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TAXONOMIC CLARIFICATION AND PHYLOGEOGRAPHY OF *FLUMINICOLA COLORADENSIS* MORRISON, A WIDELY RANGING WESTERN NORTH AMERICAN PEBBLESNAIL

Hsiu-Ping Liu[1], Jessica Walsh[1], and Robert Hershler[2]

ABSTRACT.—Herein we clarify the taxonomy of *Fluminicola coloradensis* Morrison (1940), which was described for populations in the Green River and Bonneville basins but has also been treated as restricted to the former watershed and conspecific with (currently unassigned) Snake River basin populations of *Fluminicola hindsi* sensu Taylor (1966). Bayesian analyses of DNA sequences from 2 mitochondrial genes congruently resolved *F. coloradensis* and Snake River basin populations of *F. hindsi sensu* Taylor as a strongly supported, shallowly structured clade. Haplotypes were extensively shared by Bonneville, Snake River and Green River populations; AMOVA did not detect significant variation among basins for either gene. Morphological variation was minor. Based on these results, we assign the Snake River basin populations to *F. coloradensis.* We attribute the limited differentiation of widely ranging *F. coloradensis* to its well-integrated habitats and to dispersal mediated by geologically recent drainage transfers. The broadly disjunct population in the Owyhee River drainage may be a product of translocation, as evidenced by detection of only the most common haplotypes in these snails. Our finding that *F. coloradensis* is more widely distributed than previously thought suggests that it may not require conservation attention rangewide, although some geographic subunits may be at risk.

RESUMEN.—En este resumen clarificamos la taxonomía de *Fluminicola coloradensis* Morrison (1940), que se describió en el caso de las poblaciones de las cuencas del Green River y Bonneville, pero también se consideró restringida a la anterior línea divisoria y especie congénere (actualmente sin clasificar) de las poblaciones de *Fluminicola hindsi* sensu Taylor (1966) de la cuenca del Snake River. Los análisis bayesianos de las secuencias de ADN de dos genes mitocondriales coincidieron en que las poblaciones de *F. coloradensis* y de *Fluminicola hindsi* sensu Taylor de la cuenca de Snake River constituyen un clado de estructura superficial y sólida. Los haplotipos se encontraban en gran parte de las poblaciones de Bonneville, Snake River y Green River; el análisis de varianza molecular (AMOVA) no detectó variaciones significativas entre las cuencas en el caso de ningún gen y la variación morfológica no fue significativa. Según estos resultados asignamos las poblaciones de la cuenca de Snake River a *F. coloradensis.* Atribuimos la poca diferenciación de de la variada *F. coloradensis,* a sus hábitats bien integrados y a la intervención de los flujos de desagües recientes desde el punto de vista geológico en la acción del agente dispersor. La existencia de una población dispersa en el desagüe de Owyhee River puede ser consecuencia de la traslocación, como lo demuestra el hecho de que se hayan detectado únicamente los haplotipos más comunes en estos caracoles. Nuestro hallazgo de que *F. coloradensis* se encuentra en más áreas biogeográficas de lo que suponíamos sugiere que, aunque haya algunas subunidades que se encuentran en peligro, tal vez no sea necesario tomar medidas de conservación en toda el área.

The northwestern North American genus *Fluminicola* (containing 24 currently recognized species) is composed of small (1.2–12.0 mm shell height), gill-breathing gastropods (commonly known as pebblesnails) that usually live in lotic habitats. Although *Fluminicola* is a conspicuous component of benthic communities throughout much of the region and recently has become a focus of conservation activities (e.g., USDA Forest Service and USDI Bureau of Land Management 2001), it has received little taxonomic study across most of its broad range (Hershler and Frest 1996). One of the long-standing problems is the unsettled taxonomy of *Fluminicola coloradensis* (commonly known as the Green River pebblesnail) and the numerous currently unassigned Snake River basin populations that closely resemble this species morphologically.

Morrison (1940) described *F. coloradensis* based on the large pebblesnails in the upper Green River and Bonneville basins, which he differentiated from *Fluminicola fuscus* by their wider umbilicus and lighter shell color. Taylor (1966 : fig. 14) included *F. coloradensis* (as a synonym) in *Lithoglyphus hindsii* (Baird 1863) (= *Fluminicola hindsi* [Baird, 1863]), which he envisaged as ranging widely across the upper

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Green River, Bonneville, and Snake–Columbia River basins. His brief treatment consisted of a distribution map and associated figure caption which detailed the content of *F. hindsi*. In their subsequent revision of the genus, Hershler and Frest (1996:12) synonymized the type material of *F. hindsi* (from the Kootenai River) with *F. fuscus* and resuscitated *F. coloradensis,* which they restricted to the upper Green River basin. They did not assign the Bonneville and most of the Snake River basin populations (those in the lower reaches of the Grande Ronde and Salmon rivers were allocated to *F. fuscus*), which they considered as belonging to one or more undescribed species. Hershler (1999) later reassigned the Bonneville Basin pebblesnails to *F. coloradensis,* however Frest and Johannes (2000:13) recently suggested that this species "is likely a composite taxon" as currently constituted (also see Frest 1999).

Mitochondrial DNA sequences have proved useful for delimiting species in morphologically conservative *Fluminicola* (Hershler et al. 2007). Here we use partial sequences of cytochrome *c* oxidase subunit I (COI) and cytochrome *b* (cyt*b*), together with morphological evidence, to resolve the taxonomy of *F. coloradensis.* In addition to filling an important gap in *Fluminicola* taxonomy (Hershler and Frest 1996), our findings provide additional insight into the complex biogeographic history of this genus. Our clarification of the geographic range of *F. coloradensis* may also assist state agencies in their efforts to conserve and manage this species.

METHODS

We analyzed mtDNA sequences from 18 populations of *F. coloradensis* (upper Green River basin, 6; Bonneville Basin, 12), 34 currently unassigned Snake River basin populations of *F. hindsi* sensu Taylor (1966), and 11 populations of *F. fuscus* (from the Snake–Columbia River basin), which has been delineated as the sister to *F. coloradensis* based on morphological (Hershler and Frest 1996) and molecular (Hershler et al. 2007) evidence. *Fluminicola insolitus,* which appears to be the closest relative to the *F. fuscus* + *F. coloradensis* clade (Hershler et al. 2007), was used to root the phylogenetic trees. Four COI and 3 cyt*b* sequences used in our analyses were taken from GenBank, and the remaining 242 COI and 166 cyt*b* sequences were newly obtained for this study. Sample codes, museum voucher numbers, locality details, and sample sizes are in Table 1, and the locations of sampling sites are shown in Fig. 1.

Genomic DNA was extracted from entire snails using a CTAB protocol (Bucklin 1992). Amplifications were conducted in a 25 μL total volume, containing 5 μL of 5X buffer, 0.5 μL of dNTPs (10mM), 2 μL of $MgCl_2$ (25 mM), 1.25 μL of each primer (10 μM), 1 unit Taq polymerase, 1 μL of template DNA (ca. 100 ng double-stranded DNA), and 13.8 μL of sterile water. COIL1490 (Folmer et al. 1994) and COH654 (Hershler and Liu 2012) were used to amplify a 634 bp fragment (excluding primers) of the COI gene. Cyt*b*284F and Cyt*b*757R were used to amplify a 449 bp fragment (excluding primers) of the cyt*b* gene. Cyt*b*284F (5′ATT TAT TTW CAT ATY GGW CGA GG3′) and Cyt*b*757R (5′TGG AAT RAA ATT TTC TGG GTC TG3′) were designed based on conserved regions of cyt*b* in an alignment using previously published sequences from the following gastropods: *Littorina saxatilis* (AJ132137), *Potamopyrgus antipodarum* (GQ996433), and *Oncomelania hupensis* (NC013073). Thermal cycling was performed with an initial denaturation for 2 min at 94 °C, followed by 35 cycles of 1 min at 94 °C, 1 min at 50 °C, 2 min at 72 °C, with a final extension of 10 min at 72 °C. The amplified polymerase chain reaction product was cleaned using the Exonuclease I/Shrimp Alkaline Phosphatase method. Approximately 10–20 ng of cleaned polymerase chain reaction product was used as a template in a cycle sequencing reaction using the BigDye Terminator v3.1 cycle sequencing kit (Applied Biosystem, Inc.). The following cycling conditions were used: 30 cycles of 94 °C for 20 s, 50 °C for 20 s, and 60 °C for 4 min. The cycle-sequenced product was cleaned using the ethanol precipitation method and then run on an ABI 310 genetic analyzer. Sequences were determined for both strands and then edited and aligned using Sequencher™ version 4.8. One to 10 specimens were sequenced for both genes for most of the sampled populations; we were unable to amplify and sequence cyt*b* from 4 populations (Table 1).

Sequence divergences (uncorrected p distance) were calculated using MEGA5 (Tamura

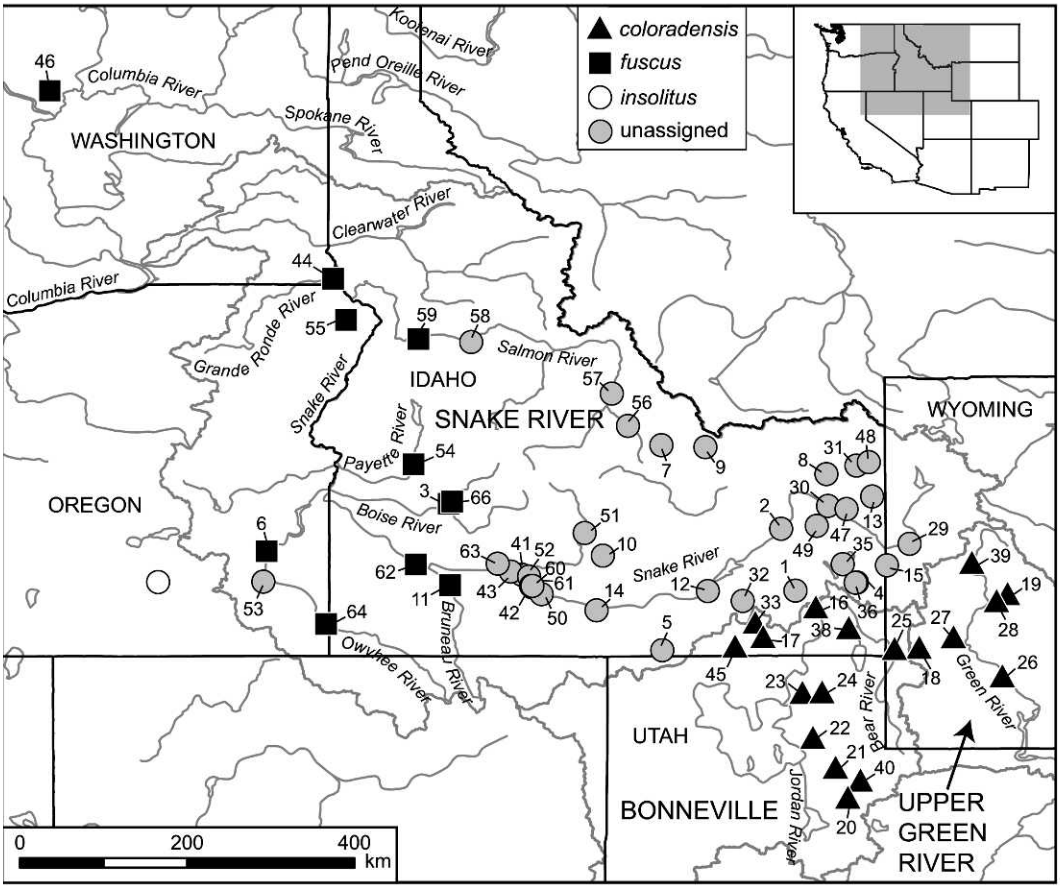


Fig. 1. Map of Idaho and portions of adjacent states showing collection localities for pebblesnail samples used in the molecular analyses. The green lines delineate the boundaries of the Bonneville, Snake River and upper Green River basins. Localities are numbered as in Table 1 (code).

