Biogeographic and taxonomic relationships among the mountain snails (Gastropoda: Oreohelicidae) of the central Great Basin

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The genus *Oreohelix* (Stylommatophora: Oreohelicidae) is widely distributed but localized throughout the Rocky Mountains, Great Basin, and southwestern regions of North America (Pilsbry 1939). Recent work (Solem 1975, Frest and Johannes 1997) has identified 2 centers of diversity in this genus, the 1st from the Salmon River drainage of Idaho and the 2nd from the northern Wasatch Mountains of Utah and Bear River Range of southern Idaho (Pilsbry 1939, Clarke and Hovingh 1991).

Pilsbry (1939) described 3 species of *Oreohelix* from the central and eastern Great Basin mountain ranges of Nevada: *O. hemphilli* Newcomb, 1869, in the White Pine Range, *O. nevadensis* Berry, 1932, in the Schell Creek Range, and *O. strigosa* Gould, 1846 (subspecies *depressa* Cockerell 1890), from the Snake Range. Roscoe (1954) listed *O. subrudis* Reeve, 1854, and *O. eurekensis* J. Henderson and Daniels, 1916, from the Deep Creek Range in western Utah. During visits in 1996 and 1997, however, the author found a medium-sized shell of *O. strigosa* and smaller-sized shell of *O. hemphilli* in the Deep Creek Range. Apparently, Roscoe (1954) misidentified these 2 species possibly due to the wide variation in shell morphology in both species as they occur throughout Utah, Colorado, and Idaho (Brandauer 1988, Clarke and Hovingh 1991, Frest and Johannes 1997).

Fieldwork in the Great Basin, begun in 1982 by Pratt (1985) and continued by Ports (1986–2002), has increased knowledge of the biogeography of the genus *Oreohelix* in the central Great Basin and suggests that this region may be a 3rd center of oreohelicid diversity as predicted by Bequaert and Miller (1973). Today these populations are fragmented and isolated on mountain ranges throughout the region with little opportunity for gene flow and dispersal across desert valleys, similar to other faunal groups such as high-elevation-adapted small mammals in the Great Basin (Brown 1971).

In this paper I describe the biogeography, shell and soft anatomy, and ecological variation in 3 little-known species of *Oreohelix* as
listed for Nevada and present as new to science a previously unknown oreohelicid from the Goshute Mountains on the Nevada–Utah border in the north central Great Basin. This new species is related to the *Oreohelix haydeni* group from the Wasatch Mountains of Utah.

**METHODS AND MATERIALS**

From 1986 to 2002, I sought land snails in 43 mountains throughout Nevada and eastern Utah. Shells were organized and stored by lots and stations in a private collection at Great Basin College. Latitude and longitude of each station were determined using U.S. Geological Survey topographic maps and confirmed using a Garmin GPS II or III.

At each station empty shells of all age classes were collected by hand and by digging into rock slides using a rock hammer. Eight to 20 live specimens were collected from each station. These specimens were relaxed in menthol for 12 hours and killed by immersing in boiling water for 30 seconds. Bodies were pulled from their shells, preserved in 75% ethanol for 24 hours, fixed in 5% formalin for 24 hours, and transferred to 50% ethanol for dissection purposes (Frest and Johannes 1997). Dissection of soft tissue was carried out under a Leica 40–60X dissection scope. Genitalia were measured in millimeters using vernier digital calipers and drawn from preserved specimens with pen and ink. The radula was prepared and studied on temporary slides using a 1% analine blue dye under a compound light microscope. Empty shells were scanned using Hewlett Packard Precision ScanPro 1.01 in apical, basal, and aperture views, following which images were saved and then printed. The taxonomic description of the new species is according to recommendations of Winston (1999). The following abbreviations were used for repository institutions: ANSP, Academy of Natural Sciences, Philadelphia, for the holotype and paratypes of *O. loisae*, topotypes of *O. nevadensis*, and *O. strigosa*; SBMNH, Santa Barbara Museum of Natural History, paratypes of *O. loisae* and topotypes of *O. nevadensis*, *O. strigosa depressa*, and *O. hemphilli*; MAP, Mark A. Ports catalogue numbers. Catalogue numbers, localities, species, and dates of collection are listed in the appendix. A Mann-Whitney U-test was used to compare morphometric data between *O. strigosa*, *O. nevadensis*, and *O. loisae*.

