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MORPHOLOGICAL AND GENETIC RELATEDNESS AMONG SUCCINEID LANDSNAILS IN THE UNITED STATES AND CANADA, WITH EMPHASIS ON THE ENDANGERED KANAB AMBERSNAIL (*OXYLOMA HAYDENI KANABENSIS*):

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EXECUTIVE SUMMARY

Introduction

Morphological analyses have indicated that the succineid landsnail genus, *Oxyloma*, is represented in North America by a dozen species, with five species in the West. Three species have been identified in the Southwest, with *O. retusa* known from New Mexico and two populations in each of two subspecies of *Oxyloma haydeni*: the Niobrara and Kanab ambersnails (*O. h. haydeni* and *O.h. kanabensis*, respectively). The Kanab ambersnail is a federally endangered species with known populations only at two springs: Three Lakes near Kanab, Utah; and Vaseys Paradise in Grand Canyon (Spamer and Bogan 1994). The Vaseys Paradise *O. h. kanabensis* population is subject to impacts during high flows from Glen Canyon Dam. Although planned floods from Glen Canyon Dam have been demonstrated to be a primary mechanism for downstream sediment and ecosystem management, the U.S. Fish and Wildlife Service 1995 and subsequent Biological Opinions (BO's) state that planned floods cannot be conducted until at least one additional *O.h. kanabensis* population has been discovered or established in Arizona.

Recent ecosystem management decisions have been based on morphological identification of *O. haydeni kanabensis*; however, recent genetics data suggest that the Vaseys Paradise population may be distinct from other southwestern *Oxyloma*. Miller *et al.* (in review) used amplified fragment length polymorphism analysis and concluded that the Vaseys Paradise *Oxyloma* population was distinctly different from those at Indian Gardens, -9 L Spring (both in AZ), and Three Lakes (UT). The taxonomic status of the endangered taxon in relation to these other populations remains a primary concern for adaptive management of the Colorado River ecosystem (Stevens *et al.* 1997a, Meretsky and Stevens 1998, Meretsky *et al.* in press).

Objectives

We investigated the relatedness of the Vaseys Paradise *Oxyloma haydeni kanabensis* population to other *Oxyloma* and succineid populations in the United States and Canada using mitochondial DNA genetic analyses and morphological taxonomic analyses. This information augments Miller *et al's*. (in review) data, and provides insight into the taxonomy of this species complex and other members of the genus and family to help resolve conflicts presented by the present state of taxonomic knowledge.

Methods

We conducted "blind", paired morphological and genetic analyses on a large series of specimens from the family Succineidae from the United States and Canada. We collected >450 specimens from 59 localities in 7 states and provinces in the United States and Canada. We had previously collected specimens from the four Four Corners Oxyloma populations cited in Miller *et al.* (in review), and added those specimens to these collections, for a total of 63 populations/ localities. Where possible, a sample of the foot from each specimen was removed and flash frozen for mitochondrial DNA analysis of a 410 bp region of the Cytochrome *b* gene at Dr. Keim's laboratory at Northern Arizona University in Flagstaff, AZ. The remainder of each specimen was preserved in 70% ethanol, and used for morphological analysis by Dr. Shi-Kuei Wu at the University of Colorado in Boulder, Colorado.

Results: Morphology

Morphological analysis of 65 specimens in 58 populations by Dr. Wu revealed 10 populations of *Catinella*, 3 populations of *Succinea*, and 31 populations of *Oxyloma*. For comparative purposes, these analyses included 4 lots of possible topotype *Oxyloma haydeni haydeni* (Binney) from Loup River, Nebraska, and 2 lots of *Oxyloma haydeni kanabensis* Pilsbry from Grand Canyon, Arizona. *Oxyloma* species identified included: *O. haydeni haydeni*, *O. h. kanabensis*, *O. nuttallina*, and *O. retusa*. Morphological analyses indicate that the ranges of all of these taxa overlap broadly. Although we collected near or at the type locality for *O. sillimani*, no specimens of this taxon were identified. We searched the type localities for *O. nuttallina chasmodes* and *O. sanibelensis*, without success, and these two taxa may have been extirpated at the type localities by agricultura; practices and suburbanization, respectively. Morphological analyses indicated that sufficient morphologically distinct populations occur within the samples to interpret genetic relatedness within the genus *Oxyloma*.

Results: Genetics

Mitochondrial genetic analyses were conducted on many of the same specimens used in the taxonomic analyses, as well as specimens from other studies. Dr. Keim and Mr. Miller sequenced 350 cytochrome b gene basepairs on 96 specimens collected from 50 different locations. A total of 146 nucleotides from the *Cytb* gene were parsimony-informative. Use of the maximum parsimony procedure revealed 32 equally parsimonious trees, each having a total length of 375 steps with consistency indices of 0.63, and we developed a midpoint-rooted majority rules consensus of these equally-parsimonious phylogenies. Morphological data were used to root alternative phylogenetic trees after both teams had submitted their data to the Grand Canyon Monitoring and Research Center. We were clearly able to distinguish among individuals of the genera *Oxyloma*, *Succinea*, and *Catinella*. Within *Oxyloma*, it appeared that there was some geographical clustering of two groups of individuals. For example, one group was comprised mainly of individuals collected in Alberta, while a second group consisted of individuals from southwestern U.S. populations in Nevada, Utah, and Arizona. Each of these clades contained multiple different morphospecies. For example, within the southwestern group, specimens were identified as *O. haydeni*, *O. kanabensis*, and *O. retusa*. Similarly, the Alberta group represented species including *O. haydeni*, *O. kanabensis*, *O. retusa*, and *O. nuttallina;* however, a neighbor-joining bootstrap consensus procedure was unable to reliably resolve many population-level relationships within *Oxyloma*.

Examination of the distribution of absolute genetic distances (number of nucleotide differences) between each pair of specimens examined in this study revealed three discrete groups of distances, falling in the ranges of 0-22, 40-54, and 66-104. Pairs of individuals with genetic distances between 0 and 25 were from the same genera. Within this range, the highest values were dominated by contrasts between the Vaseys Paradise population and individuals from the southwestern *Oxyloma* group (range: 18-20). High values in this group also characterized specimens identified as *Catinella ?mooresiana* from Arizona, and specimens identified as *C. vermata* and *C. mooresiana* from Arizona and Utah.

Towards Taxonomic Consensus

Molluscan taxonomic studies reveal both cases of morphologically indistinguishable but genetically different taxa, as well as morphologically different but genetically similar taxa (e.g.,). In addition, the genus *Oxyloma* has been cited as a biogeographically classic case of erratic long-distance dispersal on the proverbial feet of ducks (REF), allowing different taxa to exist in close proximity.

Genetic, but not morphological, analyses suggest that the Vaseys Paradise *Oxyloma* population, which has been called endangered Kanab ambersnail (KAS), is a distinctive, cryptic taxon. It is morphologically indistinguishable from the *Oxyloma* at Three Lakes, UT, but is differentiated from those in the vicinity of the presumed type locality in Kanab Canyon. Three Lakes *Oxyloma* are genetically similar (among those populátions collected) to those in the Humboldt River drainage in the Great Basin. However, the Vaseys Paradise *Oxyloma* are unique in their habitat affinities and their size. Nowhere else have we found Oxyloma inhabiting a hanging garden habitat, and showing host plant affinity for *Mimulus cardinalis*. Also, the Vaseys Paradise Oxyloma normally attain a much larger size (rather commonly $\geq$18 mm in shell length), much larger than the other Arizona *Oxyloma* or those at Three Lakes, Kanab Canyon, Carlin Nevada, or any of the Alberta populations. Although the classic morphological approach would not embrace ecological and size differences *per se* as sufficient for reclassification, such studies have not considered the possibility of evolutionary convergence or size-related morphological change.

What is required to resolve the apparent differences between morphological and genetic taxonomy of the Vaseys Paradise *Oxyloma* population. One concern is the development of a quantitative approach to morphological analyses, to help determine the extent of variation in taxonomic decision-making. Another concern is the repeatability of genetic results using other genes or techniques. In addition, several testable issues arise from this study. 1) More extensive analysis of existing specimens will provide additional insight into this taxonomic conflict. 2) Additional, more thorough, quantitative "blind" analyses of genetic and morphological variation among the *Oxyloma* populations in Utah, Arizona and Nevada may resolve this taxonomic conflict. 3) Experimental rearing of egg masses of known parentage can be used to test the role of size-related variation in morphology and genetic variability among the Vaseys Paradise, Three Lakes, Indian Gardens, -9L and Kanab Canyon *Oxyloma* populations. Lastly, 4) additional collections and analyses of eastern United States, *Oxyloma missoula*, Alberta *Oxyloma* identified as Kanab ambersnail and anomalous specimens (e.g., Alberta specimen 21.185) will help establish levels of genetic diversity, and may resolve apparent cases of convergence or anomalous distribution. Although this study does not resolve the debate over the taxonomy of the Vaseys Paradise *Oxyloma* population, it indicates that a potentially large genetic distance exists between this, Kanab ambersnail, and other *Oxyloma* populations. Also, this study suggests a high degree of genetic similarity among several western *Oxyloma* morpho-species.

CHAPTER 1: PROJECT DESCRIPTION

INTRODUCTION

The Kanab Ambersnail

Management of individual endangered species may conflict with ecosystem management (Stevens and Wegner 1995), as exemplified by issues surrounding the endangered Kanab ambersnail (*Oxyloma haydeni kanabensis*) at Vaseys Paradise (River Mile 31.5L) in Grand Canyon. The succineid landsnail genus, *Oxyloma* has been described as consisting of >12 species and subspecies in the United States and Canada (Pilsbry and Ferriss 1911, Pilsbry 1948). The species, *O. haydeni*, is represented in the American Southwest by two morphologically designated subspecies, each with two known populations. The Kanab ambersnail (*O. haydeni kanabensis* Pilsbry) is federally endangered with populations at two localities: Three Lakes, 10 km west of Kanab, Utah on Highway 89A; Kanab Canyon, 5-10 km north of Kanab, Utah; and Vaseys Paradise, 51.2 km downstream from Lees Ferry along the Colorado River in Grand Canyon National Park (U.S. Fish and Wildlife Service 1991a, 1991b, 1992; Spamer and Bogan 1994).

A recently discovered population near the type locality.("the Greens", Ferriss 1910) was tentatively described as KAS, but more detailed analysis indicates it to be the (unlisted) Niobrara ambersnail, *O. h. haydeni* Pilsbry (NAS, S.K. Wu, personal communication). NAS populations recently have been discovered at two other springs in the region: Colorado River -9L Spring, 15.5 km upriver from Lees Ferry, Arizona; and Indian Gardens, 8.0 km down the Bright Angel Trail in Grand Canyon National Park, Arizona. NAS is widely distributed, occurring in Oklahoma, Nebraska, and Alberta, and *O.h. kanabensis* has been described from central Alberta (Pilsbry 1948, Harris and Hubricht 1982). The Vaseys Paradise and Three Lakes KAS populations are large and appear healthy (Clarke 1991, Stevens *et al.* 1997b, V.J. Meretsky personal communication), while the -9L Spring NAS population exists at a low stage elevation and is directly threatened by Glen Canyon Dam operations (LES and V.J. Meretsky, personal observation). The small Indian Gardens NAS population is imperiled by human foot traffic, stock trampling and habitat alterations in its highly variable 200-1000 m^2 habitat in the midst of the most heavily visited inner canyon campground in Grand Canyon National Park (LES and V.J. Meretsky, personal observation).

The autecology of the VP KAS population has been studied intensively since 1994 to improve understanding of how discharge from Glen Canyon Dam affects habitat and population dynamics (Stevens *et al.* 1997a,b; Stevens *et al.* 1998; V.J. Meretsky, personal. communication). KAS has an approximately annual life cycle, with reproduction occurring among 9 mm or larger snails in mid-summer and young to mid-sized snails overwintering on dry substrata (driftwood, dead leaves or stems, and boulder edges). KAS is unusual in that mature snails attain lengths in excess of 18 mm, whereas such lengths do not occur at all commonly among other *Oxyloma* populations collected by LES or studied by V.J. Meretsky (personal communication).

Another unusual aspect of KAS biology is its host plant specificity. Actively feeding KAS occur primarily on native crimson monkey-flower (*Mimulus cardinalis*) and water-sedge (*Carex aquatilis*), and on non-native water-cress (*Nasturtium officinale*) and bent-grass *(Agrostis* *stolonifera*), all of which are watered by Vaseys Paradise spring outflow. Fecal pellet analyses indicate that KAS feed on live water-cress and decaying native plant matter, and possibly on fungi and bacteria associated with the decaying matter. KAS are rare or absent on other riparian plant species, with few, if any, KAS reported on bare substrata (*e.g.*, soil or rock surfaces) during the growing season. The primary host plant species have colonized downslope from the pre-dam ten year flood stage to the post-dam water's edge, increasing post-dam KAS habitat by approximately 40%. KAS has abundantly colonized the new vegetation, and thus flood control by Glen Canyon Dam probably has substantially increased the KAS population at Vaseys Paradise. In contrast, the many other populations of *Oxyloma* in North America examined by LES and V.J. Meretsky (personal communication) are associated with *Typha* spp. and *Scirpus* spp., or occasionally *Phragmites australis* (S.K. Wu, personal communication).

The U.S. Fish and Wildlife Service Kanab Ambersnail Recovery Plan calls for the establishment or discovery of at least 10 populations before KAS can be downlisted or delisted (U.S. Fish and Wildlife Service 1995). The U.S. Fish and Wildlife Service Biological Opinion (BO) on the Glen Canyon Dam Preferred (Operations) Alternative (U.S. Bureau of Reclamation 1995) and on the 1996 Bureau of Reclamation planned flood (U.S. Fish and Wildlife Service 1996) specify that at least one additional KAS population be located in Arizona. Downlisting discoveries or population establishment actions must take place before further high flows are permitted for ecosystem management of sand and sediment deposits in Grand Canyon. The Arizona Game and Fish Department and the National Park Service initiated a KAS introduction program at three sites in Grand Canyon in 1998 to fulfill those requirements, and those sites have been restocked with KAS from VP. However the duration of maintenance before such efforts can be declared a success or failure has not been established. Until a success has been declared, present dam operations are not permitted to "take" more than 10% of the KAS habitat at Vaseys Paradise. The BO's on dam operations means that KAS recovery efforts strongly influence ecosystem management.

Genetic analyses may elucidate biodiversity in morphologically similar genera, and substantial headway has been made in sequencing mitochondrial genes in Mollusca, including land snails (*e.g.*, Hatzoglou *et al.* 1995, Terrett *et al.* 1996, Yamazaki *et al.* 1997). However, genetic studies also may further complicate management. Pilsbry (1948) considered the *Oxyloma* to be among the most difficult genus in the United States from the standpoint of morphological taxonomy. Historically, succineid taxonomy has been based on internal morphology, particularly of the genitalia (*e.g.*, Pilsbry 1948, Wu 1993). In contrast, recent amplified fragment length polymorphism (AFLP) analyses by Miller *et al.* (in review) indicate that: 1) all four southwestern *Oxyloma* populations are genetically distinct; 2) the Three Lakes and Indian Gardens populations may be more closely related than the Vaseys Paradise and Three Lakes populations; and 3) these four populations may be cryptic sibling species. However, until definitive mitochondrial DNA analysis involving other populations and other members of the genus and family is completed, it will not be possible to determine the significance of this information. If all populations can be considered as members of one species complex, the significance of the historic taxonomic designation may be reduced. Alternatively, as suggested by Miller *et al.* (in review), each *O. haydeni* population may deserve unique taxonomic status, increasing the need for federal protection. Also, the genetic relatedness of the reported Canadian populations of *O. h. haydeni* and *O. h. kanabensis* to the southwestern populations remains unknown, but warrants investigation as those populations may represent additional populations of endangered KAS. The succineids are biogeographically notorious for their potential for erratic, long-distance dispersal on the feet, bills and plumage of wetland birds (Rees 1965, Dundee *et al.* 1967). Erratic long-distance dispersal may also help account for anomalous unique succineid populations in isolated habitats, such as the *Oxyloma* at Vaseys Paradise. In concert, these issues may obfuscate U.S. Fish and Wildlife Service management issues and require a policy review for the management of this taxon.

Project Objectives

We investigated the morphological and genetic relatedness of the southwestern and Canadian *O.h. haydeni* and *O.h. kanabensis* populations, along with populations of other *Oxyloma* and succineid species and genera in the United States. This information was compiled to improve understanding into the taxonomy of KAS in relation to the *O.h. haydeni* and other succineid taxa to help resolve taxonomic conflicts presented by the present state of knowledge.

Our specific objectives include the following:

1) Re-evaluate the morphological taxonomy of the *Oxyloma* species and subspecies in the Southwest and Alberta in relation to other *Oxyloma* and succineid snails in North America, using the techniques of Wu (1993).

2) Determine genetic relatedness of the *Oxyloma* species and subspecies near *O. haydeni* to other succineid genera and species in the United States and Canada, using mitochondrial DNA techniques.

3) Provide an analysis of these data for an *Oxyloma* workshop to review the status of VP KAS taxonomy in relation to other *Oxyloma* in North America.

METHODS

Specimen Collection

LES and his colleagues collected succineid landsnails across North America north of Mexico during 1998 and 1999, using the locality information provided by Pilsbry (1948), Harris and Hubricht (1982) and other sources (Table 1.1; Fig. 1.1). Localities were visited and sampled in 1998 and 1999 with the aim of collecting at least 3 specimens from each population. The Alberta populations of *Oxyloma* were of particular interest because Harris and Hubricht (1982) described an east-to-west longitudinal gradient of *O. haydeni* to *O. kanabensis* across the middle of that province, and if such populations could be verified, they might contribute to conservation efforts. Where possible, we also collected recent shells to provide Dr. Wu with a good understanding of snail size class distribution from the field.

Table 1.1: Succineid landsnail collection localities in the United States and Canada, 1996-1999.

