

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/237184409>

# Identification of the Great Lakes Quagga Mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the Basis of Allozyme Variation

Article in *Canadian Journal of Fisheries and Aquatic Sciences* · April 2011

DOI: 10.1139/f94-148

CITATIONS

71

READS

38

3 authors, including:



J. Ellen Marsden

University of Vermont

135 PUBLICATIONS 3,055 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Reef Restoration in Thunder Bay, Lake Huron, Michigan [View project](#)



Downstream Migration of Juvenile Sea Lamprey [View project](#)

# Identification of the Great Lakes Quagga Mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the Basis of Allozyme Variation

Adrian P. Spidle

Genome Variation Analysis Facility, Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA

J. Ellen Marsden

Illinois Natural History Survey, Lake Michigan Biological Station, 400 17th Street, Zion, IL 60099, USA

and Bernie May

Genome Variation Analysis Facility, Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA

Spidle, A.P., J.E. Marsden, and B. May. 1994. Identification of the Great Lakes quagga mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the basis of allozyme variation. *Can. J. Fish. Aquat. Sci.* 51: 1485–1489.

The discovery of a second dreissenid species, the quagga mussel, in the Great Lakes in 1991 prompted a search for its identity. We have identified the North American quagga mussel as *Dreissena bugensis* Andrusov on the basis of allozyme data and morphological characters. Further, a phenotypically distinct form of the quagga mussel found in Lakes Erie and Ontario also matches the electrophoretic profiles of the typical Lake Ontario quagga and European *D. bugensis*. We confirm that the white "profunda" mussel found in the deep waters of Lake Erie is a phenotype of the quagga mussel, and we conclude that the quagga mussel is *D. bugensis* which has been introduced from the Black Sea drainage of Ukraine.

La découverte en 1991 dans les Grands Lacs d'une deuxième espèce de dreissena, la moule quagga, a déclenché des recherches visant à préciser son identité. Sur la base de ses caractères morphologiques et des données relatives aux allozymes, nous avons identifié la moule quagga d'Amérique du Nord à l'espèce *Dreissena bugensis* Andrusov. Par ailleurs, une forme distincte sur le plan phénotypique de la moule quagga, que l'on retrouve dans les lacs Érié et Ontario, présente les mêmes profils électrophorétiques que celui de la moule quagga caractéristique du Lac Ontario et de la moule *D. bugensis*. Nous confirmons que la moule blanche des eaux profondes du Lac Érié est un phénotype de la moule quagga et nous concluons que la moule quagga appartient à l'espèce *D. bugensis*, qui a été introduite par le biais des eaux de la mer Noire, en Ukraine.

Received July 30, 1993

Accepted February 23, 1994

(JC030)

Reçu le 30 juillet 1993

Accepté le 23 février 1994

The Laurentian Great Lakes have been subject to invasion by an increasing number of exotic species (Mills et al. 1993b). Few of these exotic species have led to immediately detectable effects on the ecosystem of the Great Lakes basin. A notable exception is the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). It has affected food web interactions in the lakes (Hebert et al. 1991; Griffiths 1993) and also impacted industry by fouling water intake pipes along the lake shores. The quagga mussel, a second dreissenid species recently discovered Great Lakes (May and Marsden 1992), is likely to have additional, as yet unknown effects on North American ecosystems.

It has been difficult to acquire insight into the potential impact of the quagga mussel in North America because its identity is not yet known (May and Marsden 1992). Taxonomic identification of an invading species is critical for predicting the implications of its arrival in a new habitat. The lack of information about the characteristics of the quagga in its home range leaves no option but to determine its traits empirically. Preliminary studies on the quagga in the Great Lakes have indicated that it is clearly a species distinct from *D. polymorpha* (May and Marsden 1992) and that they

do not interbreed in nature (Spidle et al., unpublished data). The quagga ranges from central Lake Erie to Quebec City on the St. Lawrence River and tends to inhabit deeper areas than the zebra mussel (Mills et al. 1993a). These data plus unpublished studies suggest that quagga and zebra mussels differ in their tolerance of temperature and salinity. The presence of the quagga is also associated with a possibly drastic change in the benthic community of Lake Erie (Dermott and Munawar 1993).