et al. 2011). Genetic structuring among drainage basins was assessed by analysis of molecular variation (AMOVA) as implemented in ARLIQUIN 3.5 (Excoffier et al. 2005). Haplotype networks were generated using TCS version 1.21 (Clement et al. 2000). Because of missing data in the cyt*b* dataset, phylogenetic analyses of the 2 datasets were performed separately using Bayesian inference in MrBayes 3.2.1 (Ronquist et al. 2012). MrModeltest 2.3 (Nylander 2004) selected the HKY + I + G and HKY + G models for the COI and cyt*b* datasets, respectively, which best fit these data under the Akaike information criterion. In the Bayesian analysis Metropolis-coupled Markov chain Monte Carlo simulations were performed with 4 chains for 5,000,000 generations, and Markov chains were sampled at intervals of 10 generations to obtain 500,000 sample points. We used the default settings for the priors on topologies and HKY + I + G model parameters for COI and HKY + G model parameters for cyt*b*. The sampled trees with branch lengths were used to generate a 50% majority-rule consensus tree with the first 25% samples removed to ensure that the chain sampled a stationary portion.

Shells, radula, opercula, and soft anatomy of relevant pebblesnail collections in the Smithsonian Institution's National Museum of Natural History (USNM), the University of Minnesota Bell Museum of Natural History (UMBMNH), and the Orma J. Smith Museum of Natural History (ALBRCIDA) were studied using methods employed in recent taxonomic studies of *Fluminicola* (Hershler and Frest

TABLE 1. Species, sample codes, USNM voucher (catalog) numbers, localities, major drainage basins, and number of sequenced specimens for samples used in molecular analyses.

Species	Code	Voucher	Locality	Drainage	Zone	Easting	Northing	COI	cyt*b*
coloradensis	F18	905374	Hams Fork, Taylor Creek, Lincoln Co., WY	Upper Green River	12	526028	4661549	3	2
coloradensis	F19	1003678	New Fork and East Fork rivers, southwest of New Fork, Sublette Co., WY	Upper Green River	12	603415	4726475	5	2
coloradensis	F26	1116225	Green River, above Telephone Island, Sweetwater Co., WY	Upper Green River	12	600348	4628171	4	5
coloradensis	F27	1116226	LaBarge Creek, west-southwest of La Barge, Lincoln Co., WY	Upper Green River	12	556372	4674355	3	4
coloradensis	F28	1116227	New Fork River, Hwy. 351 bridge, Sublette Co., WY	Upper Green River	12	593855	4717675	5	5
coloradensis	F39	905307	Green River, Warren bridge, Sublette Co., WY	Upper Green River	12	571763	4763268	AY962915	AY963022
coloradensis	F16	904952	Bear River, Black Canyon, above Grace Power Plant, Carbou Co., ID	Great Salt Lake	12	434596	4709987	8	5
coloradensis	F17	1003669	Big Malad Spring, Oneida Co., ID	Great Salt Lake	12	387402	4675204	3	2
coloradensis	F20	1116219	Beaver Creek, below Thorn Creek confluence, Summit Co., UT	Great Salt Lake	12	473180	4503202	3	2
coloradensis	F21	1116220	East Canyon Creek, above East Canyon Reservoir, Summit Co., UT	Great Salt Lake	12	450644	4518471	4	3
coloradensis	F22	1116221	Strawberry Creek, above Weber River confluence, Morgan Co., UT	Great Salt Lake	12	430501	4554284	3	2
coloradensis	F23	1116222	Murray Spring, below source, Cache Co., UT	Great Salt Lake	12	421459	4608001	4	1
coloradensis	F24	1116223	Blacksmith Fork, below Big Hollow, Cache Co., UT	Great Salt Lake	12	439138	4608407	4	1
coloradensis	F25	1116224	South Fork Smiths Fork, Cokeville, Lincoln Co., WY	Great Salt Lake	12	504066	4660260	4	4
coloradensis	F33	1116232	Little Malad Spring, Oneida Co., ID	Great Salt Lake	12	380672	4692173	3	2
coloradensis	F38	1116237	North Creek, Liberty, Caribou Co., ID	Great Salt Lake	12	463469	4685107	3	2
coloradensis	F40	1123926	Provo River, above Deer Creek Reservoir, Wasatch Co., UT	Great Salt Lake	12	461672	4482641	AF520931	0
coloradensis	F45	1074880	Deep Creek, above Stone Canal, Oneida Co., ID	Great Salt Lake	12	362279	4664199	5	1
unassigned	F01	904950	Portneuf River, upper access area, Bannock Co., ID	Snake River	12	416912	4729044	6	6
unassigned	F02	1003876	Snake River, Shelley, Bingham Co., ID	Snake River	12	405364	4803200	5	2
unassigned	F04	905305	Blackfoot River, The Narrows, ca. 1.5 km above weir, Caribou Co., ID	Snake River	12	471043	4738400	3	3
unassigned	F05	1003834	Raft River, Narrows bridge, Cassia Co., ID	Snake River	12	297703	4660475	5	3
unassigned	F07	1003827	Summit Creek, BLM camp, Custer Co., ID	Snake River	12	304074	4905326	5	4
unassigned	F08	1003872	Henrys Fork, Saint Anthony, Fremont Co., ID	Snake River	12	445321	4868233	6	2
unassigned	F09	1003826	Birch Creek, Mud Creek, Lemhi Co., ID	Snake River	12	341716	4901918	5	2
unassigned	F10	905306	Little Wood River, Jim Brown bridge, Lincoln Co., ID	Snake River	11	737160	4774675	5	2
unassigned	F12	905348	Snake River, above Eagle Rock, Power Co., ID	Snake River	12	339647	4730115	5	2
unassigned	F13	1003829	Teton River, Buxton bridge, Teton Co., ID	Snake River	12	484753	4841148	5	2
unassigned	F14	1082637	Snake River, above Murtaugh, Twin Falls Co., ID	Snake River	11	733980	4709123	5	2
unassigned	F15	905412	Salt River, Freedom, Lincoln Co., WY	Snake River	12	497456	4758850	5	2
unassigned	F29	1116228	Snake River, Grand Canyon, Lincoln Co., WY	Snake River	12	517301	4784516	4	4

TABLE 1. Continued.

Species	Code	Voucher	Locality	Drainage	Zone	Easting	Northing	COI	cyt*b*
unassigned	F30	1116229	Snake River, Byington Park, Jefferson Co., ID	Snake River	12	446347	4830186	5	5
unassigned	F31	1116230	Falls River, north-northeast of Grainville, Fremont Co., ID	Snake River	12	471297	4878210	3	3
unassigned	F32	1116231	Rock Springs, Arbon Valley, Power Co., ID	Snake River	12	370312	4717572	6	4
unassigned	F35	1116234	Chubb Springs, north-northeast of Blackfoot Reservoir, Caribou Co., ID	Snake River	12	458805	4760379	3	2
unassigned	F36	1116235	Blackfoot River, mouth of The Narrows, Caribou Co., ID	Snake River	12	469816	4738036	3	3
unassigned	F41	1073422	Snake River, ca. 2.4 km below mouth of Malad River, Gooding Co., ID	Snake River	11	666980	4749610	2	0
unassigned	F42	1073427	Snake River, Thousand Springs, Minnie Miller Springs, Gooding Co., ID	Snake River	11	676558	4734783	2	0
unassigned	F43	1082642	Snake River, below Bliss Dam, Gooding Co., ID	Snake River	11	657041	4753149	1	0
unassigned	F47	1003882	Snake River, Black Canyon, Bonneville Co., ID	Snake River	12	462551	4826308	5	4
unassigned	F48	1003883	Porcupine Station Springs, Fremont Co., ID	Snake River	12	481837	4882127	5	3
unassigned	F49	905402	Willow Creek, Kepps Crossing, Bonneville Co., ID	Snake River	12	436351	4806380	5	3
unassigned	F50	905345	Snake River, Clear Lake bridge, Gooding Co., ID	Snake River	11	684946	4726773	3	2
unassigned	F51	1074895	Willow Creek, Timmerman rest stop, Blaine Co., ID	Snake River	11	720408	4801174	3	2
unassigned	F52	1082638	Big Wood River, Malad Gorge, Gooding Co., ID	Snake River	11	673403	4747854	3	2
unassigned	F53	1074940	Crooked Creek, State Wayside, Malheur Co., OR	Snake River	11	439936	4739533	4	2
unassigned	F56	1074883	Pashimeroi River, Goldburg Creek, Custer Co., ID	Snake River	12	276071	4929256	3	1
unassigned	F57	1003840	Salmon River, Kilpatrick, Lemhi Co., ID	Snake River	12	263812	4968410	3	1
unassigned	F58	1082063	Salmon River, Mackay Bar, Idaho Co., ID	Snake River	11	617390	5026758	3	2
unassigned	F60	1128547	"Len Lewis spring," Hagerman National Fish Hatchery, Gooding Co., ID	Snake River	11	675370	4736554	3	3
unassigned	F61	1128549	Thousand Springs, power plant outflow just above bridge, Gooding Co., ID	Snake River	11	676658	4736554	3	3
unassigned	F63	1128554	Snake River, King Hill SA, Elmore Co., ID	Snake River	11	645433	4762408	3	3
fuscus	F03	905343	Boise River, Willow Creek, Boise Co., ID	Snake River	11	601239	4833366	8	10
fuscus	F06	1072414	Owyhee River, below Whistling Bird Rapids, Malheur Co., OR	Snake River	11	443210	4775930	5	5
fuscus	F11	905346	Bruneau River, BLM low site, Owyhee Co., ID	Snake River	11	604160	4735760	5	4
fuscus	F44	1082059	Grande Ronde River, 0.2 km above mouth, Asotin Co., WA	Snake River	11	501191	5101192	DQ372901	DQ372902
fuscus	F46	1020712	Methow River north of Squaw Creek mouth, Okanagon Co., WA	Upper Columbia River	10	721120	5330680	5	1
fuscus	F54	1082645	Payette River, Banks Camp, Boise Co., ID	Snake River	11	570549	4880114	4	2
fuscus	F55	1074410	Imnaha River, Bare Creek, Wallowa Co., OR	Snake River	11	511997	5052195	3	3
fuscus	F59	1082627	Salmon River, Gasper Creek, Idaho Co., ID	Snake River	11	573077	5029711	3	2
fuscus	F62	1128552	Snake River, Grand View SA, Owyhee Co., ID	Snake River	11	573810	4760337	3	3

TABLE 1. Continued.