Locality	State	County	Site	Date	Collctr
1	IL	Crawford	Rt.1, 2 mi. into Crawford Co.	980513	VJM
1.5	NE	Custer	Victoria Springs State Rec. Area	980512	EN
2	NE	Cherry	Cottonwood Lake State Rec. Area	980513	EN
3	IL	Jefferson	State Rt 142, 0.5 mi into Jefferson Co.	980513	VJM
4	AZ	Coconino	Vaseys Paradise, Colo. R.Mile 31.5R, Grand Canyon N.P.	980510	JAS
5	AZ	Coconino	Saddle Canyon, CR Mile 47	980511	JAS
6	IL	White	IL 1 N. of Crossville	980513	VJM
7	IL	White	IL 14, E. of IL 1	980513	VJM
8	IL	White	IL 14, 0.2 mi. E of 1400N 400 E	980513	VJM
9	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14	980513	VJM
10	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	980512	EN
11	IL	DuPage	Slough at 75th St and Lemont Rd in Woodridge	980602	JS
12	AZ	Coconino	Roaring Springs, Bright Angel Creek, Grand Canyon N.P.	980609	JAS
13	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	980622	M. Lannoo
14	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	980622	M. Lannoo
15	UT	Kane	Best Friends Ranch, Kanab	980731	VJM+EN
16	UT	Kane	Kanab Creek, 5 mi. upstrm from Kanab	980731	VJM+EN
17	IL	White	IL 14, 0.2 mi. E of 1400N 400 E	980816	VJM
18	Alberta	N/A	3 km towards McLeod R. off Hwy 32	980918	LES
19	Alberta	N/A	Hyw 43, ca. 100 km west of Edmonton, AL	980918	LES
20	Alberta	N/A	1 km south of Hwy 16 on RGE Rd 272	980918	LES
21	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	980918	LES
22	Alberta	N/A	Two Creeks at Hwy 43, W. of Edmonton, AL	980918	LES
23	Alberta	N/A	1.5 km north of Czar, AL	980919	LES
24	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	980919	LES
25	Alberta	N/A	Highway 11, Alberta, near Condor turnoff	980919	LES
26	Alberta	N/A	Alberta Beach, SE side of Lac St. Anne	980918	LES
27	Alberta	N/A	South side of Pigeon L.	980919	LES
28	Alberta	N/A	5 km west of Amsik, ALB on Hwy 13	980919	LES
29	Alberta	N/A	0.5 km south of Lake Isoegun	980918	LES
30	WA	Stevens	A Tyla patch in a large field east of Hiway 395 at Mile 224	981106	LES
31	NV	Elko	Streamside on Maggie Cr., 4 km upstrm from Carlin	981107	LES
32	WA	Stevens	Jump-off Joe Lake along shoreline vegetation	981106	LES
33	NV	Elko	Near head of reservoir, 100 m upstrm from road across stream	981107	LES
34	WA	Stevens	Kettle lake 8km south of Chewelah on Hiway 395, Mile 200	981106	LES
37	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	990608	LES
38	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	990608	LES
39	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	990608	LES
40	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch, Kanab	990608	LES
41	UT	Kane	KOA 3 km N of Glendale	990608	LES
42	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich, Hwy 89	990608	LES
43	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	9905..	EN
44	NE	Cherry	Cottonwood Lake State Rec. Area	9905..	EN
45	UT	Kane	Separate spring @ S end of Three Lakes, Kanab	990609	EN
46	UT	Garfield	Mile 121.3 on Hwy 89	990608	LES
47	UT	Garfield	Asay Creek bridge on Hwy 89, Sevier River	990608	LES
48	UT	Garfield	Panguich, Sevier R.	990608	LES
49	UT	Garfield	Upper Valley Cr., Dixie NF border, Allen and UV Crs, Hwy 12	990809	VJM
50	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	990722	VJM
51	UT	Garfield	Calf Creek, off Escalante R., parallel to Hwy 12 on the W	990722	VJM
52A	UT	Garfield	Boulder Cr., off Escalante R., parallel to Hwy 12 on the E	990722	VJM
52B	UT	Garfield	Jct. Birch Cr and UV Cr. on Hwy 12	990722	VJM

Table 1.1: Continued

Locality	State	County	Site	Date	Collctr
53	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	990809	LES/VJM
54	WA	Pend Oreille	Betw/ W. Calispell Rd and Flowery Tr. Rd.	990809	LES/VJM
55	WA	Pend Oreille	Jct. Calispell and W. Calisplell Rd	990809	LES/VJM
56	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	990809	LES/VJM
57	UT	Garfield	Hwy 12 across Escalante R.	990725	VJM
58	WA	Stevens	Rt 395 N. of Spokane at Mile 196	990809	LES/VJM
60	AZ	Mohave	Travertine Falls, Colo. R. Mile 230, Grand Canyon N.P.	980607	LES
61*	AZ	Coconino	Vaseys Paradise, Colo. R.Mile 31.5R, Grand Canyon N.P.	970801	LES
62*	AZ	Coconino	Colo. R. Mile -9L Spring, Glen Canyon N.R.A	970901	JAS
63*	AZ	Coconino	Indian Gardens, Bright Angel Trail, Grand Canyon N.P.	960801	LES
64*	UT	Kane	Three Lakes, 5 mi. W. of Kanab on Hwy 89	961101	LES

* *Oxyloma* specimens collected prior to this study

KEY	
Number	Scientific Name
1	*?Catinella mooresiana* (Lea)
2	*Catinella vermeta* (Say)
3	*?Catinella witteri* (Shimek)
4	*Oxyloma haydeni* (Binney)
5	*Oxyloma kanabensis* Pilsbry
6	*?Oxyloma nuttallina* (Lea)
7	*Oxyloma retusa* (Lea)
8	*Succinea concordialis* Lea
9	*Succinea ovalis* Say

Figure 1.1: Localities of morphologically identified succineids in North America. A "?" before a scientific name indicates that the name has been tentatively designated. "X" indicates a type locality in which no succineids were found.

Specimen Processing

Specimens were relaxed and drowned in warm water for 8 hr prior to manipulation. If a snail specimen was sufficiently large, a sample of the foot from was removed and flash frozen for genetic analysis of the cytochrome b gene at Dr. Keim's laboratory at Northern Arizona University in Flagstaff, AZ. The remainder of each specimen was preserved in 70% ethanol, and used for morphological analysis by Dr. S.K. Wu at the University of Colorado in Boulder, Colorado. Dry shells were placed in labeled glass vials in cotton. Specimens are presently housed at Dr. Wu's laboratory in the University of Colorado museum, Boulder.

RESULTS AND DISCUSSION

Collections

We collected >450 specimens from 59 localities in 7 states and provinces in the United States and Canada (Table 1.1; Fig. 1.1; Appendix A). We had previously collected specimens from the four Four Corners *Oxyloma* populations cited in Miller *et al.* (in review), and added those specimens to these collections, for a total of 63 populations/localities. We collected as many as 30 snails per locality, striving to find the largest snails available in the population. We also collected the year's shells for a comparison of maximum size achieved by the population. In nearly all cases, large or maximum size snails were found.

We were impressed by the abundance of *Oxyloma*-like succineids throughout North America, with robust populations found at most undisturbed stands of *Typha* and *Scirpus* spp. and in many wetlands. Through the courtesy of Dr. Vicky Meretsky, we recorded many first collections, particularly in southern Utah. The *O. haydeni kanabensis* population at Vaseys Paradise remains remarkable in that it occurs on non-*Typha/Scirpus* host plants and habitat, relying instead on *Mimulus cardinalis* and *Nasturtium officinale*, as well as *Carex aquatilis* and *Agrostis stolonifera* in a hanging garden habitat.

Of the type localities visited, we failed to detect *Oxyloma sanibelensis* on Sanibel Island, Florida, or *O. nuttallina chasmodes* at Modesto, California. The type populations at these sites appear to have been extirpated or driven to extinction by urbanization and agricultural development, respectively (Fig. 1.1). Although we collected near or at the type localities for *O. hawkinsi* and *O. sillimani*, no specimens of these taxa were identified through morphological analyses.

In addition to type localities, Dr. Meretsky, Eric North and LES sampled habitat patches in the major drainages of the Colorado River, as well as the Sevier River drainage in the Great Basin, in southern Utah, localities in which we discovered relatively numerous but previously unrecognized populations of *Oxyloma haydeni* and *Catinella* spp.

Analysis Strategy

The morphological and genetics analyses were conducted in a double "blind" fashion to distinguish the differences reached between the two taxonomic approaches. The only information Dr. Wu or Dr. Keim received with their samples were specimen numbers, with no locality data. We conducted this two-way blind taxonomic comparison by subjecting nearly all specimens analyzed to both morphological and genetic analyses (Chapters 2 and 3, respectively). After the results were submitted by each team to the Grand Canyon Monitoring and Research Center, the data were matched up with locality data. This information allowed the genetics team to root the phylogenetic tree, and provided the morphologist with an expanded understanding of the ranges of morpho-species. This approach has yielded additional taxonomic controversies, but also provides clearly defined hypotheses and experimental approaches for resolving these controversies (Chapter 4).

CHAPTER 2:

MORPHOLOGICAL ANALYSIS OF KANAB AMBERSNAIL IN RELATION TO OTHER SUCCINEIDAE

Shi-Kuei Wu and Lawrence E. Stevens

INTRODUCTION

The purpose of this work was to investigate morphological variation among various populations of succineid landsnails in relation to published descriptions of physical characteristics. The specific objectives were to "re-evaluate the morphological taxonomy of the *Oxyloma* species and subspecies in the Southwest and Alberta in relation to other *Oxyloma* and succineid snails in North America, using the techniques of Wu (1993)." This morphological analysis was conducted in a blind fashion to prevent geographic information from informing the taxonomist. Therefore, the only information associated with the specimens was a specimen identification number, with no locality data, until his initial results had been presented to GCMRC. Many of these same specimens were also used in genetic analyses. After the results had been submitted, Dr. Stevens informed the teams regarding the locality data.

METHODS

Dr. Stevens sent a total of 219 specimens that had been relaxed and preserved in 70% ethyl alcohol, as well as 11 lots of dead snail shells. After reviewing the material, Dr. Wu analyzed a total of 63 specimens among 54 batches (localities). These localities included Arizona, Illinois, Indiana, Nebraska, Nevada, Utah, and Washington, as well as Alberta, Canada, as described in Chapter I (Table 2.1; Fig. 1.1).

Each snail, except dead or decayed specimens, was unscrewed out of its shell. Shells were drawn from two views: apertural and right side. The number of whorls was counted. Shell length, shell width, apertural length and apertural width were measured from the drawings.

The buccal mass was extracted and immersed in light KOH solution (4 drops of 5% KOH in 5 cc of water) for 1 d. The cleaned jaw was dehydrated and embedded in Euparal. The cleaned radula was stained with light chromic acid solution (3-4 drops of 10% chromic acid in 1 cc distilled water) for 15 minutes, and then dehydrated and flattened on a slide with the aid of 2 camel hair brushes, and finally embedded in Euparal.

The whole reproductive system, if possible, was isolated. It was then stained with light Boraz Carmine solution (3-4 drops of Borax Carmine in 2 cc of 70% ethyl alcohol) for 24 hr. Staining greatly assists with distinguishing the elements of the reproductive system, making it easier to draw under the Wild Dissecting Microscope (*e.g.*, Fig. 2.1). In order to examine the penial appendix and epiphallus of *Oxyloma*, the penial sheath was opened and both the penial appendiz and epiphallus were pinned to reveal the details of their structure.

In order to identify specimens, the shell shape was compared with holotype and paratype drawings that Dr. Wu had prepared from: the Academy of Natural Sciences of Philadelphia; the Museum of Comparative Zoology, Harvard University; the Museum of Zoology, University of

Table 2.1: Morphological identifications of succineid landsnails collected in 1998-1999. A "?" before a scientific name indicates that official names have not been designated; a "?" in front of an IDNO indicates that it was either a young specimen, or the shell and anatomical characteristics did not agree.

Scientific Name	Batch No	IDNO	Figure	STATE	LOCALITY	HABITAT	DATE	COLL'R
?*Catinella mooresiana* (Lea)	5	36		AZ	Saddle Canyon, CR Mile 47, Grand Canyon N.P.	Streamside habitat	980511	JAS
?*Catinella mooresiana* (Lea)	12	80	2.3	AZ	Roaring Springs, BA. Cr., Grand Canyon N.P.	Springs vegetation	980609	JAS
?*Catinella mooresiana* (Lea)	46	371		UT	Mile 121.3 on Highway 89	Juba along Sevier R.	990608	LES
?*Catinella mooresiana* (Lea)	47	375		UT	Asay Creek bridge on Highway 89, Sevier R. drainage	Juncus stand along Sevier R.	990608	LES
?*Catinella mooresiana* (Lea)	52A	410		UT	Boulder Cr., trib, of Escalante Cr., parallel to Highway 12 to E.	37D 49.89MN, 111D 24.49MW	990722	VJM
?*Catinella mooresiana* (Lea)	52B	413		UT	Jct. Birch Cr and UV Cr. on Hwy 12	UTM 4179460N 439233E	990722	VJM
Catinella vermeta (Say)	4	26	2.4	AZ	Vaseys Paradise, Mile 31.5R, Grand Canyon N.P.	Spring vegetation	980510	JAS
Catinella vermeta (Say)	4	28		AZ	Vaseys Paradise, Mile 31.5R, Grand Canyon N.P.	Spring vegetation	980510	JAS
Catinella vermeta (Say)	5	35		AZ	Saddle Canyon, CR Mile 47, Grand Canyon N.P.	Streamside habitat	980511	JAS
Catinella vermeta (Say)	12	79		AZ	Roaring Springs, BA. Cr., Grand Canyon N.P.	Springs vegetation	980609	JAS
?*Catinella witteri* (Shimek)	1	1		IL	Rt.1, 2-3 mi. into Crawford Co.	Roadside ditch w/ Typha&grass	980513	VJM
?*Catinella witteri* (Shimek)	1	2		IL	Rt.1, 2-3 mi. into Crawford Co.	Roadside ditch w/ Typha&grass	980513	VJM
?*Catinella witteri* (Shimek)	3	24		IL	State Rt 142, 0.5 mi into Jefferson Co.	Snails on bare soil	980513	VJM
?*Catinella witteri* (Shimek)	9	57		IL	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 4424	Grass-lined, roadside ditch	980513	VJM
?*Catinella witteri* (Shimek)	9	58	2.5	IL	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 4424	Grass-lined, roadside ditch	980513	VJM
Oxyloma haydeni (Binney)	2	9		NE	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN
Oxyloma haydeni (Binney)	14	102		IO	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab on L. Okoboji	"Oxyloma retusa" sent to M. Miller/P.	980622	M. Lannoo
Oxyloma haydeni (Binney)	14	103		IO	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab on L. Okoboji	"Oxyloma retusa" sent to M. Miller/P.	980622	M. Lannoo
Oxyloma haydeni (Binney)	15	121		UT	Best Friends Ranch on Kanab Cr., Kanab	Wet meadow	980731	VJM+EN
Oxyloma haydeni (Binney)	15	123		UT	Best Friends Ranch on Kanab Cr., Kanab	Wet meadow	980731	VJM+EN
Oxyloma haydeni (Binney)	16	129		UT	Kanab Creek, 10 km upstream from Kanab	Typha E. of Kanab Cr.	980731	VJM+EN
Oxyloma haydeni (Binney)	30	282		WA	A Tyla patch in a large field east of Highway 395, Mile 224	Tyla/sedges	981106	LES
Oxyloma haydeni (Binney)	37	288		UT	2 km N of Glendale on Highway 89-upper bridge site, Virgin R.	Streamside Juba/Salu	990608	LES
Oxyloma haydeni (Binney)	38	296		UT	4 km N of Glendale on Highway 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES
Oxyloma haydeni (Binney)	40	304		UT	The Tube' on Kanab Cr. Just off Best Friends Ranch, Kanab	Typha/Eqhy seep, 2nd seep up from	990608	LES
Oxyloma haydeni (Binney)	53	420		WA	Jct. W.Calispell Lake Rd and Highway 211	Typha at roadside marsh	990809	LES/VJM
Oxyloma haydeni (Binney)	58	432		WA	Rt 395 N. of Spokane at Mile 196	Roadside Typha marsh/pond	990809	LES/VJM
Oxyloma haydeni (Binney)	27	?252		Alberta	0.5 km west of Falun on Highway 13, south side Pigeon L.	Rare, in roadside Typha	980919	LES
Oxyloma haydeni (Binney)	28	?258		Alberta	Marsh on east side of Hwy 13	Rare in Typha/Caaq	980919	LES
Oxyloma haydeni (Binney)	28	?260		Alberta	5 km west of Amsik, AL on Highway 13	Rare in Typha/Caaq	980919	LES
Oxyloma haydeni (Binney)	34	?280		WA	A 'kettle lake' 8km south of Chewelah on Highway 395, Mile 200	Tyla+sedges	981106	LES
Oxyloma haydeni (Binney)	n/a	UCM31748	2.6	NE	36.2 km W of Albion	S.K. Wu's drawing	830728	SKWu
Oxyloma kanabensis Pilsbry	45	365		UT	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN
Oxyloma kanabensis Pilsbry	21	?185		Alberta	Tributary at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau and	980918	LES
Oxyloma kanabensis Pilsbry	21	?186		Alberta	Tributary at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau and	980918	LES
Oxyloma kanabensis Pilsbry	n/a	UCM37254	2.7	AZ	Vaseys Paradise,GCNP, Colo. R. Mi. 31.5R, 100' up from base of f	S.K. Wu's drawing	910725	EES
?*Oxyloma nuttalina* (Lea)	24	204		Alberta	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? marsh	980919	LES
?*Oxyloma nuttalina* (Lea)	25	224		Alberta	Highway 11, near Condor turnoff	Caaq streambank and Typha/Caaq	980919	LES
?*Oxyloma nuttalina* (Lea)	26	229	2.8	Alberta	Southeast end of Lac St. Anne	Very dark; active; abundant in dewat	980918	LES
?*Oxyloma nuttalina* (Lea)	36	285		NV	Streamside on Maggie Cr., 4 km upstrm from Carlin NV	Scirpus olneyi?/grasses	981107	LES

Table 2.1: Continued

Scientific Name	Batch No	IDNO	Figure	STATE	LOCALITY	HABITAT	DATE	COLL'R
Oxyloma retusa (Lea)	2	8	2.9	NE	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN
Oxyloma retusa (Lea)	10	64		NE	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN
Oxyloma retusa (Lea)	10	65		NE	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN
Oxyloma retusa (Lea)	11	74		IL	Slough at 75th St and Lemont Rd	Wetland vegetation	980602	J.Slapcinsky
Oxyloma retusa (Lea)	11	75		IL	Slough at 75th St and Lemont Rd	Wetland vegetation	980602	J.Slapcinsky
Oxyloma retusa (Lea)	11	76		IL	Slough at 75th St and Lemont Rd	Wetland vegetation	980602	J.Slapcinsky
Oxyloma retusa (Lea)	18	162		Alberta	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bidens/	980918	LES
Oxyloma retusa (Lea)	19	169		Alberta	Hyw 43, ca. 100 km west of Edmonton, AL	Caaq/grass w/ Salix overstory	980918	LES
Oxyloma retusa (Lea)	20	178		Alberta	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead Typha	980918	LES
Oxyloma retusa (Lea)	23	201		Alberta	1.5 km north of Czar, AL	Snails rare, up to 1m above ground	980919	LES
Oxyloma retusa (Lea)	41	310		UT	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Typha/C	990608	LES
Oxyloma retusa (Lea)	42	315		UT	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES
Oxyloma retusa (Lea)	43	326		NE	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of river b	9905__	EN
Oxyloma retusa (Lea)	44	351		NE	Cottonwood Lake State Rec. Area	Juncus/Carex	9905__	EN
Oxyloma retusa (Lea)	49	392		UT	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. and	Streamside, UTM 4174423N 430926	990809	VJM
Oxyloma retusa (Lea)	50	400		UT	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 419433E	990722	GSenm
Oxyloma retusa (Lea)	51	405		UT	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and the C	990722	VJM
Oxyloma retusa (Lea)	57	437		UT	Hwy 12 across Escalante R. at UTM 4180760N 462710E	Small wetland along Escalante R.	990725	VJM
Succinea concordialis Lea	8	50	2.1	IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Ditch	980513	VJM
Succinea concordialis Lea	8	52		IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Ditch	980513	VJM
Succinea concordialis Lea	8	54		IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Ditch	980513	VJM
Succinea concordialis Lea	8	55		IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Ditch	980513	VJM
Succinea concordialis Lea	17	144		IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Wide,deep ditch along road, Typha	980816	VJM
Succinea concordialis Lea	17	145		IL	IL 14, 0.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncor'd	Wide,deep ditch along road, Typha	980816	VJM
Succinea ovalis Say	13	92	2.11	IO	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	980622	M. Lannoo

