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A SURVEY OF GENETIC VARIATION AT ALLOZYME LOCI AMONG *GONIOBASIS* POPULATIONS INHABITING ATLANTIC DRAINAGES OF THE CAROLINAS

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ABSTRACT

We estimated gene frequencies at eight polymorphic enzyme loci in 12 populations of *Goniobasis* from Atlantic drainages of North Carolina, South Carolina, and Georgia. Our sample included four populations of *G. proxima* from the piedmont, five populations of *G. catenaria catenaria*, one population of *G. catenaria postellii*, and two populations of *G. catenaria dislocata* from the coastal plain. The fit to Hardy-Weinberg expectation was good within all populations of both species (F_{IS} = 0.042 *proxima*, 0.035 *catenaria*), while levels of interpopulation divergence were high (F_{ST} = 0.461 *proxima*, 0.564 *catenaria*). In spite of slightly overlapping geographic distributions, and instances of striking similarity in shell morphology between the two species, *G. proxima* and *G. catenaria* were genetically distinct (average values of Nei's D near 1.0), with no evidence of hybridization. Although their ranges are fragmented into numerous isolated and genetically distinct populations, both species remain broadly recognizable across states, drainages, and physiographic regions. The relationship between *G. catenaria postellii* and seven other nominal species and subspecies of *Goniobasis* sometime recognized from Atlantic drainages of Georgia is called into question.

Key words: electrophoresis, isozymes,freshwater, Carolina, Georgia, gastropods, pleuroceridae, *Elimia*.

INTRODUCTION

Freshwater snails of the family Pleuroceridae are abundant, widespread, and important elements of the grazing and shredding community in lotic ecosystems throughout the southeastern United States (Power et al., 1988; McCormick & Stevenson, 1991; Hill et al., 1995; Huryn et al., 1995; reviews by Feminella & Hawkins, 1995; Dillon, 2000). Their diverse and often isolated populations, easily sampled year around, have made pleurocerids attractive models for the study of divergence and speciation (Chambers 1980, 1982; Dillon 1989, 1991; Bianchi et al., 1994; Dillon & Lydeard, 1998; Lydeard et al., 1997; Holznagel & Lydeard, 2000). Yet the pleurocerid fauna of much of the southeastern United States remains obscure and poorly documented, and their systematic relationships unclear.

Goodrich (1942) listed three pleurocerid genera, 15 species, and 26 subspecies inhabiting Atlantic drainages from New England to Texas. Four of these taxa will be treated in the present work: *Goniobasis proxima* (Say, 1825) from the "highlands of North and South Carolina"; *G. catenaria dislocata* (Ravenel, 1834) inhabiting "headstreams" in Virginia, east-central North Carolina, and South Carolina; *G. catenaria catenaria* (Say, 1822) from "springs of eastern South Carolina"; and *G. catenaria postellii* (Lea, 1858) from the "Altamaha, Ogeechee, and Canoochee Rivers" of Georgia. *Goniobasis catenaria* and *G. proxima* were two of the first four species of this diverse North American genus to reach formal description.

Although altering the generic name to "*Elimia*," Burch (1982) and Burch & Tottenham (1980) generally adopted Goodrich's understanding of the pleurocerid fauna of North America as outlined above. But the systematic relationships among the Georgia representatives of this group have also been reviewed by Clench & Turner (1956), Krieger (1977), Chambers (1990), and Mihalchik (1998). Specific nomina applied to populations from Georgia Atlantic drainages have included *Goniobasis bentoniensis* (Lea, 1862), *G. boykiniana viennaensis* (Lea, 1862), *G. mutabilis* (Lea, 1862), *G. mutabilis timida* (Goodrich, 1942), *G. timida* (Goodrich, *fide* Mihalchik, 1998), *G. postellii* (Lea, 1858), and

G. suturalis (Haldeman, 1840). All these names would be junior synonyms of *G. catenaria,* to the extent that *G. catenaria* extends into Georgia, as suggested by Goodrich.