**RESULTS**

**Taxonomy and Biogeography of *Oreohelix loisae***

The oreohelicid herein is described as a new species: Order Stylommatophora; Family Oreohelicidae; Genus *Oreohelix* Pilsbry, 1904; *Oreohelix loisae* M.A. Ports, sp. nov. Holotype: ANSP 407556 (Figs. 1, 2, Table 1). Paratypes: ANSP 408362, SBMNH 345735.

**Diagnosis.**—Description of shell characteristics: Holotype (Fig. 1, 3 views of the holotype): A large shell compared with other Great Basin oreohelicids (holotype, 19.1 mm diameter and 11.4 mm height) with 5.5 whorls. Shell depressed, broadly conical, spire forming an angle of 100 degrees. Shell convex on apical and basal surfaces with a strongly rounded peripheral body whorl. Yellow-brown periostracum over the apical surface, lighter on the basal surface. Three narrow, yellow-brown bands with the peripheral band above the aperture which descends in front. No banding below. An ovate-lunate aperture, 9.4 mm in diameter and 8.5 mm in height (Table 1). Thin outer lip not deflected, parietal callus thick and reflected slightly over the umbilicus. Umbilicus deep and moderately wide, 4.6 mm in diameter, making up 23% of the shell diameter. Four faint to obsolete beaded lirae on the basal surface and 4 faint beaded lirae on the apical surface. Fine to moderately coarse, oblique striae on body whorls. Minute periostracal wreaths associated with the beaded lirae, but no periostracal fringes on the peripheral whorl. Whorl sutures moderately impressed between penultimate and body whorls, aperture descends below the body whorl.

Paratype specimens vary from the holotype in shell size (17.7–21.8 mm shell diameter; 0.59–0.61 ratio of height/diameter; Table 1), shell color (a light caulk), lack of bands or the presence of banding, distinct angular whors to rounded body whors, and degree of beaded lirae on the basal and apical surfaces. Juvenile shells are strongly angular, including aperture whorl, 4 fine and distinct complete lirae on both the apical and basal surface; juveniles have a much more depressed spire than adult shells with a large, ovate-lunate aperture. Periostracum in juveniles is dark brown, a color that accentuates the fine lirae, 3 distinct narrow brown bands, and shallow sutures, umbilicus is narrow, 3.5–whorls. The mean radula formula
for the holotype and 15 dissected paratypes is 24-1-24 (Table 1). Rows of teeth per radula ranged from 10 to 150, the central tooth is a rounded unicuspid on a tall broad plate with no ectocones; lateral teeth 1–15, have a pronounced lateral ectocone and a sharp pointed cusp; marginal teeth 16–22, degenerate from distinctly bicuspid with small, lateral ectocones to very small unicuspid marginal teeth with no ectocones, 23–24.

**DESCRIPTION OF GENITALIA OF HOLOTYPE** (Fig. 2).—The penis sac is relatively long (9.98 mm) and narrow throughout and is twisted into a tight S shape at the distal end. The distal end of the penis sac is flattened laterally and is the site of attachment for both the ribbonlike penis retractor muscle and the narrow epiphallus. Internally, 35% of the proximal end of the penis sac is lined with 4–5 regular, longitudinal pilasters, while the remaining internal surface is lined with dense papillae. The epiphallus is relatively long (5.17 mm) and slender, tapering to a thin attachment at both the distal and proximal ends. The distal end of the vas deferens runs along the side of the vagina, coiling around the base of the vagina to enter the apex of the epiphallus in the medial surface between the penis sac and the vagina. The vagina is narrow at the base and broadens at the junction of the free oviduct and the uterus. The spermathecal sac is relatively large and oval in shape and the albumin gland is short and rounded with a sharply recurved black talon. The hermaphroditic duct is highly coiled and compressed and the ovotestes are relatively short and dense.

The genitalia of 25 dissected paratypes varied in having a penis sac length of 10.1 to 12.9 mm, internal ribbed portion of penis sac of 3.79 mm to 4.39 mm in length, a ratio of penis sac length/shell diameter of 0.53 to 0.67, and a ratio of internal ribbed portion/total penis sac length of 0.34 to 0.38 (Table 1).