Reproductive system of *Succinea concordialis* Lea

Ventral view

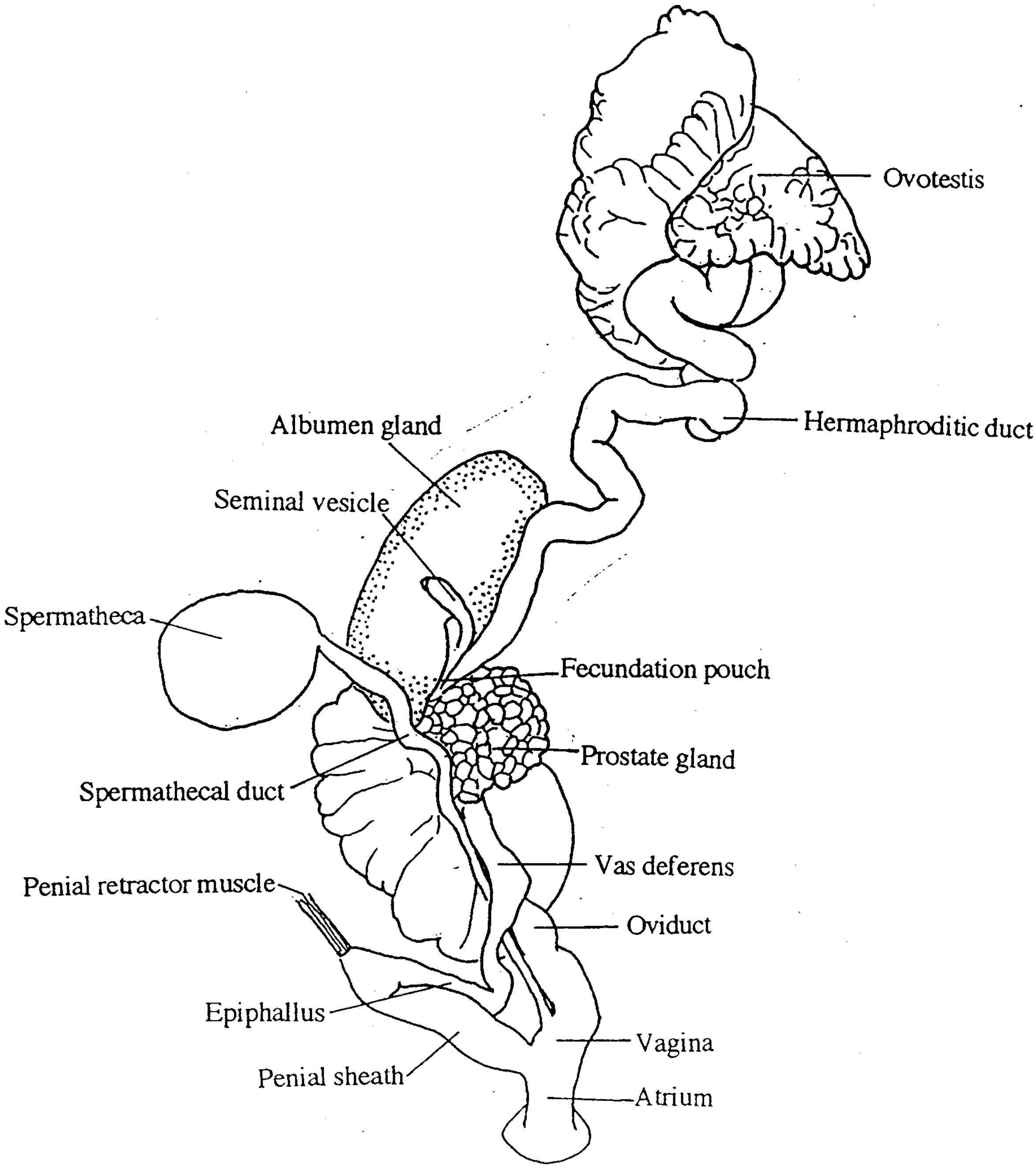


Figure 2.1: General reproductive tract scheme of succineids, using *Succinea concordialis* Lea, ventral view.

Michigan; and the U.S. National Museum. The penial sheath, penial appendix, epiphallus and seminal vesicle drawings were compared with these drawings.

For comparative purposes, 4 lots of possibly topotype specimens of *Oxyloma haydeni* (Binney) from Loup River, Nebraska, and 2 lots of *Oxyloma kanabensis* Pilsbry from Grand Canyon, Arizona, were also re-examined. This preliminary morphological analysis indicates that sufficient morphologically distinct populations occur within the samples to interpret genetic relatedness within the genus *Oxyloma*.

Specimens are currently stored at the University of Colorado Museum in Boulder, and vouchers will be stored at the Northern Arizona University National Park Service Collection in the Department of Geology at the conclusion of this project.

RESULTS AND DISCUSSION

Overall Results

A total of nine species were identified in three succineid genera, including four *Oxyloma* species (Table 2.1; Figs. 2.2-2.10). Previous taxonomic analyses had identified *O.h. kanabensis* from Vaseys Paradise in Grand Canyon, Arizona, and from Three Lakes near Kanab, Utah. Also, *O.h. haydeni* had been identified from –9L Spring and Indian Gardens, Arizona.

Biogeographic Implications

Western North American Collections: These data provide numerous new localities for the species of *Oxyloma* and *Catinella* in the western United States, and considerable new biogeographic information (Table 2.1, Fig. 2.1, Appendix A). *O. haydeni* Binney was found from the south side of Grand Canyon, throughout southern Utah, throughout western Washington, and throughout central Alberta. *O. kanabensis* Pilsbry was found at Vaseys Paradise in Grand Canyon, at and near Three Lakes outside Kanab, Utah, and possibly at one locality in western central Alberta. *O. nuttallina* (Lea) was found from Carlin, Nevada on the Humboldt River northward throughout central Alberta. *Oxyloma retusa* (Lea) was found throughout the Colorado River drainage in southern Utah and across the Great Basin drainage divide north of Panguich, Utah, as well as in the lower and central Niobrara River drainage, and across central Alberta.

Previously, the ranges of most of these western *Oxyloma* species were considered to overlap to some extent; however, these morphological data indicate a much broader overlap among the ranges of *O. haydeni* (Binney), *O. kanabensis* Pilsbry, *O nuttallina* (Lea) and *O. retusa* (Lea; Fig. 2.1) than was previously recognized.

Furthermore, these data indicate that multiple *Oxyloma* species may co-occur. For example, *O. haydeni* and *O. retusa* co-occur at Cottonwood Lake State Recreation Area in the Niobrara river drainage, Nebraska.

Alberta Collections: Morphological analyses of collections from Alberta add some insight into *Oxyloma* distributional boundaries there. Harris and Hubricht (1982) identified a boundary between *O. haydeni* and *O. kanabensis:* *O. haydeni* was reported in eastern and central Alberta, whereas *O. kanabensis* was reported in western Alberta, into the Canadian Rockies and in the

Catinella mooresiana (Lea)

Stevens #80

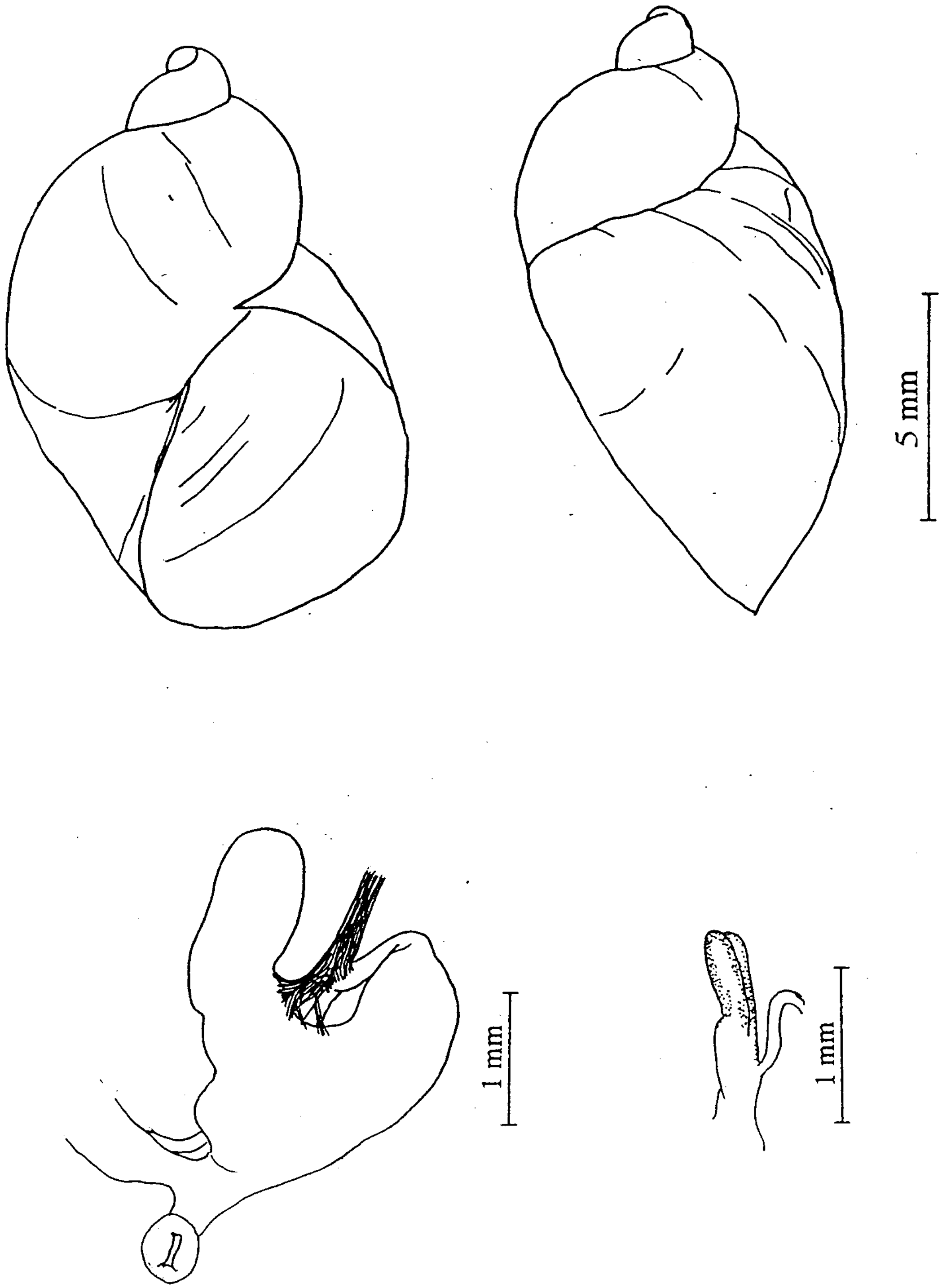


Figure 2.2: Shell and anatomy of *Catinella mooresiana* (Lea), Stevens' specimen number 80.

Catinella vermeta (Say)
Stevens #26

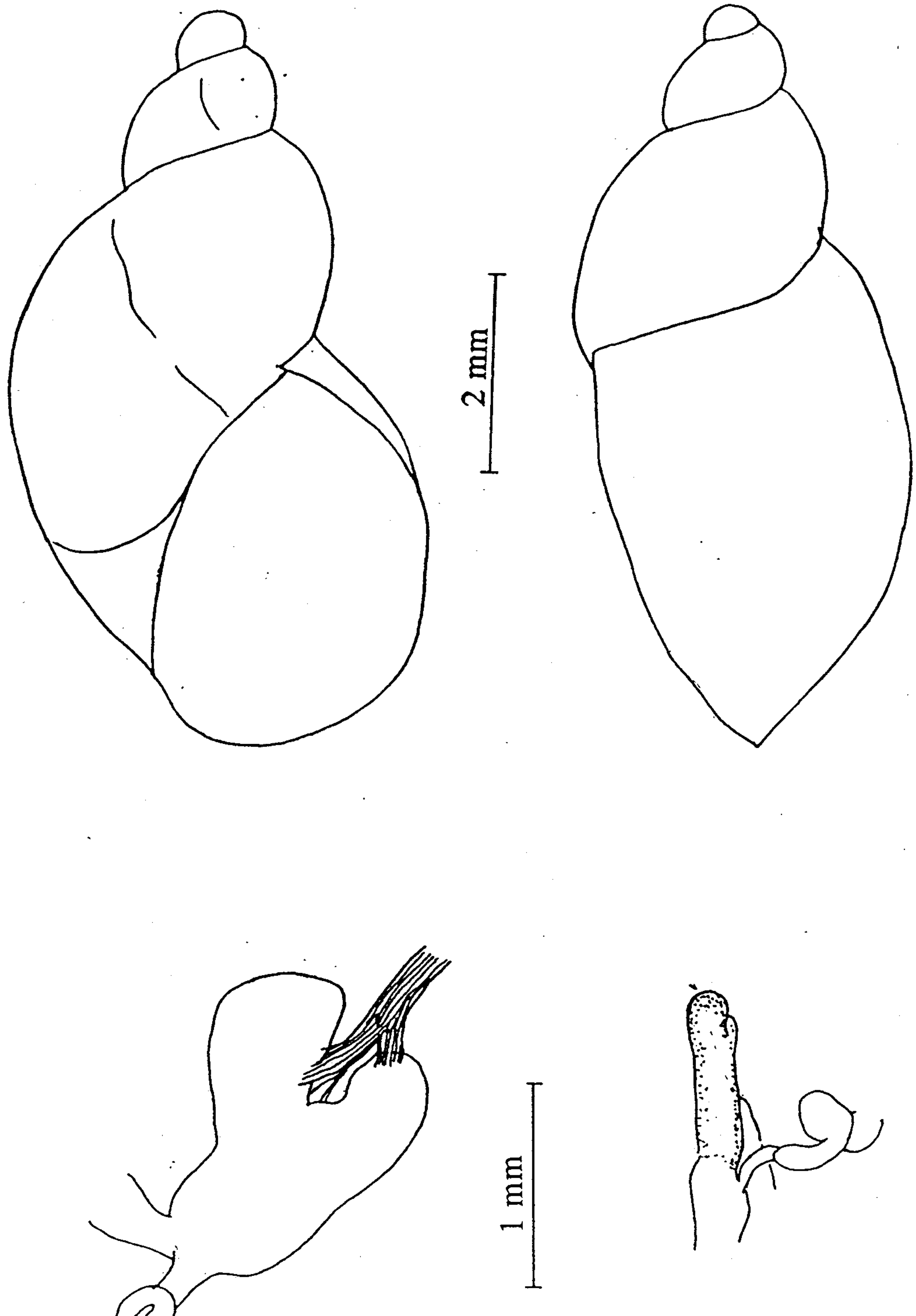


Figure 2.3: Shell and anatomy of *Catinella vermeta* (Say), Stevens' specimen number 26.

Catinella witteri (Shimek)

Stevens #58

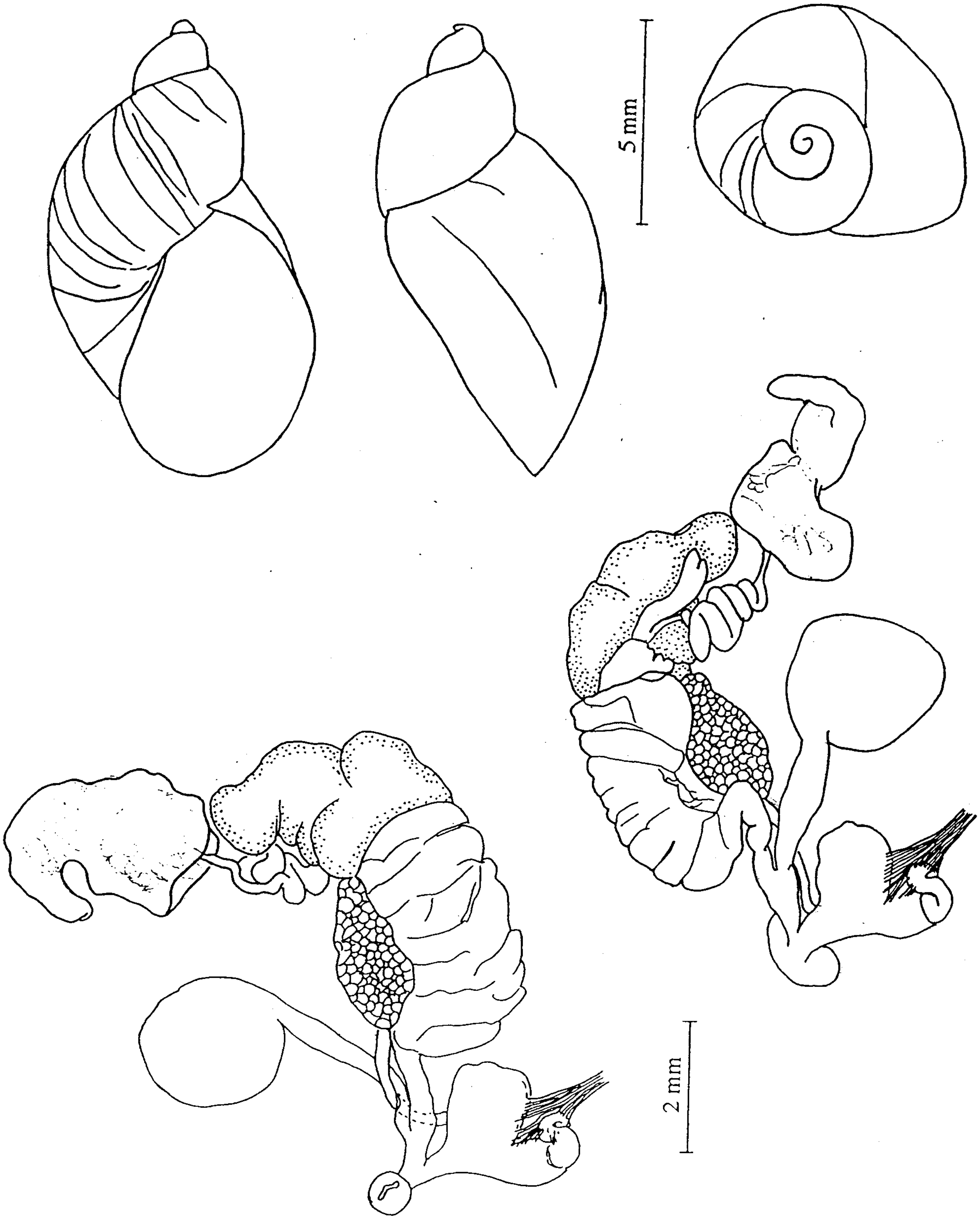


Figure 2.4: Shell and anatomy of *Catinella witteri* (Shimek), Stevens' specimen number 58.