Between 1986 and 1995, Dillon & Keferl (2000) surveyed 629 aquatic sites distributed evenly throughout South Carolina, documenting approximately 30 pleurocerid populations at 44 sites. They found ten populations of *G. proxima* in small streams in or near the Appalachian foothills, confirming Goodrich's (1942) report. Ten populations of *G. catenaria catenaria* were found at 26 sites in streams and rivers of varying size through the South Carolina midlands, expanding the known range of that species substantially from that suggested by Goodrich. The disjunct distribution of these populations suggested to Dillon & Keferl that this species may have been highly impacted by agricultural siltation and impoundment. Dillon & Keferl also reported six *G. catenaria dislocata* populations at eight sites in small streams of the coastal plain.

Goniobasis catenaria populations were occasionally found well into the South Carolina piedmont, closely neighboring populations of *G. proxima* in upstate tributaries of the Broad/Santee and Catawba/Santee. And the similarity in shell morphology between *G. proxima* and *G. catenaria dislocata* of the coastal plain was striking. The shells of both species were identically shaped and marked by a single spiral carina. *Goniobasis catenaria dislocata* shells differed from *G. proxima* only by the presence of faint axial costae near the apex, disappearing after the first 2–3 whorls. Populations of both species inhabit small, rapidly flowing streams, *G. catenaria dislocata* generally being found in those rather unusual regions of the coastal plain (often bordering large rivers) with slope and marl exposure. But whether the gross shell similarity of *G. proxima* and *G. catenaria dislocata* might reflect a genuine genetic relationship, or might be the result of convergence, Dillon & Keferl could not determine.

The genetics of North Carolina and Virginia populations of *G. proxima* have been the subject of intensive study for 20 years (Dillon & Davis, 1980; Dillon, 1984a; Stiven & Kreiser, 1994). Intrapopulation variation seems to be unusually low, and interpopulation divergence high, as might be expected from populations of such a poorly mobile animal isolated in small streams of the piedmont and mountains (Dillon, 1984b). Despite the occurrence of fixed differences at multiple enzyme loci, however, transplants and artificial introductions have revealed no evidence of reproductive isolation among *G. proxima* populations (Dillon, 1986, 1988a).

The purposes of the present work are threefold. First we compare the levels of intra- and interpopulation genetic variance observed in *G. catenaria* to the better-known *G. proxima.* Second, we evaluate the genetic distinctiveness of *G. proxima* and *G. catenaria,* paying particular attention to the possibility of hybridization. Third, we examine evidence that populations of *G. catenaria dislocata* might be extralimital *G. proxima,* rather than *G. catenaria* with shell morphology convergent on *G. proxima.*

METHODS

We sampled five populations of *G. catenaria catenaria,* two populations of *G. catenaria dislocata* from eastern South Carolina, and one *G. catenaria postellii* from Georgia. The four populations of *G. proxima* we sampled included *Yad* from northwestern North Carolina, which we have previously compared to other populations of *Goniobasis* (as *Yad* in Dillon & Davis, 1980; *Yad1* in Dillon, 1984b, 1988b) and which served as a control for the present investigation. Our Georgia site was identical to "Station X" of Krieger & Burbanck (1976) and YELD of Krieger (1977), inhabited by a population identified as "*G. suturalis*" in the former publication and "*G. boykiniana viennaensis*" in the latter. Population *Clrk* of *G. catenaria* and population *Bull* of *G. proxima* were sampled from tributaries of the Broad River separated by only about 15 km through water. The sites at which we collected all 12 populations may be located in Figure 1. Locality data for all sites are provided in the Appendix. Voucher specimens have been deposited in the Academy of Natural Sciences of Philadelphia.

