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**An Illustrated Dichotomous Key to Pleistocene and
Holocene Fossil Molluscs of Southern Nevada
and Adjacent Regions, with data
on habitats and autecology**



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Launch of LVNHM Occasional Papers

This online publication marks the beginning of a series of open-access Occasional Papers in Archaeology, Paleontology, and Natural History by the Las Vegas Natural History Museum. This series represents a contribution to the mission of the Museum “. . . to inspire a better understanding and appreciation of the natural world, the sciences, and ourselves through educational exhibits, programming, and research.”

History and Methodology of this Study

This paper has its origins in a very succinct, four-page book chapter titled “Late Pleistocene Molluscan Shells from the Tule Springs Area,” by Dwight W. Taylor, which was included in the 1967 book, *Pleistocene Studies in Southern Nevada*, published by the Nevada State Museum as *Anthropological Papers No. 13*. That book had resulted from the famous 1962-63 excavation of Pleistocene deposits of the Tule Springs area, led by geologist C. Vance Haynes. Haynes had supervised the excavation of several bulldozer trenches that were twelve feet wide and up to thirty feet deep, cut into the Pleistocene sediments of the Tule Springs area (now within the boundaries of Ice Age Fossils State Park).

In his succinct chapter on Pleistocene molluscs, Taylor, a U.S. Geological Survey paleontologist, listed seventeen genera and twenty-eight species of aquatic and terrestrial molluscs (snails and clams) that he identified in the late Pleistocene deposits of the Tule Springs area. Nearly all of these taxa are still extant today, but few of them still live in southern Nevada. Several live in northern Nevada where the climate and environmental conditions approximate the conditions that existed in the Tule Springs area during the late Pleistocene. Taylor (1967) included as much information as was available at the time about the environments in which some of these molluscs live today. However, he reported that “knowledge of the living [molluscan] fauna of Nevada is practically nil,” so he was unable to include much detail concerning the ecological constraints of most species. We now know considerably more about the habitats of these molluscan taxa (Quade and Pratt, 1989; Ports, 2021).

Conspicuously absent from Taylor’s 1967 report are photographs or sketches of the shells of the molluscs he collected, rendering his report essentially useless for helping scientists (other than biologists and paleontologists who specialize in molluscs) and interested non-scientists identify the genera and species of molluscan shells that they find, and for using them to reconstruct the environments that were present in the late Pleistocene.

In 2003, a new high school—Shadow Ridge High School—opened, directly across N. Decatur Boulevard from the exposures of the Tule Springs Fossil Beds that had been extensively excavated in 1962-63. One of the authors of this paper (SMR), along with his colleague Paul Buck of the Desert Research Institute, obtained a National Science Foundation geoscience-education grant to take advantage of the educational opportunity created by the proximity of the high school to the still-open trenches across the road. The students and their Earth science teacher, under the supervision of Buck and Rowland, were able to walk to their field area during their designated lab time, make observations, sample a specified horizon of a trench wall, and

return to their classroom with their samples. Subsequent lab activities involved grain-size analysis of the samples and identification of the tiny fossil mollusc shells recovered from the samples.

For the purpose of identifying the molluscan species, the students needed an illustrated key of some kind, so we hastily produced a booklet titled “*Dichotomous Key to the Pleistocene and Holocene Freshwater Molluscs of Southern Nevada.*” It was strictly an expedient, in-house product, with poor-quality, photocopied illustrations, using Taylor’s list of taxa. Now that Tule Springs Fossil Beds National Monument and Ice Age Fossils State Park are fully functioning protected lands, with ongoing research and interpretive activities, it is a perfect time to upgrade our mollusc key from two decades ago with high-quality images, together with ecological information about each taxon. That is the purpose of LVNHM Occasional Paper 1.

The list of genera and species included in this key began with those identified by Taylor (1967) in the Tule Springs deposits, updated where necessary to provide corrected generic names for those that are now obsolete. This list of taxa, as well as information about the environment that each taxon represents, was augmented by Las Vegas Valley regional studies by Quade (1986), Quade and Pratt (1989), and Quade et al., (1995, 1998, 2003). The insightful study by Quade and Pratt (1989) of living aquatic and terrestrial snails that occur today in the Steptoe Valley of northeastern Nevada—including several species whose shells occur in the Pleistocene/Holocene fossil record in southern Nevada—provided very useful data on habitat preferences of several taxa. Similarly, Ports (2021) study of extant terrestrial gastropods of Nevada provided very valuable accounts of the modern distribution and habitats of many terrestrial species, the shells of which are present in the Pleistocene/Holocene fossil record. One genus—the springsnail *Tryonia*—was added to the list of taxa included in this key, even though it has not been reported from Las Vegas Valley deposits; extant species of *Tryonia* occur in the Death Valley drainage system, which includes the Amargosa Valley of Clark County, Nevada. The criteria we use to distinguish genera (and some species) were informed by consulting standard sources, i.e., Burch (1982), Pennak (1989), and Dindal (1990). In the end, however, the majority of criteria we employ in this key emerged from simply comparing shells that were collected locally, together with images available online, and endeavoring to capture in words and images the simplest suite of morphological features that are unique to each taxon that occurs in this region. Our hope is that this key will be useful to paleontologists, biologists, students, and members of the general public seeking to identify living and fossil molluscan shells that they find throughout the greater southern Nevada region.

Unless otherwise specified, photos were taken by O.G. and R.M. Text and drawings are by S.M.R.

How to Use this Key

A dichotomous key is a device used by biologists and paleontologists to help them identify living or fossil organisms. Begin with a fossil shell that you want to identify, preferably viewed with the help of a microscope. Start at the beginning of this key on page 8. At each

point in the key there are two choices, “a,” and “b.” In principle, the size and shape of the specimen you are trying to identify will conform to one or the other of the two choices. Whichever one it matches will lead you to another two choices, until the specimen is finally identified. When a specimen is finally identified, confirm the identification by comparing it to the photograph. In this key, some of the specimens may be keyed out to the species level, others to the genus level, and some only to the family level. After you become familiar with the key, especially the photographs, you will be able to quickly go to the section that is most relevant for the shell you are working with.