Sympatrically collected quagga and zebra mussels are morphologically distinct, as shown by comparison of samples collected in the upper St. Lawrence River (Fig. 1). Both species have a pointed anterior and a flared posterior end. The zebra mussel has a carina, a sharp angle between the side of the valve and a flat ventral surface, while the quagga is acarinate, with the valve curving into a rounded ventral surface. The identification of the quagga is complicated by the observation of a distinct *Dreissena* phenotype found in certain deep sections of Lakes Erie and Ontario, which has been termed "profunda" (Dermott and Munawar 1993). While Lake Ontario and St. Lawrence quagga mussels closely resemble *D. bugensis* from the Dnieper River,

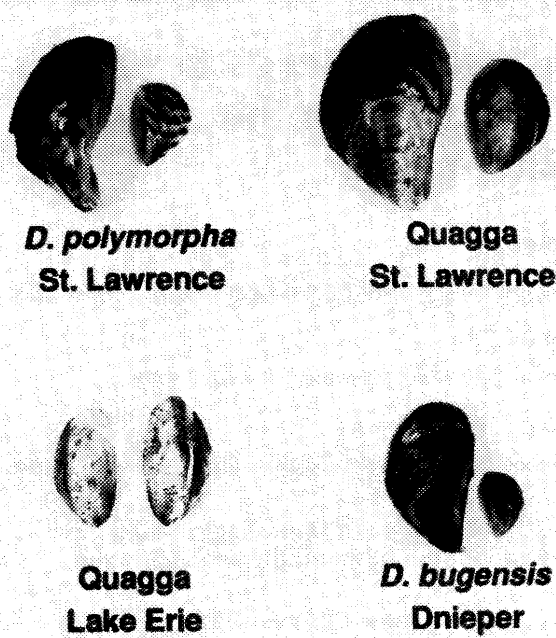


FIG. 1. Valves from samples of zebra and quagga mussels from the upper St. Lawrence River, the "profunda" phenotype of quagga from Lake Erie, and *D. bugensis* from the Dnieper River, Ukraine.

Ukraine, neither of these forms is very similar to the phenotype found in profundal zones of Lake Erie, which is most readily distinguished by its lack of a flaring posterior and its predominantly white coloration (Fig. 1). This paper reports the results of a study designed (1) to clarify the relationship between the quagga mussel and *D. bugensis* and (2) to determine if the "profunda" phenotype is indeed a third distinct species of *Dreissena* in the Great Lakes.

## Methods

### Sample Collection

A previously identified quagga mussel population was sampled by bottom trawling in the harbor of Cape Vincent, N.Y. (at the head of the St. Lawrence River). The "profunda" phenotype was collected by bottom trawling in south-eastern Lake Erie. Two samples were obtained from the Dnieper River. The first sample, labeled "*D. polymorpha*", was collected in the Kakhovka Reservoir on the Dnieper River. They were received dissected, with their shells discarded. The second sample was composed of *D. bugensis* collected from Kherson near the mouth of the Dnieper River. These latter samples were preserved in ethanol and therefore were unavailable for protein electrophoresis. All other samples were packed on dry ice and shipped overnight to the Genome Variation Analysis Facility, where they were stored at  $-70^{\circ}\text{C}$  until processed for electrophoresis.

### Electrophoresis

Extracts of whole-body tissue and one valve were prepared, and the other valve from each animal, the Kakhovka Reservoir population excepted, was archived. Horizontal starch gel electrophoresis, histochemical staining, and banding pattern interpretation were carried out according to May (1992). Gene nomenclature for protein coding loci follows

Shaklee et al., (1990). Individual zebra mussels from a population with known allele frequencies (Marsden et al. unpublished data.) were placed immediately adjacent to individuals from each population of quagga mussel to act as a standard reference for the scoring process. Eleven loci were scored. Four of these were polymorphic in the quagga mussel, i.e., the most common allele had a frequency less than 0.95 (Hartl and Clark 1989): glucose-6-phosphate isomerase 5.3.1.9 (*GPI\**), isocitrate dehydrogenase 1.1.1.42 (*IDH\**), phosphogluconate dehydrogenase 1.1.1.44 (*PGDH\**), and Triose-phosphate isomerase 5.3.1.1 (*TPI\**). The seven monomorphic loci were diaphorase 1.6.2.2 (*DIA\**), formaldehyde dehydrogenase 1.2.1.1 (*FDH\**), glyceraldehyde-3-phosphate dehydrogenase 1.2.1.12 (*GAPDH\**), malate dehydrogenase 1.1.1.37 (*MDH1,2\**), phosphoglucomutase 5.4.2.2 (*PGM1\**), and inorganic pyrophosphatase 3.6.1.1 (*PP\**). May and Marsden (1992) also used esterase 3.1.1.1 but this protein could not be reliably scored in the Ukrainian samples, presumably due to protein degradation from the length of time these samples had been stored.