At each site we collected at least 30 individual snails, which were cracked and stored in Tris-phosphate 7.4 tissue buffer at –70°C upon return. Allozyme variation was resolved from whole-animal homogenates by horizontal starch gel electrophoresis, using equipment and techniques as previously described (Dillon, 1985, 1992; Dillon & Lydeard, 1998). We initially screened ten enzyme systems and six buffers by requiring that polymorphism interpretable as the product of codominant Mendelian alleles be expressed in a

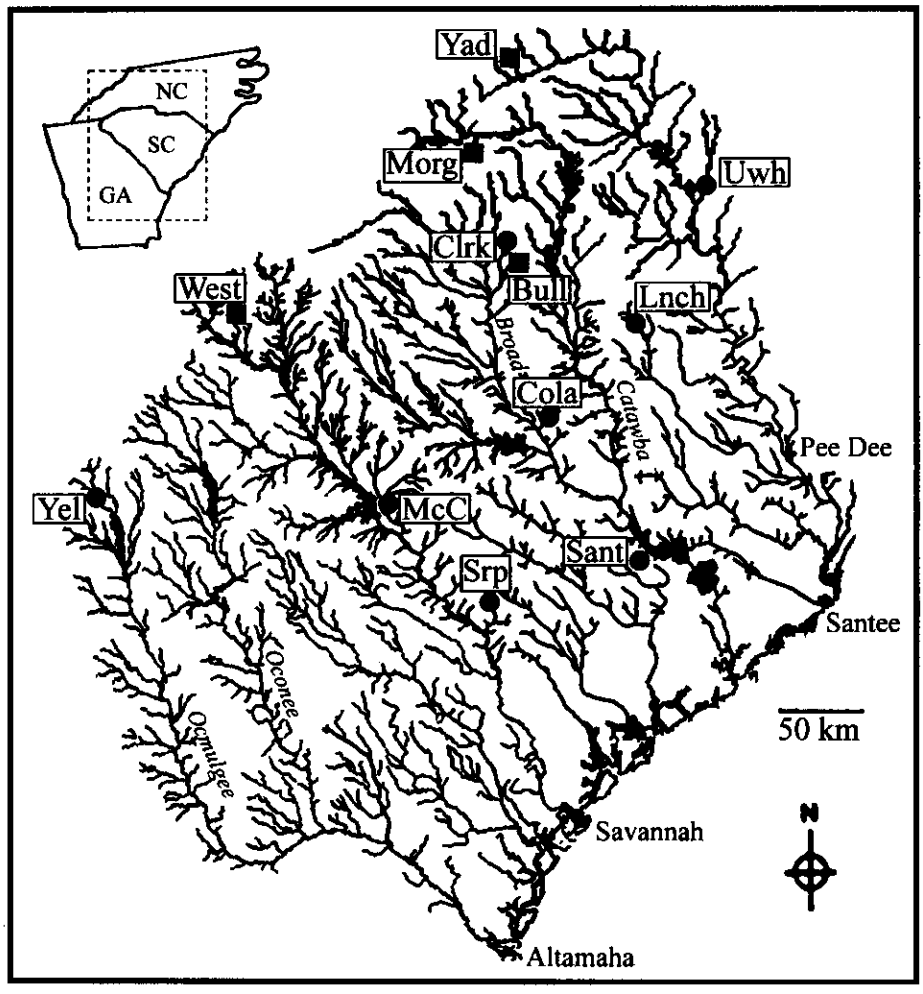

FIG. 1. The study area, showing primary drainages and sample sites. Circles indicate *G. catenaria,* and squares *G. proxima.*

comparison of *G. proxima* population *Yad, G. catenaria postellii* population *Yel,* and *G. catenaria dislocata* population *Srp.*

Ultimately, we compared all populations on the basis of eight loci, most resolved on two buffer systems, as follows. The AP6 buffer of Clayton & Tretiak (1972) was used to resolve mannose-phosphate isomerase (MPI, EC 5.3.1.8), 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44) and isocitrate dehydrogenase (IDHF and IDHS, EC 1.1.1.42 – cathodal and anodal loci, respectively). A TEB8 buffer (Shaw & Prasad 1970) was used for esterases (EST1, EC 3.1.1.2 – the strong, slow locus only), xanthine dehydrogenase (XDH, EC 1.2.1.37), MPI, and IDHF. The Poulik (1957) buffer was used for octopine dehydrogenase (ODH, EC 1.5.1.11), glucose-phosphate isomerase (GPI, EC 5.3.1.9) and EST1.