Because nearly all the genera and species included in this key are still living, as we discuss the environments that each genus or species inhabited, we use present tense. The biologists who studied and named these species were able to examine not only their shells, but also living, breathing, crawling (in the case of the gastropods) animals with soft biological tissues. Often the identification of a particular extant species is based on soft tissues; biologists may have to dissect a recently deceased snail to identify which species it belongs to. Soft tissues, of course, are not preserved in the fossil record; only the shells are preserved. In other cases the identification of individual species involves examining the characteristics of the operculum, a “hatch-cover-like” shelly structure which is present in some snail species. The operculum allows the snail to withdraw all of its soft tissues into its shell and “close the door” behind them, perhaps allowing it to survive an interval of time when the pond dries up. In the case of fossil shells there are two problems concerning the opercula: (1) they are so tiny they are difficult to collect, disappearing through the screen of our fine-mesh screen, and (2) even if we happen to find an operculum, it is separated from its shell, so we can’t be sure which shell it belongs to. And, in some cases, biologists use DNA analysis to identify different species (e.g., McKelvey et al., 2020).

For all of these reasons, when working with fossil shells, often we cannot distinguish the species to which a particular specimen belongs, but we can identify the genus. An example is the genus of bivalves (clams)—*Pisidium*—which is relatively common in the Pleistocene deposits of southern Nevada. This genus is very easy to identify from its fossil shells. Although Taylor (1967) named five species of *Pisidium* that he distinguished among the fossils he recovered from the Tule Springs deposits, we have found that individual species of this genus (as well as some other molluscan genera) are difficult or impossible to confidently identify on the basis of fossil shells obtained from these strata. Thus, in this key we identify the clam shells simply as *Pisidium* sp. The “sp.,” means “unknown species.” In some cases, especially with some of the high-spired snails with broken shells, it is even difficult to identify the genus with confidence. In such cases, paleontologists often use “cf.” which is the abbreviation for the Latin word “*confer.*” It essentially means “looks like, but I’m not completely sure.” For example, we might write “cf. *Pyrgulopsis*,” which means “this shell looks like it probably belongs to the genus *Pyrgulopsis*, but I’m not completely sure.” Or, if the genus is clearly identifiable but we’re not positive about the species, we would write “*Pyrgulopsis* cf. *P. micrococcus*.”

How to Collect Fossil Mollusc Shells

Fossil clam and snail shells occur within the sediment (sand, silt, and/or mud) that was being deposited when these animals were alive. So, the first challenge is to separate the fossil shells from the sedimentary particles. This is done with a screen, or sieve, of some sort. Fancy, scientific sieves are available, with specific size holes. For example, Quade et al. (1998) used a research-grade 0.15-mm-mesh sieve in their study of Late Pleistocene and Holocene fossils in southern Nevada. But they were seeking to recover very tiny ostracodes, in addition to mollusc shells. For a study of Pleistocene fossil molluscs, a fine-mesh, stainless steel, kitchen strainer, such as the one in this photo, works fine. The spaces between the wires in this type of strainer are about 1 mm wide, which is smaller than any of the mollusc shells we're looking for, yet large enough to allow silt and most sand grains to pass through.



If your sediment sample is not consolidated (i.e., the grains are not stuck tightly together), try simply pouring a small amount of the dry sediment sample into the strainer and gently shaking it over a bucket or trash can. Gently remove the resulting separated fraction onto a clean surface, and repeat. If your sample contains a significant amount of clay (mud-size particles), or the sample is consolidated, you will need to use water to loosen it up. Place the sediment sample in a beaker or pot of water, with a volume ratio of sediment to water of around 1:4. Add a spoonful of sodium carbonate powder (washing detergent) and a few drops of liquid hand-washing soap. If a hot plate is available, place the covered beaker or pot on the hot plate on low-to-medium heat for as long as necessary to break apart the sample, agitating or stirring occasionally (Harris and Sweet, 1989). Or you could try heating up the beaker of water and sediment in a microwave oven. If you have access to an ultrasonic machine, you can also experiment with that, to remove sediment from the shells, but only expose your samples to ultrasonics for a few seconds, to avoid damaging some of the thin-walled mollusc shells. Separating fossils from limestone and hard sandstone involves different techniques that beyond the scope of this paper.

In addition to mollusc shells, there is a category of minute, sub-millimeter-size shells that also occur in some of our Pleistocene and Holocene deposits. These are the shells of ostracodes, which are not molluscs; they are tiny, shrimp-like crustaceans (arthropods) that live in aquifers and surface-water environments. Fifteen genera and 40 species of fossil ostracodes have been reported from the deposits of southern Nevada (Forester et al., 2017). As mentioned

above, collecting ostracode shells requires a finer mesh sieve, and their identification is beyond the scope of this key.

Insightful future research projects involving Pleistocene and Holocene fossil mollusc shells in southern Nevada and adjacent regions would involve quantifying the abundance of various taxa (species and genera) within specific stratigraphic intervals. Taylor's (1967) pioneering study merely documented which taxa were present in certain stratigraphic intervals. Quade et al., (1998) were more quantitative; they weighed their sediment samples and determined the number of shells per kg of sediment. A next step in the paleontological study of these deposits would be to collect a standard volume of exposed sediment, such as 100 cubic centimeters—10 cm wide within a specific stratigraphic interval, 2 cm high perpendicular to bedding, and 5 cm deep into the cliff face—and count the number of shells of each taxon within that volume. The sediment samples should be weighed also, before screening them for fossil shells, for comparison with the results of Quade et al. (1998) and other such studies. In the field, prior to collecting the sample, the locality should be photographed and described (e.g., color and bedding characteristics of the strata). Data from such quantitative studies will reveal subtle changes in depositional environments, within and between stratigraphic intervals.

Molluscan Taxa included in this Key

Class Pelecypoda (clams)

Order Heterodonta

Family Sphaeriidae (freshwater clams)

***Pisidium* sp.**

Class Gastropoda (snails)

Order Mesogastropoda (freshwater snails)

Family Valvatidae

Valvata humeralis

Family Hydrobiidae (springsnails)

***Tryonia* sp.**

Pyrgulopsis micrococcus

***Pyrgulopsis* sp.**

Order Basommatophora (freshwater snails)

Family Lymnaeidae

***Lymnaea* sp.**

***Stagnicola* sp.**

***Fossaria* sp.**

Family Ancyliidae (pulmonate freshwater limpets)

***Ferrissia* sp.**

Family Planorbidae (pulmonate freshwater snails)

Gyraulus circumstriatus

Gyraulus parvus

Planorbella subcrenata

Promenetus umbilicatellus

Family Physidae
Physa virgata
Order Stylommatophora (terrestrial snails)
Family Pupillidae
***Pupilla* sp.**
Family Vertiginidae
Vertigo berryi
Gastrocopta tappaniana
Family Valloniidae
***Vallonia* sp.**
Family Succineidae
***Succinea* sp.**
***Oxyloma* sp.**
Family Zonitidae
Hawaiiia minuscula

How Do Freshwater Molluscs Become Dispersed Across the Landscape?