### Analysis

Sample sizes of 10 mussels from each North American population and 22 from the Kakhovka Reservoir population were chosen to ensure a reliable estimate of the genetic distance between the groups of mussels (Gorman and Renzi 1979). The software package "Genes in populations", designed by B. May and C.C. Krueger and written in C by W. Eng, was used for data analysis. Nei's genetic distance (Nei 1972) was calculated and used to construct a dendrogram by the UPGMA method. Allele frequency data from one quagga and four zebra mussel populations were used to provide reference points to demonstrate relatedness between putative quagga populations from Ukraine and Lake Erie, the known quagga population from the St. Lawrence River, and previously examined populations of zebra and quagga mussels. The zebra mussel populations were taken from Lakes Ontario and Erie as well as two sites in The Netherlands: the River Meuse near Roermond and IJsselmeer near Enkhuizerzand. The quagga mussel population was from Lake Ontario near Rochester, N.Y. (May and Marsden 1992).

## Results

Analysis of data from 11 allozyme loci indicates that the quagga mussel has the same genetic characteristics as *D. bugensis* and that they both match the Lake Erie deepwater phenotype. Allele frequencies and heterozygosity are both highly similar within, but not between, the quagga and zebra mussel populations (Table 1). The quagga mussel has one third the mean heterozygosity of the zebra mussel. The North American quagga mussel and the European *D. bugensis* match at those loci that are diagnostic between zebra and quagga mussels (*PP\**, *PGM1\**, and *MDH1\**). At the two loci that are the most variable in each species the common allele for the quagga is essentially absent in the zebra mussel (*GPI\*83* and *TPI\*88*). For seven loci that are polymorphic in the zebra mussel, the common allele is absent in the quagga (*DIA\*100*, *FDH\*100*, *MDH1\*100*, *MDH2\*100*, *PGDH\*100*, *PGM1\*100*, and *TPI\*100*).

The UPGMA dendrogram of Nei's genetic distances (Fig. 2) shows that the two putative and two known quagga mussel populations cluster together at a very short genetic dis-

TABLE 1. Allele frequencies at 11 allozyme loci in four quagga and four zebra mussel populations.

