000	0.000	0.056
80	0.017	0.071	0.083	0.036	0.000	0.000	0.000	0.018	0.021	0.000	0.050	0.028
Fis	−0.2306	−0.1096	0.1245	−0.0992	−0.0174	−0.0678	−0.1101	−0.0119	0.3801	0.6250	−0.0800	0.3665
Fis All loci	**−0.1989**	**−0.2388**	**−0.1352**	**−0.0462**	**−0.2720**	**−0.1511**	**−0.1115**	**−0.1360**	**−0.0730**	**−0.0113**	**−0.0747**	**−0.0892**

Populations											
II-ZB	II-ZC	II-ZD	II-ZE	II-ZF	II-ZG	II-ZH	II-ZJ	II-ZK	II-ZL	X-A	All Pop.
(32)	(20)	(11)	(30)	(6)	(30)	(30)	(28)	(24)	(0)	(30)	
0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	-	0.000	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.017	
1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000	1.000	-	0.983	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	
-	-	-	-	-	-	0.0000	-	-	-	0.0000	**−0.0005**
(27)	(20)	(19)	(30)	(7)	(12)	(30)	(10)	(0)	(6)	(23)	
0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	0.000	
0.019	0.025	0.000	0.033	0.071	0.042	0.050	0.150	-	0.000	0.000	
0.852	0.900	0.974	0.900	0.929	0.958	0.933	0.850	-	1.000	0.957	
0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	-	0.000	0.022	
0.130	0.050	0.026	0.067	0.000	0.000	0.000	0.000	-	0.000	0.022	
−0.1335	−0.0483	0.0000	−0.0675	0.0000	0.0000	−0.0404	−0.1250	-	-	−0.0115	**−0.0734**
(30)	(23)	(19)	(30)	(10)	(13)	(30)	(15)	(0)	(7)	(25)	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	0.000	
0.033	0.022	0.000	0.033	0.050	0.115	0.033	0.033	-	0.071	0.080	
0.767	0.761	0.816	0.867	0.750	0.808	0.783	0.833	-	0.857	0.800	
0.083	0.174	0.158	0.100	0.100	0.077	0.083	0.100	-	0.071	0.020	
0.117	0.043	0.026	0.000	0.100	0.000	0.100	0.033	-	0.000	0.100	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	0.000	
−0.0928	0.0149	−0.1667	0.0356	−0.1538	0.3333	−0.1600	0.1250	-	−0.0435	0.0879	**−0.0631**
(32)	(18)	(19)	(30)	(4)	(35)	(17)	(29)	(24)	(8)	(16)	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	
1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000	1.000	0.938	
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	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	
-	-	-	-	-	-	-	0.0000	-	-	−0.0345	**−0.0201**
(32)	(14)	(8)	(30)	(0)	(24)	(14)	(12)	(24)	(5)	(19)	
0.000	0.000	0.000	0.000	-	0.000	0.000	0.042	0.000	0.100	0.026	
0.969	0.964	1.000	1.000	-	1.000	1.000	0.958	1.000	0.900	0.947	
0.031	0.036	0.000	0.000	-	0.000	0.000	0.000	0.000	0.000	0.026	
0.000	0.000	0.000	0.000	-	0.000	0.000	0.000	0.000	0.000	0.000	
−0.0164	0.0000	-	-	-	-	-	0.0000	-	0.0000	−0.0141	**−0.0308**
(31)	(21)	(19)	(30)	(5)	(43)	(30)	(29)	(23)	(8)	(30)	
0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	
0.016	0.024	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.125	0.000	
0.968	0.976	1.000	0.967	1.000	0.988	0.983	1.000	1.000	0.875	0.983	
0.016	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.017	
−0.0084	0.0000	-	−0.0175	-	0.0000	0.0000	-	-	−0.0769	0.0000	**−0.0096**
(20)	(0)	(8)	(25)	(1)	(11)	(16)	(23)	(8)	(2)	(13)	
0.050	-	0.063	0.080	0.000	0.000	0.125	0.022	0.063	0.000	0.077	
0.950	-	0.938	0.920	1.000	1.000	0.875	0.957	0.938	1.000	0.923	
0.000	-	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	
−0.0270	-	0.0000	−0.0667	-	-	−0.1111	−0.0115	0.0000	-	−0.0435	**−0.0455**
(0)	(0)	(8)	(25)	(0)	(10)	(11)	(0)	(0)	(4)	(1)	
-	-	0.000	0.000	-	0.000	0.045	-	-	0.000	0.000	
-	-	1.000	1.000	-	1.000	0.909	-	-	1.000	1.000	
-	-	0.000	0.000	-	0.000	0.045	-	-	0.000	0.000	
											−0.0101
(26)	(13)	(19)	(30)	(5)	(6)	(30)	(30)	(23)	(8)	(29)	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
1.000	1.000	0.974	0.983	1.000	1.000	1.000	0.983	0.978	1.000	0.983	
0.000	0.000	0.026	0.017	0.000	0.000	0.000	0.017	0.022	0.000	0.017	
(90 = 80 in Schaffner et al., 2000)											
-	-	0.0000	0.0000	-	-	-	0.0000	0.0000	-	0.0000	**−0.0075**
(25)	(8)	(11)	(25)	(1)	(0)	(14)	(9)	(22)	(0)	(22)	
0.077	0.091	0.133	0.211	0.000	-	0.286	0.250	0.139	-	0.139	
0.923	0.909	0.800	0.763	1.000	-	0.714	0.667	0.833	-	0.750	
0.000	0.000	0.000	0.026	0.000	-	0.000	0.000	0.000	-	0.056	
0.000	0.000	0.067	0.000	0.000	-	0.000	0.083	0.028	-	0.056	
0.000	0.000	0.000	0.000	0.000	-	0.000	0.000	0.000	-	0.000	
−0.0833	-	0.0000	0.3143	-	-	−0.2000	1.0000	−0.1404	-	−0.1404	**0.0481**
(26)	(15)	(19)	(30)	(9)	(35)	(20)	(20)	(0)	(8)	(30)	
0.000	0.000	0.000	0.000	0.000	0.014	0.025	0.000	-	0.125	0.000	
0.731	0.733	0.816	0.983	0.556	0.743	0.800	0.800	-	0.563	0.817	
0.250	0.233	0.158	0.017	0.444	0.214	0.175	0.175	-	0.313	0.183	
0.019	0.033	0.026	0.000	0.000	0.029	0.000	0.025	-	0.000	0.000	
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	0.000	
−0.3183	−0.2800	−0.1667	0.0000	−0.7778	0.0175	0.1128	−0.1922	-	−0.4848	0.0151	**−0.1248**
(32)	(16)	(19)	(30)	(10)	(31)	(29)	(5)	(0)	(4)	(30)	
0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	-	0.000	0.000	
0.016	0.188	0.026	0.200	0.000	0.113	0.121	0.300	-	0.250	0.033	
0.969	0.781	0.947	0.750	0.900	0.742	0.759	0.700	-	0.625	0.683	
0.016	0.031	0.026	0.033	0.050	0.129	0.103	0.000	-	0.125	0.217	
0.000	0.000	0.000	0.017	0.050	0.000	0.017	0.000	-	0.000	0.067	
−0.0081	0.1477	−0.0141	−0.1617	−0.0286	0.0943	−0.1933	−0.3333	-	−0.2857	0.0458	**−0.0158**
−0.1635	**−0.0965**	**−0.1468**	**−0.0741**	**−0.3171**	**−0.0701**	**−0.1626**	**−0.1087**	**−0.1783**	**−0.2506**	**−0.0199**	