Proceedings of The Academy of Natural Sciences of Philadelphia 144: 21-68, 1993

Mollusca of the Grand Canyon and Vicinity, Arizona: New and Revised Data on Diversity and Distributions, With Notes on Pleistocene-Holocene Mollusks of the Grand Canyon

EARLE E. SPAMER AND ARTHUR E. BOGAN

Department of Malacology, Academy of Natural Sciences of Philadelphia
1900 Benjamin Franklin Parkway, Philadelphia, PA 19103-1195

ABSTRACT.—The malacofauna of the Grand Canyon region, Arizona (southwestern U.S.A.), has been largely unexamined since Pilsbry & Ferriss (1911) published the sole paper on the subject. The original locality data of Pilsbry & Ferriss are difficult to interpret from the publication, and they are refined here. Specimens from the early surveys and from sporadic later collections are held in the Academy of Natural Sciences of Philadelphia (ANSP). In 1991, collections were made during the first-ever survey for mollusks along the Colorado River through the Grand Canyon, where they are found usually in tributaries, not in the main stream; specimens are deposited in ANSP. The historical records, including unpublished data from ANSP collections, and new data from the 1991 survey, are tabulated with the perspective of modern systematics. Included among the species is the federally proposed endangered Kanab ambersnail, *Oxyloma haydeni kanabensis* Pilsbry (Gastropoda: Succineidae), the first record of this mollusk alive outside of the type locality (north of Kanab, Utah) and which extends the Recent record of the genus *Oxyloma* into Arizona and the Southwestern Molluscan Province. During the 1991 Grand Canyon survey, collections of mollusks were also made for the first time at Thunder River, a perennial cave pour-out 3 km north of the Colorado River in the Grand Canyon. The 1991 survey produced new records of occurrence and altitudinal distributions for the Grand Canyon, northern Arizona, and the state of Arizona. An examination is made of the distribution of Grand Canyon mollusks with respect to the four ecological Life Zones of the Grand Canyon area. No stratification of mollusks by Life Zone is detected, but corroboration of early studies is made, which indicate that species of higher (cooler, wetter) zones are more restricted to those zones, whereas species of lower (warmer, drier) zones more readily proliferate into higher zones. However, it is seen in the Grand Canyon that specialized riparian communities can promote the colonization of molluscan species normally found in higher Life Zones. Logistical constraints of exploration in this region are considered, and biases in collecting sites are acknowledged. And the first record of Pleistocene(?)-Holocene *Catinella* (Gastropoda: Succineidae) in the Grand Canyon is reported; the occurrence is compared to records of comparably-aged *Oreohelix* (Gastropoda: Oreohelicidae) in the canyon.

The Grand Canyon is a large complex of tributaries of the Colorado River, covering an area of about 12,000 km^2 in northwestern Arizona, the last of a series of canyons along the Colorado River in the Colorado Plateau physiographic province (Fig. 1). The Colorado Plateau is characterized largely by a series of contiguous plateaus, each offset from each other in altitude by geological faults and crustal folds, and into which drainages have excavated canyons.

Climatological conditions in the Grand Canyon region vary greatly due to elevational differences of the plateaus and the deeply incised drainages. The inner canyon is a semi-arid desert (Lower and Upper Sonoran Life Zones), largely an extension of the desert that follows the Colorado River corridor from the Basin and Range physiographic province into the Grand Canyon. The vegetation on the rims of the canyon and the adjacent plateaus ranges from semi-arid woodlands to dense evergreen forests (Transition, Boreal, and Canadian Life Zones), depending upon altitude and the localized distribution of precipitation.

In the eastern Grand Canyon, altitudes range from 730 m to 2500 m above mean sea level, over a linear distance of just 10 km. A maximum

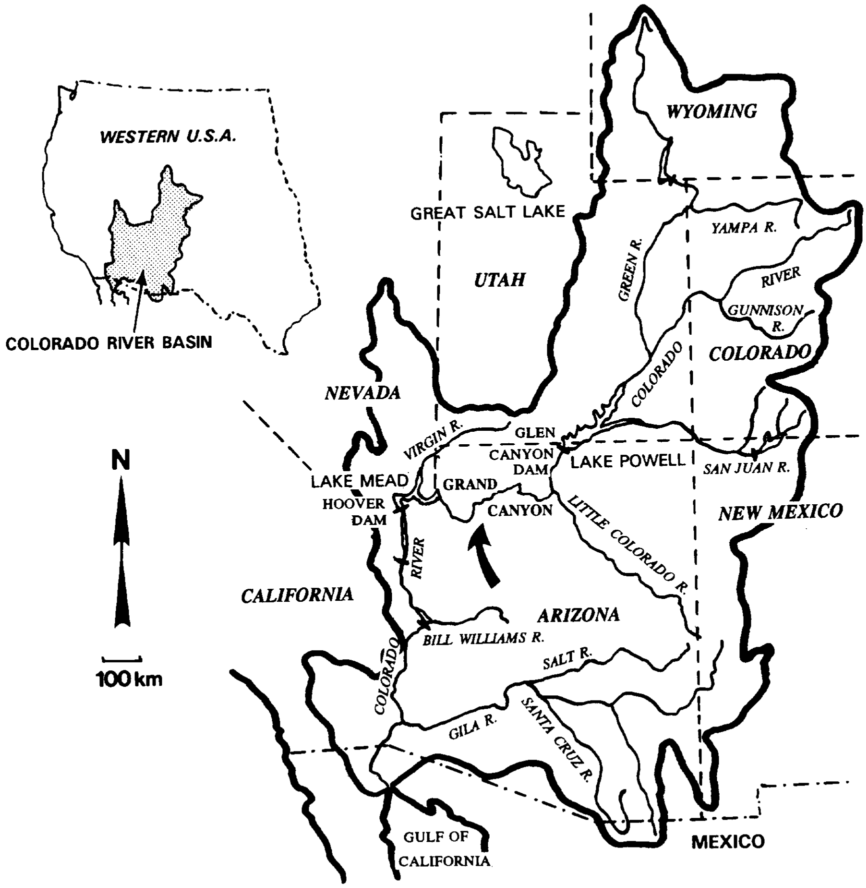

Fig. 1. Colorado River drainage basin.

regional altitude of 2800 m occurs just 8 km north of the rim of the canyon. Life Zones in this area range from Lower Sonoran to Canadian. Nowhere else in this region can as many Life Zones be encountered within a small geographic area (<1000 km^2). At the San Francisco Peaks, the highest place in the state, just north of Flagstaff and 85 km south of the Grand Canyon, Life Zones extend upward to Alpine above the timberline, but on the surrounding plateau extend downward only to the Upper Sonoran Life Zone.

Mollusks have been collected in the Grand Canyon region for a century, but few collections are available. The earliest known collection of a Grand Canyon mollusk is the type material of *Sonorella coloradoensis* (Stearns, 1890), collected in 1889 (USNM 104100, Division of Mollusks, National Museum of Natural History, Smithsonian Institution). The Academy of Natural Sciences of Philadelphia (ANSP) holds several thousand specimens from throughout northern Arizona, most of them collected by Henry A. Pilsbry and James H. Ferriss in the early part of the 20th century. A large part of those collections is comprised of terrestrial gastropods; the remainder aquatic gastropods. Sphaeriid bivalves are represented from just two localities mentioned in this paper. The entire Grand Canyon regional collection has been curated and entered into a computerized database. This is likely the most complete collection available for studying mollusks from the Grand Canyon region; it documents conditions that existed as early as 1906.

Pilsbry & Ferriss (1911) published what until now was the sole comprehensive review of mollusks of the Grand Canyon region. They did not include data from the Colorado River corridor. But in 1991, the first survey of mollusks in the river corridor was made. It was supplemented by an additional survey in another desert riparian community within the Grand Canyon, Thunder River. The results of these surveys have been summarized by Spamer & Bogan (in press); data herein are further updated based on additional examinations made in 1992. We merge these data with an updated review of the historical collections of mollusks made nearly a century ago—a broader perspective of the Mollusca of the Grand Canyon region.

The focus of this paper is the area from the South Rim of the Grand Canyon northward to the boundary between the Southwestern and Mountain Molluscan Provinces, approximately at the Arizona-Utah state line (Bequaert & Miller 1973). On the west, the study area is delineated by the Grand Wash Cliffs, the physiographic boundary between the Colorado Plateau and the Basin and Range, also the western boundary of the Grand Canyon. On the east, the study area is delineated by the Marble Canyon section of the Colorado River. Herein, we segregate discussions and listings of mollusks according to the ecological habits of these animals, i.e. aquatic mollusks (Pulmonata Limnophila mostly, but including the Bivalvia) and terrestrial mollusks (Pulmonata Geophila). This better reflects the division of current research concerns in the Grand Canyon, specifically with regard to the Glen Canyon Environmental Studies being conducted in the Colorado River corridor. Throughout this paper, references to altitudes almost all have been converted from English to metric units. Thus, apparent precision of altitude is often only a generalized figure (e.g. 762 m for a map-read altitude of ca.2500 ft).

PREVIOUS WORK

Two distinct periods of Grand Canyon molluscan research are identified here. The seminal work by Pilsbry & Ferriss (1911), described below, and miscellaneous observations scattered in the literature, delineate the first period; these constitute mostly systematic and biogeographic records. In the 1970s, federally mandated environmental studies of the Grand Canyon ecosystem were begun, principally in the Colorado River corridor, to address problems of environmental alteration caused by the operation of the hydroelectric powerplant at Glen Canyon Dam. In the 1980s, the Glen Canyon Environmental Studies (GCES) program was established within the U.S. Bureau of Reclamation, with federal, state, and Native American cooperating agencies. The most recent charge of the GCES is its contributions toward preparation of the Glen Canyon Dam Environmental Impact Statement, presently scheduled for decision in July 1994 (Randle 1992).

The GCES studies for the most part have examined plant, mammal, and bird communities in the river corridor, producing as well reports on water quality and various physical and hydrological aspects of riverbanks and rapids. In the biological studies, mollusks have been reported, but only in a cursory manner since these animals play uncertain roles in the trophic food web or other major aspects of the Grand Canyon ecosystem. The GCES studies also have presented analyses of the economic repercussions and biological and physical impacts suggested by different models of modification of the power production procedures and schedules of the Glen Canyon Dam powerplant.

Work Prior to Environmental Surveys

The preeminent malacologist, Henry A. Pilsbry (1860-1957), is the acknowledged pioneer of malacology in the American Southwest (Bequaert & Miller 1973). In the latter half of October 1906, in the company of friend and colleague James H. Ferriss (1849-1926), Pilsbry traveled to the Grand Canyon (see Pilsbry's field notes, Appendix 1 herein). Riding on the newly constructed rail line from Williams, Arizona, Pilsbry and Ferriss disembarked at the Bass Station flag stop, 6.5 km from the end of the track at Grand Canyon Village and the South Rim of the canyon. After collecting snails at Bass Station, Pilsbry and Ferriss were taken to the visitor accommodations at Bass Camp (no longer standing), on the rim of the canyon 26 km northwest of Grand Canyon Village. Their goal was the cross-canyon trail and accommodations of William Wallace Bass, Grand Canyon pioneer and self-styled Grand Canyon guide. Bass had been a copper and asbestos miner who discovered that more enjoyable profits were to be had by running a hostelry and conducting tourists into the canyon, where he had a camp and orchard along Shinumo Creek north of the Colorado River. He had developed a trail to his mines near Shinumo Creek, then expanded it to reach the Kaibab and Powell Plateaus, following ancient Native American