**TYPE MATERIAL.**—Holotype: ANSP 407556; Christmas Tree Canyon, Goshute Mountains, Elko County, NEVADA. 40 25.566′ N and –144 16.233′ W. 2784 m. Paratypes: SBMNH 345735; Felt Wash, Goshute Mountains, Elko County, NEVADA, 40 27.347′ N and –114 16.105′ W. 2477 m (Fig. 5, number 16).
ETYMOLOGY.—This species is named in honor of Lois K. Ports, my field companion, friend, and wife.

Taxonomy and Biogeography of Oreohelix nevadensis
S.S. Berry, 1932

The Schell Creek mountainsnail (O. nevadensis; SBMNH 345735) is the largest species of this genus in the Great Basin (mean diameter of 19.9 mm) and according to Pilsbry (1939) is most similar to the diverse Oreohelix haydeni (Gabb, 1869) group from north central Utah in the Wasatch Mountains. The shell of O. nevadensis (Fig. 3) has weak "spiral striae" or beaded lirae and broad, distinctive bands against a dark brown periostracum. Juvenile specimens have an angular peripheral whorl and flattened spire. Mean shell diameter is 19.9 mm, the umbilicus is deep and wide at 4.63 mm, shell height/shell diameter ratio is 0.64, and the species possesses a mean radula formula of 28-1-28 (Table 1). The genitalia (Fig. 4) of this snail are similar in size (mean 13.3 mm penis sac length) and shape to that of O. loisae. Although the penis sac length/shell diameter ratio is higher than all other species examined, the ribbed portion/penis sac length is smallest, due to the large shell size and the relatively large ribbed portion length of 2.6 mm (Table 1).

Comparisons of shell diameter ($P < 0.001$), penish length ($P < 0.001$), and the ratio of penis

<table>
<thead>
<tr>
<th>Species</th>
<th>Shell diameter</th>
<th>Shell height/shell diameter</th>
<th>Umbilicus width</th>
<th>Radula formula</th>
<th>Penis length</th>
<th>Penish length/shell diameter</th>
<th>Ribbed portion/penis length</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. nevadensis Schell Creek Range, $n = 16$</td>
<td>19.9</td>
<td>0.64</td>
<td>4.63</td>
<td>28-1-28</td>
<td>13.3</td>
<td>0.77</td>
<td>0.31</td>
</tr>
<tr>
<td>O. loisae Goshute Mountains, $n = 10$</td>
<td>19</td>
<td>0.59</td>
<td>4.91</td>
<td>24-1-24</td>
<td>10.1</td>
<td>0.53</td>
<td>0.38</td>
</tr>
<tr>
<td>O. loisae Goshute Mountains, $n = 6$</td>
<td>19</td>
<td>0.61</td>
<td>4.4</td>
<td>24-1-24</td>
<td>12.9</td>
<td>0.67</td>
<td>0.34</td>
</tr>
<tr>
<td>O. strigosa depressa Ruby Mountains, $n = 11$</td>
<td>15.2</td>
<td>0.66</td>
<td>3.35</td>
<td>30-1-30</td>
<td>10</td>
<td>0.6</td>
<td>0.35</td>
</tr>
<tr>
<td>O. strigosa depressa Ruby Mountains, $n = 13$</td>
<td>16.3</td>
<td>0.68</td>
<td>3.48</td>
<td>30-1-30</td>
<td>10.8</td>
<td>0.66</td>
<td>0.37</td>
</tr>
<tr>
<td>O. strigosa depressa Pequop Mountains, $n = 8$</td>
<td>16.5</td>
<td>0.61</td>
<td>3.54</td>
<td>30-1-30</td>
<td>10.3</td>
<td>0.62</td>
<td>0.35</td>
</tr>
<tr>
<td>O. strigosa depressa Snake Range, $n = 10$</td>
<td>17.6</td>
<td>0.63</td>
<td>4.24</td>
<td>30-1-30</td>
<td>14.1</td>
<td>0.8</td>
<td>0.38</td>
</tr>
<tr>
<td>O. strigosa depressa Schell Creek Range, $n = 8$</td>
<td>16.9</td>
<td>0.67</td>
<td>3.66</td>
<td>30-1-30</td>
<td>9.9</td>
<td>0.59</td>
<td>0.327</td>
</tr>
<tr>
<td>O. strigosa depressa Pilot Range, $n = 8$</td>
<td>18.2</td>
<td>0.70</td>
<td>3.72</td>
<td>30-1-30</td>
<td>7.7</td>
<td>0.42</td>
<td>0.37</td>
</tr>
<tr>
<td>O. strigosa depressa Deep Creek Range, $n = 8$</td>
<td>18.4</td>
<td>0.64</td>
<td>4.46</td>
<td>30-1-30</td>
<td>9.9</td>
<td>0.54</td>
<td>0.38</td>
</tr>
<tr>
<td>O. strigosa depressa Egan Range, $n = 6$</td>
<td>16.2</td>
<td>0.64</td>
<td>4.56</td>
<td>30-1-30</td>
<td>10.6</td>
<td>0.66</td>
<td>0.37</td>
</tr>
<tr>
<td>O. hemphilli White Pine Range, $n = 12$</td>
<td>11.4</td>
<td>0.6</td>
<td>2.4</td>
<td>22-1-22</td>
<td>4</td>
<td>0.36</td>
<td>0.38</td>
</tr>
<tr>
<td>O. hemphilli Snake Range, $n = 6$</td>
<td>12.5</td>
<td>0.64</td>
<td>3.1</td>
<td>24-1-24</td>
<td>4</td>
<td>0.38</td>
<td>0.6</td>
</tr>
<tr>
<td>O. hemphilli Ruby Mountains, $n = 8$</td>
<td>8.0</td>
<td>0.61</td>
<td>2.6</td>
<td>22-1-22</td>
<td>2.6</td>
<td>0.32</td>
<td>0.36</td>
</tr>
</tbody>
</table>
sac length/shell diameter were significantly different ($P < 0.001$ level) for *O. loisae* and *O. nevadensis*. Mean penis sac length and shell diameter (Table 1) separate this species from the others examined, but they are closest to *O. loisae*.