Chambers (1980) demonstrated that inheritance of allozyme phenotype is Mendelian at the 6PGD locus in *G. floridensis.* Dillon (1986) verified Mendelian inheritance at GPI, ODH, and EST1 by mother-offspring analysis in *G. proxima.* The designations of putative alleles used for population *Yad* were retained from the system of Dillon (1984b) for GPI, MPI, ODH, EST1 and XDH. For those loci which had not previously been examined for population *Yad* (6PGD, ISDHF, ISDHS), the most common *Yad* allele was named "100." Then

alleles in all other populations were named according to the mobility of their allozymes in millimeters relative to the *Yad* standard.

Data were initially analyzed using BIOSYS-1 (Release 1.7; Swofford & Selander, 1981). Genotype frequencies at all polymorphic loci were tested for conformance to Hardy-Weinberg expectation within populations using chi-square statistics, with Yates correction in 2 × 2 cases, pooling rare classes as required. Mean F-statistics (Wright, 1978) were calculated across loci for the four populations of *G. proxima* and the eight populations of *G. catenaria* separately. Values of Nei's (1978) unbiased genetic similarity and distance were calculated pairwise over all populations, as well as the chord distance of Cavalli-Sforza & Edwards (1967). The matrix of chord distances, which are Pythagorean in Euclidean space (Wright, 1978), was input to STATISTICA (Release 5.0, Statsoft, Inc.) and clustered using the method of unweighted pair-group averaging (UPGMA).

RESULTS

Example shells are shown in Figure 2. Typical *G. catenaria* bore shells with both spiral costae (or cords) and axial costae (or ribs) intersecting to form nodules. The shells of *G. proxima* had no axial costae and only a single spiral costa (or carina) becoming obsolete with age. Typical *G. catenaria* shells also tended to be wider per unit length than *G. proxima*. The shells of the *Yel* population, nominally *G. catenaria postellii,* did not differ noticeably from those of typical *G. catenaria catenaria*. But as noted by Dillon & Keferl (2000), the shells of *G. catenaria dislocata* were narrower and lacked both spiral and axial costae on later whorls, rendering them more similar to *G. proxima* than typical *G. catenaria* (Dillon & Keferl 2000).

For allozyme analysis, sample sizes averaged across loci ranged from N = 29 at *West* to N = 43 at *Yad* (Appendix). Sample sizes at all 12 × 8 loci examined were greater than 30, except N = 29 for *Bull* (XDH), N = 26 for *Bull* (EST1), N = 14 for *West* (IDH), N = 20 for *Morg,* (IDH), and N = 26 for *Morg* (GPI, XDH).

Allele frequencies are given in Table 1. Over all observations, a total of 26 loci were polymorphic by the 95% criterion, a value somewhat higher than has been observed in comparable surveys of pleurocerid population genetics previously published (Chambers, 1980; Dillon & Davis, 1980; Dillon, 1984b; Dillon & Lydeard, 1998). Fits to Hardy-Weinberg expectation were excellent within populations. Chi-square tests uncovered no significant differences between observed genotypic frequencies and those expected from Hardy-Weinberg equilibrium in any case. The values of F_{IS} for both *G. proxima* and *G. catenaria* averaged over eight loci were negligible (Table 2).