Locus	Allele	Quagga mussel				Zebra mussel			
		Kakhovka Reservoir	St. Lawrence	Lake Erie	Lake Ontario	Lake Erie	Lake Ontario	Ijsselmeer	River Meuse
<i>N</i>		22	10	10	21	243	158	40	40
<i>MDH2*</i>	100	0.000	0.000	0.000	0.000	0.864	0.894	0.897	0.936
	140	1.000	1.000	1.000	1.000	0.136	0.106	0.103	0.064
<i>MDH1*</i>	77	0.000	0.000	0.000	0.000	0.002	0.010	0.000	0.000
	100	0.000	0.000	0.000	0.000	0.591	0.587	0.679	0.808
	120	0.000	0.000	0.000	0.000	0.407	0.403	0.321	0.192
	122	1.000	1.000	1.000	1.000	0.000	0.000	0.000	0.000
<i>PGM1*</i>	88	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000
	96	0.000	0.000	0.000	0.000	0.002	0.004	0.000	0.000
	100	0.000	0.000	0.000	0.000	0.893	0.905	0.949	0.947
	107	1.000	1.000	0.950	1.000	0.002	0.004	0.000	0.000
	111	0.000	0.000	0.050	0.000	0.101	0.088	0.051	0.053
<i>IDH*</i>	91	0.091	0.000	0.100	0.100	0.306	0.293	0.692	0.667
	100	0.909	1.000	0.900	0.900	0.694	0.703	0.308	0.333
	114	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000
<i>TPI*</i>	52	0.091	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	69	0.136	0.150	0.250	0.176	0.027	0.125	0.000	0.000
	86	0.023	0.050	0.050	0.088	0.000	0.000	0.000	0.000
	88	0.750	0.750	0.700	0.735	0.000	0.000	0.000	0.000
	100	0.000	0.000	0.000	0.000	0.683	0.566	0.513	0.551
	112	0.000	0.050	0.000	0.000	0.012	0.003	0.013	0.000
	115	0.000	0.000	0.000	0.000	0.259	0.293	0.474	0.449
	121	0.000	0.000	0.000	0.000	0.019	0.013	0.000	0.000
<i>DIA*</i>	0	0.000	0.000	0.000	0.000	0.013	0.014	0.000	0.000
	100	0.000	0.000	0.000	0.000	0.623	0.683	0.973	0.969
	150	0.000	0.000	0.000	0.000	0.164	0.151	0.000	0.000
	160	0.000	0.100	0.000	0.000	0.030	0.018	0.000	0.000
	190	0.000	0.000	0.000	0.000	0.039	0.004	0.000	0.000
	200	1.000	0.900	1.000	1.000	0.131	0.130	0.027	0.031
<i>GPI*</i>	-21	0.000	0.000	0.000	0.000	0.002	0.013	0.000	0.000
	50	0.000	0.000	0.000	0.024	0.017	0.013	0.013	0.000
	83	0.405	0.450	0.600	0.619	0.006	0.000	0.000	0.000
	100	0.000	0.000	0.000	0.000	0.297	0.331	0.329	0.395
	121	0.071	0.100	0.100	0.000	0.008	0.000	0.000	0.000
	146	0.190	0.050	0.000	0.000	0.488	0.433	0.447	0.421
	188	0.024	0.050	0.000	0.000	0.004	0.006	0.000	0.013
	196	0.310	0.350	0.300	0.357	0.176	0.191	0.211	0.171
	208	0.000	0.000	0.000	0.000	0.002	0.013	0.000	0.000
	<i>PGDH*</i>	100	0.000	0.000	0.000	0.000	0.924	0.877	0.671
108		0.000	0.000	0.000	0.033	0.000	0.073	0.132	0.000
123		0.958	0.950	0.900	0.967	0.074	0.050	0.197	0.447
130		0.000	0.000	0.050	0.000	0.002	0.000	0.000	0.000
165		0.042	0.050	0.050	0.000	0.000	0.000	0.000	0.000
<i>GAPDH*</i>	97	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000
	100	1.000	1.000	1.000	1.000	0.701	0.578	0.359	0.244
	123	0.000	0.000	0.000	0.000	0.297	0.422	0.641	0.756
<i>FDH*</i>	94	1.000	1.000	1.000	0.975	0.141	0.110	0.114	0.176
	100	0.000	0.000	0.000	0.025	0.859	0.890	0.886	0.824
<i>PP*</i>	80	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000
	100	0.000	0.000	0.000	0.000	1.000	1.000	0.988	1.000
	110	1.000	1.000	1.000	1.000	0.000	0.000	0.000	0.000
Average $H_s$		0.123	0.122	0.131	0.109	0.347	0.356	0.321	0.302
SE		0.069	0.066	0.058	0.054	0.060	0.063	0.065	0.063
Average $H_0$		0.101	0.127	0.145	0.106	0.341	0.325	0.291	0.291
SE		0.068	0.081	0.065	0.059	0.058	0.061	0.062	0.065