Species	Code	Voucher	Locality	Drainage	Zone	Easting	Northing	COI	cyt*b*
fuscus	F64	1128558	Owyhee River, above Beaver Charlie Cabin, Malheur Co., OR	Snake River	11	495143	4688893	3	3
fuscus	F66	1082066	Boise River, Badger Camp, Boise Co., ID	Snake River	11	604430	4835637	4	6
insolitus	—	863507	Page Springs, Harney Co., OR	Oregon Great Basin	11	347500	4740500	AY962934	AY963040

1996, Hershler 1999, Hershler et al. 2007). Shells were cleaned with commercial bleach (to remove surface deposits) before being photographed. Fresh material was collected when needed for anatomical or molecular studies. All of the samples used for molecular studies were collected after 1990. Small samples (ca. 25–50 individuals) were collected by hand or by washing rocks and stones. Subsamples were anaesthetized overnight with menthol crystals and fixed in dilute formalin. Preservation of subsamples was in 70% ethanol for morphologic study and in 90% ethanol for molecular study.

RESULTS

Mitochondrial DNA Analyses

The alignment of COI sequences yielded 634 bp, of which 98 sites were variable (15.5%) and 46 were parsimony informative (7.3%). Average base frequencies for COI were 27.3% A, 31.7% T, 21.7% C, and 19.3% G. Base frequencies were homogeneous across all sites (χ^2 = 13.75, df = 306, P = 1.00). For cyt*b*, 449 bp were sequenced, of which 74 were variable (16.5%) and 30 were parsimony informative (6.7%). Average base frequencies for cyt*b* were 26.5% A, 35.6% T, 20.6% C, and 17.3% G. Base frequencies were homogeneous across all sites (χ^2 = 15.38, df = 222, P = 1.00). The new sequences that were generated for this study were deposited in GenBank under accession numbers JQ996156–JQ996230 (one sequence per haplotype).

In the Bayesian analysis, Metropolis-coupled Markov chain Monte Carlo simulations were performed with 4 chains for 5,000,000 generations. At the end of the analysis, the average standard deviation of split frequencies was 0.0064 for COI and 0.0059 for cyt*b* and the Potential Scale Reduction Factor (PSRF) was 1, indicating that the runs had reached convergence. Haplotypes detected in *F. coloradensis*, unassigned pebblesnails from the Snake River basin, and the lower Salmon River population of *F. fuscus* (F59) formed a well-supported (100%) but weakly structured clade (Clade "A") in both the COI (Fig. 2) and cyt*b* (Fig. 3) Bayesian trees. Haplotypes from populations in the Bonneville, upper Green River, and Snake River basins were highly intermingled within clade A (Figs. 2, 3). The 41 COI and 21 cyt*b* haplotypes detected are detailed

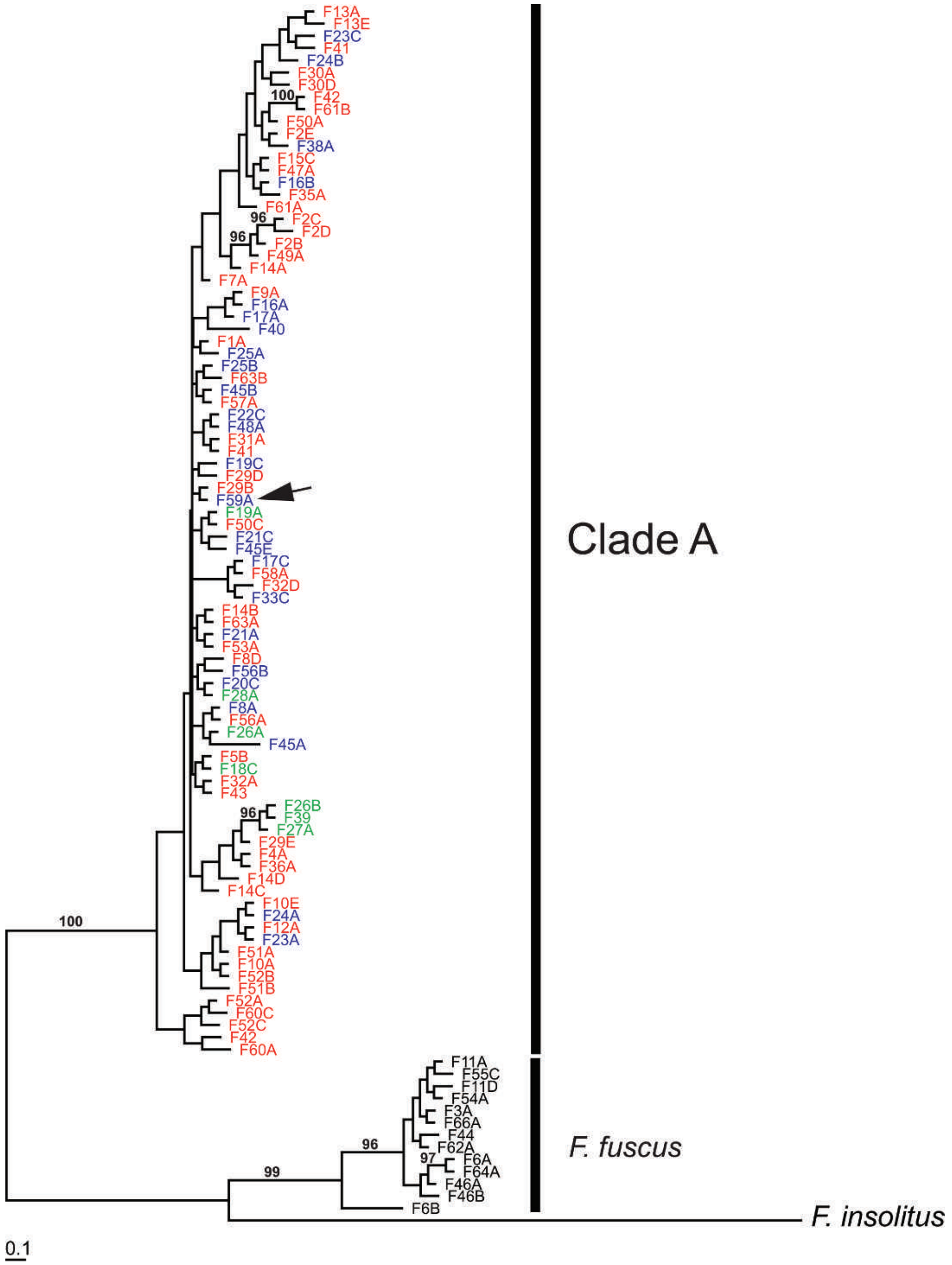


Fig. 2. Bayesian tree based on the COI data set. Sample codes as in Table 1. Terminals for *Fluminicola coloradensis* populations from the upper Green River and Bonneville basins are colored green and blue, respectively; those for the unassigned populations from the Snake River basin are colored red. The haplotype detected in the lower Salmon River population currently identified as *Fluminicola fuscus* (nested within the *F. coloradensis* clade) is indicated by an arrow. Posterior probabilities for nodes are given when ≥95%.

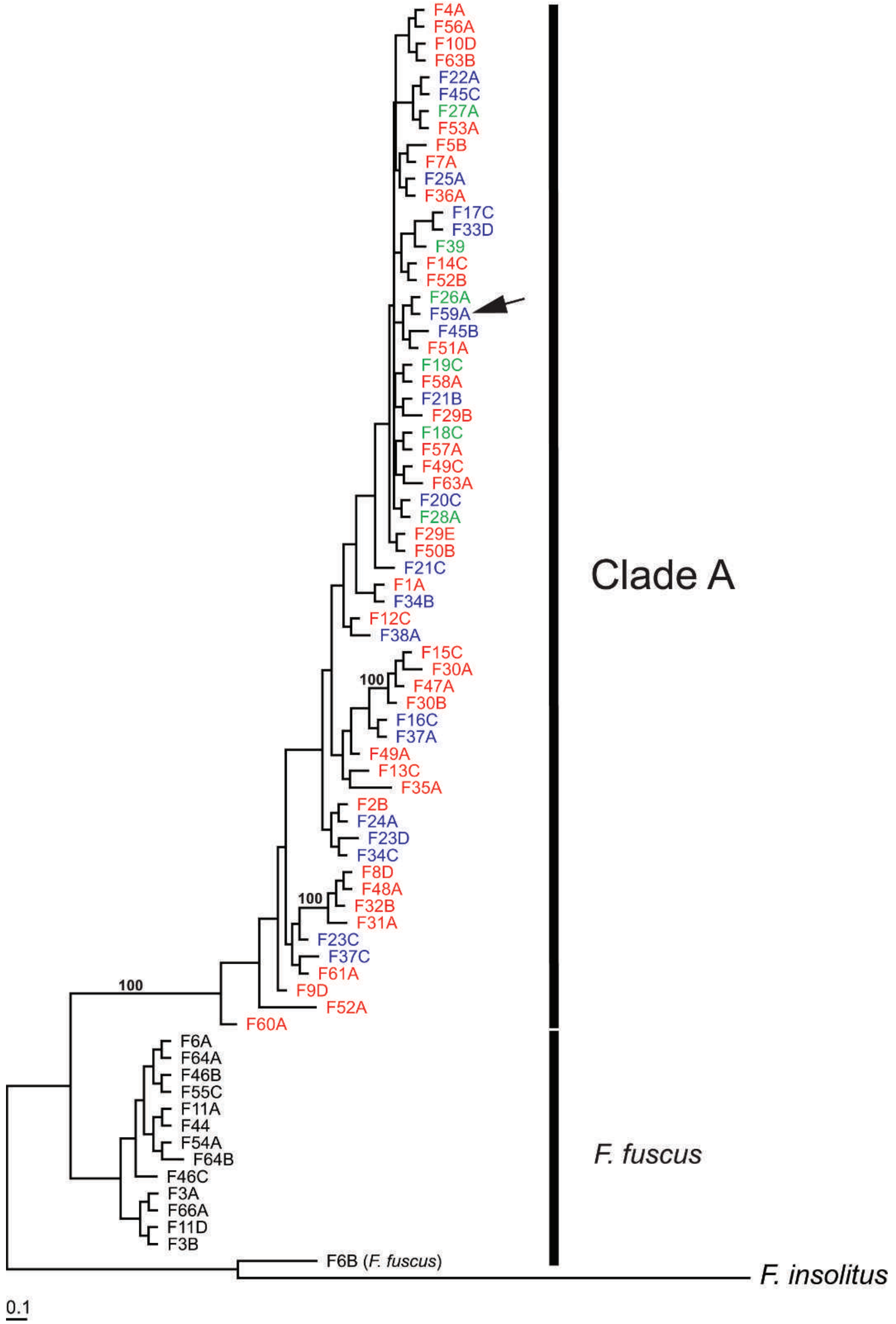


Fig. 3. Caption on page 95.