The specimens of *O. nevadensis* examined (ANSP 401885, SBMNH 345735; Appendix), come from the type locality on Cleve Creek (Pilsbry 1939) on the east slope of the Schell Creek Range and from 2 stations on the west slope. I also collected specimens on Goshute Creek and McDermid Creek in the Cherry Creek Range and on Smith Creek in the northern Snake Range (Fig. 5).

This species is limited in its distribution, typically found in small colonies and restricted to the White Pine County and southern Elko County region of Nevada.

**Taxonomy and Biogeography of *Oreohelix strigosa depressa***

Cockerell, 1890

The Rocky mountainsnail, *Oreohelix strigosa* (subspecies *depressa*), in the Great Basin has a smaller shell diameter, 4–5 mm less than the same form found in the Wasatch Range of Utah (Pilsbry 1939), and is intermediate in size between the large-shelled *O. nevadensis* and the small-shelled *O. hemphilli* (Table 1). Six of 7 populations examined are intermediate in penis sac length/shell diameter ratio to the other 3 species (Table 1). The Baker Creek sample (Pilsbry 1939) has a significantly larger penis sac length ($P < 0.001$) and a larger penis sac length/shell diameter ratio ($P < 0.001$ level) when compared with other populations of this species from the Great Basin.

The Lutts Creek population from the Ruby Mountains (Ports 1993; ANSP 401886) had a significantly smaller shell diameter ($P < 0.001$), penis sac length ($P < 0.001$), and penis sac length/shell diameter ($P < 0.001$) compared with *O. loisae* (Table 1) from the Goshute Mountains. Eight populations examined had a radula formula of 30-1-30, the same radula formula found by Jones (1940) in the Wasatch Mountains. The Lutts Creek snail has 2 to 3 distinct, brown apical bands and a periostracum exhibiting a wide range of color variation from caulk white to dark brown (Fig. 6).