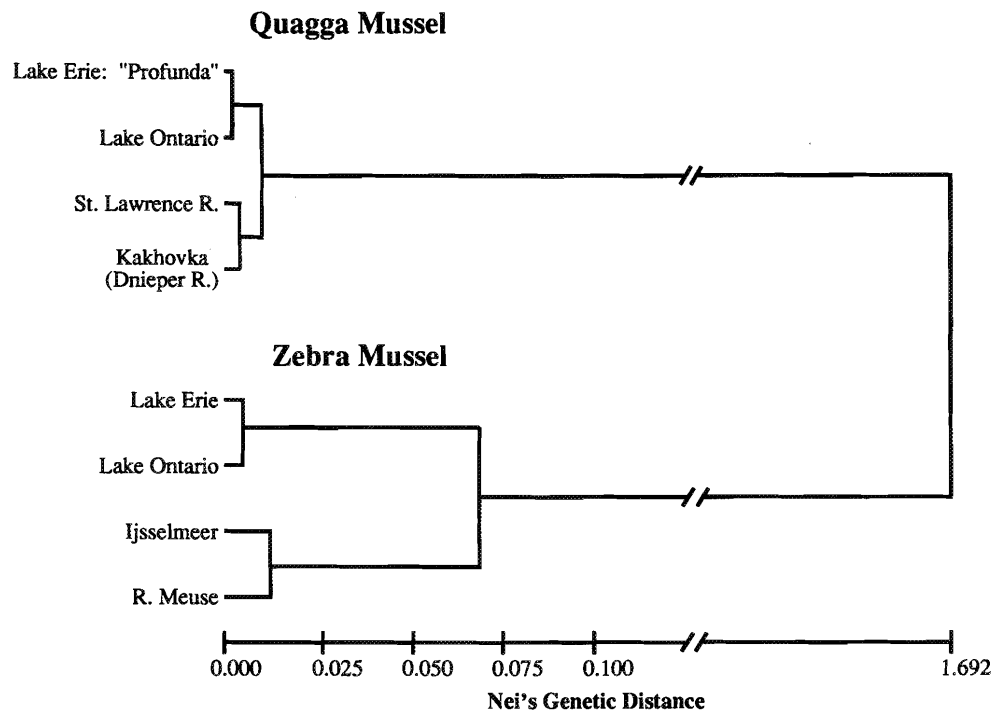


FIG. 2. UPGMA dendrogram of Nei's genetic distances between North American and European populations of zebra and quagga mussels based on 11 loci.

tance. The maximum genetic distance between quagga mussel populations is 0.005, where the cluster joining the "profunda" phenotype with the Rochester population meets the cluster joining the Ukrainian population with the upper St. Lawrence River population. The clusters of zebra mussel from North America and those from Europe are formed at genetic distances of less than 0.02, which is consistent with May and Marsden's (1992) results from the Great Lakes basin. The two continental clusters of zebra mussel join at a distance of 0.068, which is more distant, but well within the range to be expected from conspecifics with the amount of genotypic and geographic variability found in the zebra mussel (Awise and Smith 1977; Davis 1983; Thorpe 1983). In comparison, the zebra and quagga mussel populations cluster at a distance of 1.69.

## Discussion

The quagga mussel is a member of the family Dreissenidae, possessing the diagnostic septum for the attachment of anterior adductor and anterior byssal retractor muscles (Morton 1993). The genus *Dreissena* is indicated by the lack of an apophysis above the septum. The systematics of this genus is in disarray. The Russian systematist Andrusov described eight living species of *Dreissena* in 1897. Western systematists have recognized one or two extant species: *D. rostriformis* (Andrusov, 1897) and/or *D. polymorpha* (Nuttall 1990; Marelli 1991). According to Rosenberg and Ludyanskiy (1994), four living species of *Dreissena*, with a varying number of subspecies, are currently recognized in the Russian systematic literature: *D. polymorpha*, *D. rostriformis*, *D. caspia* (Andrusov, 1897), and *D. elata* (described as a subspecies of *D. polymorpha* by Andrusov in 1897 and elevated to species level by Logvinenko in 1965). While *D. bugensis*, described as a species by Andrusov (1897), has been placed into a subspecies of

*D. rostriformis* by current systematists, most Russian biologists retain Andrusov's classification (see Zolotareva et al. 1978; Pligin 1984). To conform to the body of research literature, we will use the name *D. bugensis* until an acceptable classification is worked out (see also Rosenberg and Ludyanskiy 1994).

Given the known range of *D. bugensis* and the fact that *D. polymorpha* and *D. bugensis* are the only members of the genus yet catalogued in the Dnieper River (Zhadin 1952), we conclude that the quagga mussel is synonymous with *D. bugensis*. Two pieces of evidence, one electrophoretic and one morphological, identify the quagga mussel as *D. bugensis*. Samples from the Kakhovka Reservoir showed allozyme patterns that matched loci diagnostic of the North American quagga rather than *D. polymorpha*. Morphological comparison was impossible because these samples were received without shells. The *Dreissena* population at this site was estimated to be 80–90% *D. bugensis* in 1977 (Pligin 1984). The second set of samples from the Dnieper River, identified as *D. bugensis* (T.G. Moroz, 32507 Kherson, Rabothaya, 76 a-144, Ukraine, personal communication), closely resembled the quagga mussel (Fig. 1).