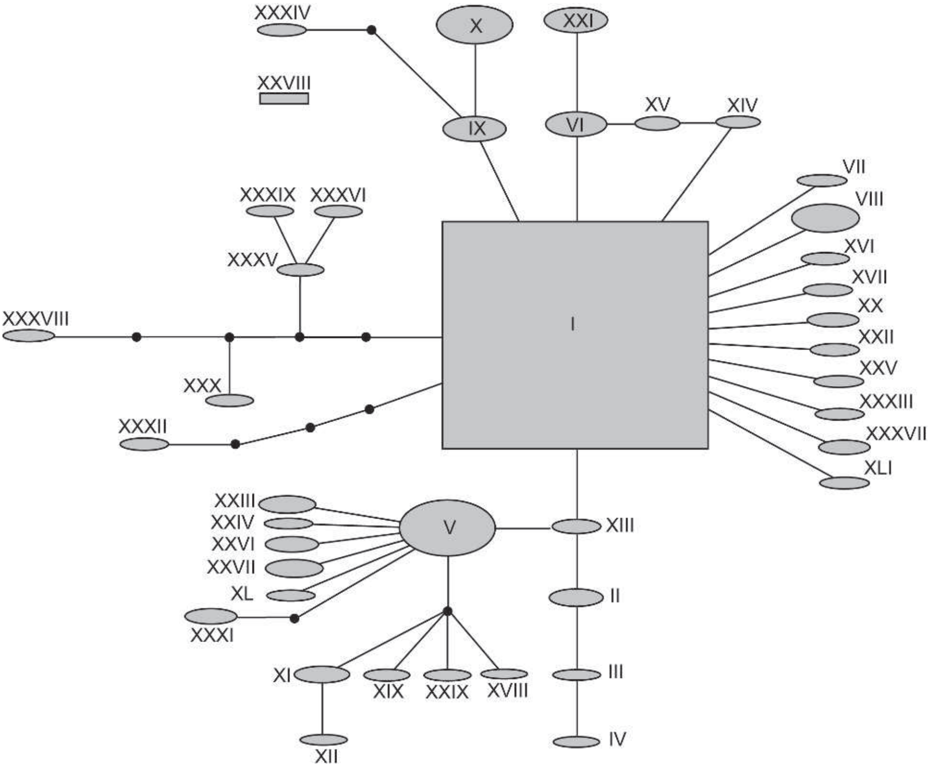


Fig. 4. Unrooted network (based on COI sequences) for the clade composed of *Fluminicola coloradensis,* unassigned pebblesnails from the Snake River basin, and *Fluminicola fuscus* from the lower Salmon River. Haplotypes are represented by gray-shaded shapes, which are sized in proportion to their frequency (Appendix 1). Branches represent mutational steps (single base pair) between haplotypes; black-filled circles represent inferred mutational steps.

TABLE 2. Analysis of molecular variance (AMOVA). Groups are upper Green River basin (samples 18, 19, 26, 27, 28, 39), Bonneville Basin (16, 17, 20, 21, 22, 23, 24, 25, 33, 37, 38, 40, 45), Snake River basin (1, 2, 4, 5, 7, 8, 9, 10, 12, 13, 14, 15, 29, 30, 31, 32, 34, 35, 36, 41, 42, 43, 47, 48, 49, 50, 51, 52, 53, 56, 57, 58, 59, 60, 61, 63).

Source of variation	df	Variance components	% of variation	Φ statistic
COI				
Among groups	2	0.02043	1.82	0.01821
Among populations within groups	50	0.72130	64.30	0.65488[a]
Within populations	150	0.38012	33.88	0.66117[a]
cyt*b*				
Among groups	2	0.02365	2.41	0.02413
Among populations within groups	45	0.83660	85.37	0.87482[a]
Within populations	82	0.11972	12.22	0.87784[a]

[a]$P < 0.01$

Fig. 3. Bayesian tree based on the cyt*b* data set. Sample codes as in Table 1. Terminals for *Fluminicola coloradensis* populations from the upper Green River and Bonneville basins are colored green and blue, respectively; those for the unassigned populations from the Snake River basin are colored red. The haplotype detected in the lower Salmon River population currently identified as *Fluminicola fuscus* (which is nested within the *F. coloradensis* clade) is indicated by an arrow. Posterior probabilities for nodes are given when ≥95%.

in Appendices 1 and 2, respectively (GenBank accession numbers JQ996156–JQ996196 for COI haplotypes I–XLI, and JQ996205–JQ996225 for cyt*b* haplotypes I–XXI). The pairwise sequence divergence among these ranged from 0.2%–1.6% for COI and 0.2%–1.8% for cyt*b*. Pairwise divergence among populations ranged from 0.0%–1.4% for COI and

0.0%–1.6% for cyt*b;* divergence within populations ranged from 0.0%–1.3% for both genes.

The most common COI haplotype (I) within clade A was detected in 5 upper Green River and 5 Bonneville basin populations of *F. coloradensis;* the lower Salmon River population of *F. fuscus;* and 18 unassigned populations spread among the upper reach, Owyhee River, and Salmon River segments of the Snake River watershed (Appendix 3). Most of the other haplotypes (30 of 40) were restricted to single populations and many were singletons. The most common cyt*b* haplotype (III) was detected in 5 upper Green River and 5 Bonneville Basin populations of *F. coloradensis;* the lower Salmon River population of *F. fuscus;* and 16 unassigned populations spread among the upper Snake, Crooked Creek, and Salmon River segments of the Snake River watershed (Appendix 4). Most of the other haplotypes (14 of 20) were restricted to single populations, and many were singletons. Haplotypes were organized in a star-like pattern (with the common haplotype centrally positioned) in both of the TCS networks (e.g., Fig. 4, the COI topology), suggesting recent population expansion and diversification (Slatkin and Hudson 1991) within this clade.

When populations belonging to clade A were grouped by major drainage basin (upper Green River, Bonneville, Snake River) most of the COI and cyt*b* variation was partitioned among populations within basins (64.3% and 85.4%, respectively) and within populations (33.9% and 12.2%); variation between basins was very small (1.8% and 2.4%) and nonsignificant (Table 2).

Morphology

Shell size, shape, and color varied considerably among populations of both *F. coloradensis* (Fig. 5A–G) and the unassigned Snake River basin pebblesnails (Fig. 5H–T). Variation was also marked within some of the populations (e.g., Fig. 5O–Q). Although most of the unassigned pebblesnails conformed well to *F. coloradensis,* some of the populations distributed along the Snake River between Murtaugh and King Hill were distinguished by their narrow, high-spired shells (Fig. 5N). The shells of the lower Salmon River populations currently identified as *F. fuscus* (e.g., Fig. 5U) also fall into the range of variation of *F. coloradensis;* note that none of the former have the well-developed subsutural angulation or keel on the later whorls that characterizes *F. fuscus* (Hershler and Frest 1996). The unassigned and lower Salmon River pebblesnails also closely resembled *F. coloradensis* anatomically, although some populations differed from previously studied material of this species in several features such as the shape of the distal section of the penis and the shape of bursa copulatrix (Fig. 6). However, similar variation was observed among populations of *F. coloradensis* that were re-studied during the course of this project. We did not observe significant differences in the number of cusps and shape of the radular teeth among *F. coloradensis* and the unassigned pebblesnails (Table 3; Fig. 7, compare with Hershler and Frest 1996 : fig. 8A–C).

DISCUSSION

Our findings do not provide any basis for restricting *F. coloradensis* to the upper Green River basin per recent proposals (Frest 1999, Frest and Johannes 2000). These results also indicate that *F. coloradensis* and the unassigned Snake River basin populations of *F. hindsi sensu* Taylor (1966) are closely similar both morphologically and genetically. Haplotypes observed in *F. coloradensis* and the unassigned populations are highly intermingled within a single, well-supported clade that lacks obvious structure. The variation among haplotypes in this clade was less than typically

Fig. 5. Photographs of shells of *Fluminicola coloradensis* (A–G), unassigned pebblesnails from the Snake River basin (H–T), and *Fluminicola fuscus* from the lower Salmon River (U): **A,** USNM 526631, Green River, WY (holotype); **B,** USNM 905307 Green River, Warren bridge, WY; **C,** USNM 905374, Hams Fork, Taylor Creek, WY; **D,** USNM 1116224, South Fork Smiths Fork, at Cokeville, WY; **E,** USNM 1003669, Big Malad Spring, Malad Valley, ID; **F,** USNM 1116219, Beaver Creek, below Thorn Creek confluence, UT; **G,** USNM 1113253, Deep Creek, above Stone Canal, ID; **H,** USNM 1144771, Snake River, Grand Canyon, WY; **I,** USNM 1003829, Teton River, Buxton bridge, ID; **J,** USNM 1003827, Summit Creek, Little Lost River drainage, ID; **K,** USNM 905368, Raft River, Narrows gauge, ID; **L,** USNM 883518, Rock Springs, Arbon Valley, ID; **M,** USNM 1082637, Snake River, Murtaugh, ID; **N,** USNM 905345, Snake River, Clear Lake bridge, ID; **O–Q,** USNM 1082642, Snake River, below Bliss Dam, ID; **R,** USNM 1074940, Crooked Creek, Owyhee River drainage, OR; **S,** USNM 1074883, Pashimeroi River, Goldburg Creek, ID; **T,** USNM 1003840, Salmon River, Kilpatrick, ID; **U,** USNM 1082061, Salmon River, Gasper Creek, ID. Scale bar = 1.0 mm.

Fig. 5. Caption on page 96.