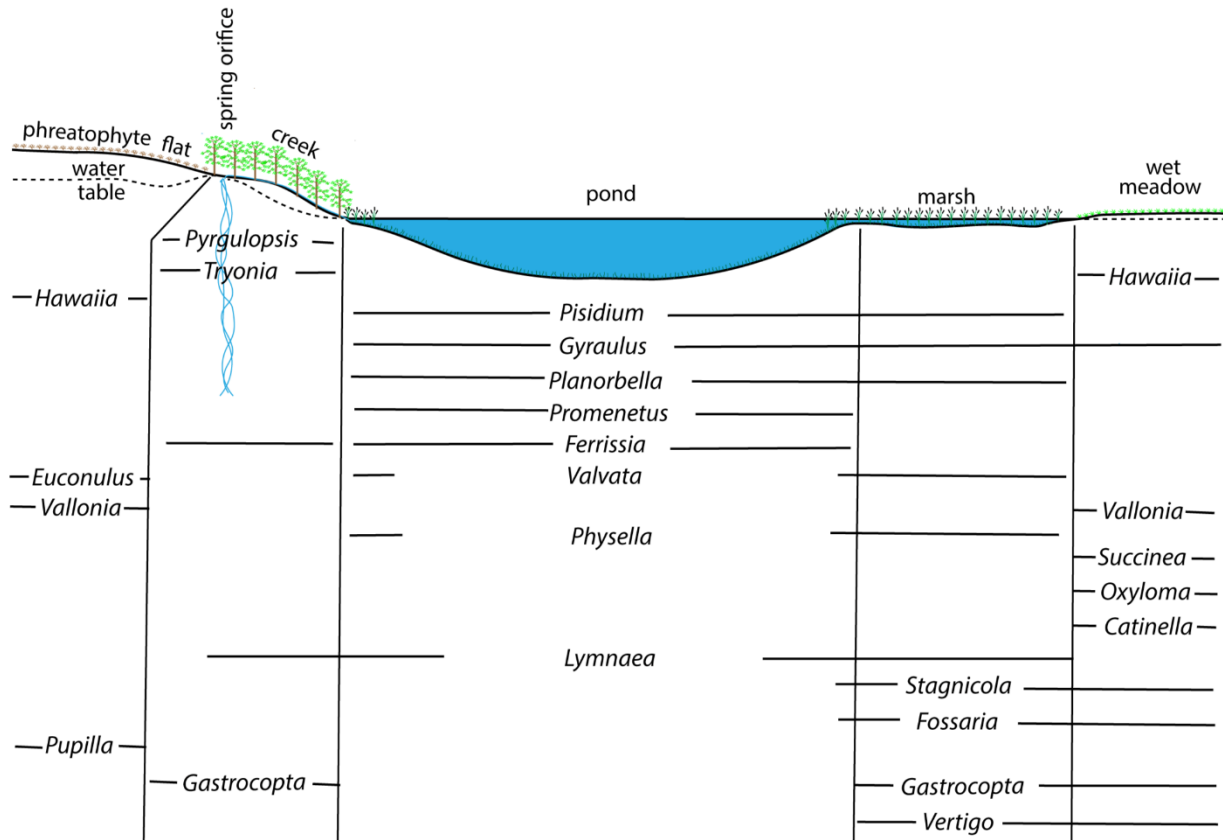
When freshwater molluscs are encountered in topographically isolated springs or basins, whether as fossils or as living populations, the question arises: How did they get there? And why do we often find the same taxa, or closely related taxa, in separate, isolated basins? In some cases, we can imagine that currently isolated paleowetland sites—such as the Tule Springs deposits, Indian Springs, and Corn Creek—may have been aquatically connected in the geologic past, when the climate was cooler and wetter, thus accounting for the presence of common fossil taxa. But it often happens that very similar molluscan faunas occur in springs and associated wetlands in isolated basins and canyons that were almost certainly never connected with surface water. Also, some of the taxa included in this dichotomous key to molluscan taxa in the southern Nevada region are widely dispersed across North America and beyond. How do these freshwater snails and clams become so widely dispersed across the landscape?

The topic of dispersal mechanisms for various species is a fascinating one. Of course, in modern times, humans are responsible for dispersing many species, often inadvertently. This includes invasive species that can be very disruptive to ecosystems; there are many published studies on this topic. An example of anthropogenic dispersal that is mentioned in this key is the globally dispersed, tiny snail *Hawaiiia minuscula* (see page 11).

With respect to the dispersal of Pleistocene and Holocene molluscs in the southern Nevada region, the leading dispersal vector is almost certainly waterbirds. Adult snails typically survive for just a single season, during which they lay a clutch of 18-50 eggs. The adult snails themselves, and also their eggs, are surrounded by sticky mucus (Van Leeuwen et al., 2012). The mucus allows the eggs to stick to the stems of aquatic plants, but it also causes them to stick to the feet and feathers of waterbirds. A study specifically addressing the distribution of the springsnail genus *Tryonia* suggests that several dispersal vectors may be involved, but the authors concluded that waterfowl are the snails' most effective dispersal partners (Wesselingh et al., 1999). This conclusion almost certainly also applies to other taxa included in this key.

Habitats

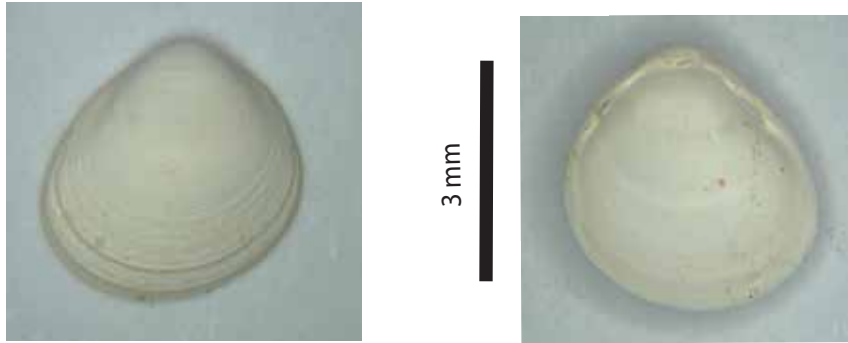
This figure is a generalized representation of wetland habitats (and an adjacent terrestrial habitat) that existed in the southern Nevada region in the late Pleistocene, showing the approximate habitat preferences of each of the twenty-one molluscan genera included in this key. Habitat preferences of each genus are also discussed in the key. These habitat data are based primarily on observed occurrences of living snails and clams in Nevada today.