As might be expected from their highly isolated population structure, divergence among the four *G. proxima* populations was high (F_{ST} = 0.461; Table 2). Table 1 shows fixed (or nearly fixed) differences at a minimum of one locus between all pairs of *G. proxima,* except *Morg–Bull*. Divergence among the eight *G. catenaria* was not as striking upon first examination, the trio of populations from the middle

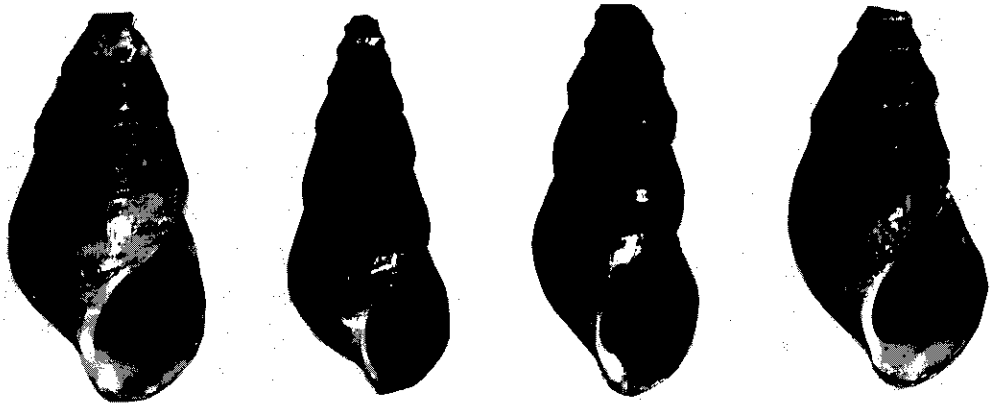

FIG. 2. Example shells from the four taxa studied. From left, *Goniobasis catenaria catenaria* (*Clrk*), *G. catenaria dislocata* (*Srp*), *G. proxima* (*Bull*), and *G. catenaria postellii* (*Yel*). The standard length of the *G. catenaria catenaria* shell is 1.75 cm, the remaining shells are figured at the same scale.

TABLE 1. Allele frequencies at 8 enzyme loci in 12 populations of *Goniobasis* from southern Atlantic drainages of the United States.

		G. proxima				*G. catenaria*							
Locus	allele	*Yad*	*West*	*Morg*	*Bull*	*Clrk*	*Uwh*	*Lnch*	*Cola*	*Sant*	*Srp*	*McC*	*Yel*
EST1	100	0.167	0.191	0.513			0.219	0.188					
	103	0.802	0.794	0.474	0.885	1.000	0.734	0.813	1.000	1.000	0.679	0.789	0.524
	106	0.031	0.015	0.013	0.115		0.047				0.321	0.211	0.012
	107												0.463
GPI	98									0.014	0.976		
	100					1.000	1.000	1.000	1.000	0.986	0.024	0.162	1.000
	102	1.000	1.000	1.000	1.000								
	105											0.784	
	110											0.054	
IDHF	93					0.953							
	97			0.125									
	99						0.016			0.319			
	100	1.000	1.000	0.750	1.000								
	103			0.050									
	105			0.075		0.047	0.984	1.000	1.000	0.681	1.000	1.000	1.000
IDHS	100	1.000	1.000	1.000	1.000								
	104					1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI	95	0.833		0.200	0.750								
	100	0.167	1.000	0.800	0.250	1.000	1.000	1.000	1.000	1.000	0.989	1.000	1.000
	103										0.011		
ODH	106	0.738	1.000	0.145									
	109F	0.125		0.855	1.000								
	111											0.118	0.431
	113F	0.138											
	114					1.000	0.969	1.000	1.000	1.000	1.000	0.882	0.569
	118						0.031						
6PGD	100	1.000	0.882	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.522
	105		0.118										0.422
	110												0.056
XDH	97		1.000	0.731	0.603				0.015	0.875	0.390		
	98	1.000		0.269	0.397	1.000	1.000	1.000	0.985	0.125	0.610	1.000	0.568
	100												0.432

TABLE 2. Values of Wright's (1978) F-statistics averaged over eight loci for four populations of *G. proxima* and eight populations of *G. catenaria*.