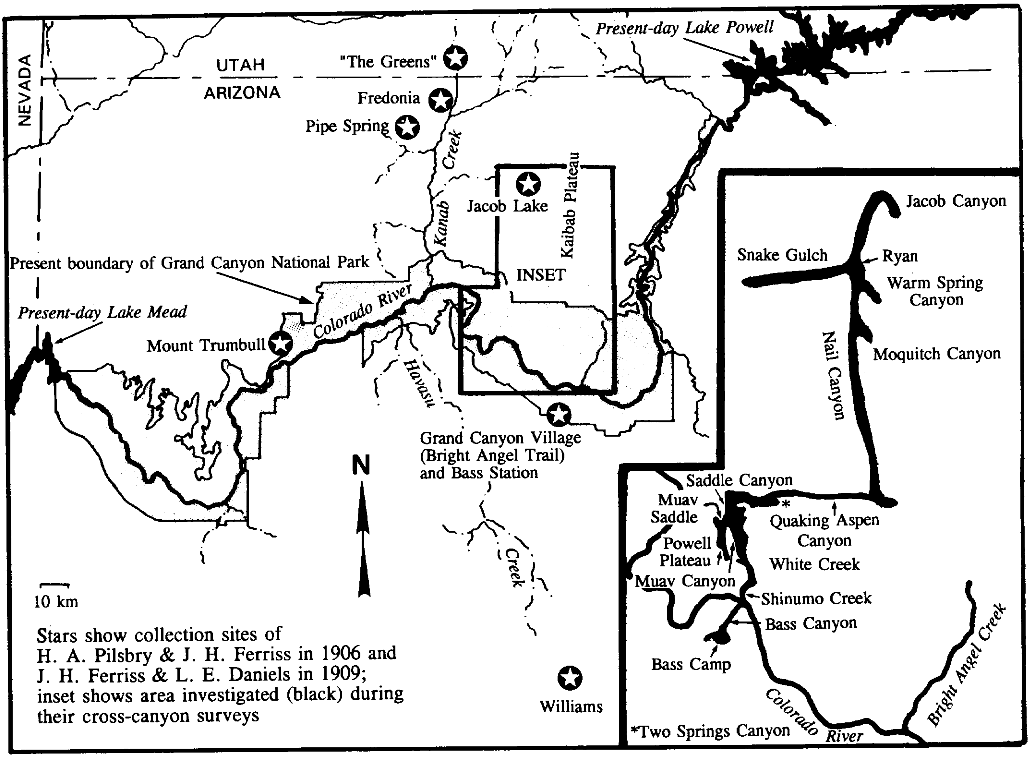

Fig. 2. Collecting sites and areas investigated by Henry A. Pilsbry, James H. Ferriss, and L. E. Daniels in 1906 and 1909. Routes and areas of investigation are as determined from Pilsbry & Ferriss (1911) and original materials held in the Department of Malacology, Academy of Natural Sciences of Philadelphia, as documented in the present paper. Geographic names are as known today.

routes and natural declivities. Today, this 34-km route is known as the South and North Bass Trails (Babbitt & Thybony 1991). These are unmaintained wilderness trails that, although improved by the Civilian Conservation Corps during the 1930s, are passable today only on foot. (It must be noted that overnight camping inside the Grand Canyon requires permits from the National Park Service. Collecting or disturbing living or dead natural objects in national parks is prohibited, and researchers must obtain collecting permits and provide appropriate reports to the National Park Service.)

After collecting near Bass Camp and localities just inside the canyon, Pilsbry and Ferriss embarked on an eight-day trip to the northern side of the Colorado River, making the first planned collection of Grand Canyon mollusks from the canyon. They crossed the Colorado River on a cable car (which no longer survives) that Bass had originally constructed when he was working his mines on the north side of the river. The site of the cable crossing is at Colorado River Mile 108.2 (174.1 km downstream from Lees Ferry). On the north side of the river, the trail crosses a saddle between the river and Shinumo Creek, then descends to the site of a camp that Bass maintained at Shinumo Creek. This was Pilsbry's and Ferriss's center of operations during the 1906 trip. They explored Shinumo Creek upstream to White Creek, then in White Creek as far as Muav Canyon.

Ascending, the North Bass Trail turns from Shinumo Creek and follows White Creek into its upper part, Muav Canyon, finally arriving at the Muav Saddle. From there ascents can be made to the Powell Plateau on the west (an erosional outlier of the North Rim) or the Kaibab Plateau on the east. That route was followed three years later by Ferriss and Daniels (see below).

After the surveys along the Bass trails, Pilsbry and Ferriss returned to Bass Camp on the South Rim, then went on to Grand Canyon Village. They spent a day there, mostly on the upper part of the Bright Angel Trail.

In 1909, Ferriss and Lorenzo E. Daniels (1852-1918) repeated the cross-canyon journey of Pilsbry and Ferriss, but they continued further up North Bass Trail to Muav Saddle and the Powell and Kaibab Plateaus (Fig. 2). They added significantly to the Grand Canyon collections and systematically sampled a segment of the area north of the Grand Canyon. They explored the Kaibab Plateau principally along Quaking Aspen Canyon, Nail Canyon, and Snake Gulch. From Muav Saddle, they traveled westward to Antelope Valley and Mount Trumbull, then followed a loop through Fredonia, Pipe Spring, Kanab (across the state line, in Utah), and Jacob Lake, eventually returning to the Muav Saddle. It should be pointed out that although this area was at that time quite remote, it was largely unprotected by the various federal agencies that today include it in the national park, national forest, and land management agencies. At that time, only the rudimentary Grand Canyon Game Preserve was in place (Hughes 1978). The collections that were made are unique; they represent a sampling of mollusk diversity and conditions as they existed before the time of federal control.

The results of the 1906 and 1909 trips were summarized by Pilsbry & Ferriss (1911), although brief note of *Sonorella* (Gastropoda: Helminthoglyptidae) collected during the trips was first made by Pilsbry & Ferriss (1910: 54). The published descriptions of the collecting stations are not precise, and we resolve this problem later in this paper. The specimens collected by Pilsbry, Ferriss, and Daniels from the Grand Canyon region were added to by more specimens that were collected by other travelers who sent them to Pilsbry (unpublished).

Prior to the collecting by Pilsbry, Ferriss, and Daniels, the only mollusk described from the Grand Canyon was *Sonorella coloradoensis* (Stearns, 1890). The species was originally described as *Helix* (*Arionta*) *coloradoensis*, collected in 1889 by C. Hart Merriam near what later would be the Hance Trail (or Red Canyon Trail), in eastern Grand Canyon (Merriam 1890: 4; Pilsbry & Ferriss 1911: 174; Pilsbry 1939: 338-339). Merriam collected the specimen during his celebrated 1889 survey of ecological zones in northern Arizona, which resulted in the seminal work on the study of Life Zones (Merriam 1890). Pilsbry (1892: 225-226) cited this species as *H. coloradoensis*, but placed it in his "Section *Lysinoe* Adams" and figured it (p. 313, and pl. 56 figs. 1-3) as *Lysinoe coloradoensis*. After briefly being included within the genus *Epiphragmophora* (Pilsbry 1894, 1897; Dall 1897; Pilsbry & Johnson 1898), Pilsbry (1900) included this species in his new genus *Sonorella*, an endemic genus of the American Southwest.

After the work of Pilsbry & Ferriss (1911), only scattered reports of mollusks of the Grand Canyon region were published; they were restricted to short notes on occurrence, comments on pathological conditions, or casual mention of mollusks in ecological surveys without generic or specific identification. Even Pilsbry's (1939-1948) epic monograph on land mollusks north of Mexico, and Bequaert & Miller's (1973) indispensable checklist of Arizona mollusks, for the most part only repeat the information given by Pilsbry & Ferriss (1911).

Daniels (1911) published notes on gravid females of *Oreohelix* (Oreohelicidae) taken during his 1909 Grand Canyon trip with Ferriss. In 1912, he published an article about abnormal shells, including brief comments and figures of sinistral and scalariform specimens of *O. strigosa depressa* (Cockerell, 1890) from the Kaibab Plateau, and a scalariform specimen of *Sonorella coloradoensis* from the Powell Plateau.

Henderson (1914) described the new species *Sonorella betheli*, which he said had been collected from the Bright Angel Trail in the Grand Canyon. But Pilsbry (1939: 174) indicated that the locality information was in error, that the specimen, reidentified by him as *Helminthoglypta traski* (Newcomb, 1861), was probably from Los Angeles, California, also visited by Henderson on that trip through the West.

Pilsbry & Ferriss (1918: 285) made a few observations on habitats and shell sizes of *Oreohelix strigosa depressa* on the Kaibab Plateau, repeating observations made by Pilsbry & Ferriss (1911).

Pilsbry (1921) published notes of occurrence of *Sonorella coloradoensis* and *Oreohelix strigosa depressa* on Bright Angel Trail. Later, he (Pilsbry 1939: 523) reidentified these shells of *O. s. depressa* as the fossil or subfossil mollusk, *O. yavapai fortis* Cockerell, 1927. In the 1921 paper, he also reported occurrences of *O. yavapai angelica* Pilsbry & Ferriss, 1911 (= *O. yavapai* Pilsbry, 1905), from Hermit's Rest (at the end of the West Rim Drive, west of Grand Canyon Village), but by his syntax it erroneously appears that the locality is on Bright Angel Trail.

Cockerell (1927) and Marshall (1929) published notes on fossil or subfossil shells of large forms of the oreohelicid, *Oreohelix yavapai* Pilsbry, erecting two new subspecies. We discuss these occurrences in more detail later in this paper, in the section, "Pleistocene-Holocene Mollusks of the Grand Canyon."

Miller (1968) provided anatomical data on the genitalia of *Sonorella coloradoensis coloradoensis*, from specimens taken on the Bright Angel Trail. He compared the genitalia with those of a new subspecies he described from western Arizona.

Miller (1984) described a new species, *Sonorella reederi*, based on animals found just west of Rampart Cave, in westernmost Grand Canyon where the environment is a part of the desert of the Basin and Range.

Records from Environmental Surveys in the Colorado River Corridor

Publications that discuss the mollusks of the Colorado River corridor through the Grand Canyon have only mentioned these animals in passing, identifying them only as "mollusks," "snails," or if systematic names were used, usually only to family level, occasionally to genus, but never to species. And although Miller's (1984) record of *Sonorella reederi* is in the Colorado River corridor, it is far more west of the environmental surveys made through the Grand Canyon.

Cole & Kubly's (1976) pioneering survey of the limnology of the Colorado River lists *Physa* (= *Physella*) (Physidae) and *Lymnaea* (Lymnaeidae) in tributaries of the Colorado. What they identified as *Lymnaea* at Vasey's Paradise, a spring along the Colorado River in the Marble Canyon portion of Grand Canyon National Park, could be the first record of what is now known to be the federally proposed endangered subspecies *Oxyloma haydeni kanabensis* Pilsbry, 1948 (Succineidae), which is discussed in more detail later in the present paper. But without preserved specimens, this supposition will remain uncorroborated.

The overview of Colorado River biotic resources by Carothers & Minckley (1981) cites only "Physidae" and "Lymnaeidae" in a checklist of aquatic invertebrates.

Tomko (1976: 48-49) reported that the gut contents of the lizard *Cnemidophorus tigris* (Reptilia: Teiidae) included "snails," also without further elaboration.

Maddux et al. (1987: 167) listed under "Mollusca" only "Undetermined species" in their census of organisms taken from plankton tows in the Colorado River. In their description of fish food resources (pp. 165-178), "molluscs" are included in volumetric analyses of fish gut contents, without further elaboration.

Carothers & Brown's (1991) volume on natural resources of the Colorado River corridor in the Grand Canyon mentions mollusks only in passing.

Three annual reports of the status of fish food stocking of the Colorado River between Glen Canyon Dam and Lees Ferry, a state-supported fishery (Stone & Queenan 1967; Stone & Rathbun 1968, 1969), mention the successful introduction of 50,000 specimens of *Physa* from below Navajo Dam on the San Juan River (a tributary of the Colorado River) in New Mexico (see Fig. 1). Some offspring of the transplanted populations may have been transferred by currents to localities further downstream in Grand Canyon National Park.

Thus is the total of published information on the mollusks of the Grand Canyon, prior to 1992. With such a diverse and largely antiquated database to rely upon, we see the necessity to bring the available information on Grand Canyon mollusks up to date, which we present here. This is in preparation for continued work in the area. The known malacofauna of the Grand Canyon region are itemized in systematic order, with remarks on known distributions, later in this paper.

LOCALITY DESCRIPTIONS

This paper combines data from historical and recent surveys. All collecting and survey stations are identified herein, and geographic coordinates are provided for them. Data on altitudes are interpreted from topographic sheets, guided also in part by published data. Precise altitudes are not implied; they are approximations limited by large topographic contour intervals. Most of the cited altitudes have been converted from English to metric units.

With the exception of the many in-canyon and Kaibab Plateau stations of Pilsbry, Ferriss, and Daniels (the 1906 and 1909 surveys), which have not been revisited, notes are provided on ecology and habitat for all stations. A few observations on these habitats were provided by

Pilsbry & Ferriss (1910, 1911, 1918), but data for individual stations are largely unrecorded. At this time, it is not known whether these habitats have changed dramatically since the early twentieth century. Data for Colorado River corridor are mostly as observed during the 1991 survey, with supplementary comments based on observations made in 1992. The Thunder River survey is based on one visit, in 1991. Some remarks on miscellaneous historical collecting stations are as interpreted from visits to these stations in recent years.