Acknowledgments

We gratefully acknowledge very helpful constructive reviews of an early draft of this publication by paleontologist Michele Jones and molluscan biologist Mark Ports.

- 1a. The shell is prominently coiled.....Proceed to 3
- 1b. The shell is *not* prominently coiled.....Proceed to 2
- 2a. The shell is roughly cup-shaped and clam-like.....*Pisidium* sp.

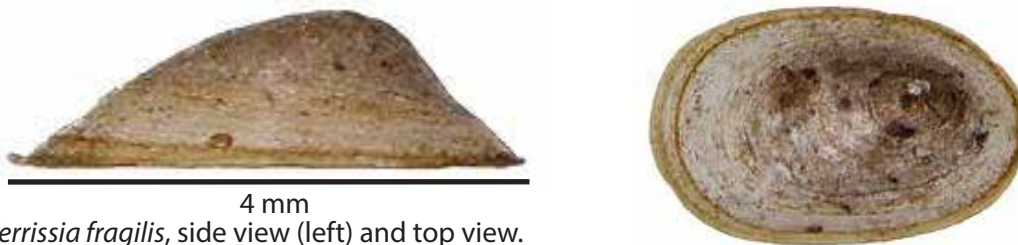


Pisidium sp., external (left) and internal views.

Pisidium is a tiny freshwater bivalve (clam), called a pea clam. There are several living species inhabiting lakes, ponds, and streams on different continents. The shells are only 3-5 mm in their longest dimension. Taylor (1967) reported five species of *Pisidium* from the Tule Springs deposits. They occur in all of the depositional units, often with multiple species occurring in the same unit. The shells of the separate species are difficult to distinguish, so we don't attempt to identify them to species level in this key.

In some cases, the presence of abundant *Pisidium* shells (or any shells) may be beneficial to the fossilization of vertebrate material. In the Dinosaur Park Formation in Alberta, Canada, dinosaur egg shells are rare, except in deposits that contain abundant *Pisidium* shells. The waters there are acidic, due to the breakdown of tannins from the local coniferous trees. Partial dissolution of the *Pisidium* shells reduces the acidity of the water, causing the egg shell fragments to not be dissolved (Tanke and Brett-Surman, 2001). Southern Nevada region waters are not acidic, so this phenomenon does not occur in our local fossil record.

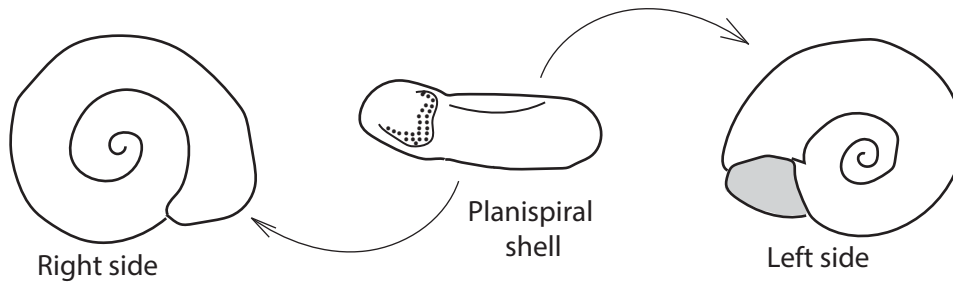
- 2b. The shell is shaped like an asymmetric volcano, with its crest off-center.....*Ferrissia* sp.



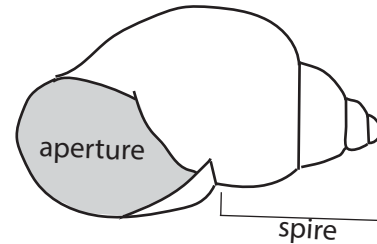
Ferrissia fragilis, side view (left) and top view.

Ferrissia is a freshwater snail. Its common name is "freshwater limpet" because its shape is similar to that of marine limpets. But it is not closely related to marine limpets. It is a very rare species in this region. Taylor (1967) reported finding *Ferrissia* in only one of his Tule Springs samples, which was a spring deposit. He did not identify the species, but *Ferrissia fragilis* occurs widely throughout North America and is likely the species that occurred in this region in the Pleistocene. Quade (1986), who sampled more widely in upper Las Vegas Valley, did not report finding any. Although *Ferrissia* is a pulmonate snail, the ancestors of which were non-aquatic air-breathers, these freshwater limpets evolved "neomorphic gills" that allow them to be entirely aquatic (McMahon, 1983).

3a. The shell is discoidal (planispiral, or nearly so), as shown in this sketch.....Proceed to 4



3b. The shell is *not* discoidal. A conspicuous spire projects asymmetrically from one side of the shell, as shown in this sketch (but not all spires are as high as this one)
.....Proceed to 7



4a. The shell is 2 cm or greater in diameter.....*Planorbella subcrenata*



Planorbella subcrenata, left side



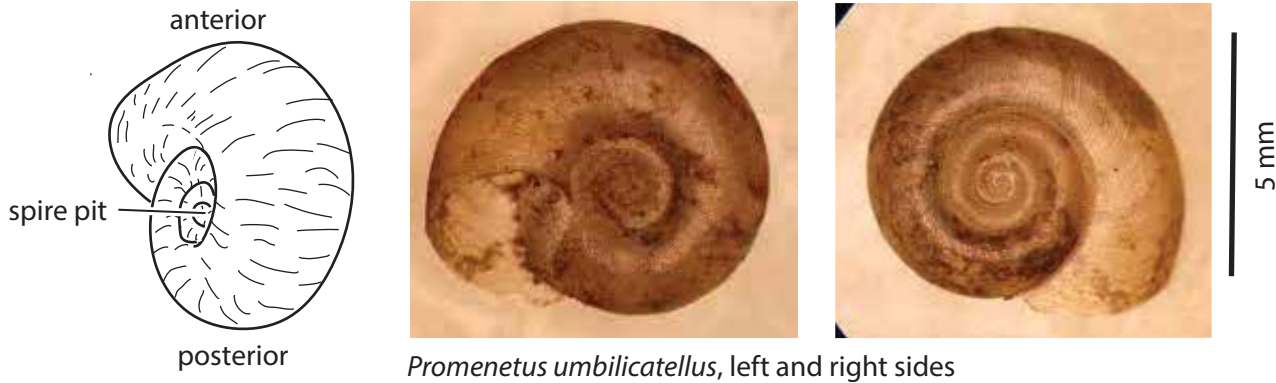
Planorbella subcrenata, right side

Planorbella, the “ram’s-horn snail,” is one of the largest molluscs in the Pleistocene and Holocene deposits of the southern Nevada region. It lives in freshwater environments, grazing on bacteria-rich organic detritus. As is the case with many aquatic snails, those within family Planorbidae, including *Planorbella*, do not have true gills; they have lungs, inherited from air-breathing, non-aquatic ancestors. So, most species (especially the larger ones, such as *P. subcrenata*) must rise to the surface of the pond from time to time to take a breath of air. A “neomorphic gill” allows some of the larger planorbid species to obtain more than 50% of their required oxygen directly from the water, via cutaneous exchange, allowing them to stay submerged for a long time (McMahon, 1983). *Planorbella* typically lives in ponds and marshes, in water up to about 1 meter deep.