	G. proxima	*G. catenaria*
F_{IS}	0.042	0.035
F_{IT}	0.484	0.580
F_{ST}	0.461	0.564

of the study area (*Uwh*—*Lnch*—*Cola*) being genetically indistinguishable. But the southern populations were more divergent. The *Yel* population of *G. catenaria postellii* had unusual alleles in high frequency at three loci (EST1, 6PGD, XDH), and both the *Srp* population of *G. catenaria dislocata* and the *McC* population of *G. catenaria catenaria* were strikingly distinct at the GPI locus. Population *Clrk* was distinguished by a unique IDHF allele. Consequently, the mean value of F_{ST} for the eight *G. catenaria* populations over the three-state region was 0.564, similar to that observed for *G. proxima.*

Nei's statistics among all populations are presented in Table 3, and the result of the UPGMA cluster analysis based on interpopulation chord distances is shown in Figure 3. Each *G. catenaria dislocata* population was more similar to its neighboring *G. catenaria catenaria* population (I = 0.86, 0.89) than the pair of *dislocata* were to each other (I = 0.81). This tends to support the hypothesis that the two populations of *G. catenaria dislocata* have lost shell sculpture independently.

Reinforcing the impression left from the F-statistics, Figure 3 suggests that the levels of interpopulation divergence within *G. proxima* and *G. catenaria* are comparably high. The four *G. proxima* populations are nevertheless quite distinct from the eight *G. catenaria* populations, sharing no alleles at three loci (GPI,

TABLE 3. Nei's (1978) statistics among pairs of *Goniobasis* populations. Unbiased genetic identity is shown below the diagonal, and unbiased genetic distance above.

	Yel	*McC*	*Srp*	*Sant*	*Cola*	*Lnch*	*Uwh*	*Clrk*	*Bull*	*Morg*	*West*	*Yad*
Yel	—	0.22	0.29	0.21	0.11	0.11	0.10	0.27	1.48	1.21	1.24	1.34
McC	0.81	—	0.15	0.24	0.10	0.10	0.11	0.24	1.08	0.96	1.06	0.92
Srp	0.75	0.86	—	0.21	0.17	0.17	0.17	0.33	1.08	0.91	0.95	1.10
Sant	0.81	0.78	0.81	—	0.12	0.13	0.13	0.21	0.96	0.80	0.73	1.23
Cola	0.90	0.91	0.84	0.89	—	0.00	0.01	0.12	1.08	0.98	1.05	0.93
Lnch	0.90	0.91	0.84	0.88	1.00	—	0.00	0.13	1.13	0.96	1.08	0.94
Uwh	0.90	0.90	0.84	0.88	0.99	1.00	—	0.13	1.14	0.95	1.09	0.95
Clrk	0.76	0.79	0.72	0.81	0.89	0.88	0.88	—	1.07	1.00	1.05	0.92
Bull	0.23	0.34	0.34	0.38	0.34	0.32	0.32	0.34	—	0.09	0.28	0.16
Morg	0.30	0.38	0.40	0.45	0.38	0.38	0.39	0.37	0.91	—	0.15	0.26
West	0.29	0.35	0.39	0.48	0.35	0.34	0.34	0.35	0.76	0.86	—	0.28
Yad	0.26	0.40	0.33	0.29	0.40	0.40	0.39	0.40	0.85	0.77	0.76	—