The four populations of quagga mussel are closely matched at allozyme loci, confirming that the "profunda" type is a phenotypic variant and not another species. The profundal phenotype is genetically closer to the Ontario quagga mussel than to the Ukraine population (Fig. 2). Dermott and Munawar (1993) suggested that these quaggas from the deeper sections of Lake Erie resemble *D. distincta*, described by Andrusov in 1897. Our results, showing that the two phenotypes are conspecific, call Andrusov's description of *D. bugensis* and *D. distincta* as separate species into question.

The difference in the genetic distances between the new and old world populations of the two species of *Dreissena* is explained by the fact that *D. bugensis* has a much more limited range in Europe than *D. polymorpha* (Zhadin 1952).

Given that *D. bugensis* is only described in two rivers in the Black Sea drainage, the old world population would not be expected to show population substructure. Mills et al. (1993a) estimated that the quagga mussel arrived in the new world in 1989. This time span does not allow for significant differentiation from the founder population in the absence of a bottleneck. Since the *D. bugensis* population is not likely to be subdivided in the old world, we would expect the new world population to be quite similar to the old world population in its electrophoretic profile. Conversely, while the new world zebra mussel has also not had sufficient time to diverge from its source population, the old world zebra mussel population has had the time and space required to develop substructure. The genetic distance between the new world population of *D. polymorpha* and any unrelated old world populations would be expected to reflect this occurrence. The extent of genetic distance between the Dutch and North American zebra mussel indicates that the North American populations could not have arisen from these Dutch populations.

In the UPGMA dendrogram (Fig. 2) the cluster of four quagga mussel populations joins with the cluster of zebra mussel at a genetic distance of 1.69, which is greater than the value of 1.22 found by May and Marsden (1992). This increase in the estimate of genetic distance is partly due to the inclusion of populations of zebra mussel from Europe in the analysis which were not used by May and Marsden and partly due to the use of a different number of loci and alleles per locus. Thorpe (1983) and others (Avisé and Smith 1977; Davis 1983) suggested that congeneric species will have a range of genetic distances between 0.16 and 1.39. Our finding that *D. polymorpha* and *D. bugensis* exceed that range may support their taxonomic classification into separate subgenera: *Dreissena* and *Pontodreissena*, respectively (Babak 1983; Nuttall 1990).

Identification of the quagga mussel as *D. bugensis* should stimulate researchers to investigate previous work which has been done on this species in its native range, in order to more readily predict its potential impacts in North America. Genetic confirmation of the existence of at least two species, *D. polymorpha* and *D. bugensis*, with two distinct phenotypes of the latter increases the taxonomic resolution of the genus. We verify that there is more than one extant species. The "profunda" phenotype indicates that considerable plasticity exists within these species. Ecological comparisons of the two extreme phenotypes of *D. bugensis* in the Great Lakes may lead to interesting insights into its morphological, and possibly physiological, plasticity.

## Acknowledgments

We thank Ron Dermott for providing the quagga samples from Lake Erie, Ximing Guo for providing the quagga sample from the Kakhovka Reservoir, and Tamara Moroz for identifying and providing intact samples of *D. bugensis* from Kherson, Ukraine. Ed Mills, Gary Rosenberg, Douglas Smith, and two anonymous reviewers each reviewed an earlier draft of this manuscript. This research was funded in part by the U.S. Environmental Protection Agency under cooperative agreement No. CR818947-01, Central Hudson Gas and Electric, Consolidated Edison, Monroe County Water Authority, New York Sea Grant, New York State Electric and Gas, and Rochester Gas and Electric. This paper is contribution No. 157 from the Cornell Biological Field Station.