Oxyloma haydeni (Binney)
UCM 31748
Nebraska: Greeley Co., Cedar River at NE hwy 91, 22.5 miles west of Albion. 28 July 1983 S. –K. Wu

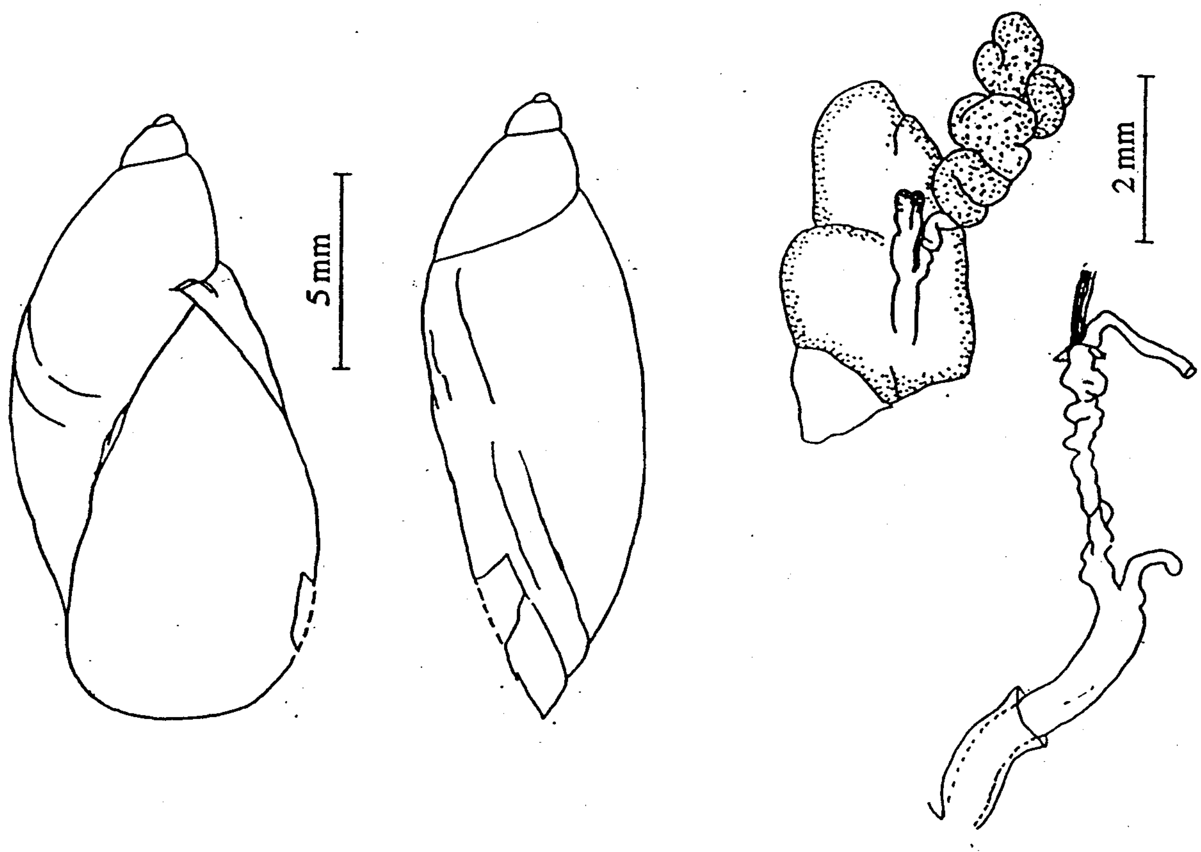


Figure 2.5: Shell and anatomy of *Oxyloma haydeni* (Binney), UCM 31748 from Nebraska: Greeley County, Cedar River at NE Highway 91, 22.5 miles west of Albion on 28 July 1983. Specimen collected by S.K. Wu.

Oxyloma kanabensis Pilsbry

UCM 37254

Arizona: Coconino Co., Vasey's Paradise,about 100 ft. up from river at base of Falls, Marble Canyon, Grand Canyon National Park. (see also ANSP A16187). 25 July 1991. M. M. Spamer & M. Shaver

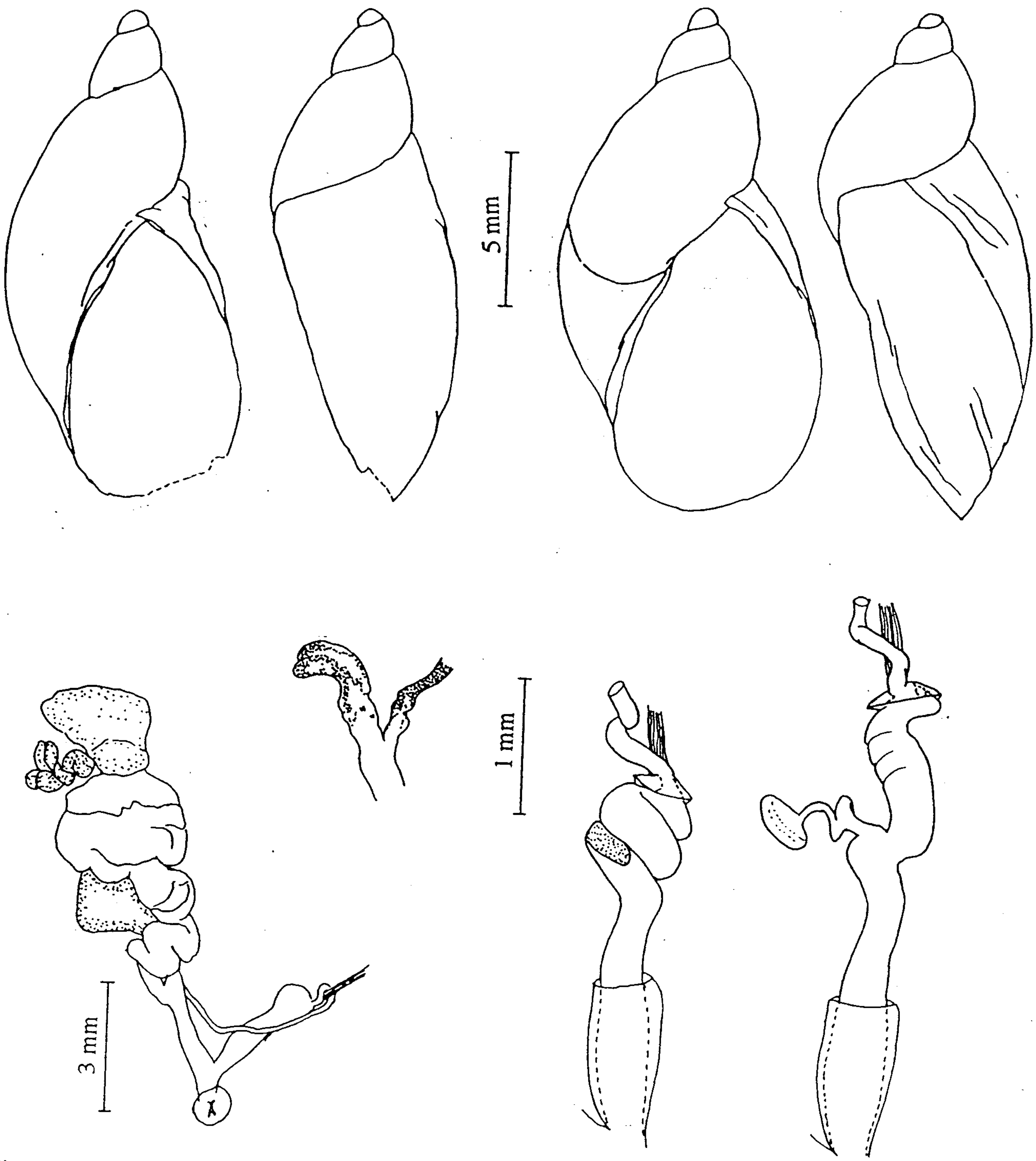


Figure 2.6: Shells and anatomy of *Oxyloma kanabensis* Pilsbry, UCM 37254 from Arizona: Coconino County, Vaseys Paradise, about 100 ft up from the Colorado River at base of falls, in Marble Canyon, Grand Canyon National Park (see also ANSP A16187), collected on 25 July 1991 by E.E. Spamer and M.M. Shaver.

Oxyloma nuttallina Lea
Stevens #229

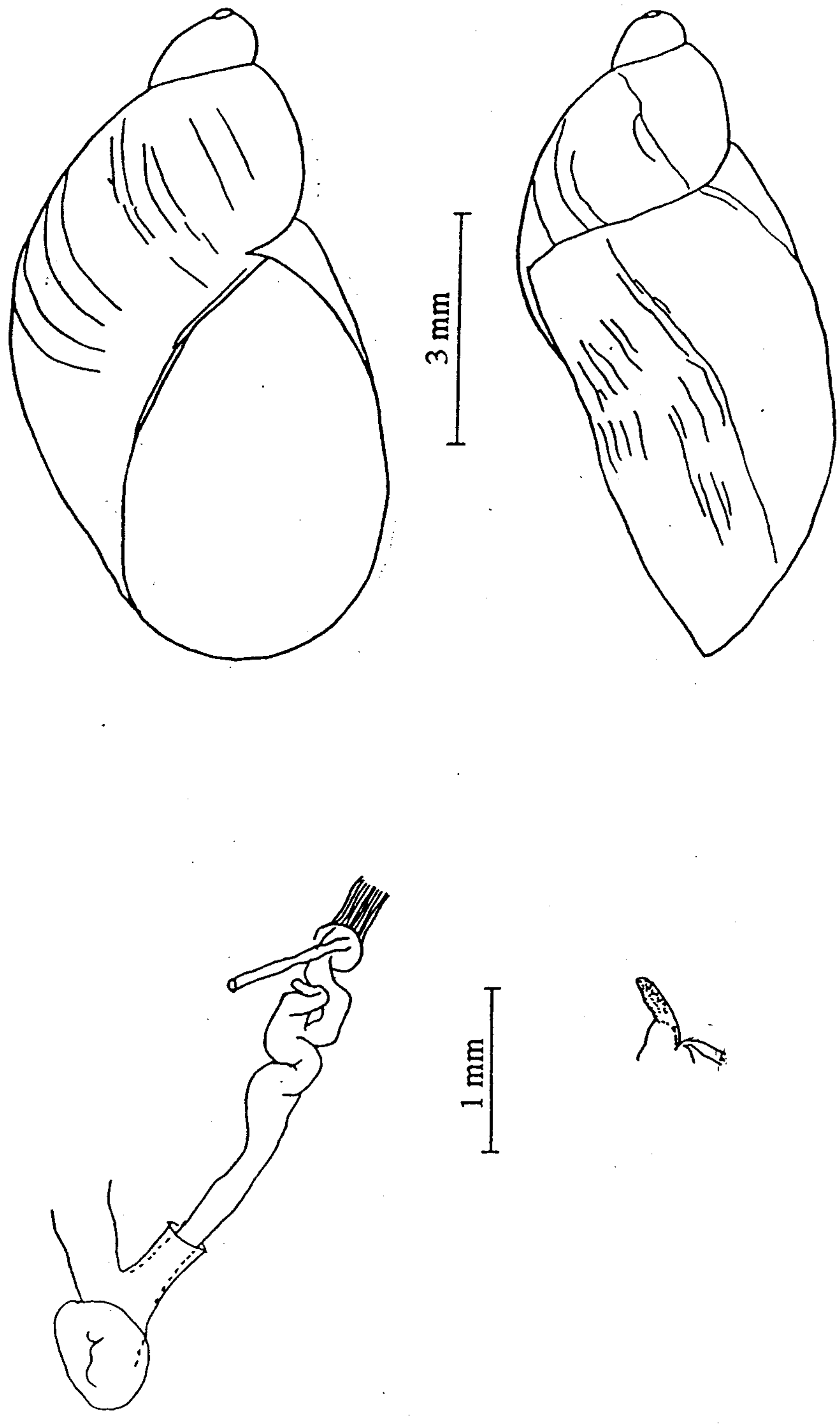


Figure 2.7: Shell and anatomy of *Oxyloma nuttallina* Lea, Stevens' specimen number 229.

Oxyloma retusa (Lea)
Stevens #8

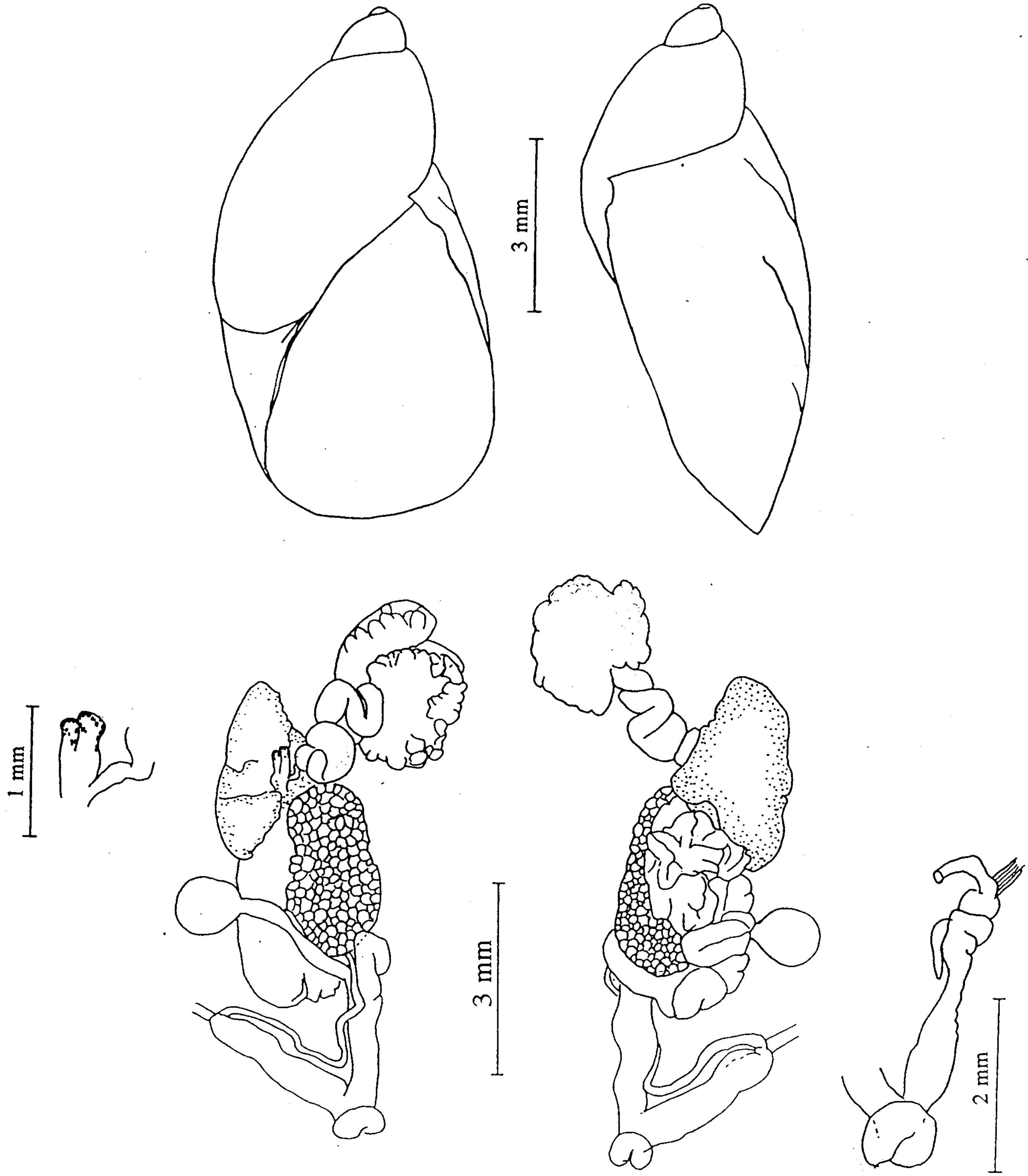


Figure 2.8: Shell and anatomy of *Oxyloma retusa* (Lea), Stevens' specimen number 8.

Succinea concordialis Lea

Stevens #50

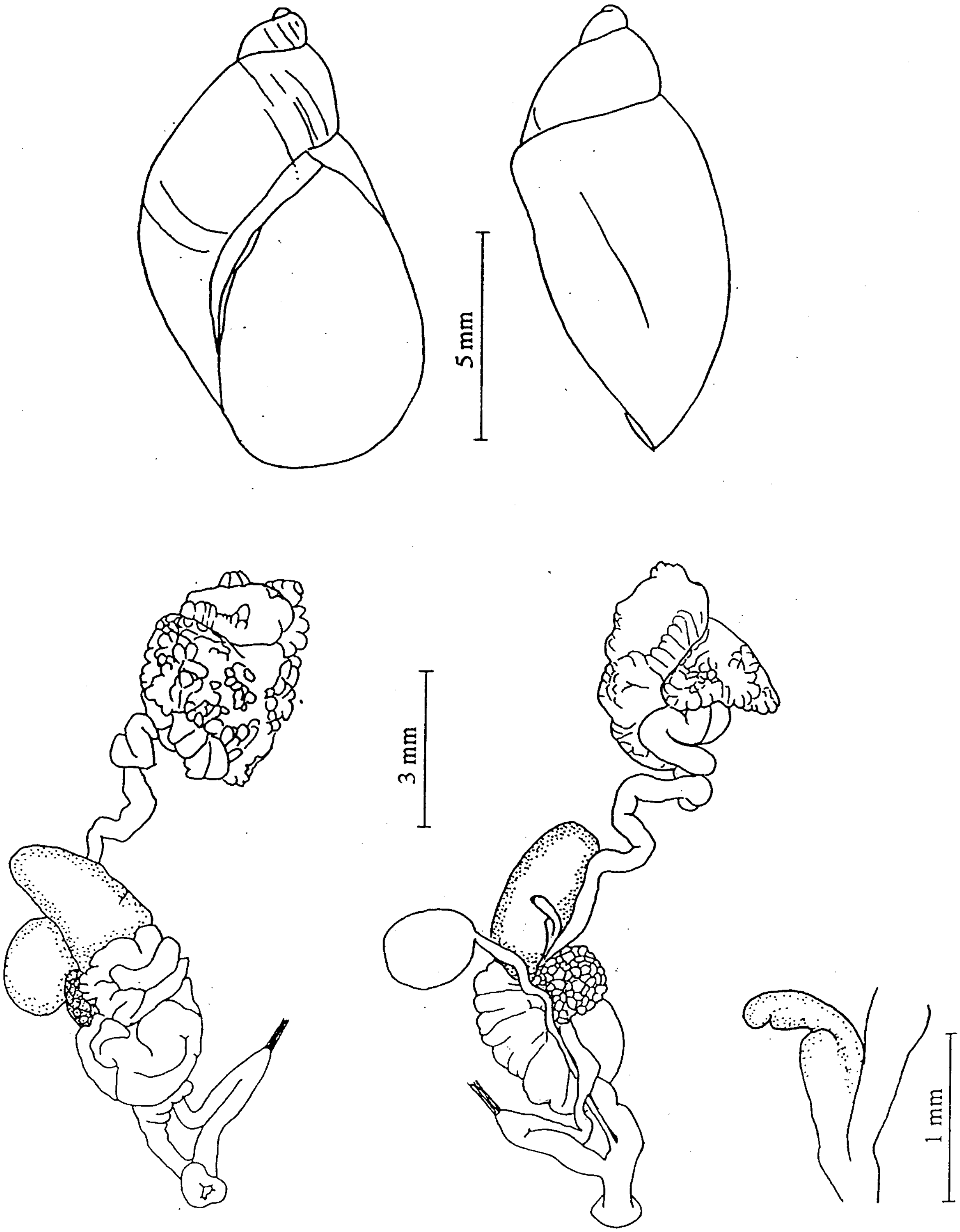


Figure 2.9: Shell and anatomy of *Succinea concordialis* Lea, Stevens' specimen number 50.