This species was located in 11 of 43 mountain ranges sampled in the central Great Basin (Appendix). Populations exist today from the...
Fig. 5. Distribution of *Oreohelix* populations in the central Great Basin of North America:

(1) Black Rock Range  
(2) Pine Forest Range  
(3) Santa Rosa Range  
(4) Tuscarora Mts.  
(5) Snowstorm Mts.  
(6) Sheep Creek Mts.  
(7) Independence Mts.  
(8) Bull Run Mts.  
(9) Jarbridge Mts.  
(10) Good Creek Mts.  
(11) Raft River Range  
(12) Oquirrh Mts.  
(13) Stansbury Mts.  
(14) Pilot Range  
(15) Toana Range  
(16) Pequop Mts.  
(17) East Humbolt Range  
(18) Goshute Mts.  
(19) Spruce Mts.  
(20) Cherry Creek Mts.  
(21) Ruby Mts.  
(22) Shoshone Mts.  
(23) Pah Rah Range  
(24) Pine Nut Mts.  
(25) Sweetwater Mts.  
(26) White Mts.  
(27) Stillwater Range  
(28) Clan Alpine Mts.  
(29) Toiyabe Range  
(30) Toquima Range  
(31) Monitor Range  
(32) Hot Creek Range  
(33) Roberts Mts.  
(34) Diamond Mts.  
(35) Pancake Range  
(36) White Pine Range  
(37) Grant Range  
(38) Egan Range  
(39) Schell Creek Range  
(40) Snake Range  
(41) Wilson Creek Range  
(42) Clover Mts.  
(43) Pine Valley Mts.  
(44) Deep Creek Range  
(45) House Range
Pilot Range (ANSP 401887) in the north, to the Egan Range in the south, as far west as the Diamond Range, east to the Deep Creek Range (ANSP 401888), and farther east to the House Range (Appendix, Fig. 5).

**Taxonomy and Biogeography of O. hemphilli** (Newcomb, 1869)

The White Pine mountainsnail (SBMNH 345737) has the smallest shell diameter (mean 8–12.5 mm; Table 1) of the Great Basin oreohelicids. Its shell also has distinct whorled lirae on the basal and apical surfaces, and a carinate, keeled, peripheral body whorl (Fig. 7). The short, swollen penis sac, short epiphalus, and stocky vagina (Fig. 8) are most similar to *O. carinifera* from Montana and *O. eurekensis* from the East Tintic Range (Pilsbry 1939). The type locality from the White Pine Range is intermediate in shell characters and soft anatomy between the 3 populations examined (Table 1). The radula formula for the type locality specimens and the Pearl Creek specimens is 22-1-22, but a radula formula of 24-1-24 was discovered for specimens from Murphy Wash (Table 1).

This species is located in 16 of 43 mountains sampled (Appendix, Fig. 5). The westernmost population is found in central Nevada in the Toiyabe Range, south to the Grant Range, north in the Pilot Range, and east to the Deep Creek Range and House Range of western Utah (Fig. 5). The last 2 localities represent the 1st records for *O. hemphilli* from Utah. In the Mojave Desert 2 very similar species exist (Pilsbry 1939): *O. handi* Pilsbry and Ferriss, 1918, from the Spring Range, and *O. californica* S.S. Berry, 1931, from Clark Mountain.

**DISCUSSION**

At present 4 species of Oreohelicidae exist in the central Great Basin of North America: *Oreohelix loisae, O. nevadensis, O. strigosa,* and *O. hemphilli.* Of 19 mountain ranges that support oreohelicids, 2 to 3 species exist in sympatry in 11 mountain ranges, within which no species were found to exist below an elevation of 2000 m (Appendix, Fig. 5). Roscoe (1954) reported both *Oreohelix subrudis* and *Oreohelix eurekensis* from the Deep Creek Range on the Nevada–Utah border. My collections from
this range suggest that these species are actually O. strigosa and O. hemphilli, based on shell morphology and genitalia. Both species pairs (O. strigosa–O. subrudis and O. hemphilli–O. eurekensis) are very similar in shell morphology and may be synonymous, as Brandauer (1988) suggested for O. strigosa and O. subrudis in Colorado. Oreohelix hemphilli and O. eurekensis are very much alike in many shell characters and may be synonymous with O. eurekensis in the East Tintic Mountains on the eastern edge of the Great Basin (Pilsbry 1939).