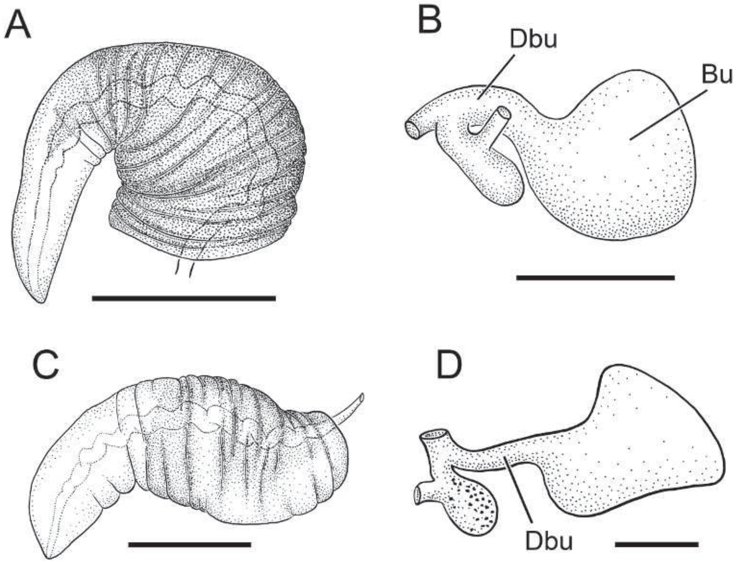
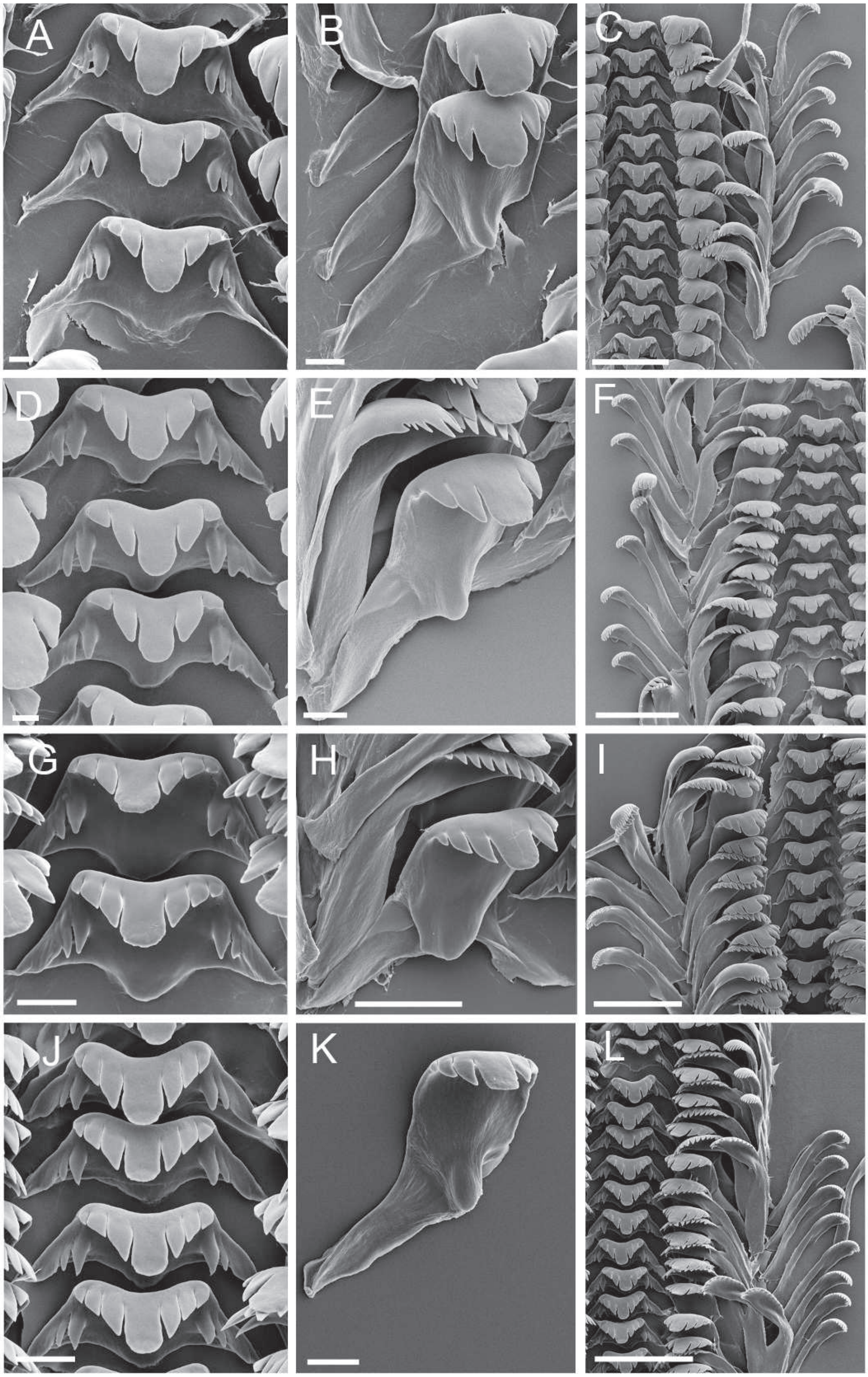


Fig. 6. Penis and female bursa copulatrix of unassigned pebblesnails from a spring along Hwy. 30 north of Hagerman, Snake River basin, ID, USNM 873464 (A and B, respectively) and *F. coloradensis* from its type locality area (C and D, respectively). Drawings C and D were modified from Hershler and Frest (1996: figs. 9a and 10b, respectively). Bu = bursa copulatrix, Dbu = bursa copulatrix duct. Scales = 1.0 mm.

TABLE 3. Variation in number of cusps on the radular teeth among populations of *Fluminicola coloradensis* and unassigned Snake River basin pebblesnails; $n = 5$ for all samples (see Hershler et al. 2007 for methods).

	Tooth type					
Species and locality	Central, cutting edge	Central, basal	Lateral, outer side	Lateral, inner side	Inner marginal	Outer marginal
Fluminicola coloradensis						
Green River, north-northeast of Bronx, WY (USNM 1003679)	2–4	2–3	2–5	2–3	10–15	11–19
Blacksmith Fork, UT (USNM 883861)	2–3	1–3	3–4	2–3	8–12	10–18
Big Malad Spring, ID (USNM 1003669)	3–5	2–4	3–5	2–5	11–14	13–23
Unassigned						
Snake River, Grand Canyon, WY (USNM 883514)	3–4	2–3	2–4	1–3	9–12	8–11
Teton River, Hog Hollow bridge, ID (USNM 905351)	3–5	2–3	2–4	2–4	9–17	11–18
Birch Creek, ID (USNM 1003826)	3–5	2–4	2–5	2–4	9–13	11–17
Snake River, Clear Lake bridge, ID (USNM 905364)	2–4	2–3	2–4	1–2	10–13	10–16
Crooked Creek, OR (USNM 1074940)	3–4	2–4	2–4	2–3	11–15	13–19
Mouth of Pashimeroi River, ID (USNM 905288)	3–4	1–3	3–5	2	10–15	12–20
Salmon River, Mackay Bar, ID (USNM 1082063)	3–4	2–3	2–4	2–3	10–14	10–17

Fig. 7 (on page 99). Scanning electron micrographs of central (A, D, G, J) and lateral (B, E, H, K) radular teeth and portions of radular ribbons (C, F, I, L) from unassigned populations of *Fluminicola* from the Snake River basin: **A–C,** USNM 883514, Snake River, Grand Canyon, WY; **D–F,** USNM 905364, Snake River, Clear Lake bridge, ID; **G–I,** USNM 1074940, Crooked Creek, Owyhee River drainage, OR; **J–L,** USNM 1082063, Salmon River, Kilpatrick, ID. Scale bars: A, D = 10 µm; B, E, G–H, J–K = 20 µm; C, F, I, L = 100 µm.


A
B
C
D
E
F
G
H
I
J
K
L

observed between congeners (>2% for both genes in most cases; Hershler et al. 2007). Based on these results we conclude that the unassigned Snake River basin populations are conspecific with *F. coloradensis.* The other taxonomic change that we are implementing based on our findings is to transfer the lower Salmon River populations currently classified as *F. fuscus* (per Hershler and Frest 1996:12) to *F. coloradensis.* The first author previously had difficulty identifying these pebblesnails because of their typically eroded shells (Fig. 5U). The material that we are newly referring to *F. coloradensis* is listed in Appendix 5.

The shallow genetic structuring of *F. coloradensis* across 3 major drainage basins (Colorado River, Snake River, Bonneville) detailed herein contrasts strikingly with the extensive diversification in the upper Sacramento River basin documented in the only previous molecular study of pebblesnails (Hershler et al. 2007) and suggests that the biogeographic history of *Fluminicola* in relation to topography and drainage has been complex. The locally extensive differentiation of pebblesnails in the upper Sacramento River watershed was attributed to the high fidelity of (most of) the members of that fauna to insular spring and spring-influenced habitats, and the complex late-Cenozoic tectonic-volcanic history of the region (Hershler et al. 2007). The limited differentiation of *F. coloradensis* across its broad geographic range may be attributed, in part, to the typical occurrence of this species in rivers and other large, well-integrated habitats. There is also abundant geologic evidence of late-Quaternary drainage exchanges between the Snake River and Bonneville watersheds—e.g., diversion of the Bear River from the former to the latter (Bouchard et al. 1998), spillover of Lake Bonneville into the Snake River basin (Malde 1968, O'Connor 1993)—that could have facilitated dispersal of *F. coloradensis* among these basins. Although there is no evidence that the Green River was integrated with either the Bonneville or Snake River basins during the late Cenozoic, dispersal of pebblesnails across the upper Green River drainage divide may have been facilitated instead by headwater stream captures. Hansen (1985, 1986) suggested that inter-basinal transfer of fishes was facilitated by (one or more of) a series of possible late-Quaternary headwater stream diversion points that he identified along this divide.

The disjunct distribution of *F. coloradensis* (as newly constituted herein) in the Snake River basin (Fig. 1) suggests additional complex aspects of biogeographic history. Most of these populations are distributed from the Snake River headwaters to just above the mouth of the Bruneau River where the ranges of *F. coloradensis* and *F. fuscus* abut. We are not aware of any sympatric occurrences of these sister species. The single, isolated occurrence of *F. coloradensis* in the middle Snake River basin (Crooked Creek), which is otherwise occupied only by *F. fuscus* (Fig. 1), may have resulted from translocation, as evidenced by the detection of only the most common COI (I) and cyt*b* (III) haplotypes in this population. The occurrence of *F. coloradensis* in the Salmon River is intriguing given that the lower (and middle) Snake River basin is otherwise occupied only by *F. fuscus.* The close proximity of *F. coloradensis* populations on either side of the divide between the upper Salmon and upper Snake River watersheds suggests that the former may have been colonized as a result of a prior headwater transfer. Ruppel (1967) provides geologic evidence of late-Quaternary reversal of flow of the Lemhi River (now tributary to the Salmon River) consistent with this hypothesis.

Fluminicola coloradensis is currently ranked as imperiled or vulnerable (G2G3) by NatureServe (2011) and imperiled (G2) by the Idaho Department of Fish and Game (2005). Our finding that this species is much more widely distributed than previously thought suggests that it may not merit these rankings, at least on a rangewide basis. Conservation measures should perhaps be focused instead on geographic subunits of this species that may be at risk owing to local habitat degradation (i.e., the relatively small number of populations in the Bonneville and upper Green River basins).

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APPENDIX 1. COI haplotypes detected within clade A. The column headings indicate base pair positions.