Historical Collecting Stations

CODED STATIONS OF PILSBRY & FERRISS. Pilsbry & Ferriss (1911) cited more than a hundred collecting stations by number and letter (Table 1). The data published for these stations are scant, and the published sketch maps (Pilsbry & Ferriss 1911, figs. 1, 2) give only a general idea of the locations of these stations. The precise positions are not clear from the published maps because they were numbered with hand-set type on a small map that had been traced from large-scale topographic sheets. The maps used to prepare the published ones are the Kaibab and Shinumo quadrangles, published by the U.S. Geological Survey in 1886 and 1908, respectively. The Kaibab quadrangle is a 1:250,000-scale sheet with 250-foot (76.2-m) topographic contour intervals, based on the original Grand Canyon surveys under the direction of the first Grand Canyon explorer, John Wesley Powell. The Shinumo quadrangle is a 1:48,000-scale topographic sheet with 50-foot (15.2-m) contours, based on 1906 surveying by François Matthes. The altitude data published by Pilsbry & Ferriss (1911) for some, but not all, of their collecting stations were interpreted from these large-scale topographic sheets, thus many of their data are approximations that can be off by tens to hundreds of meters.

METHODS USED TO RELOCATE CODED COLLECTING STATIONS. Because Pilsbry and Ferriss's (1911) published data on the location of their collecting stations is so incomplete, it is necessary to document the methods that were used to relocate these stations with more precision. We use these data in our interpretations of distribution, thus our methods must be made available for reevaluation by future workers.

In 1988, an original copy of the Kanab topographic quadrangle (1:250,000-scale, published in 1886) was found folded into one of H. A. Pilsbry's books in the library of the Department

Table 1. Identification of coded collecting stations of Pilsbry & Ferriss (1911).

Pilsbry & Ferriss (1911) and Original Labels in ANSP Collection		This Paper		
Station	Location and Published Elevation[1]	Geographical Coordinates	Alt. (m)	USGS 15' Quadrangle
A	"Spectacle Cove," at foot of Coconino Sandstone	36 11 04 N, 112 22 23 W	1830	Havasupai Point
B	Head of Starvation Tank Wash ca. 5,800 ft	36 11 15 N, 112 21 46 W	1770	Havasupai Point
C	Bay ca. 1/2 mile W of Bass Camp, a few hundred feet below rim	36 10 57 N, 112 22 50 W	1920	Havasupai Point
D	Bass Trail, Redwall Limestone, 5,000 ft	36 11 49 N, 112 22 15 W	1350	Havasupai Point
E	Bass Trail, foot of Redwall Limestone, 3,850 ft	36 12 19 N, 112 21 50 W	1175	Havasupai Point
F	Shinumo Creek, near camp, ca. 2,500 ft	36 15 05 N, 112 20 04 W	762	Powell Plateau
G	White Creek, ca. 1 mi. from confluence with Shinumo Creek	36 16 00 N, 112 19 26 W	975	Powell Plateau
H	Mojave Amphitheatre, below Redwall Limestone, W side Muav Canyon	36 17 00 N, 112 20 42 W	1300	Powell Plateau
1	"North of the Grand Canyon"	—	—	—
2	Near South Bass Trail, ca. 200 ft below rim	36 10 57 N, 112 22 23 W	1950	Havasupai Point
3	Box of Shinumo Creek, 2,750 ft	36 15 13 N, 112 19 13 W	900	Powell Plateau
4	—	36 18 39 N, 112 20 30 W	1860	Powell Plateau
5	East of Muav Canyon, near Muav Saddle, 6,717 ft	36 19 08 N, 112 20 18 W	2010	Powell Plateau
6	—	36 20 00 N, 112 21 05 W	2200	Powell Plateau
7	Kaibab Saddle and Plateau	30 18 54 N, 112 20 24 W	1950	Powell Plateau
8	East side of Powell Plateau [near Dutton Point]	36 17 08 N, 112 21 48 W	2300	Powell Plateau
9[2]	Box of Muav Creek, 4,000 ft	36 18 00 N, 112 20 30 W	1220	Powell Plateau

9[2]	East side of Powell Plateau, 7,500 ft	36 17 14 N, 112 21 39 W	2300	Powell Plateau
10	East side of Powell Plateau	36 19 13 N, 112 22 10 W	2327	Powell Plateau
11	—	36 20 22 N, 112 21 05 W	1950	Powell Plateau
11	1/2 = Station 49			
12[3]	Shinumo Creek, Big Spring Canyon	36 19 05 N, 112 16 00 W	2040	Powell Plateau
13	Northern end of Powell Plateau	36 20 22 N, 112 21 45 W	2045	Powell Plateau
14	Northern end of Powell Plateau	36 20 35 N, 112 22 02 W	2134	Powell Plateau
15	Northern end of Powell Plateau	36 20 32 N, 112 21 54 W	1982	Powell Plateau
16	Northern end of Powell Plateau	36 20 06 N, 112 21 55 W	2043	Powell Plateau
17	Off northern end of Powell Plateau	36 20 59 N, 112 21 45 W	2240	Powell Plateau
18	Upper part of saddle trail, Powell Plateau, 6,700 ft	36 19 16 N, 112 22 08 W	2350	Powell Plateau
19	Western side of Powell Plateau	36 19 46 N, 112 22 30 W	2330	Powell Plateau
20	Western side of Powell Plateau	36 19 16 N, 112 22 40 W	2330	Powell Plateau
21	Western side of Powell Plateau	36 19 08 N, 112 22 45 W	2330	Powell Plateau
22	Western side of Powell Plateau	36 18 54 N, 112 22 40 W	2300	Powell Plateau
23	Horse Tank Canyon, western side of Powell Plateau, 7,000 ft	36 18 43 N, 112 22 45 W	2300	Powell Plateau
24	Western side of Powell Plateau	36 18 39 N, 112 22 50 W	2300	Powell Plateau
25	Western side of Powell Plateau, 6,700 ft	36 18 32 N, 112 23 00 W	2300	Powell Plateau
26	Quaking Aspen Canyon	36 21 54 N, 112 17 18 W	2415	Powell Plateau
27	Upper Two Spring	36 21 54 N, 112 17 53 W	2385	Powell Plateau
28	Quaking Aspen Canyon	36 21 58 N, 112 18 28 W	2350	Powell Plateau
29	Lower Two Spring	36 22 02 N, 112 18 24 W	2295	Powell Plateau
30	Quaking Aspen Canyon	36 22 12 N, 112 18 38 W	2290	Powell Plateau
31	Castle Canyon, [Castle Spring?] [= Station 79?]	36 35 10 N, 112 20 29 W	2195	Big Springs
32	Nail Canyon, [Mourning Dove Spring?]	36 36 58 N, 112 20 52 W	2135	Big Springs
33	Nail Canyon, [near Mangum Springs?]	36 37 20 N, 112 21 00 W	2085	Big Springs
34	Nail Canyon, near Mangum Springs	36 37 40 N, 112 20 50 W	2070	Big Springs
35	Nail Canyon, [near Moquitch Camp?]	36 38 25 N, 112 20 38 W	2040	Big Springs
36	Oak Canyon	36 40 30 N, 112 20 24 W	2010	Big Springs
37	North side of mouth of "Smelter Gulch," near Ryan, 5,750 ft	36 42 25 N, 112 22 20 W	1770	Big Springs
38	Fredonia	36 56 44 N, 112 31 33 W	1425	Fredonia
39	Pipe Spring [Pipe Spring National Monument]	36 51 43 N, 112 44 11 W	1510	Fredonia
40	Antelope Valley [area of Mount Trumbull Road]	36 40 — N, 112 50 — W	1500	Heaton Knolls
43	—	36 26 — N, 113 09 — W	2010	Mt. Trumbull NW[4]
44	[Coyote Spring?]	36 24 57 N, 113 07 59 W	2200	Mt. Trumbull NW[4]
45	—	36 26 — N, 113 09 — W	2010	Mt. Trumbull NW[4]
46	Hurricane fault [Hurricane Cliffs], near Mt. Trumbull, 6,000 ft	36 24 — N, 113 17 — W	1875	Jones Hill[4]
49	Snake Gulch, below Coconino Smelter [Ryan]	36 41 29 N, 112 21 08 W	1890	Big Springs
50	Snake Gulch, 5,500 ft	36 42 40 N, 112 22 29 W	1740	Big Springs
51	Snake Gulch	36 42 45 N, 112 23 24 W	1720	Big Springs
52	Snake Gulch	36 42 45 N, 112 23 48 W	1710	Big Springs
53	Snake Gulch	36 42 38 N, 112 24 08 W	1690	Big Springs
54	Snake Gulch	36 42 30 N, 112 24 35 W	1690	Big Springs
55	Snake Gulch, 5,500 ft	36 42 22 N, 112 25 05 W	1675	Big Springs
56	Snake Gulch	36 42 27 N, 112 25 52 W	1677	Big Springs
57	Snake Gulch	36 42 25 N, 112 26 43 W	1615	Big Springs
58	Snake Gulch	36 42 48 N, 112 27 35 W	1585	Big Springs
59	Warm Springs Canyon	36 41 23 N, 112 20 28 W	1920	Big Springs
60	Warm Springs Canyon	36 41 26 N, 112 20 06 W	1965	Big Springs
61	Warm Springs Canyon	36 41 29 N, 112 19 35 W	1920	Big Springs
62	Warm Springs Canyon	36 41 36 N, 112 20 02 W	1980	Big Springs
63	Warm Springs Canyon	36 41 39 N, 112 19 03 W	2040	Big Springs
64	Warm Springs Canyon	36 41 39 N, 112 18 47 W	2070	Big Springs
65	Warm Springs Canyon	36 41 35 N, 112 18 33 W	2100	Big Springs
66	First gulch facing west, north of Warm Springs Canyon	36 42 30 N, 112 20 02 W	2075	Big Springs
67	Below mouth of Jacob Canyon, 2nd gulch north of Warm Springs Canyon	36 42 55 N, 112 19 35 W	2100	Big Springs

68	Jacob Canyon	36 43 28 N, 112 18 22 W	2075	Big Springs
69	Jacob Canyon	36 43 36 N, 112 17 53 W	2135	Big Springs
70	Jacob Canyon	36 44 07 N, 112 17 42 W	2160	Big Springs
71	Jacob Canyon	36 44 18 N, 112 17 10 W	2225	Big Springs
72	Jacob Canyon	36 44 28 N, 112 16 27 W	2240	Big Springs
73	Warm Springs Canyon	36 41 35 N, 112 20 06 W	2070	Big Springs
74	Warm Springs Canyon	36 41 44 N, 112 20 06 W	2180	Big Springs
75	Moquitch Canyon, [Moquitch Spring?]	36 37 59 N, 112 19 32 W	2225	Big Springs
76	Moquitch Canyon	36 38 07 N, 112 19 48 W	2134	Big Springs
77	Nail Canyon	36 36 06 N, 112 20 57 W	2100	Big Springs
78	Nail Canyon, Big Spring	36 36 06 N, 112 20 57 W	2100	Big Springs
79	Castle Spring, Castle Canyon [= Station 31?]	36 35 10 N, 112 20 29 W	2195	Big Springs
80	—	36 35 00 N, 112 20 35 W	2165	Big Springs
81	Riggs Canyon[5]	36 33 42 N, 112 19 36 W	2293	Big Springs
82	Bee Spring area[5]	36 27 — N, 112 17 — W	2380	Big Springs
83	Quaking Aspen Canyon, head, 8,250 ft	36 23 28 N, 112 13 45 W	2515	De Motte Park
84	Quaking Aspen Canyon	36 22 53 N, 112 15 21 W	2430	Powell Plateau
85	Quaking Aspen Canyon, [Watts Spring?][6]	36 22 48 N, 112 16 30 W	2435	Powell Plateau
86	Quaking Aspen Canyon, [Quaking Aspen Spring?]	36 22 43 N, 112 16 54 W	2375	Powell Plateau
87	Quaking Aspen Canyon	36 21 52 N, 112 18 52 W	2195	Powell Plateau
88	Quaking Aspen Canyon	36 21 54 N, 112 19 13 W	2135	Powell Plateau
89	Quaking Aspen Canyon	36 22 00 N, 112 20 00 W	2000	Powell Plateau
90	Quaking Aspen Canyon	36 22 06 N, 112 20 42 W	1920	Powell Plateau
91	Quaking Aspen Canyon, 7,000 ft	36 22 34 N, 112 20 30 W	2040	Powell Plateau
92	Quaking Aspen Canyon	36 22 12 N, 112 21 06 W	1890	Powell Plateau
93	Quaking Aspen Canyon	36 22 19 N, 112 21 23 W	1890	Powell Plateau
94	Quaking Aspen Canyon	36 22 23 N, 112 21 45 W	1890	Powell Plateau
95	Quaking Aspen Canyon	36 22 19 N, 112 21 00 W	1950	Powell Plateau
96	Quaking Aspen Canyon	36 22 23 N, 112 22 02 W	1890	Powell Plateau
97	Quaking Aspen Canyon	36 22 34 N, 112 22 02 W	1860	Powell Plateau
98	Quaking Aspen Canyon, lower end, 6,500 ft	36 22 40 N, 112 21 55 W	1950	Powell Plateau
99	Quaking Aspen Canyon	36 22 27 N, 112 21 23 W	1950	Powell Plateau
100	Muav Saddle[7]	36 21 51 N, 112 21 38 W	2040	Powell Plateau
101	North end of Powell Plateau	36 20 32 N, 112 22 50 W	2350	Powell Plateau
102	—	36 18 51 N, 112 22 02 W	2320	Powell Plateau
103	East side of Powell Plateau	36 18 28 N, 112 22 10 W	2320	Powell Plateau
104	East side of Powell Plateau	36 18 16 N, 112 22 02 W	2295	Powell Plateau
105	Muav Saddle area, [Grass Canyon?]	36 21 — N, 112 18 — W	2350	Powell Plateau
106	Muav Saddle area, [Grass Canyon?]	36 21 — N, 112 18 — W	2350	Powell Plateau
107	—	36 17 32 N, 112 20 24 W	1220	Powell Plateau
108	[= Station F?]	—	—	—
109	South Bass Trail, Redwall Limestone, 5,000 ft	36 11 49 N, 112 22 15 W	1350	Havasupai Point