Succinea ovalis Say
Stevens #92

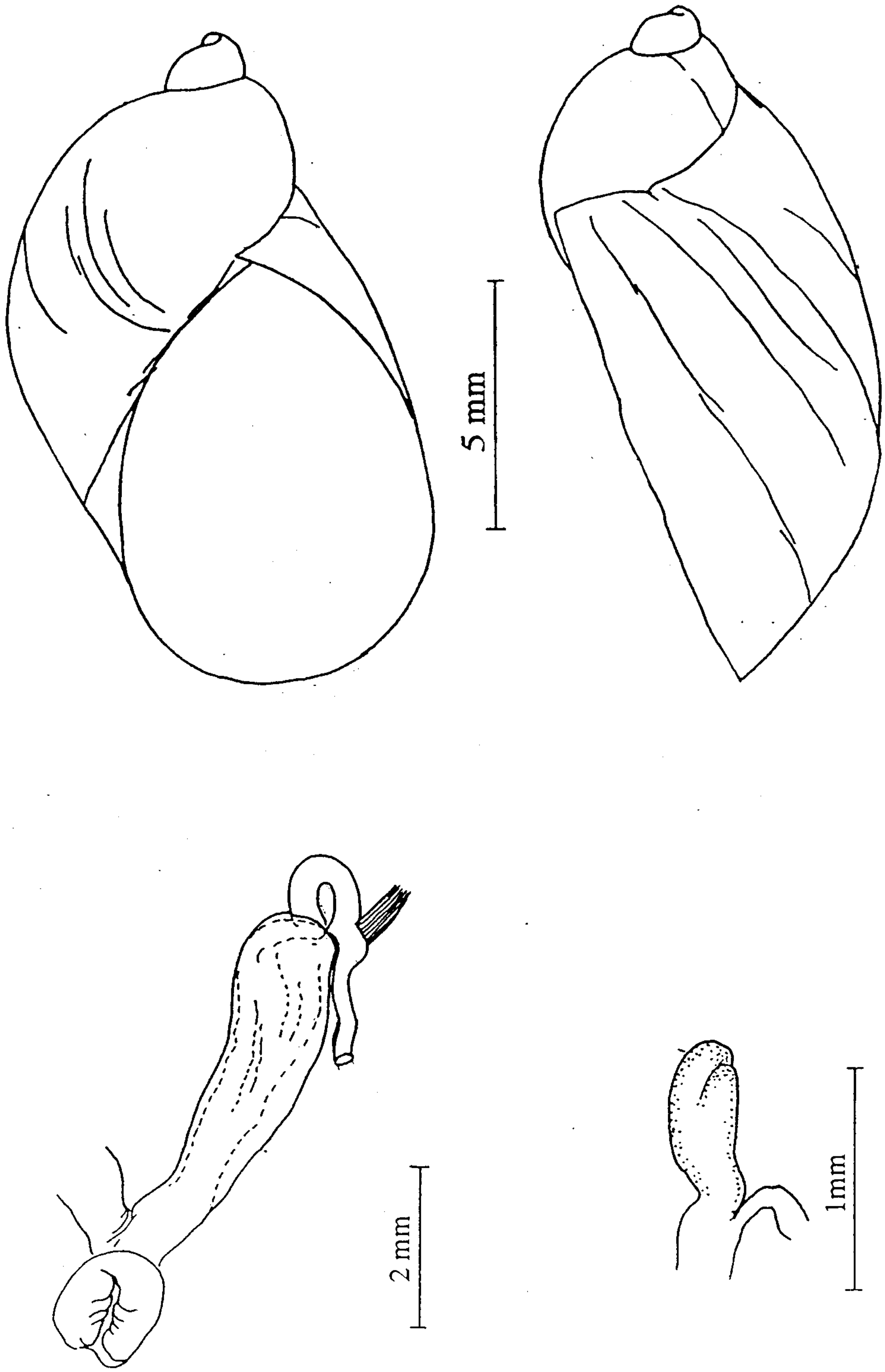


Figure 2.10: Shell and anatomy of *Succinea ovalis* Say, Stevens' specimen number 92.

muskeg. Our data generally supports this pattern, with specimens tentatively assigned to *O. h. kanabensis* found just west of Edmonton, Alberta. However, Harris and Hubricht (1982) identified *O. kanabensis* from the south side of Pigeon Lake, a locality that presently supports *O. h. haydeni*. This represents a slight western range extension for *O. haydeni*, or a misidentification on the part of those authors.

We found *?Oxyloma nuttallina* (Lea; the *O. nuttalliana* of Harris and Hubricht 1982) to be widely distributed across Alberta, bridging Harris and Hubricht's (1982) eastern range boundary of the Continental Divide. Harris and Hubricht's (1982) extensive collections in the region had indicated that this species was restricted to the west of the Continental Divide. Also, we found *O. retusa* widely across central Alberta, well north of Harris and Hubricht's (1982) northern limit at Cobden Lake, southern Alberta. Dr. Wu's analyses indicate broad overlap of the ranges of several *Oxyloma* in Alberta.

***O.h. kanabensis* Type Locality Collections:** The present work also provided large specimens for analysis from the Kanab Creek drainage from very near the presumed type locality of *Oxyloma h. kanabensis*. Three smaller specimens had been previously examined from this locality and considered to be *O. h. kanabensis*; however, analysis of four larger specimens in the present study revealed only *O. h. haydeni*. Additional specimens should be examined to determine whether the type locality population of *O. h. kanabensis* has shifted to *O. h. haydeni*, or whether the two taxa co-occur there.

CHAPTER 3:

A MOLECULAR PHYLOGENY OF THE GENUS *OXYLOMA* (PULMONATA: SUCCINEIDAE) IN WESTERN NORTH AMERICA WITH RESPECT TO THE ENDANGERED KANAB AMBERSNAIL (*OXYLOMA HAYDENI KANABENSIS*)

Mark P. Miller, Lawrence E. Stevens, and Paul Keim

INTRODUCTION

The Kanab ambersnail (KAS; *Oxyloma haydeni kanabensis*) is known from only two locations in the United States: one at Three Lakes, Utah and one at Vaseys Paradise along the Colorado River in Grand Canyon National Park. This taxon, protected under the endangered species act as an endangered subspecies, has received considerable attention because its presence at Vaseys Paradise has implications for the ecosystem-wide management of the Colorado River. In 1996, an experimental high-water discharge from Glen Canyon Dam destroyed or degraded approximately 16% of KAS habitat at Vaseys Paradise (Stevens *et al.* 1997). This planned flood release was designed to let resource managers evaluate an alternate strategy for Glen Canyon Dam operations that would allow the restoration of more natural flow regimes throughout the Grand Canyon. The ultimate goal was to mimic natural events that occurred in the canyon prior to the completion of dam construction in 1963. As a result of the habitat destruction at Vaseys Paradise during the flood event, the U.S. Fish and Wildlife Service (1996, 1997) ruled that no further experimental floods could be conducted until additional Kanab ambersnail populations were discovered or established. Because of this ruling, a situation then existed where the management of a single endangered species was in direct opposition of the management of an entire ecosystem. In a study by Miller et al. (in review), Amplified Fragment Length Polymorphism (AFLP) diversity was characterized in individuals from the two known KAS populations as well as individuals from the only two known southwestern populations of the widespread, non-endangered, NAS (*Oxyloma haydeni haydeni*) from Indian Gardens in Grand Canyon National Park and the -9 Mile spring upriver from Lees Ferry along the Colorado River. A controversial result of this analysis was the suggestion that the KAS population at Three Lakes was more closely related to a non-endangered NAS population at Indian Gardens in Grand Canyon National Park. In addition, the Vaseys Paradise population appeared to be distinct from the other three populations. This relationship was further corroborated with the use of DNA sequence data from two mitochondrial genes and raised multiple questions about the taxonomic status of the KAS and the protected status it receives from the Endangered Species Act (Miller *et al.*, in review).

The objective of this study was to generate a molecular phylogeny of western North American ambersnails with respect to the taxonomic status of the Vaseys Paradise population. New *Oxyloma* populations discovered in Utah and Nevada (L.E. Stevens and V.J. Meretsky, personal communication), as well as Miller *et al's.* (in review) four previously sampled *Oxyloma* populations were included in analyses to help provide a better understanding of patterns of genetic differentiation and relationship among populations of this taxon in the Southwest. Overall, we obtained sequence data from a 350 bp region of the *Cytb* gene for 96 individuals from 50 locations to elucidate the genetic relationships of succineids at both the species and population levels.

METHODS

Specimens received at Dr. Keim's laboratory were identified by a single number which was used later to provide collection location and in some instances species identification information. Ethanol-preserved tissue was stored at -20°C while non-preserved tissue was stored at -80°C until use. DNA extractions from specimens were performed using standard proteinase-K digestions coupled with phenol/chloroform protein extraction methods. Whole genomic DNA was precipitated with isopropanol and subsequently washed with 70% ETOH prior to drying and resuspending in 50 mM Tris, 0.1 mM EDTA, pH 8.

A ~410 bp region of the *Cytb* gene was amplified and sequenced using the universal molluscan primers (U*Cytb*151F and U*Cytb*270R) designed by Merritt *et al.* (1998). Amplification of this gene fragment was performed in 1X PCR buffer (Sigma) 2.5 mM $MgCl_2$, 200 mM dNTPs, 0.5 pmol/□l each primer, and 2 U *Taq* DNA polymerase (Sigma). Thermal cycling was performed using an initial heat soak at 94°C for 2 min. and then 40 cycles of the following: 10 sec. at 94°C to denature, 10 sec. at 45°C to anneal primers, and 10 sec. at 72°C for product extension. In most instances, duplicate PCR reactions were performed for each specimen to ensure that sufficient quantities of product would be available for sequencing. All PCR products were purified using Qiagen PCR purification spin-columns following the manufacturer-specified procedure. Sequencing took place using an Applied Biosystems, Inc. Model 377 automated flourescent sequencer. Cycle-sequencing reactions were conducted for both strands of the PCR amplicon using d-Rhodamine di-deoxyribonucleotide terminators (Applied Biosystems, Inc.) following the manufacturers protocols, except that annealing temperatures of sequencing reactions were changed to 45°C. Unincorporated dye terminators were removed from sequence reaction product using an ethanol/sodium acetate precipitation procedure prior to re-suspending products in 2 □l of loading dye for analysis on the DNA sequencer. After gel runs, sequences were aligned and manually edited using Sequence Navigator (Applied Biosystems, Inc.). Because of the highly degenerate nature of the *Cytb* primers used, data from 5' ends of sequence data were frequently difficult to unambiguously interpret. As a result, only 350 bp of internal sequence information was used for analyses. Overall, we were able to obtain data for 96 specimens collected from 50 different locations.

Aligned and edited sequence data were entered into MegAlign (Lasergene), which was used to create input files for PAUP* (Swofford 1999). In PAUP*, sequence data were analyzed via maximum parsimony using a heuristic search and with a Neighbor-Joining procedure. Genetic distances used for the latter procedure were calculated using the method of Jukes and Cantor (1969). Additional support for the Neighbor-Joining tree was obtained though the use of a bootstrap procedure consisting of 100 bootstrap replicates. We also obtained descriptive information of the sequence data using MEGA (Kumar *et al.* 1993), which calculated absolute numbers of nucleotide differences between each pair of specimens included in our analysis. This information was plotted as a histogram to observe patterns of genetic distances among individuals within and between genera. Once data were analyzed, we received information on collection locations and species identifications for the individuals studied that was subsequently mapped onto dendrograms.

RESULTS

A total of 181 of the 350 nucleotides from the *Cytb* gene were constant across all of the specimens studied. Of the remaining variable characters, 146 were parsimony-informative. Use of the maximum parsimony procedure found 32 equally parsimonious trees, each having a total length of 375 steps with consistency indices of 0.63. A midpoint-rooted majority rules consensus of the 32 equally-parsimonious phylogenies is shown in Fig. 3.1. Based on our data, we were clearly able to distinguish among individuals of the genera *Oxyloma*, *Succinea*, and *Catinella*, which appeared as separate groups. Figure 3.2 is an example of one of the 32 equally-parsimonious trees and can be used to obtain a general feel for branch lengths on the dendrogram. Branch lengths and locations of taxa on the remaining 31 trees are identical except for rearrangements within southwestern group A.

Within *Oxyloma,* it appeared that there was some geographical clustering of individuals. For example, one group was comprised mainly of individuals collected in Alberta (indicated by point "B" on Figs. 3.1-3.3) while a second group consisted of individuals from southwestern U.S. populations in Nevada, Utah, and Arizona (indicated by point "A" on Figs. 3.1-3.3). Each of these clades contains multiple different morphospecies: the southwestern group included morpho-species identified as *O. haydeni*, *O. kanabensis*, and *O. retusa*. Similarly, the Alberta group represented species including *O. haydeni*, *O. kanabensis*, *O. retusa*, and *O. nuttallina*.

The Neighbor-Joining bootstrap consensus tree is presented in Fig. 3.3. Overall, there is excellent support at the genus level for the taxa studied. Specimens from the genus *Catinella* were grouped 84% of the time while a separate group containing *Oxyloma* specimens was observed in all 100 bootstrap replicates. Of interest is specimen 21.185 from Alberta, which was identified as *O. kanabensis*. While shown on a branch between two *Succinea* groups in Fig. 3.3, it should be noted that the presented arrangement occurred in only 53 of the 100 bootstrap replicates. In the remaining 47 replicates, that taxon instead was placed between the Vaseys Paradise population and the *Succinea* group consisting of specimens from locations 8 and 17.

The bootstrap procedure was unable to reliably resolve many of the population-level relationships within *Oxyloma*, as indicated by the branching of many individuals from the large central polytomy (Fig. 3.3). The majority of high bootstrap values were associated with individuals from the same population. A high value (87), however, was associated with the clustering of individuals in the southwestern group (indicated by the branch at point "A"). Similarly, in 71 bootstrap replicates, the Vaseys Paradise population was placed on its own distinct branch separate from its congeners. The Alberta group (indicated by the branch at point "B") was supported in only 60 replicates.

Examination of the distribution of absolute genetic distances (number of nucleotide differences) between each pair of specimens examined in this study revealed several trends (Figs. 3.4, 3.5). Three discrete groups of distances were observed, which fell in the ranges of

Fig. 3.1. Midpoint rooted, majority rules consensus tree of the 32 equally-parsimonious phylogenies obtained from parsimony analysis. Numbers along branches of tree indicate the proportion of the 32 trees that agreed with the arrangement shown. Nodes with less than 50% consensus are collapsed to form polytomies. Alphanumeric codes along terminal branches identify collection location, state or province where the specimen was collected, and specimen number. For example, the code "13.97IN" indicates specimen 97 from location13 in Iowa. Individuals marked with a tilde (~) before their designation were analyzed both morphologically and genetically. Symbols following state or province designation indicate presumed species identity of *Oxyloma* specimens based on the assumption that all individuals from the same collection location are the same species. * = *Oxyloma haydeni*; ! = *Oxyloma kanabensis*; $ = *Oxyloma retusa*. Taxonomic designations are absolute only for those individuals examined by Dr. Wu. Specimens with names enclosed by a box indicate sequences from individuals examined in the preliminary study by Miller *et al.* (in review).