This species is not especially common in our local fossil record, except in specific paleo-environments. Taylor (1967), who did not report abundances, reported finding *Planorbella* in several stratigraphic intervals of the Tule Springs deposits. He did not identify which species he collected. However Quade (1986) identified shells of *Planorbella subcrenata* in Upper Las Vegas Valley deposits. He reported recovering a small number of specimens in Unit D of Lower Corn Creek Flat, in deposits that he interpreted to represent well-oxygenated seasonal and permanent ponds. Quade and Pratt (1989) reported finding no specimens of this taxon in Indian Springs Valley.

4b. The shell is 1 cm or less in diameter (typically ~5 mm).....Proceed to 5

5a. The shell diameter is greater than 4 mm, and the depression on the left side of the shell (the “spire pit”) is relatively deep and narrow, as shown in the sketch on the left.....*Promenetus umbilicatellus*



Promenetus umbilicatellus, left and right sides

Promenetus belongs to the same family of pulmonate, aquatic gastropods (Planorbidae) as *Planorbella*, and *Gyraulus*. Snails in these genera have similar ecological and physiological characteristics; they are aquatic, but they need to ascend to the surface from time to time to capture a breath of air. *Promenetus* is much less common in our region than are *Planorbella* and *Gyraulus*. Taylor (1967) reported finding *Promenetus* at only one Tule Springs site, near the orifice of a Pleistocene spring. Quade (1986) reported finding no *Promenetus* shells at all in these deposits.

5b. The shell diameter is no larger than 4 mm, and the spire pit is shallow and wide.....Proceed to 6

6a. The shell is perfectly planispiral; the aperture is bisected by the plane of the coiled shell, as shown in the right-hand photo below.....*Gyraulus circumstriatus*



Gyraulus circumstriatus

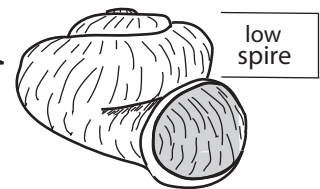
6b. The shell is not perfectly planispiral; the aperture is conspicuously displaced toward the left side of the shell, as shown in the right-hand photo, below.....*Gyraulus parvus*



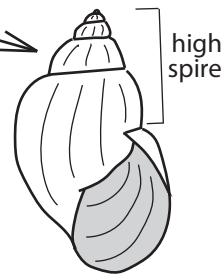
Gyraulus parvus

Both species of this tiny aquatic gastropod are very common in the Tule Springs deposits and other Pleistocene deposits of the southern Nevada region. Like *Promenetus* and *Planorbella*, they are members of family Planorbidae. As with *Promenetus* and *Planorbella*, they are aquatic, living in ponds and marshes, but they acquire most of their oxygen from the air, by projecting a snorkel-like structure above the surface of the water from time to time. *G. parvus* is very abundant today in the Step-toe Valley of northeastern Nevada, along with *Pisidium* sp., dominating the aquatic fauna of small ponds and sluggish flowing water (Quade and Pratt, 1989).

7a. The shell is low-spired, with a profile similar to the shell in this sketch
Proceed to 8



7b. The shell is high-spired, more like the shell in this sketch
Proceed to 11



8. Low-spired shells

8a. The shell is larger than 2 mm in diameterProceed to 9

8b. The shell diameter is 2 mm or smaller.....*Hawaiiia minuscula*

Taylor (1967) reported *Hawaiiia minuscula* to be rare in the Tule Springs deposits; it appeared in only two of his samples, both of which came from ancient spring orifice deposits (but see below). However, Quade et al. (1998) found this species to be quite abundant in their samples from black-mat horizons at Corn Creek Flat, Cactus Springs, and Pahrump Valley.

This species currently has a very wide distribution globally, having been dispersed by human activity. It lives mainly in greenhouses. Prior to its anthropogenic dispersal, it lived widely in North and Central America. These snails can occupy a wide variety of **non-aquatic** habitats, including bare ground, dunes, meadows, leaf litter of deciduous and mixed forests, shrubland, and among stones on grassy slopes (Kaszuba and Stworzewicz, 2008). This contradicts Taylor's (1967) implication that their preferred habitat is spring orifices.



Hawaiiia minuscula

9a. The shell has a dome-shaped profile with five or more whorls.....*Euconulus fulvus*



Euconulus fulvus, apical view



profile view

Euconulus is a terrestrial snail that is understandably rare in the groundwater-discharge deposits. Ports (2021) describes it as occurring today in mountain woodland habitats of Nevada, at elevations of 2000 meters and higher. Taylor (1967) did not report its presence in his Tule Springs samples, nor did Quade and Pratt (1989) report it occurring in Indian Springs Valley deposits. However, Quade et al. (1998) reported recovering a few specimens in Corn Creek Flat and Sandy Valley.

9b. The profile is not dome-shaped, and the number of whorls is fewer than five.....Proceed to 10

10a. The shell has conspicuous surface microstructure in the form of parallel ridges that are perpendicular to the direction of the whorls, as seen in the shell on the left below, and the margin of the aperture is conspicuously flared.....*Vallonia* sp.

Vallonia is a terrestrial genus whose species inhabit an extraordinarily wide diversity of habitats in Nevada today, ranging from shrubland steppe to pinyon-juniper woodland to wetlands (Ports, 2021). It is the most abundant terrestrial taxon recovered from groundwater-discharge deposits in our region. Taylor (1967) reported recovering two species, *V. cyclophorella* and *V. gracilicosta*, but from only a few stratigraphic intervals of the Tule Springs deposits.



Vallonia sp., apical view showing parallel-ridge microstructure



Apertural view, showing deep spire pit and large aperture with flared margin

We don't distinguish the different species in this key. Abundant shells of *Vallonia* have been reported from "black mat" intervals, representing organic-rich settings, at Cactus Springs and Corn Creek Flat (Quade et al., 1998). Today, in Steptoe and Butte valleys of northeastern Nevada, Quade and Pratt (1989) observed *Vallonia* snails living in marshy seep/wet meadow environments. Moist areas with tufts of grass are interspersed with ponds 20 to 40 cm deep. *Vallonia* occurs in the grass tuft areas. Presumably these snails inhabited the same environment in our region in the Pleistocene.