Haplotype	14	22	40	45	52	55	58	67	73	82	101	118	127	145	158	178	187	190
I (F1A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
II (F2B)	T	G	C	C	G	A	C	G	A	A	G	T	C	T	C	C	C	A
III (F2C)	T	A	C	C	G	A	C	G	A	A	G	T	C	T	C	C	C	A
IV (F2D)	T	A	C	C	G	A	C	G	A	A	G	T	C	T	C	C	C	A
V (F2E)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
VI (F4A)	T	G	C	C	A	A	T	G	A	A	G	T	C	T	C	C	C	A
VII (F8D)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
VIII (F9A)	C	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
IX (F10A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
X (F10E)	T	A	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XI (F13A)	T	A	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XII (F13E)	T	A	C	C	A	A	C	G	A	A	A	T	C	T	C	C	C	A
XIII (F14A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XIV (F14C)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XV (F14D)	T	G	C	C	A	A	T	G	A	A	G	T	C	T	C	C	C	A
XVI (F19C)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XVII (F21C)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	G
XVIII (F23C)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XIX (F24B)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XX (F25A)	T	G	C	C	A	A	C	G	G	A	G	T	C	T	C	C	C	A
XXI (F26B)	T	G	C	C	A	A	T	G	A	G	G	T	C	T	C	C	C	A
XXII (F29D)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXIII (F30A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXIV (F30D)	T	G	C	C	A	A	C	G	A	A	G	T	T	T	C	C	C	A
XXV (F32D)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	T	C	C	A
XXVI (F35A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXVII (F38A)	T	G	C	C	A	G	C	G	A	A	G	T	C	T	C	C	C	A
XXVIII (F40)	–	–	C	G	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXIX (F41A)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	T	A
XXX (F42A)	T	G	C	C	A	A	C	A	A	A	G	T	C	T	C	C	C	A
XXXI (F42B)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXXII (F45A)	T	G	C	C	A	A	C	G	A	A	G	C	C	T	C	C	C	A
XXXIII (F45E)	T	G	C	C	A	A	C	G	A	A	G	T	C	C	C	C	C	A
XXXIV (F51B)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXXV (F52A)	T	G	C	C	A	A	C	A	A	A	G	T	C	T	C	T	C	A
XXXVI (F52C)	T	G	C	C	A	A	C	A	A	A	G	T	C	T	C	T	C	A
XXXVII (F56B)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XXXVIII (F60A)	T	G	C	C	A	A	C	A	A	A	G	T	C	T	T	C	C	A
XXXIX (F60C)	T	G	C	C	A	A	C	A	A	A	G	T	C	T	C	T	C	A
XL (F61A)	T	G	A	C	A	A	C	G	A	A	G	T	C	T	C	C	C	A
XLI (F63B)	T	G	C	C	A	A	C	G	A	A	G	T	C	T	C	C	T	A

214	229	340	353	364	368	373	374	376	417	451	474	490	500	520	559	565	574	578	596	610	628
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	G	A	A	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	G	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	G	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	G	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	G	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	A	G	G	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	C	G	G	G	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
T	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	T	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	G	C	–	–
C	A	C	A	C	G	G	G	C	T	G	G	G	T	A	G	A	G	C	T	C	T
C	A	T	A	C	G	A	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	G	C	A	C	G	G	G	C	T	G	G	A	C	A	G	A	G	C	T	C	T
C	A	C	G	C	G	G	G	T	T	G	G	A	T	G	A	A	G	C	T	C	C
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	G	C	A	C	G	G	G	T	T	A	G	A	T	A	A	G	G	C	T	C	T
C	A	C	A	C	G	A	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	A	G	T	T	G	A	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	G	A	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	T	A	C	A	A	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T
C	A	C	A	C	G	A	G	T	T	G	G	A	T	A	A	A	G	C	T	T	T
C	A	C	A	C	G	G	G	C	T	G	G	A	T	A	G	A	G	C	T	C	T
C	A	C	A	C	G	G	G	T	T	G	G	A	T	A	A	A	G	C	T	C	T

APPENDIX 2. Cyt*b* haplotypes detected within clade A. The column headings indicate base pair positions.

Haplotype	4	22	29	73	103	133	136	151	175	185	193	199	226	229	301	319	328	342	364	373	383	385	404	421	422	444
I (F1A)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	A	G	T	A	C	A	A	A	T	T
II (F2B)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
III (F4A)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	G	G	T	A	C	A	A	A	C	T
IV (F5B)	G	T	T	A	G	T	T	T	G	T	G	A	G	G	T	T	G	G	T	A	C	A	A	A	C	T
V (F8D)	G	T	C	A	A	T	T	T	G	T	A	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
VI (F13C)	G	T	C	A	G	C	T	T	G	T	G	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
VII (F15C)	G	T	C	A	G	T	T	T	A	T	G	A	G	G	T	T	A	G	T	A	C	C	A	A	C	T
VIII (F16C)	G	T	C	A	G	T	T	T	A	T	G	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
IX (F17C)	G	T	C	A	G	T	T	T	G	T	G	A	G	A	T	T	G	G	T	A	C	A	A	A	C	T
X (F21C)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	G	G	T	A	C	A	A	A	T	T
XI (F23D)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	C	T	A	G	T	A	C	A	A	A	C	T
XII (F29B)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	G	G	T	A	C	A	G	A	C	T
XIII (F30A)	G	T	C	A	G	T	T	C	A	T	G	A	G	G	T	T	A	G	T	A	C	C	A	A	C	T
XIV (F31A)	G	T	C	A	A	T	T	T	G	T	A	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
XV (F35A)	G	T	C	A	G	T	T	T	G	T	G	T	G	G	T	T	A	G	C	C	C	A	A	A	C	T
XVI (F37C)	G	T	C	A	G	T	C	T	G	T	G	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
XVII (F38A)	G	T	C	A	G	T	T	T	G	G	G	A	G	G	T	T	A	G	T	A	C	A	A	A	C	T
XVIII (F45B)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	T	G	G	T	A	C	A	A	A	C	C
XIX (F52A)	G	C	C	A	G	T	T	T	G	T	G	A	A	G	T	T	A	A	T	G	C	A	A	G	C	T
XX (F60A)	A	T	C	G	G	T	T	T	G	T	G	A	G	G	T	T	A	G	T	A	T	A	A	G	C	T
XXI (F63A)	G	T	C	A	G	T	T	T	G	T	G	A	G	G	T	C	G	G	T	A	C	A	A	A	C	T

APPENDIX 3. Distribution of COI haplotypes detected in clade A. Line shading is to assist the reader.

	Sample																			
Haplotype	F1	F2	F4	F5	F7	F8	F9	F10	F12	F13	F14	F15	F16	F17	F18	F19	F20	F21	F22	F23
I	6			5	5	5					1			1	3	4	3	3	3	
II		1																		
III		1																		
IV		1																		
V		2										5	7							
VI			3																	
VII						1														
VIII							5						1	2						
IX								4												
X								1	5											3
XI										4										
XII										1										
XIII											2									
XIV											1									
XV											1									
XVI																1				
XVII																		1		
XVIII																				1

	Sample																			
Haplotype	F24	F25	F26	F27	F28	F29	F30	F31	F32	F33	F35	F36	F38	F39	F40	F41	F42	F43	F45	F47
I		2	2		5	2		3	5	3						1		1	3	
II																				
III																				
IV																				
V																				5
VI						1						3								
VII																				
VIII																				
IX																				
X	3																			
XI																				
XII																				
XIII																				
XIV																				
XV																				
XVI																				
XVII																				
XVIII																				
XIX	1																			
XX		2																		
XXI			2	3																
XXII						1														
XXIII							4													
XXIV							1													
XXV									1											
XXVI											3									
XXVII													3							
XXVIII															1					
XXIX																1				
XXX																	1			
XXXI																	1			
XXXII																			1	
XXXIII																			1	

APPENDIX 3. Continued.

	Sample												
Haplotype	F48	F49	F50	F51	F52	F53	F56	F57	F58	F59	F60	F61	F63
I	5		1			4	1	3	3	3			2
II		3											
III													
IV													
V			2										
VI													
VII													
VIII													
IX				2	1								
X													
XI													
XII													
XIII													
XIV													
XV													
XVI													
XVII													
XVIII													
XIX													
XX													
XXI													
XXII													
XXIII													
XXIV													
XXV													
XXVI													
XXVII													
XXVIII													
XXIX													
XXX													
XXXI												2	
XXXII													
XXXIII													
XXXIV				1									
XXXV					1								
XXXVI					1								
XXXVII							2						
XXXVIII											2		
XXXIX											1		
XL												1	
XLI													1

APPENDIX 4. Distribution of cyt*b* haplotypes detected in clade A. Line shading is to assist the reader.

	Sample																			
Haplotype	F1	F2	F4	F5	F7	F8	F9	F10	F12	F13	F14	F15	F16	F17	F18	F19	F20	F21	F22	F23
I	5																			
II	1	2					2		2											1
III			3		4			2			2				2	2	2	2	2	
IV				3																
V						2														
VI										2										
VII												2								
VIII													4							
IX														2						
X																		1		
XI																				1

APPENDIX 4. Continued.

	Sample																			
Haplotype	F1	F2	F4	F5	F7	F8	F9	F10	F12	F13	F14	F15	F16	F17	F18	F19	F20	F21	F22	F23
XII																				
XIII																				
XIV																				
XV																				
XVI													1							

	Sample																			
Haplotype	F24	F25	F26	F27	F28	F29	F30	F31	F32	F33	F35	F36	F38	F39	F40	F41	F42	F43	F45	F47
I																				
II	3																			
III		4	5	4	5	1						3							1	
IV																				
V									4											
VI																				
VII							4													4
VIII																				
IX										2										
X																				
XI																				
XII						3														
XIII							1													
XIV								3												
XV											2									
XVI																				
XVII													2							
XVIII																			1	

	Sample												
Haplotype	F48	F49	F50	F51	F52	F53	F56	F57	F58	F59	F60	F61	F63
I													
II		2										2	
III		1	2	2	1	2	1	1	2	2			1
IV													
V	3												
VI													
VII													
VIII													
IX													
X													
XI													
XII													
XIII													
XIV													
XV													
XVI													
XVII													
XVIII													
XIX					1								
XX											2		
XXI													1

Appendix 5. Snake River basin material referred to *Fluminicola coloradensis.* Universal transverse mercator (UTM) coordinates (NAD83) were estimated for some localities based on original township and range data.