Oreohelix loisae is found in only a few dry canyons of the limestone-dominated Goshute Range in north central Great Basin. A large- to medium-sized snail, this species is adapted to limestone rockslides with an understory of Symphoricarpus oreophilus, Rhus trilobata, Artemisia tridentata, and Holodiscus dumosus, beneath an overstory of white fir (Abies concolor), limber pine (Pinus flexilis), and Great Basin bristlecone pine (Pinus longaeva).

Oreohelix loisae is found from the highest elevation of the range at 2750 m (bristlecone pine and white fir) to 2450 m in the pinyon pine (Pinus edulis) and Utah juniper (Juniperus osteosperma) woodlands. Except for spring snowmelt and rare summer showers as sources of moisture, there is no open or flowing water in this range. This snail is found in the same rockslides with O. hemphilli, but the other 2 species discussed were not detected in this range.

Because of similar shell characters and soft anatomy, I assume that O. nevadensis and O. loisae are related to, and possibly holophyletic with, Oreohelix haydeni from the northern mountains of Utah (Pilsbry 1939). As of this writing, O. nevadensis exists in 3 parallel mountains separated by 2 valleys: the North Snake Range on Smith Creek, the Schell Creek Range on Cleve Creek (the type locality; Pilsbry 1939), and on Goshute Creek in the Cherry Creek Range (Appendix, Fig. 5). In each of these ranges, O. nevadensis is associated with perennial springs or streams lined with narrow-leaf cottonwood (Populus angustifolia), willow (Salix sp.), red-osier dogwood (Cornus stolonifera), and wild rose (Rosa woodsii). At each locality O. nevadensis is sympatric with O. strigosa in the drainages and O. hemphilli on the drier, brush-covered, rocky slopes above the drainage. It is not unusual to find more than 1 species of oreohelicid on a single, isolated mountain range, as shown by Metcalf and Smartt (1997) in New Mexico. Adaptation to microhabitats and dispersal biogeography (Pratt 1985) into the Great Basin mountains may explain why 2 to 3 species coexist in the same mountains. In Logan Canyon of the northern Wasatch Range, I found O. strigosa and O. haydeni together (Pilsbry 1939), while in the Stansbury Range on the east side of the Great Basin, I found O. strigosa and O. eurekensis together in the same canyon. Colonization from the east into the Great Basin also may explain why certain species exist where they do today, as suggested for the distribution of montane mammals in the Great Basin by Brown (1971). Pratt (1985) suggests that several species of land snails that have been isolated on mountains in the Great Basin are at risk of extinction.

The most mesic stations in the central Great Basin are occupied primarily by O. strigosa. All of the stations listed for this species (Fig. 5, Appendix) are on perennial streams in limestone or metamorphic ranges in woodlands dominated by quaking aspen (Populus tremuloides), limber pine, and white fir with an understory of wild rose, red-osier dogwood, and common chokecherry (Prunus virginiana). This species of land snail is generally restricted to rock slides and boulders but occasionally is found in forest litter. Similar habitat associations have been described by Henderson (1924).
for oreohelicids at many stations throughout the West.

Much less is known about the biogeography, anatomy, and habitat association of *Oreohelix hemphilli* (Pilsbry 1939). The source of origin may possibly be the East Tintic Mountains, where the similar *Oreohelix eurekensis* exists, or *O. hemphilli* may be endemic to the central Great Basin and has spread east from the central Great Basin. Stations where *O. hemphilli* is found in the Great Basin (Fig. 5, Appendix) are typically xeric and associated with limestone rocksides. An understory of shrubs is usually present, including snowberry, mountain ninebark (*Physocarpus monogynus*), and Rocky Mountain maple (*Acer glabrum*). Overstory trees consist of mixed conifer woodlands of pinyon pine, Utah juniper, and Rocky Mountain juniper (*Juniperus scopulorum*) at mid-elevations (2250 m). At higher elevations (2450 m) the conifers consist of bristlecone pine, limber pine, white fir, and Douglas-fir (*Pseudotsuga menziesii*).

More work, including genetic analysis, is currently underway in order to understand the historical biogeography and taxonomic relationships among these 4 species and their relationships with the species of oreohelicids from the eastern edge of the Great Basin and the Wasatch Mountains.

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LITERATURE CITED


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Appendix on the following page.
APPENDIX

SPECIMENS EXAMINED