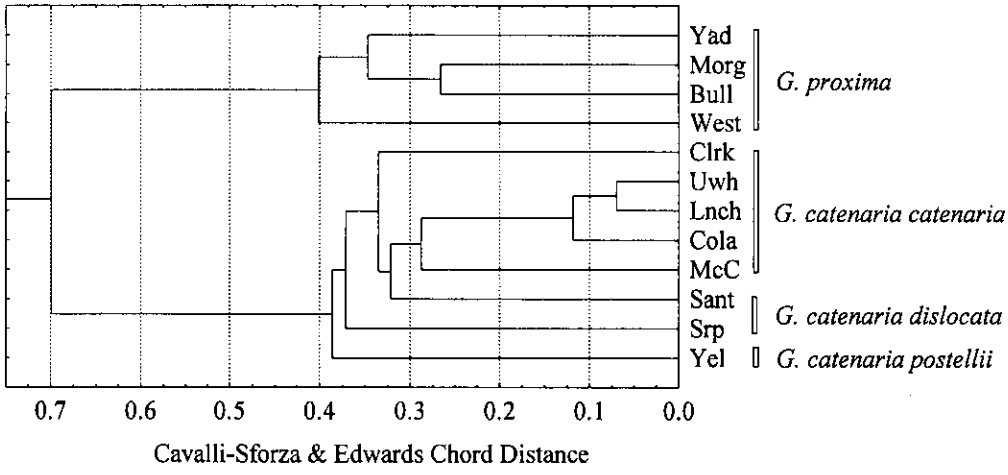

FIG. 3. UPGMA Cluster analysis of the 12 study populations, based on a matrix of genetic distances calculated using the chord method of Cavalli-Sforza & Edwards (1967).

ODH, IDHS) and almost completely distinct at IDHF. Table 1 shows no evidence of hybridization between the species, in the Broad/Santee drainage between *Clrk* and *Bull* or elsewhere.

DISCUSSION

Although inhabiting a more moderate climate and a less mountainous environment, the population genetic structure of *G. catenaria* does indeed resemble that of the better-studied *G. proxima*. The similarity of the *G. catenaria* populations inhabiting the Pee Dee drainage (*Uwh* and *Lnch*) and the (apparently isolated) Santee populations (particularly *Cola*) was unexpectedly high. But the overall values of Wright's F-statistics and most values of Nei's genetic distances among *G. catenaria* populations were comparable to values obtained from *G. proxima*.

Values of genetic similarity and distance weakly suggest that our two *dislocata* populations may have independently lost shell sculpturing, *Sant* deriving from *Cola* and *Srp* from *McC*. But as indicated in Figure 3 and Table 3, the two putative source *G. catenaria catenaria* populations, *Cola* and *McC*, are more similar to each other than either is to its *G. catenaria dislocata* neighbor. *Sant* and *Srp* do share a unique allele (GPI98) not found in any other population, and are also more similar to each other at the XDH locus than either is to *G. catenaria catenaria*. Additional data will be required before the origin of *G. catenaria dislocata* can be proposed with any confidence.

It is clear, in any case, that *G. catenaria dislocata* populations are not extralimital *G. proxima*, nor do they bear more genetic similarity

to *G. proxima* than to other *G. catenaria* of more typical shell morphology. We found no evidence of hybridization between the two species, in the upper Santee tributaries where they are closely neighboring or elsewhere. *Goniobasis proxima* and *G. catenaria* are quite distinct.

As might be predicted from its geographic situation on the periphery of the study area, population *Yel* was the most genetically distinctive of the populations here identified as *G. catenaria* (Fig. 3). But the level of divergence displayed clearly does not warrent the removal of this population to another specific name. Population *West* is more different from other *G. proxima* than population *Yel* is from other *G. catenaria*. Goodrich's (1942) suggestion that *Goniobasis* populations from this region of Georgia be referred to *G. catenaria* as a subspecies *postellii*, rather than distinguished as a separate species, would seem to have considerable merit.