IDAHO. ***Bannock County:*** Mink Creek, Cherry Springs, zone 12, 385885 E, 4734040 N, USNM 1074941. Marsh Creek, Goodenough Creek, zone 12, 399555 E, 4720456 N, USNM 1003831. McCammon, zone 12, 402094 E, 4723727 N, UMBMNH uncat. Marsh Creek, Arimo, zone 12, 402648 E, 4713481 N, USNM 1003841. Portneuf River, upper access, zone 12, 416912 E, 4729044 N, USNM 904950. Portneuf River, upper access area, zone 12, 416946 E, 4729108 N, USNM 1116233. ***Bingham County:*** McTucker Creek, spring, zone 12, 367555 E, 4765851 N, USNM 905347, USNM 1080262. Ferry Butte, upper springs, zone 12, 376449 E, 4775027 N, USNM 1082636. Snake River, Firth, zone 12, 403992 E, 4796177 N, USNM 905340, USNM 1074884. Snake River, Shelley, zone 12, 405364 E, 4803200 N, USNM 1003876. Blackfoot River, Wolverine-Cedar, zone 12, 416770 E, 4787188 N, USNM 1074939. Blackfoot River, Trail Creek, zone 12, 425990 E, 4775487 N, USNM 905357. Rawlins Creek, low, zone 12, 428138 E, 4774742 N, USNM 905356. Willow Creek, Pole Bridge, zone 12, 439116 E, 4788762 N, USNM 905411. Poison Creek, Warm Spring, zone 12, 441409 E, 4763564 N, USNM 905349. ***Blaine County:*** Silver Creek, BLM north site, zone 12, 256788 E, 4792992 N, USNM 1002786. Silver Creek, BLM south site, zone 12, 256827 E, 4792468 N, USNM 905377, USNM 1002790. Snake River, McTucker Ramp, zone 12, 364544 E, 4765210 N, USNM 1074879. Willow Creek, Timmerman rest stop, zone 11, 720408 E, 4801174 N, USNM 1074881, USNM 1074895. Grove Creek, Gannett Spring, zone 11, 728869 E, 4802978 N, USNM 1002791. Stalker Creek and Mud Creek, zone 11, 729596 E, 4799267 N, USNM 1002787. Grove Creek, Thompson Creek, zone 11, 730000 E, 4801460 N, USNM 1002792. Loving Creek, Hayspur High, zone 11, 731391 E, 4802341 N, USNM 904964, USNM 1003870. Silver Creek, west site, zone 11, 734506 E, 4800992 N, USNM 904956. Silver Creek, upper U.S. 20 bridge, zone 11, 734803 E, 4800146 N, USNM 1002788. Silver Creek East, zone 11, 736042 E, 4801612 N, USNM 1003888. ***Bonneville County:*** Snake River, Idaho Falls Canal, zone 12, 414487 E, 4819762 N, USNM 1082635. Snake River, Payne, zone 12, 414674 E, 4826257 N, USNM 1003832. Snake River, Osgood, zone 12, 415282 E, 4824216 N, USNM 1094138, USNM 1094139. Willow Creek, Kepps Crossing, zone 12, 436351 E, 4806380 N, USNM 905303, USNM 905402. Snake River, Byington Park, zone 12, 446347 E, 4830186 N, USNM 1116229. Snake River, Black Canyon, zone 12, 462551 E, 4826308 N, USNM 1003882. Snake River, Spring Creek access boat launch, zone 12, 467960 E, 4810630 N, USNM 1073420. Salt River, west side at McCoy Creek Road (FS 87), just upstream of Palisades Reservoir, zone 12, 496085 E, 4776964 N, USNM 1144429. ***Caribou County:*** Little Blackfoot River, Henry, zone 12, 456810 E, 4750734 N, USNM 904958. Little Blackfoot River east of ID 34 bridge on north end of Henry East of Blackfoot Reservior, zone 12, 456900 E, 4750520 N, USNM 1144924. Meadow Creek, mouth, zone 12, 457930 E, 4752515 N, USNM 905401. Chubbs Spring northeast of Blackfoot Reservoir, zone 12, 458805 E, 4760379 N, USNM 1116234. Chubb Springs (south), zone 12, 458820 E, 4759930 N, USNM 1144353. Chubb Springs (north), zone 12, 458900 E, 4760190 N, USNM 1144352. Blackfoot River, The Narrows, zone 12, 469816 E, 4738036 N, USNM 1116235. Blackfoot River, The Narrows, zone 12, 471043 E, 4738400 N, USNM 905305. ***Cassia County:*** Raft River, zone 12, 292407 E, 4659930 N, UMBMNH uncat. Raft River Narrows gage, zone 12, 297370 E, 4660129 N, USNM 905368. Raft River Narrows bridge, zone 12, 297703 E, 4660475 N, USNM 1003834. ***Clark County:*** Birch Creek, zone 12, 342162 E, 4899226 N, UMBMNH uncat. Birch Creek, Kaufman, zone 12, 342317 E, 4899681 N, USNM 905291. Salmon River, river km 411.1, bridge near Morgan Creek road, zone 11, 724935 E, 4943235 N, USNM 1144764. ***Custer County:*** Grandview Canyon, Willow Creek on ID 93, zone 12, 267669 E, 4891469 N, USNM 1144713. Pashimeroi River, Goldburg Creek, zone 12, 276071 E, 4929256 N, USNM 1074883. Summit Creek at hwy. crossing, zone 12, 303905 E, 4905388 N, USNM 1123928. Summit Creek, BLM Camp, zone 12, 304074 E, 4905326 N, USNM 892155, USNM 1003827. Summit Creek, Sawmill Canyon bridge, zone 12, 310493 E, 4901113 N, USNM 905300, USNM 905372, USNM 1003842. Salmon River near ID 75 road km 321.3, zone 11, 677519 E, 4903501 N, USNM 883740. Salmon River, Penal Gulch, zone 11, 724052 E, 4936289 N, USNM 1003874. Salmon River, Spring Gulch, zone 11, 726442 E, 4946159 N, USNM 1003853, USNM 1082646. Pashimeroi River, mouth, zone 11, 733901 E, 4952909 N, USNM 905288, USNM 1003837. Pashimeroi River, Burstedt Lane, zone 11, 735590 E, 4949912 N, USNM 1026462. ***Elmore County:*** Snake River, C.J. Strike Reservoir, main arm, zone 11, 585967 E, 4755761 N, ALBRCIDA 73101. Snake River, zone 11, 606575 E, 4754710 N, ALBRCIDA 7011. Snake River, zone 11, 608430 E, 4755365 N, ALBRCIDA 47384. Snake River, between island and rocky bar, zone 11, 614542 E, 4754858 N, ALBRCIDA 57131. Snake River, zone 11, 614676 E, 4754615 N, ALBRCIDA 7012. Snake River, zone 11, 618084 E, 4755096 N, ALBRCIDA 27322. Snake River, zone 11, 620293 E, 4755382 N, ALBRCIDA 27308. Snake River, zone 11, 621572 E, 4754709 N, ALBRCIDA 27274. Snake River, zone 11, 622753 E, 4753820 N, ALBRCIDA 27219. Snake River, zone 11, 624255 E, 4753936 N, ALBRCIDA 27138. Snake River, 3/4 down down Schoff's Island, zone 11, 627620 E, 4754672 N, ALBRCIDA 29879. Snake River, 3/4 way down midstream island, zone 11, 629527 E, 4755277 N, ALBRCIDA 27505. Snake River, 0.5 km into The Narrows, zone 11, 631408 E, 4756030 N, ALBRCIDA 29897. Snake River, zone 11, 632924 E, 4756781 N, UMBMNH uncat. Snake River, midway part of island, zone 11, 633061 E, 4756502 N, ALBRCIDA 29750. Snake River, midway part of island, zone 11, 635057 E, 4755619 N, ALBRCIDA 29715. Snake River, zone 11, 635806 E, 4755361 N, ALBRCIDA 26115. Snake River, 20 m below large center island, zone 11, 637842 E, 4755062 N, ALBRCIDA 26134. Snake River, zone 11, 640508 E, 4757318 N, ALBRCIDA 26949. Snake River, 75 m below ranch on opposite bank, zone 11, 641134 E, 4759012 N, ALBRCIDA 26700. Snake River, 45 m above large island, zone 11, 642473 E, 4759009 N, ALBRCIDA 44797. Snake River, 40 m above series of small islands, zone 11, 643668 E, 4760493 N, ALBRCIDA 44955. Snake River, 0.5 km above King Hill creek, zone 11, 644330 E, 4761456 N, ALBRCIDA 45642. Snake River, King's Hill SA, zone 11, 645433 E, 4762408 N, USNM 1128554. Snake River, zone 11, 650481 E, 4755051 N, UMBMNH uncat. Snake River, adjacent to Bancroft Springs at river km 889.5, zone 11,

Appendix 5. Continued.

APPENDIX 5. Continued.

650556 E, 4754900 N, USNM 1073424. Bancroft Springs, main outlets at south end of complex, river km 889.5, zone 11, 650561 E, 4754897 N, USNM 1073428, USNM 1144624. ***Fremont County:*** Henry's Fork River, Saint Anthony, zone 12, 445321 E, 4868233 N, USNM 1003872. Henry's Fork River, Del Rio bridge, zone 12, 447742 E, 4869003 N, USNM 905370, USNM 1025884. Teton River, Hog Hollow bridge, zone 12, 451080 E, 4864701 N, USNM 905351. Henry's Fork River, Ashton dock, zone 12, 463525 E, 4884358 N, USNM 905341, USNM 905381, USNM 1025966. West side of Henrys Fork at Riverside Campground, ca. 2.09 km southeast of U.S. 20/I-91, zone 12, 463820 E, 4901820 N, USNM 1144427. Henry's Fork River, U.S. 20 bridge north of Ashton, zone 12, 464111 E, 4884317 N, USNM 883745. Henry's Fork River, Osborne bridge, zone 12, 464181 E, 4907725 N, USNM 905386. Falls River, Hwy. 32, zone 12, 465637 E, 4874224 N, UMBMNH uncat. Buffalo River, U.S. 20, zone 12, 470364 E, 4918813 N, USNM 905385, USNM 905398. Falls River north-northeast of Grainville, zone 12, 471297 E, 4878210 N, USNM 1116230. Robinson Creek, mouth, zone 12, 474082 E, 4884619 N, USNM 905403. Lucky Dog Creek, low bridge, zone 12, 477584 E, 4925704 N, USNM 892157, USNM 1003873. Lucky Dog Creek, low bridge (mouth), zone 12, 477910 E, 4925792 N, USNM 903631. Henry's Fork River, water railhead, zone 12, 478400 E, 4927123 N, USNM 905315. Henry's Fork River, Big Springs, zone 12, 479728 E, 4927252 N, USNM 854977. Large spring pool and source spring run just south of John Sack Cabin East side of Big Springs complex east of ID 84, zone 12, 479820 E, 4927100 N, USNM 1144428. Rock Creek, Robinson Creek, zone 12, 479938 E, 4884287 N, USNM 903630, USNM 1003830. Porcupine Station Springs, zone 12, 481837 E, 4882127 N, USNM 1003883. ***Gooding County:*** Snake River, rapids ca. 100 m above confluence with Clover Creek, zone 11, 647929 E, 4762412 N, USNM 873470. Snake River, below Bliss Dam, zone 11, 657041 E, 4753149 N, USNM 1082642. Snake River, Bliss bridge, zone 11, 665813 E, 4753455 N, USNM 905394, USNM 1082640. Snake River, at river km 916.3, zone 11, 666980 E, 4749610 N, USNM 1073422, USNM 1123797. Snake River, zone 11, 670025 E, 4749650 N, UMBMNH uncat. River Road spring run, 4.83 km southeast of Bliss, zone 11, 670065 E, 4749860 N, USNM 1073421, USNM 1144700. Unnamed spring, pool above river road (old Hwy. 30) at Snake River Pottery turnoff, zone 11, 670097 E, 4750052 N, USNM 873460. Headwater alcove of unnamed spring, middle of Hwy. 30 grade, at base of basalt cliffs, zone 11, 670808 E, 4749548 N, USNM 873464. Snake River at river km 919.2, zone 11, 670972 E, 4748801 N, USNM 1073423. Snake River just downstream (ca. 18.3 m) of outflow of Malad River Power Plant on east side of river, river km 918.8, zone 11, 670972 E, 4748010 N, USNM 1144695. Snake River just off-shore on east side of river, ca. 0.16 km north of mouth of Malad River at river km 919.2, zone 11, 671153 E, 4747620 N, USNM 1144696. Upper Salmon Falls, zone 11, 672211 E, 4737061 N, UMBMNH uncat. Malad River, zone 11, 672557 E, 4747897 N, UMBMNH uncat. Birch Creek, just below spring source, zone 11, 673017 E, 4746743 N, USNM 874587. Big Wood River, Malad Gorge, zone 11, 673403 E, 4747854 N, USNM 1082638. Hagerman State Hatchery outlet, zone 11, 673779 E, 4736840 N, USNM 904959. "Len Lewis Spring," Hagerman National Fish Hatchery, zone 11, 675370 E, 4736554 N, USNM 1128547

APPENDIX 5. Continued.