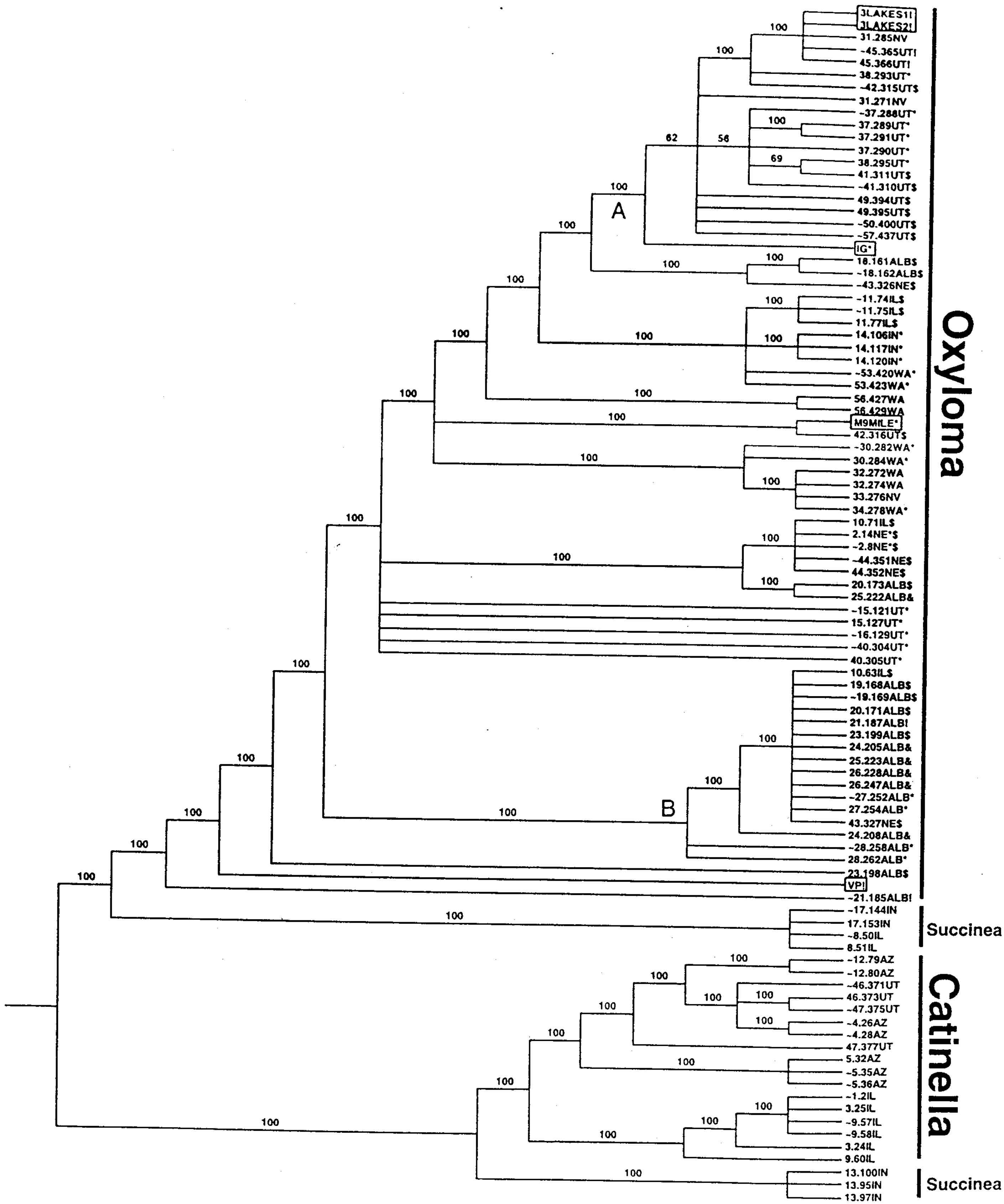
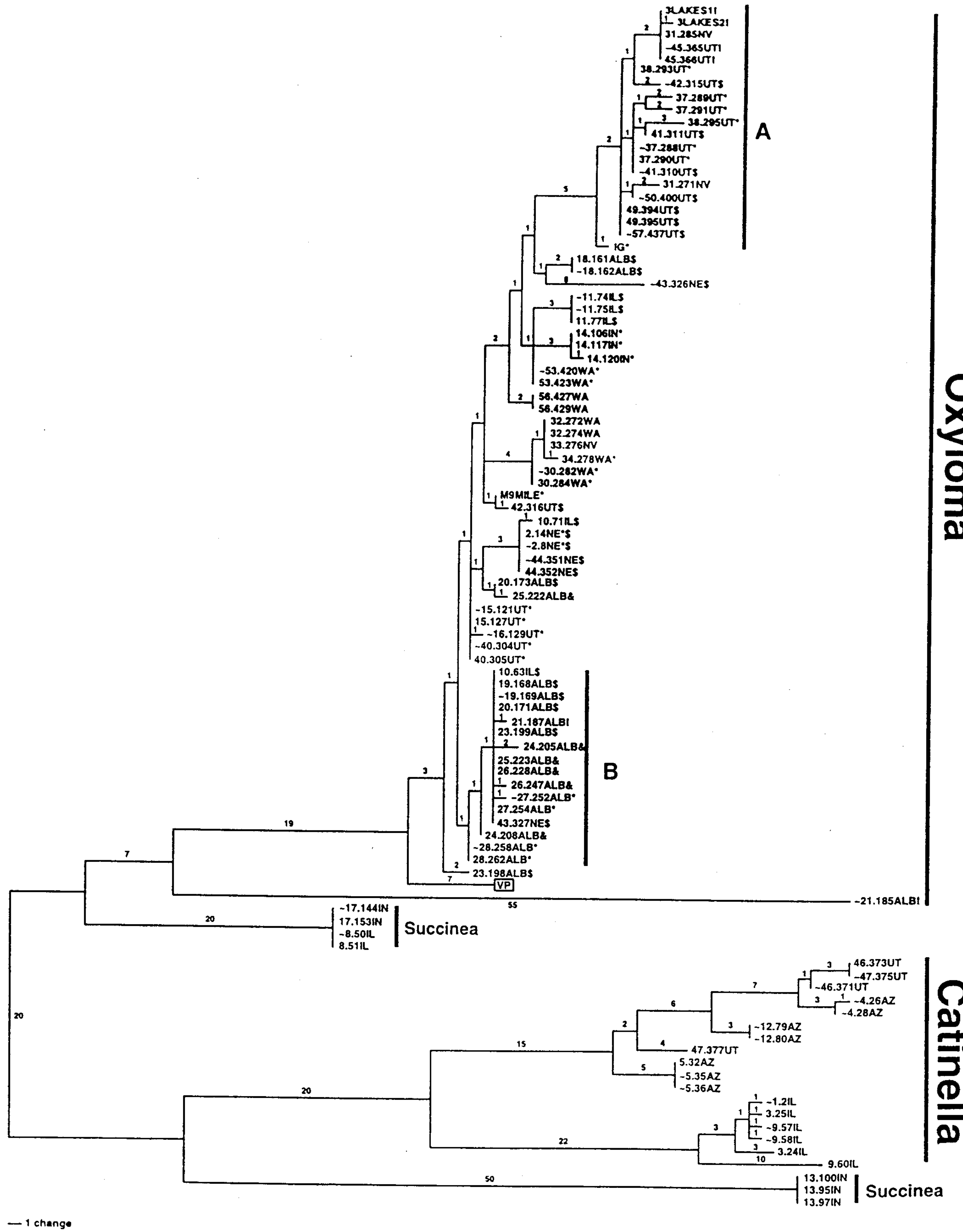
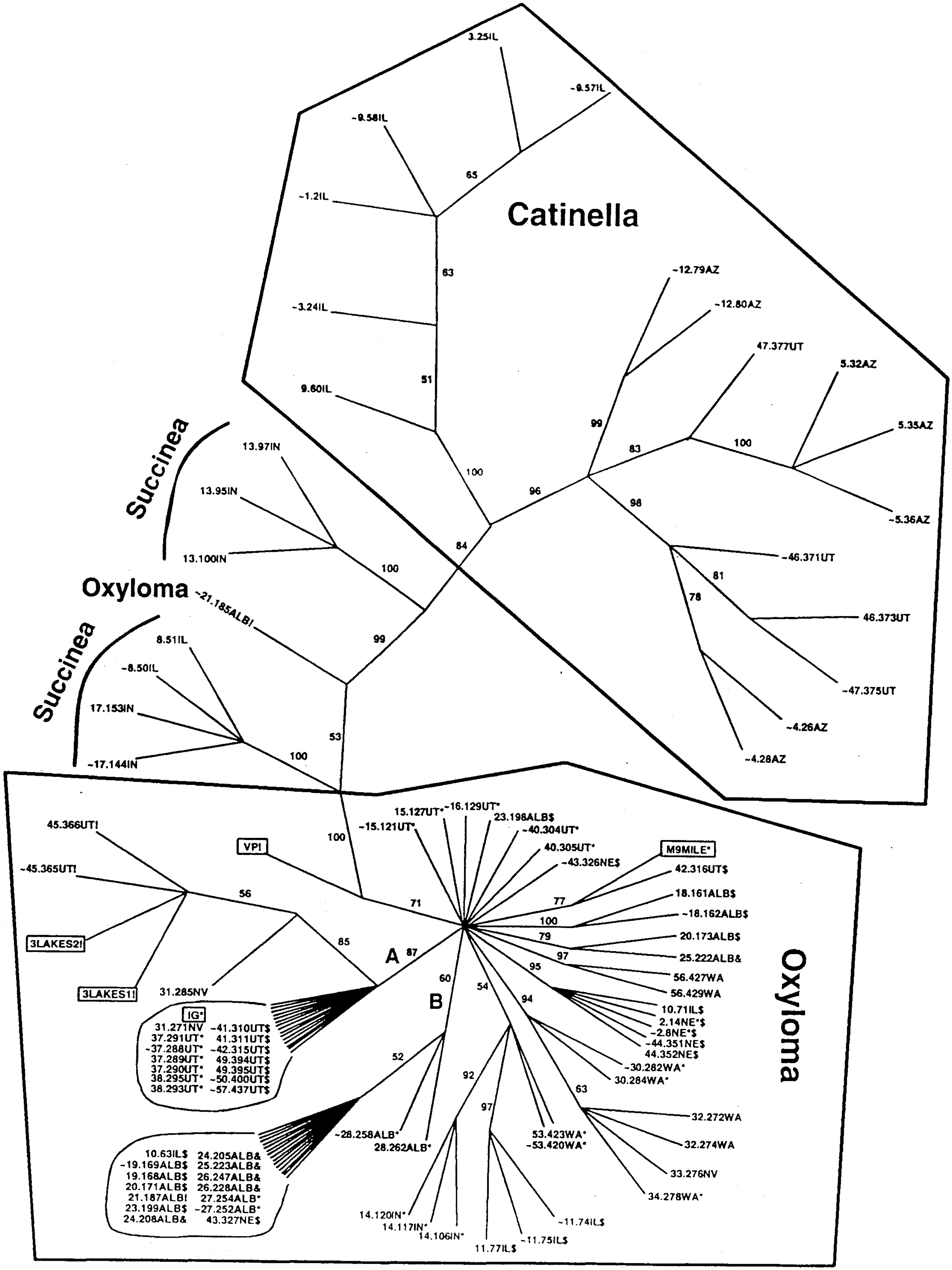

Oxyloma
Succinea
Catinella
Succinea
A
B
3LAKES1!
3LAKES2!
31.285NV
~45.365UT!
45.366UT!
38.293UT*
~42.315UT$
31.271NV
~37.288UT*
37.289UT*
37.291UT*
37.290UT*
38.295UT*
41.311UT$
~41.310UT$
49.394UT$
49.395UT$
~50.400UT$
~57.437UT$
IG*
18.161ALB$
~18.162ALB$
~43.326NE$
~11.74IL$
~11.75IL$
11.77IL$
14.106IN*
14.117IN*
14.120IN*
~53.420WA*
53.423WA*
56.427WA
56.429WA
M9MILE*
42.316UT$
~30.282WA*
30.284WA*
32.272WA
32.274WA
33.276NV
34.278WA*
10.71IL$
2.14NE*$
~2.8NE*$
~44.351NE$
44.352NE$
20.173ALB$
25.222ALB&
~15.121UT*
15.127UT*
~16.129UT*
~40.304UT*
40.305UT*
10.63IL$
19.168ALB$
~19.169ALB$
20.171ALB$
21.187ALB!
23.199ALB$
24.205ALB&
25.223ALB&
26.228ALB&
26.247ALB&
~27.252ALB*
27.254ALB*
43.327NE$
24.208ALB&
~28.258ALB*
28.262ALB*
23.198ALB$
VP!
~21.185ALB!
~17.144IN
17.153IN
~8.50IL
8.51IL
~12.79AZ
~12.80AZ
~46.371UT
46.373UT
~47.375UT
~4.26AZ
~4.28AZ
47.377UT
5.32AZ
~5.35AZ
~5.36AZ
~1.2IL
3.25IL
~9.57IL
~9.58IL
3.24IL
9.60IL
13.100IN
13.95IN
13.97IN

Fig. 3.2. An example of one of the 32 equally-parsimonious trees obtained in this study. The remaining 32 trees are identical save for rearrangements within southwestern group A. Numbers along branches indicate the number of changes or differences for a given individual or group. See Fig. 3.1 caption for a description of alphanumeric codes along terminal branches.



Oxyloma
A
B
3LAKES11
3LAKES21
31.285NV
~45.365UT!
45.366UT!
38.293UT*
~42.315UT$
37.289UT*
37.291UT*
38.295UT*
41.311UT$
~37.288UT*
37.290UT*
~41.310UT$
31.271NV
~50.400UT$
49.394UT$
49.395UT$
~57.437UT$
IG*
18.161ALB$
~18.162ALB$
~43.326NE$
~11.74IL$
~11.75IL$
11.77IL$
14.106IN*
14.117IN*
14.120IN*
~53.420WA*
53.423WA*
56.427WA
56.429WA
32.272WA
32.274WA
33.276NV
34.278WA*
~30.282WA*
30.284WA*
M9MILE*
42.316UT$
10.71IL$
2.14NE*$
~2.8NE*$
~44.351NE$
44.352NE$
20.173ALB$
25.222ALB&
~15.121UT*
15.127UT*
~16.129UT*
~40.304UT*
40.305UT*
10.63IL$
19.168ALB$
~19.169ALB$
20.171ALB$
21.187ALB!
23.199ALB$
24.205ALB&
25.223ALB&
26.228ALB&
26.247ALB&
~27.252ALB*
27.254ALB*
43.327NE$
24.208ALB&
~28.258ALB*
28.262ALB*
23.198ALB$
VP
~21.185ALB!
~17.144IN
17.153IN
~8.50IL
8.51IL
Succinea
Catinella
46.373UT
~47.375UT
~46.371UT
~4.26AZ
~4.28AZ
~12.79AZ
~12.80AZ
47.377UT
5.32AZ
~5.35AZ
~5.36AZ
~1.2IL
3.25IL
~9.57IL
~9.58IL
3.24IL
9.60IL
13.100IN
13.95IN
13.97IN
Succinea
1 change

Fig. 3.3. Neighbor-Joining bootstrap consensus tree of all individuals studied. Numbers along branch lengths indicate the percent of 100 bootstrap replicates that supported the arrangement shown. Groups with less than 50% support are collapsed to form polytomies. See Fig. 3.1 caption for a description of alphanumeric codes along terminal branches.



Catinella
Succinea
Oxyloma
Succinea
Oxyloma
3.25IL
~9.57IL
~9.58IL
65
~1.2IL
63
~3.24IL
51
9.60IL
100
96
84
~12.79AZ
~12.80AZ
47.377UT
5.32AZ
5.35AZ
99
83
100
~5.36AZ
98
~46.371UT
81
78
46.373UT
~47.375UT
~4.26AZ
~4.28AZ
13.97IN
13.95IN
13.100IN
100
~21.185ALBI
99
8.51IL
~8.50IL
17.153IN
~17.144IN
100
53
100
45.366UT!
~45.365UT!
56
3LAKES2!
3LAKES1!
31.285NV
85
VP!
71
A
87
~15.121UT*
15.127UT*
~16.129UT*
23.198ALB$
~40.304UT*
40.305UT*
~43.326NE$
M9MILE*
42.316UT$
77
18.161ALB$
100
~18.162ALB$
79
20.173ALB$
97
25.222ALB&
95
56.427WA
56.429WA
10.71IL$
2.14NE*$
~2.8NE*$
~44.351NE$
44.352NE$
94
~30.282WA*
30.284WA*
63
32.272WA
32.274WA
33.276NV
34.278WA*
53.423WA*
~53.420WA*
IG*
31.271NV ~41.310UT$
37.291UT* 41.311UT$
~37.288UT* ~42.315UT$
37.289UT* 49.394UT$
37.290UT* 49.395UT$
38.295UT* ~50.400UT$
38.293UT* ~57.437UT$
60
B
54
52
92
97
10.63IL$ 24.205ALB&
~19.169ALB$ 25.223ALB&
19.168ALB$ 26.247ALB&
20.171ALB$ 26.228ALB&
21.187ALBI 27.254ALB*
23.199ALB$ ~27.252ALB*
24.208ALB& 43.327NE$
~28.258ALB*
28.262ALB*
14.120IN*
14.117IN*
14.106IN*
11.77IL$
~11.75IL$
~11.74IL$

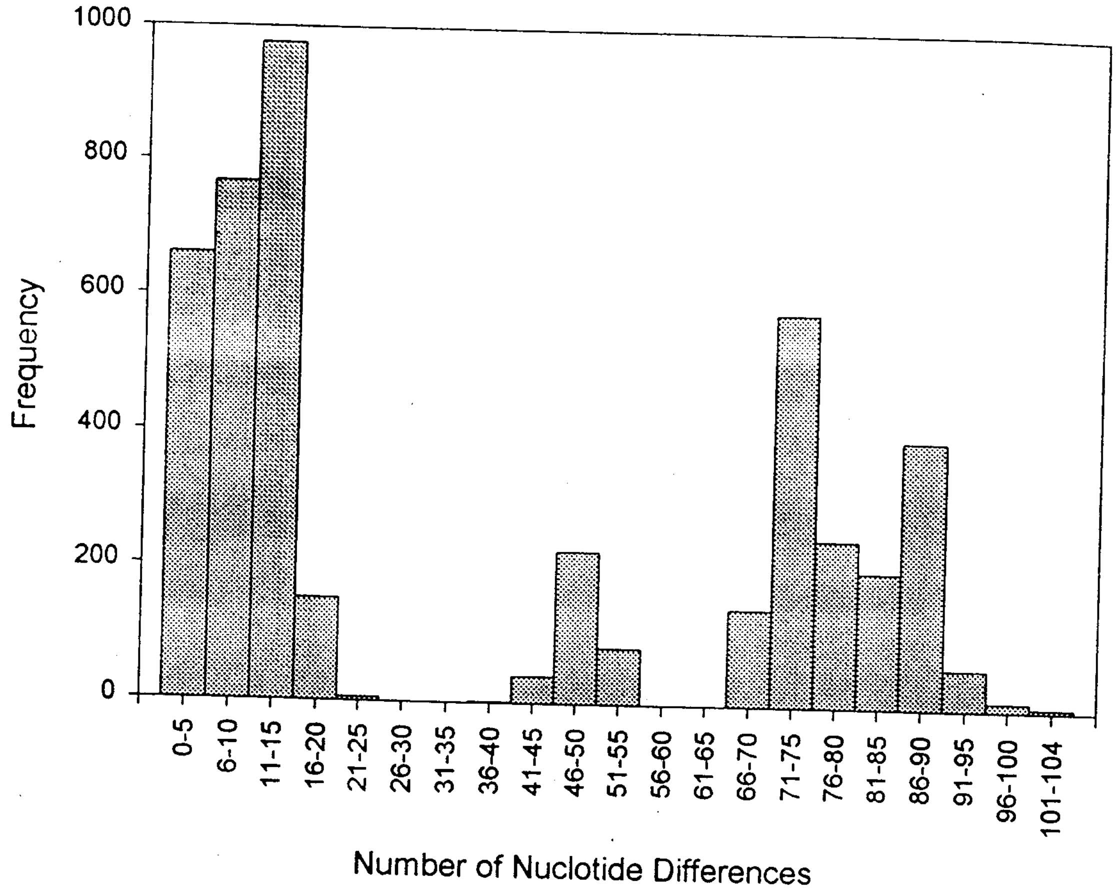


Fig. 3.4. Histogram of the distribution of absolute genetic distances (number of nucleotide differences) between all pairs of specimens examined in this study.

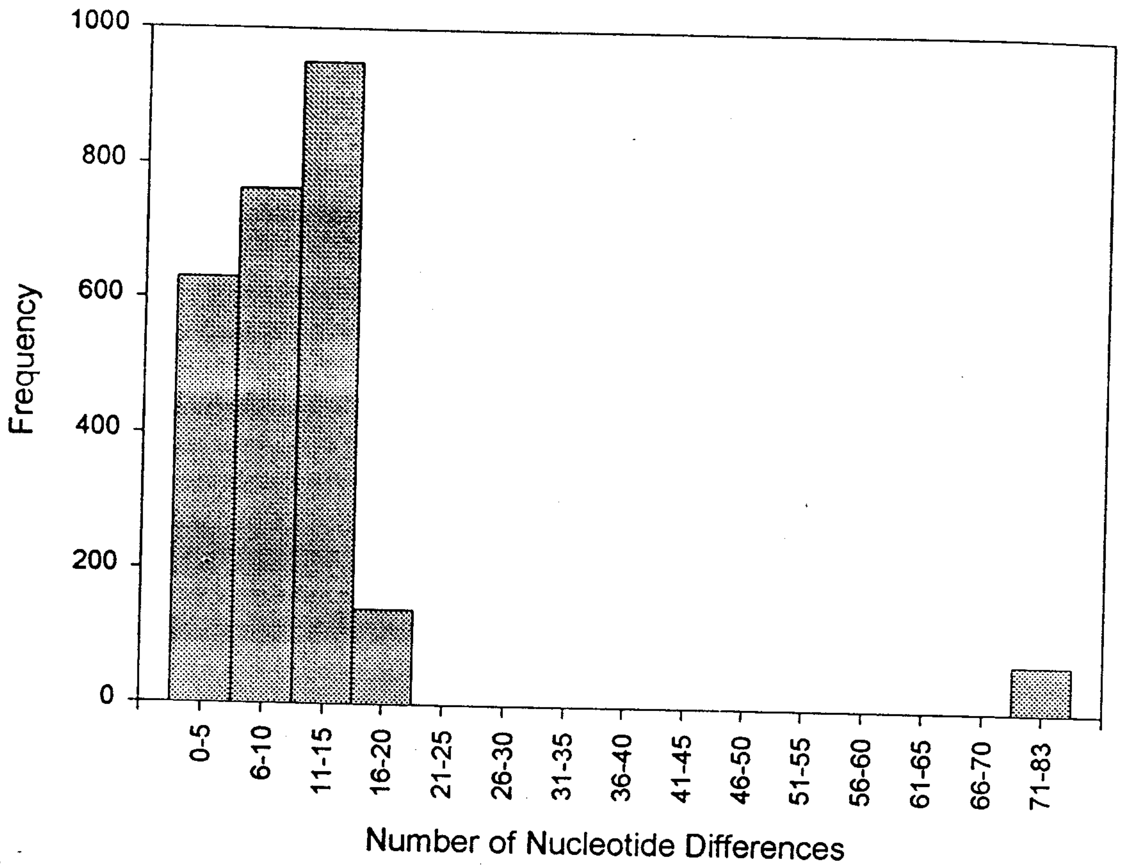


Fig. 3.5. Histogram of the distribution of absolute genetic distances (number of nucleotide differences) between all pairs of specimens identified as *Oxyloma*. The Vaseys Paradise Oxyloma population displayed genetic distances of 16-20. The anomalous specimen number 21.185 from Alberta Beach, west of Edmonton, Alberta had 71-83 nucleotide differences from other populations.