Based on a comparison of his freshly collected shells to shells in the University of Michigan collections, Krieger (1977) identified Georgia populations of *Goniobasis* from the Atlantic drainages as *G. postellii* in the Oconee River, *G. suturalis* (= *G. mutabilis*) in the Yellow River above Porterdale, and *G. boykiniana viennaensis* in the Apalachee River and in the Yellow/Ocmulgee River below Porterdale. Mihalcik (1998) identified a population of *Goniobasis* from Snapping Shoals on the South River, a tributary of the Ocmulgee 20 km west of Porterdale, as *G. mutabilis*. She identified a population from an Ocmulgee tributary downstream about 350 km from Porterdale as *G. timida*, and suggested that a third population from the Atlantic tributaries of Georgia, Rocky Creek of the Oconee drainage, might be an undescribed "Species C." Mihalcik referred *Goniobasis* populations from the Savannah River to *G. bentoniensis*.

Neither Krieger nor Mihalchik examined populations from South Carolina, nor did either researcher consider the possibility that Georgia *Goniobasis* might be referable to the older name *G. catenaria*. Resolution of the longstanding systematic confusion regarding the *Goniobasis* of Georgia would seem a fertile direction for future studies.

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APPENDIX

Identification and locality data for study populations. The sample sizes given are averaged over the 8 enzyme loci reported in Table 1.

Bull—G. proxima (N = 31). Bullock's Creek at SC 889 bridge (Boheler Road), 10.9 km NNW of York, York Co., South Carolina. 81°19′W, 35°05′N. Same as site 20p of Dillon & Keferl (2000).

Clrk—G. catenaria catenaria (N = 32). Clarks Fork Creek at SC 55 bridge, 16.1 km NW of York, York Co., South Carolina. 81°24′W, 35°05′N. Same as site 17c of Dillon & Keferl (2000).

Cola—*G. catenaria catenaria* (N = 34). Big Cedar Creek at SC 59 bridge (Wildflower Road), 21.3 km N of Forest Acres, Richland Co., South Carolina. 81°06′W, 34°11′N. Same as site 23c of Dillon & Keferl (2000).

Lnch—*G. catenaria catenaria* (N = 32). Lynches River at SC 265 bridge, 3.8 km SW of Jefferson, Chesterfield/Lancaster Cos., South Carolina. 80°26′W, 34°38′N. Same as site 40c of Dillon & Keferl (2000).

McC—*G. catenaria catenaria* (N = 38). Stevens Creek at SC 23 bridge, 24.6 km WSW of Edgefield, Edgefield/McCormick Cos., South Carolina. 82°11′W, 33°44′N. Same as site 4c of Dillon & Keferl (2000).

Morg—*G. proxima* (N = 33). Small tributary of Clear Creek at bridge 50 m N of U.S. 64, 5 km S of Morganton, Burke Co., North Carolina. 81°45′W, 35°40′N.

Sant—*G. catenaria dislocata* (N = 36). Head of Chapel Branch, Santee, Orangeburg Co., South Carolina 80°29′W, 33°30′N. Same as site 28d of Dillon & Keferl (2000).

Srp—*G. catenaria dislocata* (N = 39). Lower Three-Runs Ck at SC 70 bridge, 9 km S of Snelling, Barnwell Co., South Carolina. 81°27′W, 33°11′N. Same as site 6d of Dillon & Keferl (2000).

Uwh—*G. catenaria catenaria* (N = 32). Uwharrie River at NC 109 bridge, 1 km NW of Uwharrie, Montgomery Co., North Carolina. 80°01′W, 35°26′N.

West—*G. proxima* (N = 29). Small tributary of the Chauga River at SC 196 bridge, 1km W of Mountain Rest, Oconee Co., South Carolina. 83°10′W, 34°52′N.

Yad—*G. proxima* (N = 43). Naked Creek at NC 1154 bridge, 5.2 km N of Ferguson, Wilkes Co., NC. 81°22′W, 36°09′N. Same as *Yadk* of Dillon & Davis (1980), *Yadl* of Dillon (1984).

Yel—*G. catenaria postellii* (N = 40). Yellow River below dam at Porterdale, Newton Co., Georgia. 83°53′W, 33°34′N.