10b. The surface of the shell is smooth, without prominent microstructure, and the margin of the aperture is not conspicuously flared.....*Valvata humeralis*



Valvata sp.



Valvata humeralis is an aquatic snail that lives on submerged vegetation. Shells of this species are very abundant in some intervals of the Pleistocene and Holocene deposits of the southern Nevada region, especially in Unit D of the Tule Springs deposits (Taylor, 1967) and also Unit D of lower Corn Creek Flat (Quade, 1986). These sediments were interpreted by Quade (1986) to represent quiet, well-oxygenated water with vegetation that projected above the water level. However, in other localities and other units of the Pleistocene strata they are rare or absent.

11. High-spired shells

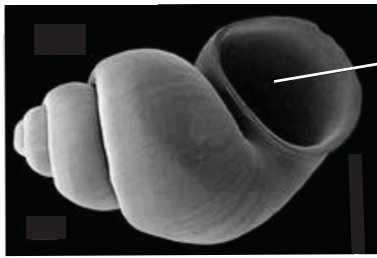
11a. The shell consists of conspicuously wide whorls, nearly all the way to the tip of the spire, as in this photo. These are called "whorl snails."Proceed to 20



11b. The spire does not consist of conspicuously wide whorls nearly all the way to the tip. Rather, the apex has a relatively sharp point, as in this photo. Even if the whorl adjacent to the aperture (called the "body whorl") is large, the next whorl is conspicuously smaller.....Proceed to 12



12a. The aperture is approximately round or oval, as seen in the shell on the left below, without a sharp corner on the posterior margin.....Proceed to 18



oval aperture



asymmetrical aperture with sharp corner on posterior margin

12b. The aperture is distinctly asymmetrical, as seen in the shell on the right above, with a sharp corner on the posterior margin.....Proceed to 13

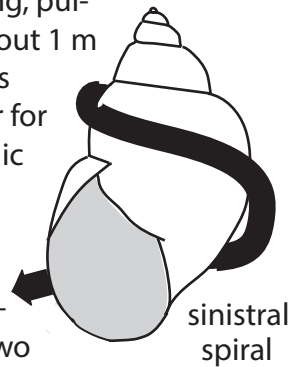
13a. The shell is sinistral (counterclockwise, when viewed from the apical end).....

.....*Physella virgata*



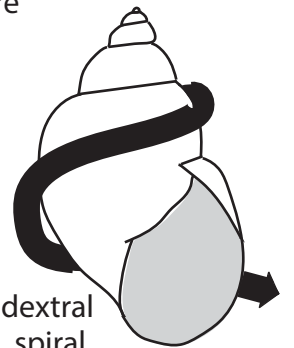
Physella virgata

The sinistral-coiled snail *Physella virgata* is an air-breathing, pulmonate, aquatic snail. These snails live in water up to about 1 m deep in slowly flowing streams and small perennial ponds (Quade et al., 1995). Although they are dependent on air for most of their oxygen needs, they also have a "neomorphic gill" that allows them to absorb some oxygen while submerged, thus enabling them to stay submerged for long intervals (McMahon, 1983). Crayfish prey upon *Physella virgata*. Experiments have shown that these snails sometimes crawl out of the water and stay out for as long as two hours when a caged crayfish, along with crushed snails, are placed in their tank (Dillon, 2000).



sinistral spiral

Taylor (1967), who called this species *Physa virgata* (now an obsolete name), reported it to be present in nearly every stratigraphic interval of the Tule Springs deposits. However, Quade et al. (1998) found it to be very rare in "black mat" intervals (representing organic-rich environments such as springs, wet meadows, and marshes) in Corn Creek Flat, Sandy Valley, and Pahrump Valley.

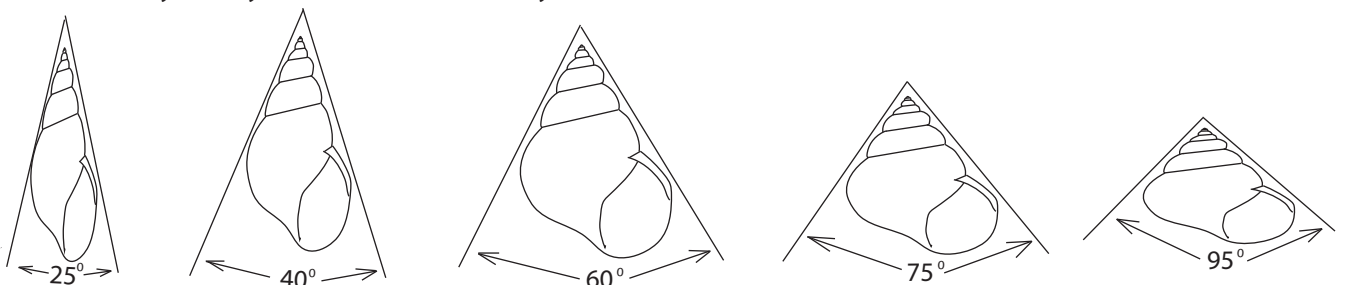


dextral spiral

13b. The shell's spiral is dextral (clockwise, when viewed from the apical end).
.....Proceed to 14

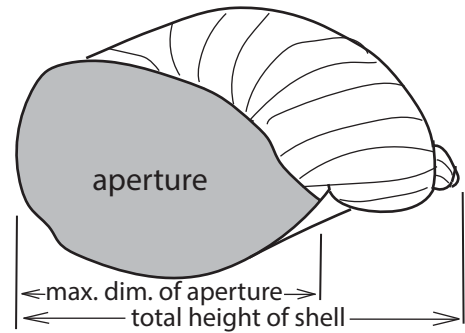
Spire Angles

Among high-spired gastropods, the angle of the spire is often a characteristic feature of each genus. The sketches below show examples of shells with spire angles ranging from 25° to 95°. In the remaining pages of this key, spire angles are sometimes used to distinguish among genera. Refer to these sketches as you key out fossil shells that you find.



14a. The spire angle is greater than 60° (see figures on the bottom of page 11); in some cases the maximum dimension of the aperture is greater than half the total height of the shell, as in this sketch.....Proceed to 15

14b. The spire angle is less than 60°; the maximum dimension of the aperture is less than half the total height of the shell..... Proceed to 16



15. **Succineidae** (ambersnails) is a family of terrestrial snails that typically live in wet meadows, adjacent to ponds and streams. Three genera of succineid fossil snails, shown below, have been reported from the southern Nevada region's fossil record. *Oxyloma* has an exceptionally large aperture, representing about 75% of the total height of the shell. It is very rare in our fossil record. Both Taylor (1967) and Quade (1998) reported the occurrence of *Oxyloma* in only one stratigraphic interval in the Tule Springs



Oxyloma sp.