0-22, 40-54, and 66-104. Pairs of individuals with genetic distances between 0 and 25 were from the same genera. Within this range, the highest values were dominated by contrasts between the Vaseys Paradise population and individuals from the southwestern *Oxyloma* group (range: 18-20) and by contrasts between specimens from location 5 (identified as *Catinella ?mooresiana* from Arizona) and specimens from locations 4, 12, 46, and 47 (identified as *C. vermata* and *C. mooresiana* from Arizona and Utah). Genetic distances between 36-45 corresponded mainly to contrasts between *C. witteri* specimens from locations 1, 3, and 9 (representing different Illinois populations) and *C. vermata* and *C. mooresiana* specimens from locations 4, 5, 12, 46, and 47 in Arizona and Utah. Distances between 46 and 55 mainly represented comparisons of *Oxyloma* specimens and *Succinea* specimens from locations 8 and 17 (Illinois). Distances between presumed *S. ovalis* specimens from location 13 (Iowa) and *Oxyloma* individuals ranged from 85-90. Distances representing the relationships between *Oxyloma* and *Catinella* specimens occurred frequently in the range of 66-95 while contrasts including *Succinea* and *Catinella* occurred from 71 to 80. Specimens presumably corresponding to *S. ovalis* (location 13, Iowa) and *S. concordialis* (locations 8 and 17 from Illinois, respectively) all had genetic distances of 85 when compared to each other. Distances involving specimen 21.185, presumably identified as *O. kanabensis* from Alberta, were among the highest observed in the data set. Another specimen from this site (21.187), also morphologically identified as *O. h. kanabensis*, clustered with the *O.h. haydeni* complex (Group B in Fig. 3.2). The lowest value observed for this individual was 68, which is the observed difference between it and *S. concordialis* specimens from locations 8 and 17. Genetic distances of specimen 21.185 and the other specimens identified as *Oxyloma* in this data set ranged from 75 to 83. All distances greater than 95 were between specimen 21.185 and *Catinella* specimens.

DISCUSSION

Overall, results from this study corroborate findings of the previous study by Miller *et al.* (in review). The 3 Lakes and Indian Gardens populations, when included with a sample of a more diverse set of populations, continue to form part of the same evolutionary clade. Similarly, the Vaseys Paradise population, which appeared to be distinct from the other three populations examined in the previous study, appears in its own basal group outside of the majority of other *Oxyloma* specimens included in this study (Figs. 3.1-3.3). Genetic distances between the Vaseys Paradise population and the rest of the southwestern *Oxyloma* group were among the greatest within the range of 0-20 (Figs. 3.4, 3.5). While the development of a more rigorous phylogenetic framework would be necessary to confirm it, the data suggest that the Vaseys Paradise population may in fact be a distinct species. It remains possible that related populations may have existed upstream along the Colorado River prior to construction of the Glen Canyon Dam, however, the genetic dissimilarity of Vaseys Paradise individuals and individuals from the upstream -9 Mile spring population suggest that not to be the case.

A significant result of this study is the finding that the current morphological criteria used to distinguish *Oxyloma* species may be phylogenetically misleading. For example, the well-supported southwestern U.S. group (Fig. 3.1-3.3, designated as "A") contained specimens identified as *O. haydeni*, *O. kanabensis*, and *O. retusa*. Similarly, the Alberta group (Fig. 3.1-3.3, designated as "B"), although not as well defined, contained specimens identified as *O. haydeni*, *O. kanabensis*, *O. retusa*, and *O. nuttallina*. In addition, specimens identified as *O. kanabensis* from Vaseys Paradise and Alberta (specimen 21.185) appear to be distantly related to the rest of the *Oxyloma* specimens examined in this study (Fig. 3.1-3.3). Similar conflicting patterns were also observed within the genus *Catinella*. Specimens identified as *C. vermata* (location 4 from Arizona) formed a well-defined clade with individuals identified as *C. mooresiana* (locations 46 and 47 from Utah; Fig. 3.3).

Two alternate explanations can be invoked to account for the observed discrepancy between the molecular and morphological data. First, it could be considered that the genetic information may be insufficient to resolve species and subspecies-level relationships in the genus *Oxyloma*. This may be possible considering the relatively small amount of sequence data available for analysis. While 350 bp of data were obtained, only 42 nucleotides were parsimony-informative within the genus *Oxyloma*. It remains possible that a better understanding of relationships could be obtained if data for the entire *Cytb* gene were available. Alternately, rapidly-evolving regions of the mitochondrial genome, such as the non-coding d-loop, may be capable of providing better resolution. Second, it could be considered that the data are sufficient, but the morphological characters used to describe species and subspecies are evolutionarily insignificant. Such a scenario would result, in part, in the patterns observed with the molecular data from this study.

Morphological variation has long been a confounding factor in molluscan systematics. For example, species designations of freshwater Unionids has historically been based on shell morphological characters. Many of these characters, however, have since been interpreted as phenotypic variation found within species (Johnson 1970, Lydeard and Roe 1998, Williams and Mulvey *et al.* 1997). Often, molecular techniques have been required to resolve taxonomic issues in these instances. In a study by Mulvey *et al.* (1997), identical 16S rRNA haplotypes were found in the unionids, *Megalonaias boykiniana* and *M. nervosa*. Allozyme data provided similar evidence to suggest that these taxa were likely not separate species. In contrast, putative morpho-species of the bivalve *Potamilus inflatus* from geographically isolated populations have been shown to be separate evolutionary entities that are genetically as different as other morphologically distinct species in the genus (Roe and Lydeard 1997). Examples such as these also exist for pulmonates. Recent studies by Remigio and Blair (1997a, 1997b) showed little genetic differences among three species of lymnaeids in the genus *Stagnicola*: *S. catascopium*, *S. emarginata*, and *S. elodes*. These studies, which were based on comparisons of nuclear ribosomal ITS sequences and rRNA genes among taxa, suggested that these three species were in fact not distinct and supported prior evidence from breeding, morphological, ecological, and allozyme studies (Clarke 1973, Burch and Ayers 1973, Rudolph and Burch 1989).

Given these examples of both cryptic genetic and taxonomically-insignificant morphological variation, it appears likely that similar situations exist in the genus *Oxyloma*. In this study, we have showed that different specimens with the same anatomical features may in fact be unique evolutionary entities. In contrast, we also identified genetically-related specimens with different morphological attributes that have conventionally been considered to indicate different species. Given the findings of this study, it is apparent that the taxonomy of this genus is problematic. In all likelihood, its resolution will require significant new data on ecology, life history, morphology, and genetics to develop a complete understanding of the evolution of *Oxyloma*.

CHAPTER 4: SYNTHESIS AND RECOMMENDATIONS

INTRODUCTION

This study provides a great deal of new information on the taxonomic relationships and distribution of succineid landsnails in the United States and Canada, particularly the genus *Oxyloma* and the endangered taxon *O. haydeni kanabensis* at Vaseys Paradise. Rather than achieving consensus on the taxonomy of the endangered Vaseys Paradise Kanab ambersnail, our data indicate that a substantial discrepancy exists between morphological and genetic taxonomic designations. Molluscan taxonomic studies reveal both cases of morphologically indistinguishable but genetically different taxa, as well as morphologically different but genetically similar taxa, as referenced in Chapter 3. The former case may apply to the Vaseys Paradise *Oxyloma*, while the latter may apply to some or many of the western *Oxyloma*. Our genetic, but not morphological, analyses suggest that the Vaseys Paradise *Oxyloma* population, which has been considered to be endangered Kanab ambersnail, is a distinctive, cryptic taxon. It is morphologically indistinguishable, but genetically unique from, *Oxyloma* at Three Lakes UT, which is genetically most similar (among those populations collected) to a population in the Humboldt River drainage in the Great Basin. However, the Vaseys Paradise *Oxyloma* are morphologically differentiated from those in the vicinity of the presumed type locality in Kanab Canyon.

Despite morphological similarity to Three Lakes *Oxyloma*, those at Vaseys Paradise are unique in their habitat affinities and their size. The many other populations of *Oxyloma* in North America examined by LES and V.J. Meretsky (personal communication) in 1998 and 1999 are associated with *Typha* spp. and *Scirpus* spp., or occasionally *Phragmites australis* (S.K. Wu, personal communication). Nowhere else have we found *Oxyloma* inhabiting a hanging garden habitat, and showing considerable host plant affinity for *Mimulus cardinalis*. Also, the Vaseys Paradise *Oxyloma* normally attain a much larger size (rather commonly $\geq$18 mm in shell length) than that of the other Arizona *Oxyloma* populations, of those at Three Lakes, Kanab Canyon, Carlin Nevada, or any Alberta populations. This may be attributable to the longer growing season and warm temperatures at this lowest elevation, most southerly population of *Oxyloma haydeni*-related snails; however, it appears to be a distinctive trait. Although the classic morphological approach do not embrace ecological or size differences *per se* as sufficient cause for reclassification, morphological studies have not considered the possibility of evolutionary convergence or size-related morphological change.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Resolving Conflicting Taxonomic Views

While morphological versus genetic taxonomic conflicts are far from rare among the Mollusca, they are important in the United States because of the Endangered Species Act directs management activities and affects large federal actions and expenditures. What is required to resolve the apparent differences between morphological and genetic taxonomy of the Vaseys Paradise *Oxyloma* population? In this section, we suggest further research and experiments that may distinguish between these conflicting views.

Suggested Future Studies

Further Analyses of Existing Specimens: Less than one quarter of the material collected was analyzed in this study. Additional insight into the distribution of morpho-species and genetic clades, as well as the co-occurrence of different *Oxyloma* species, can be developed from further analyses of these materials.

Numerical Morphological Studies: One practice that would help determine the extent of variation in morphology would be the development of a quantitative analytical approach. Establishment of an ordinal scale for similarity to the various morphological traits of interest would help determine the extent of variation in those morphological characteristics.

Additional Genetic Analyses: The repeatability of genetic results may be determined using other genes or techniques.

More Thorough Analyses of Four Corners Oxyloma: Additional, more thorough, quantitative "blind" analyses of genetic and morphological variation among the *Oxyloma* populations in Utah, Arizona and Nevada may resolve issues of relatedness among these populations. In particular, analysis of multiple individuals from populations, such as that at Three Lakes, would help determine the constancy of genetic make-up within populations.

Size-related Morphological Variation: Experimental rearing of egg masses of known parentage can be used to test the role of size-related variation in morphology and genetic variability among the Vaseys Paradise, Three Lakes, Indian Gardens, -9L and Kanab Canyon *Oxyloma* populations.

Additional Collections of Oxyloma: Determination of genetic relationships among eastern *Oxyloma* and *Oxyloma missoula* (Harris and Hubricht 1982) will improve understanding of the the number of *Oxyloma* taxa in the United States. Snails putatively morphologically identified as Kanab ambersnail, and genetically anomalous specimens (*e.g.*, Alberta specimen 21.185) may help resolve apparent cases of convergence or anomalous distribution. Although a lower priority, such data will ultimately improve the understanding of diversity in this taxonomically challenging genus.

Improving Management

One of our objectives was to "provide an analysis of these data for an *Oxyloma* workshop to review the status of VP KAS taxonomy in relation to other *Oxyloma* in North America." We provided morphological and mitochondrial data on the *cytb* gene to an expert review panel convened by the Arizona Game and Fish Department in Phoenix on 1-3 December 1999. This panel reviewed the existing state of information on the taxonomy and management of the Vaseys Paradise *Oxyloma* population, and has prepared a report that fairly critiques our approach and preliminary results. We intend to continue to assist the Kanab Ambersnail Working Group and the managing agencies work to understand and resolve scientific issues related to this problem.

SUMMARY

Although this study does not resolve the debate over the taxonomy of the Vaseys Paradise *Oxyloma* population, it has brought to light the potentially large genetic distance between this and all other *Oxyloma* populations analyzed to date. Conversely, this study suggests that morphological similarity of the Vaseys Paradise *Oxyloma* population to the Three Lakes (but not the Kanab Creek) populations may not reflect genetic differentiation of this highly isolated population. Resolution of this debate remains an important task, as the snail's endangered status is a function of habitat endangerment in southern Utah, not the health of the population at Vaseys Paradise, which has substantially increased as a function of flood control by Glen Canyon Dam. The dam-augmented population at Vaseys Paradise does not necessarily mean increased population health: the relaxation of a previously intense flood-related selection regime, may permit the genetic drift or the accumulation of deleterious mutations over time. Such changes may lead to a long term shift in genetic constitution in this regulated wetland habitat.

ACKNOWLEDGEMENTS

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ADMINISTRATIVE REPORT

This project is nearing completion, and the Northern Arizona University accounting of the project indicates that $2,210.27 remains unexpended as of 5 January 2000 (Table 5.1). This project is still in the process of reimbursing Dr. Wu for his taxonomic services, and we expect additional comments on the final report, which will require additional analyses and staff writing time. Therefore, we expect that this project will xero out with the completion of the final report.

Table 5.1: Administration of BOR 98-FC-40-1230 (BIO 355L), as of 5 January 2000.

Budget Category	Budgeted	Encumbered	Spent	Remaining
Salaries	11,917.00	$ -	$8,567.86	
Grad. Asst.		$ -	$4,562.69	
ERE	$1,423.00	$ -	$1,297.01	
Subtotal	**$13,340.00**	**$ -**	**$14,427.56**	**$(1,087.56)**
Operations	$8,200.00	$ -	$ -	
Supplies	$ -	$1,402.15	$13,624.93	
Dues/Subsc			$125.00	
Reg/Con Fees			$21.00	
Subtotal	**$8,200.00**	**$1,402.15**	**$13,770.93**	**$(6,973.08)**
Outside Services	**$4,000.00**	**$ -**	**$ -**	
Subtotal	**$4,000.00**		**$ -**	**$4,000.00**
Travel-Instate	$9,350.00		$702.18	
Travel-OutState		$ -	$2,376.91	
Subtotal	**$9,350.00**	**$ -**	**$3,079.09**	**$6,270.91**
Equipment	$ -	$ -	$ -	
	$ -	$ -	$ -	$ -
Indirect Costs	$5,048.00	$99.62	$4,948.38	
Subtotal	**$5,048.00**	**$99.62**	**$4,948.38**	**$ -**
Totals	$39,938.00	$1,501.77	$36,225.96	$2,210.27

APPENDIX A:

SUCCINEID LANDSNAIL COLLECTION DATA

IN THE UNITED STATES AND CANADA,

1998-1999

Appendix A: Succineid collections in the United States and Canyon, 1998-1999.

Batch No	IDNO	STATE	COUNTY	LOCALITY	HABITAT	DATE	COLLCTR	Wu ID
1	1	IL	Crawford	Rt.1, 2-3 mi. into Crawford Co.	Roadside ditch w/ Typha&gras	980513	VJM	?Catinella witteri (Shimek)
1	2	IL	Crawford	Rt.1, 2-3 mi. into Crawford Co.	Roadside ditch w/ Typha&gras	980513	VJM	?Catinella witteri (Shimek)
1	3	IL	Crawford	Rt.1, 2-3 mi. into Crawford Co.	Roadside ditch w/ Typha&gras	980513	VJM	
1.5	4	NE	Custer	Victoria Springs State Rec. Area	Small stream/Populus/Saex/Ty	980512	EN	
1.5	5	NE	Custer	Victoria Springs State Rec. Area	Small stream/Populus/Saex/Ty	980512	EN	
2	7	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	8	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	9	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	Oxyloma retusa (Lea)
2	10	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	Oxyloma haydeni (Binney)
2	11	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	12	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	13	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	14	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	15	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	16	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	17	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	18	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	19	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	20	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	21	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
2	22	NE	Cherry	Cottonwood Lake State Rec. Area	Saex/Typha/grass	980513	EN	
3	23	IL	Jefferson	State Rt 142, 0.5 mi into Jefferson Co.; 350200.3 4231403.8	Snails on bare soil; ditch/strea	980513	VJM	
3	24	IL	Jefferson	State Rt 142, 0.5 mi into Jefferson Co.	Snails on bare soil	980513	VJM	?Catinella witteri (Shimek)
3	25F	IL	Jefferson	State Rt 142, 0.5 mi into Jefferson Co.	Snails on bare soil	980513	VJM	
4	26	AZ	Coconino	Vaseys Paradise, Mile 31.5R	Spring vegetation	980510	JAS	Catinella vermeta
4	27	AZ	Coconino	Vaseys Paradise, Mile 31.5R	Gave to M.Miller for freezing as	980510	JAS	
4	28	AZ	Coconino	Vaseys Paradise, Mile 31.5R	Spring vegetation	980510	JAS	Catinella vermeta
4	29	AZ	Coconino	Vaseys Paradise, CR Mile 31.5R	Spring vegetation	980510	JAS	
4	30	AZ	Coconino	Vaseys Paradise, CR Mile 31.5R	Spring vegetation	980510	JAS	
4	31	AZ	Coconino	Vaseys Paradise, CR Mile 31.5R	Spring vegetation	980510	JAS	
5	32	AZ	Coconino	Saddle Canyon, CR Mile 47	Gave to M.Miller for freezing as	980511	JAS	
5	33	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
5	34	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
5	35	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	Catinella vermeta
5	36	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	?Catinella mooresiana (Lea)
5	37	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
5	38	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
5	39	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
5	40	AZ	Coconino	Saddle Canyon, CR Mile 47	Streamside habitat	980511	JAS	
6	41	IL	White	IL 1 N. of Crossville	Ditch w/ good flow	980513	VJM	
6	42	IL	White	IL 1 N. of Crossville	Ditch w/ good flow	980513	VJM	
6	43	IL	White	IL 1 N. of Crossville	Ditch w/ good flow	980513	VJM	
6	44	IL	White	IL 1 N. of Crossville	Ditch w/ good flow	980513	VJM	
6	45	IL	White	IL 1 N. of Crossville	Ditch w/ good flow	980513	VJM	
7	46	IL	White	IL 14, E. of IL 1	Stream	980513	VJM	
7	47	IL	White	IL 14, E. of IL 1	Stream	980513	VJM	
7	48	IL	White	IL 14, E. of IL 1	Stream	980513	VJM	
7	49	IL	White	IL 14, E. of IL 1	Stream	980513	VJM	
8	50	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	Succinea concordialis Lea
8	51	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	
8	52	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	Succinea concordialis Lea
8	53	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	
8	54	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	Succinea concordialis Lea
8	55	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Ditch	980513	VJM	Succinea concordialis Lea

9	56	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	
9	57	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	
9	58	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	?Catinella witteri (Shimek)
9	59	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	?Catinella witteri (Shimek)
9	60	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	
9	61	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	
9	62	IL	White	0.45 mi. E of Rt 14 Rt 1 intersection on Rt 14; UTM 407569.7 44242	Grass-lined, roadside ditch	980513	VJM	
10	63	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	64	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	Oxyloma retusa (Lea)
10	65	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	Oxyloma retusa (Lea)
10	66	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	67	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	68	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	69	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	70	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	71	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	72	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
10	73	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Sedges/Carex wet meadow	980512	EN	
11	74	IL	DuPage	Slough at 75th St and Lemont Rd	Wetland vegetation	19980602	J.Slapcinsky	Oxyloma retusa (Lea)
11	75	IL	DuPage	Slough at 75th St and Lemont Rd	Wetland vegetation	19980602	J.Slapcinsky	Oxyloma retusa (Lea)
11	76	IL	DuPage	Slough at 75th St and Lemont Rd	Wetland vegetation	19980602	J.Slapcinsky	Oxyloma retusa (Lea)
11	77	IL	DuPage	Slough at 75th St and Lemont Rd	Wetland vegetation	19980602	J.Slapcinsky	
11	78	IL	DuPage	Slough at 75th St and Lemont Rd	Wetland vegetation	19980602	J.Slapcinsky	
12	79	AZ	Coconino	Roaring Springs	Springs vegetation	19980609	JAS	Catinella vermeta
12	80	AZ	Coconino	Roaring Springs	Springs vegetation	19980609	JAS	?Catinella mooresiana (Lea)
12	81	AZ	Coconino	Roaring Springs	Springs vegetation	19980609	JAS	
12	82	AZ	Coconino	Roaring Springs	Springs vegetation	19980609	JAS	
12	83	AZ	Coconino	Roaring Springs	Springs vegetation	19980609	JAS	
13	84	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	85	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	86	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	87	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	88	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	89	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	90	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	91	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	92	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	Succinea ovalis Say
13	93	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	94	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	95	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	96	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	97	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	98	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	99	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
13	100	IO	Dickinson	Iowa Lakeside Lab grounds, west side of Lake Okoboji	Lab grounds	19980622	M. Lannoo	
14	102	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	Oxyloma haydeni (Binney)
14	103	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	Oxyloma haydeni (Binney)
14	104	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	105	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	106	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	107	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	108	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	109	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	110	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	111	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	112	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	
14	113	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo	