[1] Current names of locations are used, as determined in this paper. Pilsbry & Ferriss's (1911) locations usually were generalized (e.g. "Quaking Asp Canyon"), with the more precise location of the station indicated on their published maps (figs. 1, 2). Altitudes are as determined from readings on the cited topographic maps, and sometimes with reference to current geologic map (Huntoon et al. 1976) (e.g. station 109). Omitted station numbers appear nowhere in Pilsbry & Ferriss (1911), Ferriss's manuscript map, or with specimens in ANSP collection.

[2] Two stations carry the number 9.

[3] Station 12 not published; shown on Ferriss's original map below South Big Spring, along Shinumo Creek, Big Spring Canyon.

[4] 7.5' series quadrangle

[5] Pilsbry & Ferriss (1911) list Station 82 as Riggs Spring; Ferriss's detailed manuscript map shows Station 82 in the area of Bee Spring.

[6] Station not indicated on Pilsbry & Ferriss's (1911) map.

[7] Pilsbry & Ferriss (1911) give three different localities for Station 100: 1) "third amphitheatre north of the Kaibab Saddle, 6,700 feet" (pp. 181-182), 2) "Kaibab-Powell Saddle, 6,700 feet" (p. 190), and 3) "near Oak Springs" (p. 197).

of Malacology, ANSP. On it were penned station numbers and various locality names for stations visited, and routes travelled, by J. H. Ferriss and L. E. Daniels during the 1909 expedition. This is apparently the map that is mentioned in a letter from Ferriss to Pilsbry (Ferriss 1910), but this is not the field map used by Ferriss and Daniels because it is quite unworn. It appears to be an accurate transcription of Ferriss's original map, apparently by Ferriss, which he sent to his friend Pilsbry for the purpose of preparing the published sketch maps of their collecting stations.

With this map in hand, more than 100 stations were translated to modern topographic sheets. Control of position was maintained by comparing 1) the relative position of each station with the topographic pattern of drainages, cliff faces, other major topographic features, 2) relative position between stations as shown on the published maps (and manuscript map in ANSP), 3) the proximity to the known route travelled by the collectors, and 4) reference to altitude data that was published and that accompanies specimens in ANSP collections. The supporting data that were sometimes available from original labels in the ANSP collections are written in the hands both of Pilsbry and Ferriss.

If the modern map indicated an impossible or very improbable position for a translated station (e.g. on a sheer cliff, or in a canyon below the rim of the plateau on which the collectors were known to be traveling), a nearby position was identified that physiographically made more sense, and the altitude for that position read from it. In the case of some imprecise translations, apparent errors were due more to the inaccuracy of surveying for the 1886 map than they were to an inaccuracy in Ferriss's positioning of station numbers.

When all translations were completed, geographic coordinates were read off of the modern topographic sheet (Table 1), to the nearest second of arc. These coordinates are presented with the understanding that the translations may not be entirely precise, although accurate within the constraints of topographic expression and relative positions of all stations. No rounding of values for plotted coordinates was done (e.g. to the nearest minute or 15-second interval of arc) because such rounding was discovered to yield plotted positions that were topographically (and sometimes ecologically) impossible—with respect to accessibility and from the resultant reading of altitude.

Many of Pilsbry & Ferriss's (1911) geographic names, which also appear on original labels throughout ANSP collections, had to be reidentified to current terminology. Work with the original maps assisted in making these determinations. A key to the older and informal

Table 2. Geographic names and terminology of Pilsbry & Ferriss (1911) and Pilsbry's field notes.

Name Used	Current Name
Ash Springs	=? Powell Spring
Bass Camp	site of W. W. Bass's hotel, South Bass trailhead, ~36°12'00" N, ~112°22'30" W
Bass Station	no longer in existence; flag stop on Grand Canyon Railroad (36°00'35" N, 112°11'30" W; 1950 m; Bright Angel quadrangle)
bay	amphitheater
Coconino Smelter	smelter at Ryan (or Coconino City)
Cross-bed sandstone	Coconino Sandstone
Horse Tank Canyon	informal name, on west side of Powell Plateau
Jacob's Canyon	Jacob Canyon
Kaibab Saddle, Kaibab-Muav Saddle	Muav Saddle
Mojave Amphitheatre	amphitheater below Masonic Temple
Mojave Canyon	Muav Canyon
Moquitch Gulch	Moquitch Canyon
Muav Box	box (narrows) of Muav Creek
Mystic Spring Trail	South Bass Trail
Oak Springs	=? unnamed springs below Muav Saddle, or Powell Spring (not Oak Spring of Kaibab Plateau)
Oreohelix Talus	informal name; collecting station off of South Bass Trail below the Coconino Sandstone

Quaking Asp Canyon	Quaking Aspen Canyon
Red Wall	Redwall Limestone
Seep Spring	Unnamed spring 3.2 km west of South Bass Trail; 36°10′48" N, 112°23′56" W; Havasupai Point quadrangle
Shinumo Box	box (narrows) of Shinumo Creek
Shinumo Canyon	Snake Gulch [not Shinumo Canyon]
Smelter Gulch	informal name, lower Warm Springs Canyon
Snake Gulch	some localities = Nail Canyon
Spectacle Cove	informal name, amphitheater below and east of Bass Camp
Starvation Tank Wash	informal name, drainage just east of Bass Camp
Two Springs	Upper Two Spring
Two Springs Canyon	Quaking Aspen Canyon (branch)
Warm Spring Canyon	Warm Springs Canyon

names is presented in Table 2.

OTHER HISTORICAL COLLECTING STATIONS. In addition to the coded stations published by Pilsbry & Ferriss (1911), many other localities along the canyon rims or on nearby plateaus were cited by these authors or have appeared in other literature. Descriptions of these localities are provided below. (Some of these localities are plotted in Fig. 3, later in this paper.)

Pilsbry & Ferriss (1911) also published records of occurrence for the area of Williams, Arizona; but these data are omitted in the present paper. The altitudinal data for the specimens from Williams, mostly from Bill Williams Mountain, are wanting. The same is true for unpublished ANSP specimens from the San Francisco Peaks, near Flagstaff, which is unfortunate since the Peaks are the "type area" for the recognition and development of the concept of Life Zones (Merriam 1890). None of these specimens can be justifiably included in the discussions of altitudinal zonation and Life Zones, but data on them are provided in Table 3, for the sake of completeness of systematic information. Furthermore, no collection of specimens is known to have been published—nor are there any in ANSP collections—from the broad area between Williams/Flagstaff and the Grand Canyon. Contrarily, on the northern side of the canyon, significant collections have been made across the plateaus to the Arizona-Utah state line; these have good station data. The state line is near the physiographic transition between plateaus and approximates the boundary between the Mountain and Southwestern Molluscan Provinces (Bequaert & Miller 1973). Thus the study area of the present paper encompasses the northern extremity of the Southwestern Molluscan Province in Arizona, southward to the South Rim of the Grand Canyon.

South Side of Grand Canyon. The Rampart Cave locality is in Mohave County; all others are in Coconino County. Localities are listed from west to east.

Rampart Cave Area. Rampart Cave is in the Muav Limestone near Colorado River Mile 274.7 (Km 439.5), Left; 36°05'56" N, 113°55'57" W (518 m). The locality is in westernmost Grand Canyon, just east of the Grand Wash Cliffs that delineate the physiographic boundary between the Colorado Plateau and Basin and Range provinces. It overlooks the impounded channel of the Colorado River (Lake Mead), in a dry desert environment characteristic of the lower elevations of the Basin and Range. Specimens of *Sonorella* have been reported from near this locality by Bequaert & Miller (1973) and Miller (1984); it is the northwesternmost occurrence of the genus (Bequaert & Miller 1973).

Seep Spring West of South Bass Trail. 36°10'48" N, 112°23'56" W (1830 m). Pilsbry & Ferriss (1911) and Pilsbry's field notes (Appendix 1 herein) indicate that the seep spring is 2 miles (3.2 km) west of Bass Trail, at the base of the Coconino Sandstone and the talus below it. The position of the west-facing spring shown on the Havasupai Point topographic sheet is in the Toroweap Formation.

Hermit's Rest. At the end of the West Rim Drive; this is a structure built in the 1930s near the Hermit trailhead; 36°03'43" N, 112°12'37 W (2012 m). The locality is in a pinyon-juniper forest on the rim of the canyon. This site is very heavily visited by tourists.

Bass Station. Site along the Grand Canyon Railroad, 6.5 km south of the end of the line at Grand Canyon Village, a flag stop used by visitors traveling to or from Bass Camp; in an open wash tributary to Bright Angel Wash;

Table 3. Mollusks reported from the vicinities of Bill Williams Mountain and the San Francisco Peaks, south of the Grand Canyon. Occurrences are as reported by Pilsbry & Ferriss (1911), Bequaert & Miller (1973), and specimens in ANSP collections.[1]

Taxon	Vicinity of Williams	Bill Williams Mtn.	San Francisco Mtn.	Elden Mtn.	G.C.[2]
AQUATIC MOLLUSKS					
Physidae					
Physella gyrina (Say, 1821)	•				
P. virgata (Gould, 1855)	•				
Planorbidae					
Helisoma tenue (Dunker, 1850)[3]	•		•		
Gyraulus parvus (Say, 1817)	•		•		•
TERRESTRIAL MOLLUSKS					
Cochlicopidae					
Cionella lubrica (Müller, 1774)			•		•
Vertiginidae					
Vertigo concinnula Cockerell, 1897		•	•		
V. gouldii (Binney, 1843)[4]		•	•		
V. modesta (Say *in* Keating, 1824)			•		
Pupillidae					
Gastrocopta pilsbryana (Sterki, 1890)[5]		•	•	•	•
G. quadridens Pilsbry, 1916[6]		•			
Pupoides nitidulus (C. B. Adams, 1841)			•		
Pupilla hebes (Ancey, 1881)	•		•	•	•
P. muscorum (Linné, 1758)			•[11]		
P. syngenes (Pilsbry, 1890)			•		•
Valloniidae					
Vallonia cyclophorella Sterki, 1892		•	•		•
Vallonia sp.			•		
Punctidae					
Punctum californicum Pilsbry, 1898			•		
Discidae					
Discus cronkhitei (Newcomb, 1865)		•	•		•
D. shimekii (Pilsbry, 1890)			•[11]		
Succineidae					
Catinella avara (Say, 1824)			•		•
Succinea sp.				•	
Charopidae					
Radiodiscus millecostatus Pilsbry & Ferriss, 1906			•		
Helicarionidae					
Euconulus fulvus (Müller, 1774)[7]			•		•
Zonitidae					
Hawaiia minuscula (Binney, 1841)[8]		•	•	•	•
Zonitoides arboreus (Say, 1817)		•	•	•	•
Glyphyalinia indentata (Say, 1823)[9]		•	•		•
Striatura meridionalis (Pilsbry & Ferriss, 1906)[10]		•	•		
Vitrinidae					
Vitrina alaskana Dall, 1905		•	•		•

Thysanophoridae			
Thysanophora hornii (Gabb, 1866)		•	•
Microphysula ingersollii (Bland, 1875)	•	•	•
Oreohelicidae			
Oreohelix sp.		•	

[1]The localities itemized in this table are cited in some previous literature on the Grand Canyon region, but for reasons explained in the text they are excluded from the study area of the present paper. They are cited here so as to provide comparable coverage with the previous literature. Some cosmopolitan species may be present at localities for which no information is given here. This may be due to the lack of citations for specific localities in the literature referred to for this paper.