Succinea sp.



Catinella sp.

beds. *Succinea* and *Catinella* are morphologically identical. This similarity has apparently led to inconsistent identification by previous workers. Taylor (1967) reported the occurrence of *Succinea* in many Tule Springs stratigraphic intervals, and a complete absence of *Catinella*. In contrast, Quade (1986) and Quade et al., (1998) reported *Catinella* to be one of the most abundant and widespread genera of fossil snails in the Tule Springs fossil beds, as well as in the fossil-rich beds of Cactus Springs, Corn Creek Flat, and Sandy Valley. Because of this confusion and the similarity of these two genera, we recommend identifying *Catinella*-like and *Succinea*-like fossil shells as ?*Catinella*, or simply as Succineidae.

16. **Lymnaeidae** (pond snails). Three genera of fossil lymnaeid snails occur in our region: *Lymnaea*, *Fossaria*, and *Stagnicola*. These are amphibious, air-breathing, pulmonate snails that typically live at the margins of ponds. They only occasionally submerge beneath the water surface, and rarely deeper than 25 cm, then returning to the surface to replenish their air supply (McMahon, 1983). A key difference between *Lymnaea* and the other two genera is their sizes. *Lymnaea* can be up to 3 cm in height, while *Fossaria* and *Stagnicola* are shorter.

16a. The shell is 1.5 cm high or shorter.....Proceed to 17

16b. The shell is greater than 1.5 cm in height (up to 3.0 cm).....*Lymnaea* sp.

Lymnaea is a large, aquatic, pond snail. The extant species *L. stagnalis*—the “giant pond snail”—is well known to aquatic biologists; it occurs in the quiet margins of freshwater lakes and ponds in North America, Europe, and Asia. Taylor (1967) reported the occurrence of two species, *L. caperata* and *L. montanensis*, in the Tule Springs deposits. They presumably lived in seasonal ponds. Quade (1986) found abundant specimens of *L. caperata* in Units E1 and E2 of the Tule Springs beds, which he interpreted to represent “flowing streams with some spring action, [with] marshy borders.”



Lymnaea sp.

17a. The shell is greater than 1.0 cm in height.....*Stagnicola* sp.



Stagnicola sp.



Fossaria sp.

17b. The shell is less than 1.0 cm in height.....*Fossaria* sp.

These two genera, together with *Lymnaea*, are morphologically very similar. Size is the best criterion for distinguishing them. Taylor (1967) reported the presence of two *Fossaria* species, *F. dalli* and *F. obrussa*, in the Tule Springs deposits. We don't distinguish those species in this key. He also identified several specimens as "*Lymnaea (Stagnicola) sp.*," apparently being unable to decide which genus they represented.

Although Lymnaeids are commonly referred to as aquatic snails, this is an over-simplification of the the habitat versatility of some species. As discussed on page 14, Lymnaeids are amphibious. They typically inhabit moist areas bordering permanent water (Quade and Pratt, 1989), and some species of *Stagnicola* and *Fossaria* have been shown to survive dry periods (Quade et al., 1998).

18. **Hydrobiidae** (springsnails). Hydrobiids are tiny snails, never exceeding 9 mm in height. Most of the species are considerably smaller, and some are only 2 or 3 mm in height. Two genera, *Pyrgulopsis* and *Tryonia* occur as living snails in the greater southern Nevada region, however *Pyrgulopsis* is the only one that has been reported from the Las Vegas Valley fossil record. Hydrobiids are fully aquatic snails. They live in the orifices and pools of springs and in flowing water.

18a. The shell's spire angle is 40° or less (see drawings on page 13).....*Tryonia*

Fossil Tryonia shells have not been reported from the Tule Springs deposits, nor from other Pleistocene and early Holocene sites in the Las Vegas Valley region. Living populations of several species of *Tryonia*, as well as *Pyrgulopsis*, occur in the Death Valley drainage system, which includes Ash Meadows in Nye County, NV (Hershler, 1989, 1999). Fossil *Tryonia* shells were reported from Kokoweef Cave in San Bernardino County, California (Roth and Reynolds, 1990).



Two species of *Tryonia*, showing the range of shell surface microstructure. Adapted from Hershler et al., 1999.

A study of the distribution of living and fossil *Tryonia* concluded that waterbirds play an important role in their dispersal (Wesselingh et al., 1999). See the discussion of dispersal vectors of freshwater molluscs on page 6 of this paper.

18b. The shell's spire angle is 60° or greater.....19

19. *Pyrgulopsis*. These springsnails are called “pyrgs” by the biologists who study them. In his study of the fossil molluscs of Tule Springs, Taylor (1967) used the name *Fontelicella* for these snails, but this is now an obsolete name for this genus. Today, in the Steptoe Valley of northeastern Nevada, where flowing water issues from spring orifices, pyrgs are abundant in watercress along the margins of clear, flowing, oxygenated springs and creeks (Quade and Pratt, 1989), so we can infer that was the environment that they inhabited in southern Nevada in the Pleistocene. Taylor (1967) and Quade (1986) reported finding only small numbers of shells of this genus in the Tule Springs deposits, in only a few of their samples. So, this genus is rare in the southern Nevada fossil record. But when found, it indicates a very specific environment.

19a. The spire angle is conspicuously greater than 60°*Pyrgulopsis micrococcus*
P. micrococcus is the only local species of this genus whose shell shape is distinctive enough to be identified to the species level based on fossil shells. The others can only be identified as *Pyrgulopsis* sp.



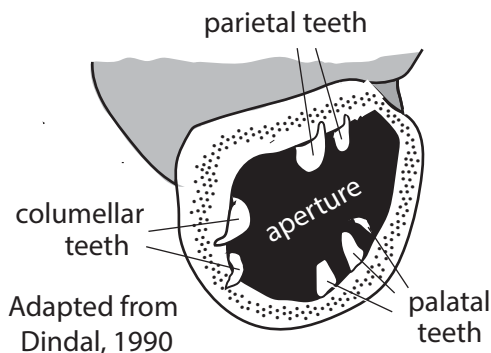
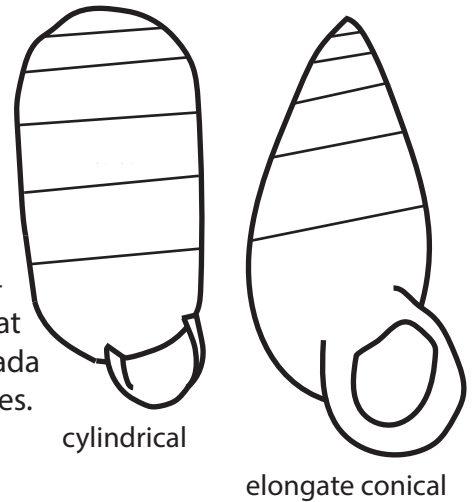
Pyrgulopsis micrococcus



Pyrgulopsis sp.