14	114	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	115	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	116	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	117	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	118	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	119	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
14	120	IO	Dickinson	Gull Point Wetland, 1 km S. of Iowa Lakeside Lab	Gull Point Wetland	19980622	M. Lannoo			
15	121	UT	Kane	Best Friends Ranch	Wet meadow	980731	VJM+EN	Oxyloma haydeni (Binney)		
15	122	UT	Kane	Best Friends Ranch	Wet meadow	980731	VJM+EN			
15	123	UT	Kane	Best Friends Ranch	Wet meadow	980731	VJM+EN	Oxyloma haydeni (Binney)		
15	124	UT	Kane	Best Friends Ranch	Typha, N of wet meadow	980731	VJM+EN			
15	125	UT	Kane	Best Friends Ranch	Typha, N of wet meadow	980731	VJM+EN			
15	126	UT	Kane	Best Friends Ranch	Typha, N of wet meadow	980731	VJM+EN			
15	127	UT	Kane	Best Friends Ranch	Typha, N of wet meadow	980731	VJM+EN			
16	128	UT	Kane	Kanab Creek	Typha E. of Kanab Cr.	980731	VJM+EN			
16	129	UT	Kane	Kanab Creek	Typha E. of Kanab Cr.	980731	VJM+EN	Oxyloma haydeni (Binney)		
16	130	UT	Kane	Kanab Creek	Typha E. of Kanab Cr.	980731	VJM+EN			
16	131	UT	Kane	Kanab Creek	Typha E. of Kanab Cr.	980731	VJM+EN			
17	132	IL	White	14W,	Wide,deep ditch along road, wi	980816	VJM			
17	133	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	134	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	135	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	136	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	137	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	138	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	139	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	140	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	141	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	142	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	143	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	144	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM	Succinea concordialis Lea		
17	145	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM	Succinea concordialis Lea		
17	146	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	147	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	148	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	149	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	150	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	151	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	152	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	153	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	154	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	155	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	156	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	157	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	158	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	159	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
17	160	IL	White	IL 14, o.2 mi. E of 1400N 400 E: 386336.7 4215729.9 uncorrected	Wide,deep ditch along road, wi	980816	VJM			
18	161	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	162	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES	Oxyloma retusa (Lea)		
18	163	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	164	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	165	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	166	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	167	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
18	161A	Alberta	N/A	3 km towards McLeod R. off Hwy 32	Marshy pond/stream; Typha/Bi	19980918	LES			
19	168	Alberta	N/A	Beaver-dammed stream	Caaq/grass w/ Salix overstory	19980918	LES			
19	169	Alberta	N/A	Beaver-dammed stream	Caaq/grass w/ Salix overstory	19980918	LES	Oxyloma retusa (Lea)		

19	170	Alberta	N/A	Beaver-dammed stream	Caaq/grass w/ Salix overstory	19980918	LES			
20	171	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	172	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	173	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	174	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	175	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	176	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	177	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	178	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	179	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES	Oxyloma retusa (Lea)		
20	180	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	181	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	182	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	183	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	184	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	268	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	171A	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	171B	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
20	171C	Alberta	N/A	1 km south of Hwy 16 on RGE Rd272	Dormant; <30 cm up on dead	19980918	LES			
21	185	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES	?Oxyloma kanabensis Pilsbry		
21	186	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES	?Oxyloma kanabensis Pilsbry		
21	187	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	188	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	189	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	190	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	191	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	192	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
21	191A	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES			
22	193	Alberta	N/A	Beaver pond, South of Hwy 43	Typha/Caaq/grasses/Sphagnu	19980918	LES			
23	194	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	195	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	196	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	197	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	198	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	199	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	200	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	201	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
23	202	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES	Oxyloma retusa (Lea)		
23	194A	Alberta	N/A	1.5 km north of Czar, AL	Marsh, snails rare, <1m above	19980919	LES			
24	203	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Marsh, snails rare, <1m above	19980919	LES			
24	204	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	205	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES	?Oxyloma nuttalina (Lea)		
24	206	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	207	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	208	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	209	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	210	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	211	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	212	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	213	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	214	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	215	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	216	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	217	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	218	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	219	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			
24	220	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES			

24	221	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES	
24	269	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES	
24	203A	Alberta	N/A	5 km west of Wetaskiwin, Alberta on Hwy 13	Abundant in Scirpus olneyi? m	19980919	LES	
25	222	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
25	223	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
25	224	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
25	225	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	?Oxyloma nuttalina (Lea)
25	265	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
25	222A	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
25	222B	Alberta	N/A	Highway 11, near Condor turnoff	Caaq streambank and Typha/C	19980919	LES	
26	226	Alberta	N/A	Southeast end of Lac St. Anne	Caaq streambank and Typha/C	19980919	LES	
26	227	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	228	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	229	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	230	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	?Oxyloma nuttalina (Lea)
26	231	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	232	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	233	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	234	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	235	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	236	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	237	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	238	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	239	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	240	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	241	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	242	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	243	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	244	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	245	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	246	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	247	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	248	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	249	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	250	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	251	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	266	Alberta	N/A	Trib. at bridge, NE shore, Lac St. Anne	At shoreline boundary of Phau	19980918	LES	
26	226A	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	226B	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	226C	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
26	226D	Alberta	N/A	Southeast end of Lac St. Anne	Very dark; active; abundant in	19980918	LES	
27	252	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
27	253	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	Oxyloma haydeni (Binney) ?
27	254	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
27	255	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
27	256	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
27	257	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
27	252A	Alberta	N/A	South side of Pigeon L.	Rare, in roadside Typha	19980919	LES	
28	258	Alberta	N/A	Marsh on east side of Hwy 13	Rare, in roadside Typha	19980919	LES	
28	260	Alberta	N/A	Marsh on east side of Hwy 13	Rare in Typha/Caaq	19980919	LES	Oxyloma haydeni (Binney) ?
28	261	Alberta	N/A	Marsh on east side of Hwy 13	Rare in Typha/Caaq	19980919	LES	Oxyloma haydeni (Binney) ?
28	262	Alberta	N/A	Marsh on east side of Hwy 13	Rare in Typha/Caaq	19980919	LES	
28	263	Alberta	N/A	Marsh on east side of Hwy 13	Rare in Typha/Caaq	19980919	LES	
28	258A	Alberta	N/A	Marsh on east side of Hwy 13	Rare in Typha/Caaq	19980919	LES	
29	264	Alberta	N/A	0.5 km south of Lake Isoegun	Rare in Typha/Caaq	19980919	LES	
30	270	WA	Stevens	A Tyla patch in a large field east of Hiway 395 at milepost 224	Caaq/Typha/grass along the s	19980918	LES	
30	282	WA	Stevens	A Tyla patch in a large field east of Hiway 395 at milepost 224	Tyla/sedges	981106	LES	
					Tyla/sedges	981106	LES	Oxyloma haydeni (Binney)

30	284	WA	Stevens	A Tyla patch in a large field east of Hiway 395 at milepost 224	Tyla/sedges	981106	LES			
31	271	NV	Elko	Streamside on Maggie Cr., 4 km upstrm from Carlin NV	Scirpus olneyi?/grasses	981107	LES			
32	272	WA	Stevens	Jump-off Joe Lake along shoreline vegetation	Tyla/sedges/grasses	981106	LES			
32	273	WA	Stevens	Jump-off Joe Lake along shoreline vegetation	Tyla/sedges/grasses	981106	LES			
32	274	WA	Stevens	Jump-off Joe Lake along shoreline vegetation	Tyla/sedges/grasses	981106	LES			
32	275	WA	Stevens	Jump-off Joe Lake along shoreline vegetation	Tyla/sedges/grasses	981106	LES			
33	276A	NV	Elko	Near head of reservoir, 100 m upstrm from road across stream	Saex+sedges/grasses in a beav	981107	LES			
34	278	WA	Stevens	Kettle lake 8km S.of Chewelah on Hiway 395, Milepost 200	Tyla+sedges	981106	LES			
34	280	WA	Stevens	Kettle lake 8km S.of Chewelah on Hiway 395, Milepost 200	Tyla+sedges	981106	LES	Oxyloma haydeni (Binney) ?		
34	276B	WA	Stevens	Kettle lake 8km S.of Chewelah on Hiway 395, Milepost 200	Tyla+sedges	981106	LES			
36	285	NV	Elko	Streamside on Maggie Cr., 4 km upstrm from Carlin NV	Scirpus olneyi?/grasses	981107	LES	?Oxyloma nuttalina (Lea)		
36	287	NV	Elko	Streamside on Maggie Cr., 4 km upstrm from Carlin NV	Scirpus olneyi?/grasses	981107	LES			
37	288	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	Streamside Juba/Salu	990608	LES	Oxyloma haydeni (Binney)		
37	289	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
37	290	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
37	291	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
37	292	UT	Kane	2 km N of Glendale on Hwy89-upper bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
38	293	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES			
38	294	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES			
38	295	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES			
38	296	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES	Oxyloma haydeni (Binney)		
38	297	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES			
38	298	UT	Kane	4 km N of Glendale on Hwy 89-Hidden Lake Ranch	Streamside rush/sedge	990608	LES			
39	299	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
39	300	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
39	301	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
39	302	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
39	303	UT	Kane	2 km N of Glendale on Hwy89-lower bridge site on Virgin R.	Streamside Juba/Salu	990608	LES			
40	304	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES	Oxyloma haydeni (Binney)		
40	305	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES			
40	306	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES			
40	307	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES			
40	308	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES			
40	309	UT	Kane	The Tube' on Kanab Cr. Just off Best Friends Ranch	Typha/Eqhy seep, 2nd seep up	990608	LES			
41	310	UT	Kane	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Ty	990608	LES	Oxyloma retusa (Lea)		
41	311	UT	Kane	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Ty	990608	LES			
41	312	UT	Kane	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Ty	990608	LES			
41	313	UT	Kane	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Ty	990608	LES			
41	314	UT	Kane	KOA 3 km N of Glendale	Spring rill or Irrigation ditch;Ty	990608	LES			
42	315	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES	Oxyloma retusa (Lea)		
42	316	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES			
42	317	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES			
42	318	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES			
42	319	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES			
42	320	UT	Garfield	TNC Autumn Buttercup Preserve, 9 mi. N of Panguich on Hwy 89	Juncus/Typha spring marsh	990608	LES			
43	321	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	322	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	323	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	324	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	325	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	326	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN	Oxyloma retusa (Lea)		
43	327	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	328	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	329	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	330	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	331	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	332	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			

43	333	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	334	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	335	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	336	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	337	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	338	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	339	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	340	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	341	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	342	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	343	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	344	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	345	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	346	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	347	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	348	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
43	349	NE	Cherry	Smith Falls State Park, 15 mi. E of Valentine on Niobrara R.	Eleocharis patch on S side of ri	9905..	EN			
44	350	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905	EN			
44	351	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN	Oxyloma retusa (Lea)		
44	352	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	353	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	354	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	355	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	356	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	357	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	358	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	359	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	360	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	361	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	362	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	363	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
44	364	NE	Cherry	Cottonwood Lake State Rec. Area	Juncus/Carex	9905..	EN			
45	365	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN	Oxyloma kanabensis Pilsbry		
45	366	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN			
45	367	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN			
45	368	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN			
45	369	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN			
45	370	UT	Kane	Separate spring @ S end of 3 Lakes	Wetland vegetation	990609	EN			
46	371	UT	Garfield	Mile 121.3 on Hwy 89	Juba along Sevier R.	990608	LES	?Catinella mooresiana (Lea)		
46	372	UT	Garfield	Mile 121.3 on Hwy 89	Juba along Sevier R.	990608	LES			
46	373	UT	Garfield	Mile 121.3 on Hwy 89	Juba along Sevier R.	990608	LES			
46	374	UT	Garfield	Mile 121.3 on Hwy 89	Juba along Sevier R.	990608	LES			
47	375	UT	Garfield	Sevier R.	Juncus stand along Sevier R.	990608	LES	?Catinella mooresiana (Lea)		
47	376	UT	Garfield	Sevier R.	Juncus stand along Sevier R.	990608	LES			
47	377	UT	Garfield	Sevier R.	Juncus stand along Sevier R.	990608	LES			
47	378	UT	Garfield	Sevier R.	Juncus stand along Sevier R.	990608	LES			
47	379	UT	Garfield	Sevier R.	Juncus stand along Sevier R.	990608	LES			
48	380	UT	Garfield	Sevier R.	Streamside Juncus/Nasturtium	990608	LES			
48	381	UT	Garfield	Sevier R.	Streamside Juncus/Nasturtium	990608	LES			
48	382	UT	Garfield	Sevier R.	Streamside Juncus/Nasturtium	990608	LES			
48	383	UT	Garfield	Sevier R.	Streamside Juncus/Nasturtium	990608	LES			
49	392	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM	Oxyloma retusa (Lea)		
49	393	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			
49	394	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			
49	395	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			
49	396	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			
49	397	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			

49	398	UT	Garfield	Upper Valley Cr. At Dixie NF boundary, SW of jct. of Allen Cr. & UV	Streamside, UTM 4174423N 4	990809	VJM			
50	399	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm			
50	400	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm	Oxyloma retusa (Lea)		
50	401	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm			
50	402	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm			
50	403	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm			
50	404	UT	Garfield	Springs NE of Henrieville Springs on Henrieville Cr. on Hwy 12	Springs, UTM 4162065N 4194	990722	GSenm			
51	405	UT	Garfield	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and	990722	VJM	Oxyloma retusa (Lea)		
51	406	UT	Garfield	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and	990722	VJM			
51	407	UT	Garfield	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and	990722	VJM			
51	408	UT	Garfield	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and	990722	VJM			
51	409	UT	Garfield	Calf Creek, a major trib pf Escalante, parallel to Hwy 12 on the W	Betw/ Lower Calf Cr. Falls and	990722	VJM			
52A	410	UT	Garfield	Boulder Cr., a major trib pf Escalante, parallel to Hwy 12 on the E	37D 49.89MN, 111D 24.49MW	990722	VJM	?Catinella mooresiana (Lea)		
52A	411	UT	Garfield	Boulder Cr., a major trib pf Escalante, parallel to Hwy 12 on the E	37D 49.89MN, 111D 24.49MW	990722	VJM			
52A	412	UT	Garfield	Boulder Cr., a major trib pf Escalante, parallel to Hwy 12 on the E	37D 49.89MN, 111D 24.49MW	990722	VJM			
52B	413	UT	Garfield	Jct. Birch Cr and UV Cr. on Hwy 12	UTM 4179460N 439233E	990722	VJM	?Catinella mooresiana (Lea)		
52B	414	UT	Garfield	Jct. Birch Cr and UV Cr. on Hwy 12	UTM 4179460N 439233E	990722	VJM			
52B	415	UT	Garfield	Jct. Birch Cr and UV Cr. on Hwy 12	UTM 4179460N 439233E	990722	VJM			
52B	416	UT	Garfield	Jct. Birch Cr and UV Cr. on Hwy 12	UTM 4179460N 439233E	990722	VJM			
53	420	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM	Oxyloma haydeni (Binney)		
53	421	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
53	422	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
53	423	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
53	424	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
53	425	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
53	426	WA	Pend Oreille	Jct. W.Calispell Lake Rd and Hwy 211	Typha at roadside marsh	990809	LES/VJM			
54	435	WA	Pend Oreille	Betw/ W. Calispell Rd and Flowery Tr. Rd.	Typha at roadside marsh	990809	LES/VJM			
54	436	WA	Pend Oreille	Betw/ W. Calispell Rd and Flowery Tr. Rd.	Typha at roadside marsh	990809	LES/VJM			
54	436	WA	Pend Oreille	Betw/ W. Calispell Rd and Flowery Tr. Rd.	Typha at roadside marsh	990809	LES/VJM			
55	441	WA	Pend Oreille	Jct. Calispell and W. Calisplell Rd	Typha at roadside marsh	990809	LES/VJM			
55	442	WA	Pend Oreille	Jct. Calispell and W. Calisplell Rd	Typha at roadside marsh	990809	LES/VJM			
55	443	WA	Pend Oreille	Jct. Calispell and W. Calisplell Rd	Typha at roadside marsh	990809	LES/VJM			
56	427	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
56	428	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
56	429	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
56	430	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
56	431	WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
56		WA	Stevens	Rt 395 N. of Spokane at Stevens Co. line	Typha in RR marsh	990809	LES/VJM			
57	437	UT	Garfield	Hwy 12 across Escalante R. at UTM 4180760N 462710E	Small wetland along Escalante	990725	VJM	Oxyloma retusa (Lea)		
57	438	UT	Garfield	Hwy 12 across Escalante R. at UTM 4180760N 462710E	Small wetland along Escalante	990725	VJM			
57	439	UT	Garfield	Hwy 12 across Escalante R. at UTM 4180760N 462710E	Small wetland along Escalante	990725	VJM			
57	440	UT	Garfield	Hwy 12 across Escalante R. at UTM 4180760N 462710E	Small wetland along Escalante	990725	VJM			
58	432	WA	Stevens	Rt 395 N. of Spokane at Mile 196	Roadside Typha marsh/pond	990809	LES/VJM	Oxyloma haydeni (Binney)		
58	433	WA	Stevens	Rt 395 N. of Spokane at Mile 196	Roadside Typha marsh/pond	990809	LES/VJM			
58	434	WA	Stevens	Rt 395 N. of Spokane at Mile 196	Roadside Typha marsh/pond	990809	LES/VJM			
60	445	AZ	Mohave	Travertine Falls along creek at ca. OHW line	Dead typha stems	980607	LES			

– end of report –

Extra Copy

NORTHERN ARIZONA UNIVERSITY
DEPARTMENT OF BIOLOGICAL SCIENCES

Ms. Claudette Piper
Sponsored Research Office
Northern Arizona University
Flagstaff, AZ 86011

5 January 2000

Dear Ms. Piper:

Enclosed are our draft final technical and administrative reports for the project entitled, "Genetic Relatedness between Ambersnail Populations (Succineidae: *Oxyloma* spp.) in the United States and Canada" by myself and Dr. Paul Keim. This project was funded by the Grand Canyon Monitoring and Research Center and the Bureau of Reclamation as 98-FC-40-1230, and was supported by Northern Arizona University as BIO 355L.

We have taken the liberty of submitting 2 copies for review to Dr. Barry Gold (Grand Canyon Monitoring and Research Center, and one copy each to Dr. Shi-Kuei Wu and Mr. Mark Miller, who are collaborating on the project with us. All data will be submitted in electronic form with the final report.

Please inform us of your comments regarding this report at your convenience.

Sincerely,

Lawrence E. Stevens, PhD

Paul Keim, PhD

encl: draft 1999 technical and administrative report
cc: B. Gold (2), M. Miller (1), S-K Wu (1)