[2]Species also occurs in the vicinity of the Grand Canyon, as discussed in the present paper.

[3-10]Pilsbry & Ferriss (1911) cited these taxa as: [3]*Planorbis tenuis* Phil., [4]*Vertigo coloradoensis arizonensis* Pilsbry & Vanatta, 1900, [5]*Bifidaria pilsbryana* Sterki, [6]*Bifidaria quadridentata* Sterki, 1899 (Bill Williams Mountain is the northwesternmost station of this species; Bequaert & Miller 1973), [7]*Euconulus fulvus alaskensis* (Pilsbry), [8]*Zonitoides minuscula* (Binney), [9]*Vitrea indentata umbilicata* "Singleton" Cockerell, [10]*Zonitoides milium meridionalis* Pilsbry.

[11]Arctic-Alpine Life Zone only (Bequaert & Miller 1973).

36°00'35" N, 112°11'30" W (1950 m). Bass Station was no longer a stop after Bass Camp closed in 1926. The railway, between Williams and Grand Canyon, ceased operation in 1967, but operations continued again with steam locomotives in 1989.

Bright Angel Trail. Several stations have been collected between the rim and Indian Gardens, a trail distance of 7.4 km; generalized coordinates for this part of the trail are 36°03'30" N, 112°08'30" W (1140-2070 m). It is heavily used by hikers and mules.

Indian Gardens. Spring area along Bright Angel Trail, 36°04'44" N, 112°07'12" W (1140 m). This is a cool, heavily vegetated area at one of the rare spring heads on the south side of the canyon. A campground and mule corral are here, and the area is heavily used. The locality was visited briefly by the senior author in June 1992. Due to time constraints, the spring was not examined, and a brief survey of plants and shaded plant litter near the mule corral revealed no terrestrial mollusks.

Yavapai Point. Collecting station "just below rim," 36°03'57" N, 112°07'01" W (2130 m). The locality is in a pinyon-juniper forest on the rim of the canyon; a small museum (formerly the "Yavapai Observation Station") was built here in the 1930s. This site is very heavily visited by tourists.

Grandview Point. 35°59'46" N, 111°59'07" W (2255 m). At the turn of the 19th-20th century, a hotel stood near here, and it was a staging area for mules working back and forth between a copper mine down Grandview Trail, so the area has at times experienced some considerable human impact. The locality is in a pinyon-juniper forest on the rim of the canyon. This site today is heavily visited by tourists.

Hance Trail Area. Hance trailhead is near the head of Red Canyon; it is this area in 1889 that C. Hart Merriam descended into the canyon during his pioneering survey of ecological Life Zones; ca.36°00' N, ca.111°56' W (ca.2200 m altitude at the canyon rim in this area). Unfortunately there is no record of whether Merriam descended over the rim randomly, or whether he followed what is known today as the Old Hance Trail (actually nothing more than a route), the original trail built by prospector/hosteler John Hance that was obliterated by landslides shortly after the time Merriam visited. The Old Hance Trail is to the west of the present Hance Trail; the route eventually connects with the present trail. Merriam's collecting area is still virtually unvisited wilderness. Hance Trail, also built and maintained by John Hance in the 1890s, is rugged and not maintained; it receives only very light use.

North Side of Grand Canyon. Bright Angel Point, Jacob Lake, and Ryan are in Coconino County. The community of Fredonia is in Coconino County, but Kanab Creek, alongside which it is, is the boundary between Coconino and Mohave Counties. The other localities listed here are in Mohave County. These sites are listed approximately from east to west.

Bright Angel Point. 36°11'35" N, 112°02'53" W (2482 m). The locality is in a pine forest on a narrow point extending into the canyon. The site is near a hotel and is heavily visited by tourists. This is the site of Wylie's Camp, cited with specimens in ANSP.

Jacob Lake. 36°42'26" N, 112°13'49 W (2400 m). Jacob Lake is in a forest of ponderosa pine, generally cool and wet with heavy winter snows.

Ryan. 36°41'18" N, 112°20'55" W (1951 m). Ryan, or Coconino City, was the site of a copper-smelting operation, receiving ore from several prospects in the area (G. H. Billingsley, MS.). In 1905, water was delivered to the smelter through a wooden pipe from Big Spring, 8 km south of Ryan in Nail Canyon, and a narrow-gauge rail line ran into Warm Springs Canyon; Ryan also provided itself with electric power (Cox 1982). The smelter probably was not in operation when Ferriss and Daniels visited in 1909, but still the specimens collected in the area may record the effects of this polluting operation. A steam-operated pumping plant in Warm Springs Canyon was built to support a mill nearby, but it was destroyed by fire ca. 1902, before either became operational (G. H. Billingsley, MS.). The area experienced intermittent activity through the 1920s, and again during World War II (Tainter 1947), which certainly had an effect on the local environment. Thus, the area around Ryan uniquely presents itself as an ecological zone once affected by polluting industries, in the midst of a largely wilderness setting.

Fredonia. 36°56'44" N, 112°31'33" W (1424 m); the northernmost collecting locality in the study area.

Pipe Spring. Now Pipe Spring National Monument; 36°51'43" N, 112°44'11" W (1509 m), at the Vermilion Cliffs.

Antelope Valley. Precise position of locality unknown; 36°35' N, 113°00' W (ca. 1600 m); area is along the Hurricane Cliffs, on the Shivwits Plateau. (The Hurricane Cliffs are the physiographic boundary, created by offset along the Hurricane fault, between the Shivwits and Uinkaret Plateaus.)

Mount Trumbull. Precise locality unknown; 36°24' N, 113°10' W (ca. 1600 m). Mount Trumbull is a wooded volcanic peak on the Shivwits Plateau. Vegetation in the area provides adequate shelter for terrestrial mollusks in plant litter.

Mount Logan. 36°21'38" N, 113°12'44" W (2398 m) (coordinates and altitude for summit). This locality is another volcanic peak on the Shivwits Plateau; listed here based on records cited by Bequaert & Miller (1973).

Localities of the 1991 Grand Canyon Survey

The 1991 Grand Canyon survey of mollusks included localities in the Colorado River corridor and near a major spring (Thunder River) 3 km from the Colorado River. Some supplementary data are added from examinations of localities in 1992.

STUDY AREA AND PARAMETERS OF OBSERVATIONS. As defined herein, the Colorado River corridor includes the lower extremity of tributaries as well as the main stream and its banks. While all localities are in Grand Canyon National Park, those between Lees Ferry and Nankoweap Creek are within the Marble Canyon section of the Colorado River (Fig. 3). With the exception of Thunder River, all productive collecting stations were in wet tributaries in this corridor. Most sites are accessible only from the Colorado River; access to them requires travel by whitewater craft from Lees Ferry (the only place between Glen Canyon Dam and Diamond Creek that can be reached by vehicle) through some of the largest navigable rapids in the world.

Some of the tributary confluences mentioned below are also accessible from trails that descend from the canyon rims—Saddle Canyon, Nankoweap Creek, Little Colorado River, Lava Canyon, Bright Angel Creek, Phantom Creek, Hermit Creek, Shinumo Creek, Tapeats Creek, Deer Creek, Havasu Creek. Of these trails, only Bright Angel Creek can be reached on maintained trails; others are unmaintained trails and wilderness routes requiring both experience in desert hiking and stamina for mountain hiking. The Bright Angel confluence also is the only confluence that can be reached from either the North Rim or the South Rim, via the North Kaibab Trail (from the North Rim) or the South Kaibab or Bright Angel Trails (from the South Rim); this is possible because two suspension footbridges have been built over the Colorado River near Bright Angel Creek.

By convention since 1923, distances upstream and downstream along the Colorado River are measured in miles beginning at Lees Ferry (e.g. Stevens, 1987). The locality descrip-

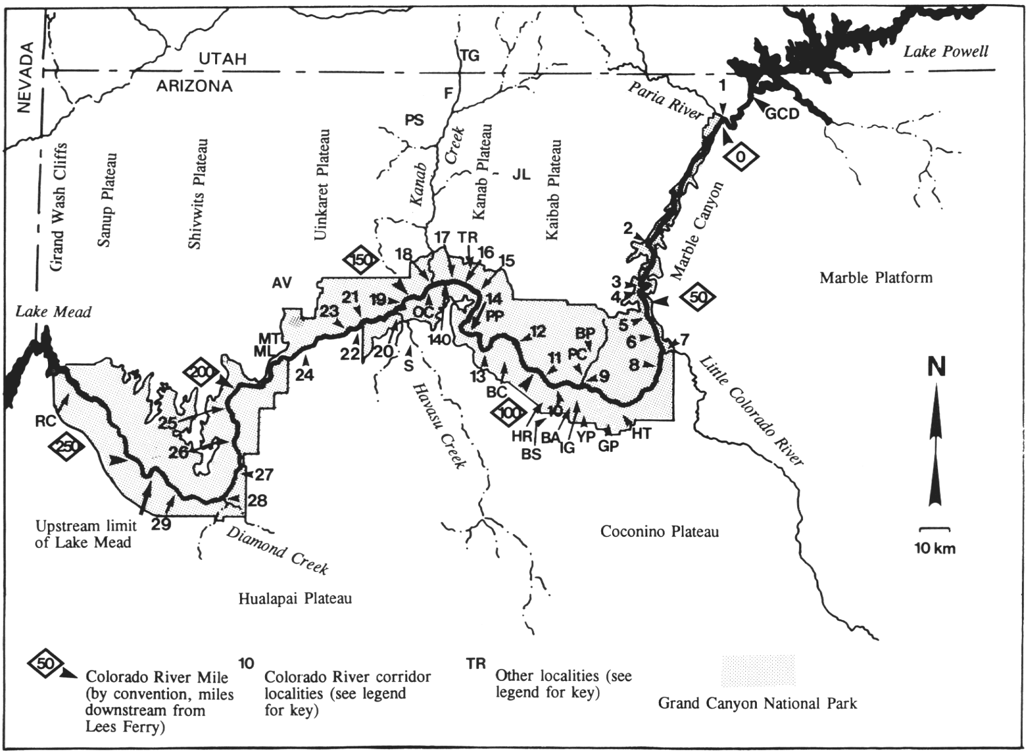

Fig. 3. Molluscan prospecting localities of the Grand Canyon and vicinity, discussed in the present report. These localities include both productive and unproductive localities (as reported herein), combining historical collecting sites (see also Fig. 2 for details of 1906/1909 surveys), sites of the early Colorado River ecological surveys, and the 1991 Colorado River corridor survey. Arrows for river corridor localities are positioned on the side of the river from which tributaries enter. GCD = Glen Canyon Dam.

Colorado River localities:

1	Lees Ferry
2	Vasey's Paradise
3	Buck Farm Canyon
4	Saddle Canyon
5	Nankoweap Canyon
6	Kwagunt Canyon
7	Little Colorado River
8	Lava Canyon, Chuar Creek
9	Bright Angel Creek
10	Hermit Creek
11	Crystal Creek
12	Shinumo Creek
13	Elves Chasm, Royal Arch Creek
14	Blacktail Canyon
15	Stone Creek
16	Tapeats Creek
17	Deer Creek
18	Kanab Creek
19	The Ledges
20	Havasu Creek
21	Tuckup Canyon
22	National Canyon
23	Fern Glen, Fern Glen Canyon
24	Lava Falls Spring
25	Spring Canyon
26	Spring opposite Pumpkin Springs
27	Three Springs Canyon
28	Diamond Creek
29	Bridge Canyon

Other Localities:

140	140 Mile Canyon
AV	Antelope Valley
BA	Bright Angel Trail
BC	Bass Camp and Bass Canyon
BP	Bright Angel Point
BS	Bass Station
F	Fredonia
GP	Grandview Point
HR	Hermit's Rest
HT	Hance Trail
IG	Indian Gardens
JL	Jacob Lake
OC	Olo Canyon
ML	Mount Logan
MT	Mt Trumbull
PC	Phantom Creek
PP	Powell Plateau
PS	Pipe Spring
RC	Rampart Cave
S	Supai
TG	"The Greens"
TR	Thunder River
YP	Yavapai Point

tions include the river mileage (kilometers included by multiplying miles by 1.609) for the confluence of each tributary with the Colorado River, and the side of the river (facing downstream) from which it enters. The geographic coordinates are read from topographic sheets or taken from the Arizona volume of the *National Gazetteer* (U.S. Geological Survey 1987). Township and range lines have not been surveyed in the Grand Canyon. Altitudes are approximate, estimated from topographic sheets or from the strip map of Stevens (1987); readings in feet have been converted to meters throughout this paper by multiplying feet by 0.3048. Both the geographic coordinates and altitudes are for the mouth of the tributary or, if otherwise appropriate, for the exact area of collecting further up the tributary. All Colorado River survey sites are in Coconino County, except Kanab Creek which is on the Coconino-Mohave county boundary, and Diamond Creek which is in Mohave County.