19b. The shell’s spire angle is approximately 60°*Pyrgulopsis* sp.

20. **Pupillidae** and **Vertiginidae** (whorl snails)--pupa-shaped terrestrial snails. Three genera of pupillid snails have been reported from Pleistocene and Holocene sediments in the southern Nevada region: *Pupilla* (in family Pupillidae) and (in family Vertiginidae) *Vertigo*, and *Gastrocopta*. Morphological features that are used to describe and identify genera and species of these snails usually involve the overall shape of the shell, together with detailed features associated with the aperture. The two shell shapes that are relevant for identifying fossil whorl snails in the southern Nevada region are *cylindrical* and *elongate conic*, as shown in these sketches.



The features associated with the aperture are technically called apertural lamellae and folds, but they are informally called “teeth.” These snails don’t actually chew, like vertebrate animals chew, so their “teeth” are not directly analogous to teeth in vertebrates. But their arrangement and size are critical for distinguishing between genera. The teeth occur along three margins of the aperture, as shown in this sketch.

20a. The shell has a cylindrical shape, and there are no conspicuous teeth in the aperture.....*Pupilla hebes*

Taylor (1967) reported the occurrence of *Pupilla* sp. in a few stratigraphic intervals of the Tule Springs deposits, without identifying the species. Quade (1986) recovered a relatively large number of specimens that he identified as *P. hebes*, from deposits of Tule Springs, Indian Springs, and Corn Creek Flat.

Pupilla hebes is an extant species. It has a wide distribution within the Rocky Mountain Molluscan Province, which covers most of Nevada (Ports, 2021). It occurs today in the Spring Mountains and Sheep Range of southern Nevada (Ports, 2021), where its habitat includes the shrubland steppe community dominated by sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), greasewood (*Sarcobatus* spp.), and antelope bitterbrush (*Pershia tridentata*). In this community it inhabits leaf litter in the limestone gravel beneath individual shrubs or clusters of shrubs (Ports, 2021). But it also occurs in xeric pinyon-juniper woodlands with poor litter development for land snails. *P. hebes* and *Vallonia cyclophorella* are the only gastropods that occur in that community (Ports, 2021).

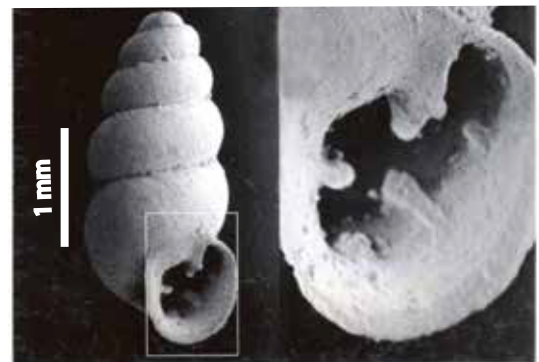


Pupilla hebes (The aperture is packed with sediment, so the presence or absence of teeth cannot be determined in this specimen.)

20b. The shell has an elongate conical shape, and the aperture contains conspicuous teeth.....
.....Proceed to 21

21a. The two parietal teeth have converged and partially united, so that a prominent forked tooth extends from the posterior margin of the aperture, as shown in these SEM images.....*Gastrocopta tappaniana*

The partially-united parietal teeth of *Gastrocopta* have given this genus the nickname “snaggletooth.” Both Taylor (1967) and Quade (1986) identified *G. tappaniana* as the only species of this genus in the fossil record of the southern Nevada region. Living specimens of this species occur in Clark and Nye counties of Nevada, in perennial streams, marshes, and wet meadows (Ports, 2021). Taylor (1967) reported its occurrence in many intervals of the Tule Springs strata, while Quade (1986), whose study included Corn Creek Flat and Indian Springs, in addition to the Tule Springs deposits, reported recovering a total of only two specimens of this species. Both of Quade’s specimens came from the same layer, which was not at Tule Springs; they came from a black-mat horizon at Corn Creek Flat. This species is one of the most common in black-mat intervals, which record shallow ponds and wet meadows (Quade et al., 1998). The surprising differences in the reported abundance of this species between the studies of Taylor (1967) and Quade (1986) are presumably due to differences in the scope of the two studies. *Gastrocopta tappaniana* also occurs in late Pleistocene groundwater deposits in the central Mojave Desert, at Valley Wells, California (Pigati et al., 2011).



Gastrocopta sp., scanning electron micrographs (SEM images) showing the forked tooth that is a characteristic feature of this genus. USGS image in the public domain.

21b. The two parietal teeth are *not* partially united into a forked tooth; one of the parietal teeth is large, while the other is a small nubbin.
.....*Vertigo berryi*

Vertigo berryi is one of the most ubiquitous and abundant molluscan species in the southern Nevada region's Pleistocene fossil record. Taylor (1967) reported finding it in all of the Tule Springs stratigraphic units. Quade (1986) reported recovering 155 individuals of this species in the Corn Creek Flat black-mat interval; this is more than two and a half times the number of individuals representing all other species combined from that interval. Black-mat intervals record the former presence of shallow ponds and wet meadows (Quade et al. 1998). This species also occurs in groundwater discharge deposits at Valley Wells, California, in the central Mojave Desert (Pigati et al., 2011). Ports (2021) reported the occurrence of two species of *Vertigo*--*V. modesta* and *V. ovata*--living today in mountain woodlands of Clark County, Nevada, while one of these, *V. ovata*, also occurs in perennial streams, meadows, and marshes.



Vertigo berryi

What is the function of apertural teeth in pupillid and vertiginid snails?

A study of the genus *Vertigo* suggests that apertural teeth evolved as a defense mechanism against predaceous beetles. Presumably they inhibit the beetles from getting into the snail shells and eating the soft tissues of the snails. Apertural teeth are highly "plastic" across genera and species, in an evolutionary sense, which means that their shapes and sizes are highly variable. For this reason they may not be a highly reliable feature to use to define genera and species (Nekola et al., 2018).

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