## References

- ANDRUSOV, N.I. 1987. Fossil and living Dreissenidae of Eurasia. Proc. Saint Petersburg Soc. Nat. Dep. Geol. Mineral. 25: 285–286.
- AVISE, J.C., AND M.H. SMITH. 1977. Gene frequency comparisons between sunfish (Centrarchidae) populations at various stages of evolutionary divergence. Syst. Zool. 26: 319–335.
- BABAK, E.V. 1983. The Pliocene and Quaternary Dreissenidae of the Evksin Basin. Tr. Paleontol. Inst. Akad. Nauk SSSR 204: 104 p. (In Russian)
- DAVIS, G.M. 1983. Relative roles of molecular genetics, anatomy, morphometrics and ecology in assessing relationships among North American Unionidae (Bivalvia), p. 193–222. In G.S. Oxford and D. Rollinson [ed.] Protein polymorphism: adaptive and taxonomic significance. Academic Press, New York, N.Y.
- DERMOTT, R., AND M. MUNAWAR. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. Can. J. Fish. Aquat. Sci. 50: 2298–2304.
- GORMAN, G.C., AND J. RENZI, JR. 1979. Genetic distance and heterozygosity estimates in electrophoretic studies: effects of sample size. Copeia 2: 242–249.
- GRIFFITHS, R.W. 1993. The changing environment of Lake St. Clair. Proceedings of the Third International Zebra Mussel Research Conference, Toronto, Ont. (Abstr.)
- HARTL, D.L., AND A.G. CLARK. 1989. Principles of population genetics. 2nd ed. Sinauer, Sunderland, Mass. 682 p.
- HEBERT, P.D.N., C.C. WILSON, M.H. MURDOCH, AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. Can. J. Zool. 69:405–409.
- LOGVINENKO, B.M. 1965. Changes in the fauna of Caspian molluscs *Dreissena* after intrusion of *Mytilaster lineatus* (Gmelin). Nauchn. Dokl. Vyssh. Shk. Biol. Nauki 4: 14–19.
- MARELLI, D. 1991. Zhadin's systematic account of *Dreissena*: are the species valid? *Dreissena polymorpha* Inf. Rev. 2(4): 3. New York Sea Grant, Brockport, N.Y.
- MAY, B. 1992. Starch gel electrophoresis of allozymes, p. 1–27 and 271–280. In A.R. Hoelzel [ed.] Molecular genetic analysis of populations: a practical approach. IRL Press, Oxford.
- MAY, B., AND J.E. MARSDEN. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. Can. J. Fish. Aquat. Sci. 49: 1501–1506.
- MILLS, E.L., R.M. DERMOTT, E.F. ROSEMAN, D. DUSTIN, E. MELLINA, D.B. CONN, AND A.P. SPIDLE. 1993a. Colonization, ecology, and population structure of the "quagga" mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 50: 2305–2314.
- MILLS, E.L., J.H. LEACH, J.T. CARLTON, AND C.L. SECOR. 1993b. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. 19(1): 1–54.
- MORTON, B. 1993. The anatomy of *Dreissena polymorpha* and the evolution and success of the Heteromyarian form in the Dreissenoidae, p. 185–216. In T.F. Nalepa and D.W. Schloesser [ed.] Zebra mussels: biology, impacts, and control. Lewis Publishers, Inc., Boca Raton, Fla.
- NEI, M. 1972. Genetic distances between populations. Am. Nat. 106: 283–292.
- NUTTALL, C.P. 1990. Review of the Caenozoic heterodont bivalve superfamily Dreissenacea. Palaeontology 33: 707–737.
- PLIGIN, Y.V. 1984. Extension of the distribution of *Dreissena bugensis*. Malacol. Rev. 17: 143–144. (Abstr.)
- ROSENBERG, G. AND M.L. LUDYANSKIY. 1994. A nomenclatural review of *Dreissena* (Bivalvia: Dreissenidae), with identification of the quagga mussel as *Dreissena bugensis*. Can. J. Fish. Aquat. Sci. 51: 1474–1484.
- SHAKLEE, J.B., F.W. ALLENDORF, D.C. MORIZOT, AND G.S. WHITT. 1990. Gene nomenclature for protein-coding loci in fish. Trans. Am. Fish. Soc. 119: 2–15.
- THORPE, J.P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation, p. 131–152. In G.S. Oxford and D. Rollinson [ed.] Protein polymorphism: adaptive and taxonomic significance. Academic Press, New York, N.Y.
- ZHADIN, V.I. 1952. Molluscs of fresh and brackish waters of the U.S.S.R. Academy of Sciences of the U.S.S.R. Israeli Program for Scientific Translations, Jerusalem. xvi + 368 p.
- ZOLOTAREVA, V.I., A.V. MAKHONINA, AND A.K. DYGA. 1978. The filtration ability of *Dreissena bugensis* Andrusov. Malacol. Rev. 11: 96–97. (Abstr.)