Descriptions are provided both for productive and unproductive localities so as to also review the conditions seen in unproductive areas. The unproductive localities may indicate only non-collection, however; mollusks may be found there by more thorough examination. Conditions are as recorded during the 1991 mollusk survey (July-August), and supplemented by data obtained in May and June 1991 and in May and June 1992. These data provide a baseline against which future studies of diversity and distribution can compare their results.

We point out that tributary water flows and environmental conditions change seasonally, and all tributaries are susceptible to flash flooding at any time of the year. A good example of this was seen in May 1992, when an unusually wet May produced much runoff in the region. At every wet tributary visited, there was evidence of higher water flows some time shortly before inspection of these localities; in some instances some newly deposited sediments were seen. Rain fell each day during this trip; however, rainfalls were not significant enough to initiate large floods or debris flows.

Because flash floods obviously have an impact upon the molluscan communities in tributaries, we provide data on tributary discharge rates when they are known. Except for Bright Angel Creek, where the U.S. Geological Survey maintains a stream gaging station, no data are available for discharge rates at the times that the tributaries were visited in 1991 and 1992. We include with some of the locality descriptions data on the significant hydrologic event of December 1966 (described more fully in the section, "Observations on Aquatic Mollusks"). Storm-generated debris flows of this event certainly devastated the molluscan populations of the affected tributaries, and as a recent historical maximum for discharge rates we include these data as an aspect of ecological conditions in these tributaries. Quantitative data on this event and on more usual discharge rates are from Johnson & Sanderson (1968) and Cooley et al. (1977). Discharge rates are cited in the present paper in m^3/s; to convert to ft^3/s (cfs), multiply the figure by 35.29.

LOCALITIES IN THE COLORADO RIVER CORRIDOR. *Lees Ferry.* Mile 0.0 (Km 0.0), Right; 36°52'03" N, 111°35'40" W (3107 ft, 946 m). Productive. Specimens and data were sent to the authors by the Glen Canyon Environmental Studies office. The GCES sampling site was at the Lees Ferry cobble bar, near which also are deposits of anaerobic black clay. This locality

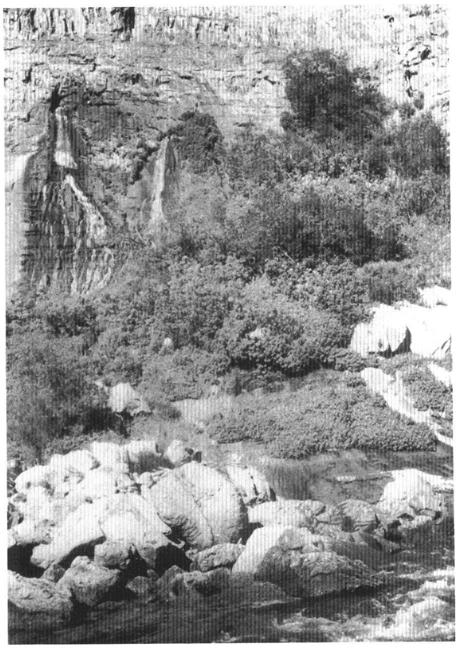

Fig. 4. Vasey's Paradise, Marble Canyon (Colorado River Mile 31.8, Km 51.2); this view from the Colorado River encompasses virtually the entire site. These springs in the Redwall Limestone support a localized community of riparian vegetation. The community hosts the only known population of *Oxyloma haydeni kanabensis* Pilsbry living in natural conditions. Photo 25 July 1991, by E. E. Spamer.

yielded physid gastropods and sphaeriid bivalves. The area between Lees Ferry and Glen Canyon Dam sees moderately heavy recreational use by boaters, but only whitewater craft continue downstream through Marble and Grand Canyons. Species found: *Pisidium variabile, P. walkeri, Physella* sp.

Vasey's Paradise. Mile 31.8 (Km 51.2), Right; 36°29'45" N, 111°51'36" W (2900 ft, 884 m) (Fig. 4). Productive. From the 1991 survey, this was the most diverse and productive river corridor molluscan locality examined. The locality is a richly diverse riparian vegetational community at a perennial spring in the Redwall Limestone (flow ≤0.3 m^3/s; Johnson & Sanderson 1968). Vegetation is primarily redbud trees, poison ivy, and coyote willow, with watercress, cardinal monkey flower, maidenhair ferns, and helleborine orchids (Stevens 1987). Even though this locality is a popular stop on river trips, the steep, wet, slippery ledges and poison ivy discourage much human impact on the site. Visitation is usually restricted to the river edge. Clear water cascades in falls down bare rock walls to ca. 30 m above the river, after which it flows down steep ledges and forms pools <1 m deep along several different runs to the river. It is in this ca. 30-m zone in which mollusks were collected. The substratum of the pools is sand and bedrock, with algae and sometimes silt. This is the only known natural habitat of the federally proposed endangered *Oxyloma haydeni kanabensis* Pilsbry, 1948, the Kanab ambersnail (Succineidae), (see also discussions later in this paper). Species found: *Fossaria obrussa, Physella* sp., *Catinella avara, Oxyloma haydeni kanabensis, Hawaiia minuscula. H. minuscula* was dead collected only.

Buck Farm Canyon. Mile 41.0 (Km 66.0), Right; 36°24'18" N, 111°52'48" W (2900 ft, 884 m). Unproductive. No running water, but several wet seeps were inspected; these were surrounded by moss and vegetation. Channel filled with gravel and cobbles on bedrock. Mature vegetation along the streamcourse indicated no recent, significant flash floods.

Saddle Canyon. Mile 47.0 (Km 75.6), Right; 36°22'00" N, 111°53'32" W (3200 ft, 976 m; locality upstream ca. 0.5-1 km along creek). Productive. A trail ascends from the heavy vegetation of the creek delta up talus slopes, then follows contours up the canyon until the creek is reached. Up in this stretch, until the streamcourse narrows into a defile that is blocked by a waterfall, it is heavily shaded by hackberry, redbud, barberry, and box elder; thistles are common (Stevens 1987). Water flow is slight, across rocks and sand. (The hot, dry part of the trail, ascending, is the locality at which fossil or subfossil succineids were found (see the section in this paper, "Pleistocene-Holocene Mollusks of the Grand Canyon").) Species found: *Catinella avara.*

Nankoweap Creek. Mile 52.1 (Km 83.8), Right; 36°18'18" N, 111°51'28" W (2790 ft, 851 m). Productive. River level was ebbing at the time of collection; many pools were seen in the creek delta, some still with communication to the river. The streamcourse was composed of rocks, gravel, sand, and silt; pools were usually lined with silt. Some streamside vegetation is present, but otherwise the area is exposed to hot sun. Gastropods were found only in the lower end of the creek and in these pools, including one pool that was in communication with the river. Several gastropods were collected by a kayaker from a pool that was in communication with the river, about 50 m upstream from the northern (upstream) end of the delta; some trickles of river water still were passing through the pool. A reconnaissance ca. 2.5 km upstream along Nankoweap Creek revealed many algae- and silt-lined pools along the streamcourse, seeps in the canyon wall, and much vegetation, but no mollusks were seen. The spring further upstream was not reached. There was no evidence of a recent flash flood, although some evidence was seen of recently ebbing streamflow (known normal discharges of <0.09 m^3/s (Johnson & Sanderson 1968); estimated flood discharge in December 1966 storm 84.0 m^3/s (Cooley et al. 1977)). Species found: *Fossaria obrussa, Physella* sp.

Kwagunt Creek. Mile 56.0 (Km 90.1), Right; 36°15'48" N, 111°49'41" W (2770 ft, 844 m). Unproductive. Only a little water in creek, which disappeared into sand and gravel before reaching the river. Delta area widely exposed to hot sun; streamcourse composed mostly of gravel and cobbles. River level was ebbing, and several pools were seen near the river; no stranded snails were seen. In May 1992, this creek was examined for 3 km along its course, beginning ca. 0.5 km from the creek mouth. No mollusks were seen, and potential habitats were similar to those that had been observed in Nankoweap Creek. (Estimated flood discharge in December 1966 storm 33.6 m^3/s; Cooley et al., 1977.)

Little Colorado River. Mile 61.4 (Km 98.8), Left; 36°11'28" N, 111°48'11" W (coordinates for mouth of river) (2700 ft, 823 m). Unproductive. The Little Colorado River drains 62,000 km^2 of semi-arid high desert, with headwaters in mountainous areas of eastern Arizona and westernmost New Mexico. Through much of its course, water usually flows only during spring runoff from higher elevations. In the Grand Canyon, the Little Colorado is perennial; the source is Blue Springs (flow 6.2 m^3/s) 21 km upstream from the confluence with the Colorado River. The Blue Springs discharge is a milky blue due to mineral contents principally of chloride, sodium, calcium, and bicarbonate (Johnson & Sanderson 1968). The streamcourse is silty with cobble bars and boulders. Riparian vegetation is dense in places along the banks. In May 1992, due to regional storms, the Little Colorado River was heavily laden with silt, with a very dark chocolate color.

Lava Canyon, Chuar Creek. Mile 65.5 (Km 105.4), Right; 36°08'23" N, 111°49'01" W (2650 ft, 808 m). Unproductive. Examinations were made from the mouth upstream ca. 0.75 km; very shallow, narrow stream of sun-warmed water. Streamcourse composed mostly of gravel and cobbles, with some silt in small pools. Area vegetation light except in the riparian regime at the confluence with the Colorado River. (Estimated discharge in December 1966 storm 22.4 m^3/s; Cooley et al., 1977.)

Bright Angel Creek. Mile 87.8 (Km 141.3), Right; 36°05'56" N, 112°05'33" W (2425 ft, 740 m). Productive. Bright Angel Creek, near its confluence with the Colorado River, is a heavily used area, the most congested locale inside the Grand Canyon. Here, three trails—two from the South Rim and one from the North Rim—converge on Phantom Ranch and Bright Angel Campground, in the lower 1 km of Bright Angel Creek. Mule riders, hikers, and river travelers all take advantage of the amenities offered by the Fred Harvey Company concession at Phantom Ranch. A mule corral and sewage treatment facility are near the creek. Bright Angel Creek is perennial and of substantial flow (1 m^3/s; record peak discharge, in 1936, was 123 m^3/s; Anderson & White 1979). Vegetation is heavy and diverse, although large numbers of cottonwood trees were removed by a flash flood during the December 1966 storm (112 m^3/s; Cooley et al. 1977). In the area near the campground, the creek banks have been rip-rapped with cobbles and wire mesh to help reduce erosion. Collecting sites in Bright Angel Creek were between the upstream end of the campground and a point ca. 200 m downstream from the lower end of the campground. The creek was examined from this point to its mouth. The water is clear, swift and cool; the substratum is made up of rocks, gravel, sand, and algae, with vegetational debris in the water. Except in the swiftest current, physids were found on everything—on rocks, vegetation, sand, silt, algae (including nestled in the algae), but were found mostly on rocks. Organic enrichment of the water, due to the heavy use of the area, may contribute to the abundance of gastropods.

Bright Angel Creek was examined again in June 1992 between its mouth and the confluence of Phantom Creek 3 km from the Colorado River. Evidence of higher creek flows was seen, the result of recent storms. Few physids were found at any given place along the creek between the campground and the Colorado River, although higher, swift water made examinations more difficult than when the site was visited in 1991. Some collecting stations that were productive in 1991 hosted no snails when examined in 1992.

Upstream from Phantom Ranch, the creek flows through a narrow canyon in the Vishnu Schist; its bed is rocky and sediment accumulations in different places along the banks permit growth of riparian grasses and shrubs. Rocks in the creek host algae, and some moderate soil development is seen in protected, vegetated lengths of the stream bank. Succineid snails were discovered in vegetation along the banks, and physids were seen along the edges of the creek, on submerged bare and algae-covered rocks. On the creek delta (a broad expanse of boulders and cobbles with some vegetation), a single physid was found just 10 m from the mouth of the creek. At the rate of flow of the Colorado River at that time (4 June), the creek flowed abruptly into the river; the river level was not high enough to inundate or develop pools over any significant part of the delta. The Colorado River was silt-laden (a light brown color), the result of runoff from recent storms, and if the observed physid was washed into it death was assured. Species found: *Physella* sp., *Catinella avara*.