Snake River, second inlet 1 near mouth of second inlet east side Ritter Island channel, zone 11, 676387 E, 4734829 N, USNM 1073425. Snake River, Thousand Springs, Minnie Miller springs inlet 1, zone 11, 676558 E, 4734783 N, USNM 1073427. Thousand Springs, power plant outflow just above bridge, zone 11, 676658 E, 4736554 N, USNM 1128549. Snake River, Thousand Springs north inlet 3, springs at and near talus base, zone 11, 676699 E, 4734545 N, USNM 1073426, USNM 1144880. Blueheart Spring, zone 11, 677732 E, 4730988 N, UMBMNH uncat. Snake River, zone 11, 677928 E, 4730728 N, UMBMNH uncat. Banbury Springs, zone 11, 678521 E, 4728860 N, USNM 905363. Box Canyon Creek, falls, zone 11, 679403 E, 4730561 N, USNM 905367. Snake River, Clear Lake bridge, zone 11, 684946 E, 4726773 N, USNM 905345, USNM 905364. Cutright Spring, zone 11, 669046 E, 4751315 N, ALBRCIDA 73285. Wood Spring, zone 11, 669635 E, 4750651 N, ALBRCIDA 73252. "Bowler Spring," north fork, zone 11, 670245 E, 4749946 N, ALBRCIDA 73240. Dorita Spring, zone 11, 670570 E, 4749430 N, ALBRCIDA 73261. Unnamed spring, zone 11, 673324 E, 4743712 N, ALBRCIDA 73277. Cove Creek, zone 11, 674046 E, 4748223 N, ALBRCIDA 48962. Billingsley Creek, zone 11, 676107 E, 4738102 N, ALBRCIDA 48932. Sand Springs, zone 11, 678658 E, 4732484 N, ALBRCIDA 48953. Niagara Springs, zone 11, 690186 E, 4726065 N, ALBRCIDA 48958. Crystal Springs, zone 11, 692523 E, 4726017 N, ALBRCIDA 75572. ***Gooding–Twin Falls Counties:*** Snake River, zone 11, 683467 E, 4726694 N, UMBMNH uncat. ***Idaho County:*** Salmon River at Boles Bridge, to east of bridge for 0.4 km, zone 11, 545683 E, 5084361 N, USNM 1144761. Salmon River by Hwy. 95, zone 11, 553071 E, 5060071 N, UMBMNH uncat. Salmon River, km 93.2–98.5, Skookumchuck Creek access, zone 11, 553202 E, 5061045 N, USNM 1144785. Salmon River, west side, Hwy. 95, zone 11, 553217 E, 5031471 N, UMBMNH uncat. Salmon River at Skookumchuck Creek access, river km 93.2–93.8, zone 11, 553271 E, 5061247 N, USNM 883520. Salmon River at south end of Lyons Bar, zone 11, 553287 E, 5072536 N, USNM 1150362. Salmon River, river km 134.5–134.8 north of Riggins, zone 11, 553829 E, 5032601 N, USNM 883516, USNM 1144787, USNM 1145094. East side of Salmon River at river km 135.2, below pull off west of U.S. 95 and 0.24 km northeast of Riggins bridge above Time Zone rapids, zone 11, 553859 E, 5032700 N, USNM 1144358. Salmon River, zone 11, 554817 E, 5043993 N, UMBMNH uncat. Salmon River, Music Bar, River of No Return, zone 11, 563788 E, 5029150 N, USNM 1144769. Salmon River, Spring Bar, km 156.1 east of Riggins, zone 11, 566351 E, 5030617 N, USNM 883510, USNM 1144786. Salmon River, Gasper Creek, zone 11, 573077 E, 5029711 N, USNM 1082061, USNM 1082627. Salmon River, km 173.1, zone 11, 579133 E, 5031338 N, USNM 1144784. Salmon River, Mackay Bar, zone 11, 617390 E, 5026758 N, USNM 1082063. ***Jefferson County:*** Snake River Eagle Rock, zone 12, 339602 E, 4730065 N, USNM 526354. Snake River, Roberts, zone 12, 412533 E, 4841548 N, USNM 905408, USNM 1075205, USNM 1082634. Snake River, Menan Buttes, zone 12, 421127 E, 4844795 N, USNM 1074882. Snake River, Lorenzo, zone 12, 430025 E, 4842399 N, USNM 597735. ***Jerome County:*** Shoshone Falls, zone 11, 713121 E, 4719232 N, USNM 58956. Blue Lake spring, Jerome, zone 11, 707340 E, 4720977 N, USNM 1120937.

APPENDIX 5. Continued.

APPENDIX 5. Continued.

Lemhi County: Salmon River, Kilpatrick, zone 12, 263812 E, 4968410 N, USNM 1003840. Salmon River, Elevenmile ramp, zone 12, 270067 E, 4990006 N, USNM 1003828, USNM 1082648. Salmon River, Red Rock, zone 12, 270676 E, 5026358 N, USNM 1002789. Salmon River, Tower Rock, zone 12, 272137 E, 5021644 N, USNM 1003855. Salmon River, Shoup bridge, zone 12, 272289 E, 4997879 N, USNM 1003838. Salmon River, Tower Rock, zone 12, 272439 E, 5022930 N, USNM 1144819. Salmon River, Salmon, zone 12, 272459 E, 5007027 N, USNM 1003868. Birch Creek, Mud Creek, zone 12, 341716 E, 4901918 N, USNM 905286, USNM 905302, USNM 1003826, USNM 1074894. Salmon River, Corn Creek ramp, zone 11, 681005 E, 5026653 N, USNM 1003866. Salmon River, zone 11, 681251 E, 5026461 N, UMBMNH uncat. Middle Fork Salmon River, mouth, zone 11, 688498 E, 5018500 N, USNM 1003886. Salmon River, Long Tom rapids, zone 11, 689738 E, 5019271 N, USNM 1003836. Salmon River, zone 11, 702677 E, 5022128 N, UMBMNH uncat. Lemhi, Salmon River, Spring Creek, zone 11, 715393 E, 5030115 N, USNM 1003851. Salmon River, bridge near Morgan Creek Road, ID 75 road km 411.1, zone 11, 724935 E, 4943235 N, USNM 883744. Salmon River, zone 11, 729549 E, 5029526 N, UMBMNH uncat. Salmon River and North Fork, zone 11, 734100 E, 5032507 N, USNM 1003884, USNM 1082649. Salmon River, Deer Gulch, zone 11, 734289 E, 4954247 N, USNM 1003839, USNM 1003885, USNM 1026470. ***Lincoln County:*** Little Wood River, Shoshone, zone 12, 272132 E, 5021733 N, USNM 126783. Little Wood River, Jim Brown bridge, zone 11, 737160 E, 4774675 N, USNM 905306, USNM 905378. Little Wood River–Bear Tracks FAS, zone 11, 739630 E, 4782121 N, USNM 1133688. Little Wood River, Preacher bridge, zone 11, 742217 E, 4786217 N, USNM 904965, USNM 1003887. ***Madison County:*** Snake River, Beaver Dick Park, zone 12, 427228 E, 4852701 N, USNM 1082631. Henrys Fork River, ID 33 bridge, zone 12, 427328 E, 4853011 N, USNM 894761, USNM 905380. Snake River, Lorenzo, zone 12, 429983 E, 4842419 N, USNM 905369, USNM 1025885. ***Owyhee County:*** Snake River, at tip of island, zone 11, 605368 E, 4754551 N, ALBRCIDA 48220. Snake River, 0.8 km below pumping station, zone 11, 610451 E, 4756456 N, ALBRCIDA 49205. Snake River, 0.3 km above pumping station, zone 11, 612079 E, 4756817 N, ALBRCIDA 50094. Island east of Indian Cove Bridge north channel, zone 11, 619941 E, 4755529 N, USNM 1144853. ***Power County:*** Benson Springs south of road to Domesea Farms Hatchery, ca. 0.64 km west of Fall Creek Road on Benson Springs Road, zone 12, 330620 E, 4719510 N, USNM 1144382. Snake River, Eagle Rock, zone 12, 339647 E, 4730115 N, USNM 905348. American Falls Hatchery, outlet, zone 12, 345890 E, 4736650 N, USNM 904970. East Fork Rock Creek, camp, zone 12, 352969 E, 4713810 N, USNM 905314, USNM 904967, USNM 1075368. Rock Springs, Arbon Valley, zone 12, 370312 E, 4717572 N, USNM 883518, USNM 1116231. Batiste Springs, zone 12, 375824 E, 4752676 N, USNM 1002524. ***Teton County:*** Teton River, Harrops bridge, zone 12, 481200 E, 4852540 N, USNM 892156, USNM 894817, USNM 905316. Teton River, ID 33 bridge west of Tetonia, zone 12, 481216 E, 4852451 N, USNM 1144932. Teton River at ID 33 bridge, on south side of bridge, ca. 7.08 km west of Tetonia, road km 82.9, zone 12, 481360 E, 4852240 N, USNM 1144383. Teton River, zone 12, 481227 E, 4852391 N, UMBMNH uncat. Teton River at Cache Bridge, on south side of bridge, west side of river, at south side public access, ca. 4.18 km west of site of Cache, river km 90.6, zone 12, 483180 E, 4847440 N, USNM 1144384. Teton River at Cache Bridge, on south side of bridge, west side of river, at south side public access, ca. 4.18 km west of site of Cache, river km 95.2, zone 12, 483180 E, 4847440 N, USNM 1145588. Teton River, Buxton bridge, zone 12, 484753 E, 4841148 N, USNM 1003829, USNM 1075674. Public access to Teton River about 0.16 km west of Buxton Bridge, zone 12, 484890 E, 4840940 N, USNM 1144354, USNM 1144743. Both sides of Bates Bridge on Teton River at river km 103.0, zone 12, 486740 E, 4837980 N, USNM 1144355. Woods Creek fen, zone 12, 487941 E, 4841341 N, USNM 1116704. ***Twin Falls County:*** Salmon Falls Creek, zone 11, 668372 E, 4712124 N, UMBMNH uncat. Salmon Falls Creek, zone 11, 675318 E, 4730667 N, UMBMNH uncat. Salmon Falls Creek, zone 11, 676010 E, 4701868 N, UMBMNH uncat. Snake River, Kanaka Rapids, zone 11, 680131 E, 4725946 N, USNM 854624. Snake River, Shoshone Falls, zone 11, 713175 E, 4719184 N, UMBMNH uncat. Snake River, 0.8 km below bridge, Hansen, zone 11, 721392 E, 4716392 N, USNM 597739. Snake River, Murtaugh, zone 11, 733980 E, 4709123 N, USNM 905366, USNM 1082637.

OREGON. ***Malheur County:*** Crooked Creek, State Wayside, zone 11, 439936 E, 4739533 N, USNM 1074940. Crooked Creek, south side of U.S. 95, Crooked Creek State Wayside, zone 12, 440000 E, 4739100 N, USNM 1144657.

WYOMING. ***Lincoln County:*** Salt River, King Creek, zone 12, 496476 E, 4771554 N, USNM 1025967. Salt River, Freedom, zone 12, 497456 E, 4758850 N, USNM 905412. Salt River, Thayne, zone 12, 498759 E, 4750899 N, USNM 905384. Salt River, Afton, zone 12, 502275 E, 4733897 N, USNM 905373. Salt River, at WY 238 bridge, 0.48 km from U.S. 89 and ca. 5.95 km northeast of Auburn, zone 12, 517301 E, 4784516 N, USNM 883462. Snake River, east end of Grand Canyon, zone 12, 517301 E, 4784516 N, USNM 883514, USNM 1116228, USNM 1144771.