Hermit Creek. Mile 95.0 (Km 152.8), Left; 36°05'56" N, 112°12'32" W (2340 ft, 714 m). Productive. Hermit Creek had just experienced a flash flood when visited. Grasses were flattened and light shrubs were disrupted; banks of gravel and silt had been deposited in some areas, and older deposits had been partly dissected. Water was flowing clearly, but became turbid when the bottom was even slightly disturbed. An examination of the sediment and remaining vegetation indicated that the flood waters at the mouth of the creek contained more fine- than coarse-grained material. Only two specimens were found, both dead, on a cobble bar ca. 200 m upstream from the creek mouth; one a physid, the other a succineid. Species found: *Physella* sp., *Catinella avara*.

Crystal Creek. Mile 98.1 (Km 157.8), Right; 36°08'13" N, 112°14'45" W (2300 ft, 701 m). Unproductive. The creek was examined for a distance of ca. 1 km from the Colorado River. The stream banks were heavily overgrown in places, with no evidence of recent flash flood. Known normal discharges are ≤0.056 m^3/s (Johnson & Sanderson 1968). The streamcourse was silty and covered thickly in places by algae. In December, 1966, a catastrophic debris flow generated from the Kaibab Plateau storm, more than four orders of magnitude greater than normal flows, cascaded down Crystal Creek and a major tributary, Dragon Creek (estimated discharge in Crystal Creek drainage 816.6 m^3/s; Cooley et al. 1977), creating a major rapids in the Colorado River. Certainly the entire molluscan population living in the creek was destroyed during this event. But unlike the debris fans at other tributaries that discharged runoff from this storm (see above), the debris fan here is composed mostly of boulders, and high river flows no longer breach habitable portions of the mouth of the creek. Molluscan populations might not have recolonized this tributary from the river.

Shinumo Creek (lower). Mile 108.8 (Km 175.1), Right; 36°14'12" N, 112°20'58" W (2175 ft, 663 m). Productive. The area is a well-sheltered narrow chasm (ca. 10 m wide, from mouth of creek a couple of hundred meters to the first waterfall), with a streamcourse incised in bedrock and filled with cobbles and gravel. Passage is only by wading, and a shallow plunge pool is found a short distance upstream; the waterfall blocks passage along the streamcourse. Moss and vegetation are found on the walls at the plunge pool, and only moss is found in the dark recess beneath the waterfall. The water is pleasantly cool, perennial, with a good rate of flow, thus making the site a popular stop by river travelers. No mollusks were seen here in 1991, but in May 1992 two succineids were found on dead sticks and debris in the only accumulation of silt and vegetation in this defile—an area of just a couple of square meters. The snails no doubt were washed down from above during recent storms, since the higher reach does host ample habitats for these snails (see below). It would seem that molluscan colonization of this site is impossible because the narrow defile offers no protection from flash floods, inadequate nutrient resources, and because it is heavily used by people who are forced to wade in the stream while there. (Estimated discharge from the December 1966 storm 46.5 m^3/s; Cooley et al. 1977.) Species found: *Catinella avara*.

Shinumo Creek (locality upstream). 36°14'15" N, 112°20'58" W (2250 ft, 686 m; locality ca. 0.5 km upstream from mouth of creek). Productive. The locality was reached along the lower route of North Bass Trail, which passes through the first saddle in the ridge that forms the divide between the Colorado River and Shinumo Creek. The trail then drops to the bed of Shinumo Creek, where the channel is filled mostly with gravel and cobbles. Streamside vegetation is riparian and patchy. The collecting station was on the eastern side of the creek just upstream of the place where the trail reaches the creek. Specimens were collected alongside the stream in the shady shelter of a stand of *Equisetum*. (During the 1906 and 1909 surveys, Pilsbry and colleagues probably followed the higher trail that crosses the next higher saddle and meets Shinumo Creek further upstream.) Species found: *Catinella avara*.

Elves Chasm, Royal Arch Creek. Mile 116.6 (Km 187.6), Left; 36°11'47" N, 112°27'00" W (2300 ft, 702 m). Productive. The area is not heavily vegetated, and there are large boulders and travertine-mantled talus slopes. Boulders of travertine and travertine-cemented talus litter the drainage. The creek flows down smooth chutes, eroded in bedrock, from pool to pool during its descent to the river. Known normal discharges are ≤0.007 m^3/s (Johnson & Sanderson 1968). Elves Chasm is a grotto at the base of a waterfall, with a plunge pool ca. 1.5 m deep. There, moss covers darkened areas of rock, particularly beneath and behind the overhanging chocks that create the waterfall. The flow of water is small, but the flow is swift down chutes between pools. Physids were found abundantly on either side of the air-water interface on the walls of the plunge pool; they were found both in sunlight and in dark shade of the overhang. Disturbance of the bottom by visitors apparently discourages habitation of physids even in the shallower parts of the plunge pool. Along the descent to the river, physids inhabited silt-lined pools and the algae-covered sides of chutes. Even though the area is heavily visited by river travelers, their impact is not great along the chutes and pools because the usual access route bypasses them. Only in the plunge pool is there frequent contact between people and snails. Unlike the Shinumo Creek plunge pool area, however, adverse conditions here apparently are not significant enough to eliminate the molluscan colony. One dried bedrock pool, lined with silt, contained the remains of a large number of stranded physids. The shells were not clustered at the bottom, suggesting that they may have died due to solar heating of the water rather than from a water level lowered by evaporation.

Elves Chasm was visited in May 1992, shortly after storms caused a flash flood in Royal Arch Creek. Grasses in the lower end of the tributary were flattened, but no significant amounts of sediment were seen. The physid population in the plunge pool and along the chutes and pools to the river was absent, nor were stranded snails seen in drying and dried pools. Only in the final 10-30 m of the creek, below the chutes and out onto the small debris fan, were physids found in small numbers. Carothers & Minckley (1981) reported finding unidentified specimens of Lymnaeidae at Elves Chasm, but no further data are available. Species found: *Physella* sp.

Blacktail Canyon. Mile 120.1 (Km 193.2), Right; 36°14'24" N, 112°28'17" W (2090 ft, 637 m). Productive. This tributary is a dark, narrow defile incised in bedrock. Water flow was very shallow and slow, with nearly stagnant pools. Substratum of the streamcourse was mostly of silt and gravel. Species found: *Physella* sp.

Stone Creek. Mile 131.8 (Km 212.1), Right; 36°20'48" N, 112°27'13" W (1975 ft, 602 m). Unproductive. Vegetation was heavy in this tributary, with much sawgrass (*Cladium californicum*) and small stands of *Equisetum*. No mollusks were seen in the water or at the waterfall, where the plunge pool is shallow. Known normal discharges are ≤0.008 m^3/s (Johnson & Sanderson 1968). The area between the Colorado River and the waterfall is used moderately by river travelers.

Tapeats Creek (mouth). Mile 133.7 (Km 215.1), Right; 36°22'14" N, 112°28'07" W (1950 ft, 594 m). Unproductive. The substratum at the creek mouth is largely sand and gravel, and the stream flows rather swiftly. Known normal discharges are ≤7.9 m^3/s (Johnson & Sanderson 1968). No habitat suitable for aquatic gastropods was seen. (See discussions under Thunder River, later in this paper, for specimens collected further up Tapeats Creek.) (Estimated discharge from December 1966 storm 11.2 m^3/s; Cooley et al. 1977.)

Deer Creek. Mile 136.1 (Km 219.0), Right; 36°23'17" N, 112°30'29" W (1940 ft, 591 m). Productive. During visits in 1991 and 1992, mollusks (dead or alive) were not seen in the confluence area below the waterfall. But Carothers & Minckley (1981) reported finding unidentified specimens of Physidae at Deer Creek. Presumably, the occurrence is in the upper part of the creek, not near the river, but no further data are available.

Deer Creek plunges as a waterfall virtually into the Colorado River. A well-developed plunge pool is at the base of the fall, and due to the flow of water cascading from above, access into the pool is limited. Known normal discharges are ≤0.23 m^3/s (Johnson & Sanderson 1968). Along the run between the pool and the river, no suitable molluscan habitat was seen. A popular scenic spot, the area is heavily visited by river travelers. A trail ascends the talus to reach the narrow defile of Deer Creek, then proceeds along bedrock until it reaches the stream, where the area is vegetated and some suitable molluscan habitats are available. Above here is a broad valley in which suitable habitats are probable, particularly at Deer Spring. (Estimated discharge from December 1966 storm 8.4 m^3/s; Cooley et al. 1977.)

140 Mile Canyon. Mile 140.0 (Km 225.3), Left; 36°23'49"N, 112°33'59"W (1900 ft, 580 m). Productive. T. Martin (pers. comm. 1991, 1992) has reported seeing aquatic snails in a pool on the debris fan of this tributary, above the controlled high-water level of the Colorado River. Not visited by the senior author, and no specimens available at the time this is written.

Kanab Creek. Mile 143.4 (Km 230.7), Right; 36°23'32" N, 112°37'45" W (1880 ft, 573 m), on the Coconino-Mohave county boundary. Productive. At the time of visitation, Kanab Creek was a slow, shallow stream. Known normal discharges are ≤0.11 m^3/s (Johnson & Sanderson 1968). The level of the Colorado River was somewhat high, as an algae strand in Kanab Creek was 10-15 cm below the water level. The creek is a significant regional drainage, with headwaters in Utah; it is geomorphologically mature, with a mostly gentle grade throughout its length. The streamcourse at the mouth was filled with gravel and rocks. Vegetational cover was relatively light except for dense stands near the confluence. No mollusks were seen for a distance of ca. 0.5 km upstream from the Colorado, where a single pool 1 m deep and about 4 x 5 m in area, isolated from the main flow of Kanab Creek, was filled with hundreds of mature physids. The pool bottom was lined with silt and algae; it was like many other uninhabited pools seen in other tributaries, and the population in it may have been in a critical situation. The pool was exposed to direct sunlight, but since the water temperature was pleasant there was some subsurface communication with the creek through the gravel. A nearby, damp, silt-lined pool had no stranded snails. (No known significant discharge from December 1966 storm.) Species found: *Physella* sp.

Olo Canyon. Mile 145.6 (Km 234.3), Left; 36°22'14"N, 112°38'53"W (1850 ft, 564 m), Left. Productive. T. Martin (pers. comm. 1992) has reported seeing aquatic snails at this tributary. Not visited by the senior author, and no specimens available at the time this is written.

The Ledges. Mile 151.5 (Km 243.8), Right; 36°20'55" N, 112°43'25" W (1825 ft, 556 m). Unproductive. Seep spring in the Muav Limestone; some vegetation around seep. Area very hot in sunlight.

Havasu Creek. Mile 156.8 (Km 252.3), Left; 36°18'28" N, 112°45'40" W (1825 ft, 556 m). Productive. Havasu Creek is a mineralized stream that deposits significant and beautiful accumulations of travertine along its course. The water was silty, with accumulations of white calcium carbonate in quiet pools. Water flow is swift between pools. Some of the pools are very deep. Known normal discharges are ≤1.86 m^3/s (Johnson & Sanderson 1968). The substratum, where sediment accumulates along the creek, ranges from gravel to sand to silty carbonate muck. The area is very heavily visited by river travelers and to a lesser extent by hikers who descend Havasu Canyon. Organic enrichment of the water is due to the heavy use of the area as well as from the community of Supai, in the Havasupai Indian Reservation further up the creek. Physids were reported in Havasu Creek by Carothers & Minckley (1981), but during three visits in 1991 the senior author of the present paper saw no mollusks in the lower 1 km of the tributary; and dried pools showed no evidence of stranded snails. The creek experienced a significant flash flood in September 1990, which destroyed most of the vegetation along the creek. The flood may have destroyed the molluscan population, too. Since the mouth of Havasu Creek has no emergent debris fan, due to the narrow channel and swift current of the Colorado River here, there is little likelihood for redeposition of aquatic mollusks that have been flushed out from tributaries upstream. Instead, recolonization of this creek may initiate from populations that live in many suitable environments further up in the canyon of Havasu Creek.

In May 1992, Havasu Creek was examined at a locality 2 km up from its mouth. A recent flash flood had deposited small amounts of silt along the banks of the creek. At this locality (approximate coordinates 36°17'30"N, 112°44'45"W), a single dead physid snail was seen on moist mud left in a bedrock depression at streamside, corroborating the existence of these snails further upstream. Species found: *Physella* sp.

Tuckup Canyon. Mile 164.5 (Km 264.7), Right; 36°16'47" N, 112°52'30" W (1750 ft, 534 m). Productive. Shallow pools with almost no running water were seen to contain a small number of physids. The lower end of the tributary is a narrow defile incised in bedrock; the substratum of the streamcourse is bedrock, gravel, and sand, although some pools are lined with silt. Specimens appeared to have been redeposited from habitats further upstream, perhaps by a flash flood. Species found: *Physella* sp.

National Canyon. Mile 166.4 (267.7), Left; 36°15'24" N, 112°53'29" W (1740 ft, 530 m). Unproductive. There had been a flash flood in National Canyon a couple of weeks before visited during the 1991 survey. Water was found in the streamcourse ca. 0.5 km upstream from the mouth of the canyon. The substratum was largely gravel and rocks, and pools were filled with gravel and sand, sometimes with silt. Some pools were clogged with *Cladophora*. The streamcourse was followed as far as the large chockstone ca. 0.8 km from the mouth. National

Canyon is a popular place visited by river travelers. When this locality was visited in May 1992, water flow in the creek was somewhat higher than when seen during the 1991 visit, but otherwise all conditions remained essentially the same.

Fern Glen, Fern Glen Canyon. Mile 168.0 (Km 270.3), Right; 36°15'35" N, 112°55'05" W (1740 ft, 530 m). Unproductive. Virtually no water was seen in this usually wet tributary with mineralized water. The spring (not visited) is 1 km up the tributary, in the Muav Limestone; there, maidenhair fern dominates the vegetational community (L. E. Stevens, pers. comm.). A few pools were clogged with algae, and there were silt-lined pools that usually are favored by physids; but no snails were seen. This is a popular locality to river travelers.

Lava Falls Spring. Mile 179.4 (Km 288.6), Left, at the bottom of Lava Falls Rapids; 36°11'51" N, 113°05'00" W (1670 ft, 509 m). Productive. This warm spring and marsh is protected from visitation by dense stands of sawgrass (*Cladium californicum*). Known normal discharges are ≤0.42 m^3/s (Johnson & Sanderson 1968). Large, still pools in direct sunlight are surrounded by vegetation; the substratum is sand and silt, with algae and vegetational debris. Small physids were found in abundance at a depth of 5-10 cm in areas of very slight current. Most of the specimens were found dead; their shells, bleached white, were quite malleable. A few succineids also were found beneath a monkey flower at this locality. Species found: *Physella* sp., *Catinella avara.*

Spring Canyon. Mile 204.3 (Km 328.7), Right; 36°01'N 113°21'W (1500 ft, 458 m). Productive. The lower end of the canyon is heavily overgrown, watered by a spring in the Bright Angel Shale not far from the Colorado River; the stream is shallow, with a substratum of cobbles and gravel. The stream disappeared into the gravel upstream from the river. This locality was visited twice during the 1991 reconnaissance, and an attempt was made to reach the spring pour-out. Dense vegetation was impassable near the pour-out. No aquatic mollusks were seen anywhere along the streamcourse. But at the limit of accessibility there was a small cascade (<0.5 m) of water (one of two cascades in the area, the other only heard). Sifting of the silt below this cascade resulted in a collection of *Hawaiia minuscula* shells, all from a plot <0.3 m^2 in size. During the 1991 survey, this was the only locality other than Vasey's Paradise that yielded this species. Species found: *Hawaiia minuscula.*

Unnamed Spring Opposite Pumpkin Springs. Mile 212.9 (Km 342.6), Right; 35°55'00" N, 113°20'08" W (1600 ft, 488 m). Unproductive. A small, dripping seep in shade was at the limit of accessibility up the drainage, where sawgrass (*Cladium californicum*) and moss was in abundance, and minor accumulations of silt were found on small ledges and under stones. No mollusks were found near the water or in the vegetation. (Note: Pumpkin Springs is a small, travertine-mantled pool alongside the Colorado River, left bank, in an area of exposed bedrock ledges; the water is warm (28° C) and has a sulfurous smell.)

Diamond Creek. Mile 225.7 (Km 363.2), Left; 35°45'58" N, 113°22'22" W. Unproductive. Diamond Creek experienced a flash flood the day before it was visited during the 1991 survey; only the area near the mouth was examined. Known normal discharges are ≤0.06 m^3/s (Johnson & Sanderson 1968). This is a principal regional drainage, and its grade is geomorphologically mature. The substratum of the streamcourse is mostly sand and gravel. No suitable molluscan habitats were seen in the examined area.

OTHER LOCALITY RECORDS IN THE RIVER CORRIDOR. Carothers & Minckley (1981) reported the results of investigations at several localities that were not visited during the 1991 survey. Among these localities, they found mollusks at: *Three Springs Canyon* (Mile 215.7, Km 347.1, Left, Coconino County; mollusks identified only as Physidae, with no further data) and *Bridge Canyon* (Mile 235.2, Km 378.4, Left, Mohave County; Physidae).

Carothers and Minckley (1981) found no mollusks at several localities. Coconino County localities: *Paria River* (Mile 0.0, Km 0.0, Right), *Pipe Creek* (Mile 88.9, Km 143.0, Left), *155 Mile Creek* (Mile 155.7, Km 250.5, Right), *190 1/2 Mile Creek* (Mile 190.3, Km 306.2, Left), *Trail Canyon* (*219 Mile Canyon* of Carothers & Minckley, Mile 219.2, Km 352.7, Right). Mohave County localities: *Travertine Canyon* (Mile 229.0, Km 368.5, Left), *Travertine Falls* (Mile 230.5, Km 370.9, Left), *Bridge City* (Mile 235.2, Km 378.4, Left), or *Spencer Canyon* (Mile 246.0, Km 395.8, Left).

Sonorella reederi Miller 1984, even though from a river corridor locality (west of Rampart Cave, Colorado River Mile 275.0, Km 442.5, Left, Mohave County), is, as we have said, probably an element of the fauna of the Basin and Range province. *Sonorella coloradoensis*, however, is known from throughout the Grand Canyon; it is a species that, normally living in the lower Life Zones, also ranges into the higher Life Zones. It would be of interest to establish the ranges of these two species within the Grand Canyon.

LOCALITIES OUTSIDE OF THE RIVER CORRIDOR. During the 1991 survey, to investigate the biologic community at Thunder River, it was necessary to hike from the Colorado River 3 km up Tapeats Creek. In June 1992, when lower Bright Angel Creek was reinvestigated, a brief survey was also made of lower Phantom Creek, a tributary to Bright Angel Creek 3 km from the Colorado River. Locality descriptions are as follows.

Tapeats Creek (near Thunder River). 36°23'N, 112°27'W (2400 ft, 732 m), not far downstream from Upper Tapeats Campground, where the trail makes the second stream crossing (as one travels up from the Colorado River). Species found: *Catinella avara*.

Thunder River. A perennial stream issuing from Thunder Cave, in the Muav Limestone, one of just three major springs that drain the Kaibab Plateau (Huntoon 1970); tributary to Tapeats Creek (Fig. 5). Geographic data for confluence of Thunder River and Tapeats Creek, a collecting station: 36°23'31" N, 112°27'02" W (2500 ft, 762 m). Geographic data for the collecting station near the base of the waterfall from Thunder Cave: 36°23'42 N, 112°27'35" W (3280 ft, 1000 m). Because the terrain of the Kaibab Plateau is karst, there is virtually no surface water there. Most precipitation evaporates, and the remainder percolates into the carbonate rocks (mostly limestones and dolostones) and follows natural bedding planes and joint structures to springs in the canyon wall (Huntoon 1970). Johnson & Sanderson (1968) reported a discharge of 0.46 m^3/s for Thunder River. Significant amounts of limestone talus litter the drainage of Thunder River, and limestone-derived soils have developed within the riparian zone along its banks—very favorable, sheltered conditions for terrestrial mollusks.

At the confluence with Thunder River, the trail turns northwestward, climbing steeply alongside Thunder River for a short distance before turning away to climb steep talus of the Surprise Valley Landslide, in the semi-arid environs outside the riparian zone. Nearer to the

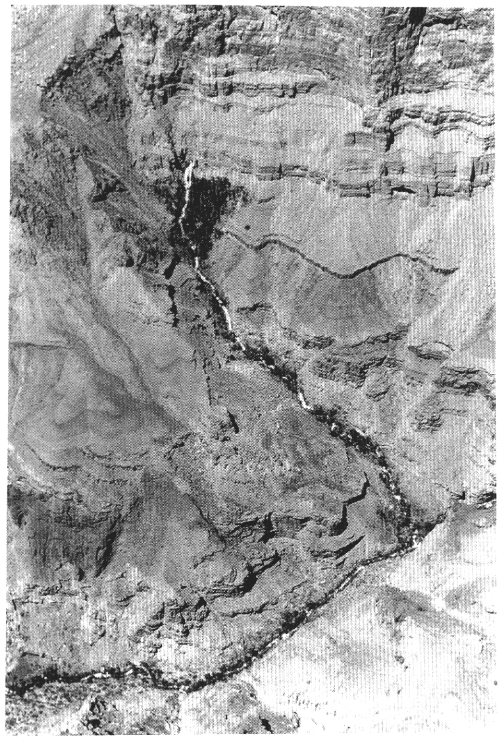

Fig. 5. Thunder River, a tributary to Tapeats Creek below the Kaibab Plateau, hosts a riparian vegetational community in which live molluscan species of mixed ecological Life Zones. It is this site for which new minimum-altitude records are reported herein for several Arizona mollusks. The stream issues from Thunder Cave, in the Muav Limestone. Along the 0.9-km run of Thunder River, altitudes range between 1000 m (base of waterfall, in more densely vegetated area near top of photo) and 762 m (confluence with Tapeats Creek, at right-angle of creek bed near bottom of photo) (altitudes read from topographic sheets and converted from English to metric units). Photo 4 April 1957, courtesy of J. Harvey Butchart via George H. Billingsley. A photo taken by Billingsley on 18 April 1980, from nearly the same vantage point, shows no significant changes to vegetation.

bottom of the falls from Thunder Cave, the trail crosses over to again reach the lush, cooler riparian community. No evidence of snails was seen outside of the riparian zone. Species found: *Cionella lubrica*, *Discus cronkhitei*, *Catinella avara*, *Glyphyalinia indentata*, *Zonitoides arboreus*, *Oreohelix strigosa depressa*, *Sonorella coloradoensis*, *Deroceras laeve*.

Phantom Creek. 36°06'58"N, 112°05'14"W (2760 ft, 841 m). Productive. The lower part of Phantom Creek contains perennial water. The creek here was filled with cobbles and small boulders, with a somewhat steeper gradient than Bright Angel Creek; stream width was ca. 3 m. Some small pools had depths of 50-75 cm. Streamsides were vegetated along small terraces of poorly sorted sediment banked against cliff walls. In the creek, rocks were algae-covered, and in places the bottom was coated by a mineralized substratum, indicating that large floods have not recently come down this tributary. Water flow was moderately swift and clear, with evidence of ebbing flows following recent storms. The water temperature was warmer than that of Bright Angel Creek. Physids were found on rocks and submerged vegetation in the creek, to a depth of 50 cm. Succineids were found on streamside vegetation. No snails were found within ca. 15 m of the mouth of Phantom Creek, where water flow was somewhat more swift and without pools. Species found: *Physella* sp., *Catinella avara.*

GRAND CANYON SURVEY: 1991

Between 24 July and 4 August 1991, the senior author joined a Glen Canyon Environmental Studies research trip on the Colorado River, traveling by whitewater raft 363.2 km from Lees Ferry to Diamond Creek. He examined 28 river corridor localities (Fig. 3) for mollusks, finding them at 14 of these stations. Both aquatic and terrestrial mollusks were sought. Voucher specimens for these surveys are listed in Appendix 2 herein. Constraints of time and logistics precluded employing detailed survey techniques, so the results of the survey provide only a minimal view of diversity and distribution of mollusks in the river corridor. The logical next step in the investigation of Grand Canyon mollusks is to determine more precisely the aspects of their diversity and distribution, and to gain some understanding of their levels of productivity, mechanisms of dispersal, and position in the trophic food web of the inner canyon. The remoteness of the desert inner canyon poses many logistical problems that will make any survey both lengthy and costly. But the area is unique as a protected wilderness with multiple ecological zones that are in communication with riparian communities and nearby plateaus with ecological conditions ranging from cool, wet forests to warmer, dry expanses.

Not all of the visited wet tributaries were seen to contain mollusks. Since both terrestrial and aquatic habitats were examined, much time was spent prospecting promising habitats (Spamer & Bogan in press); sometimes with success, other times not. No quarrying of talus slopes was attempted during the survey, but such prospecting sites abound throughout the inner canyon, along the mainstream of the Colorado River and in tributary canyons.

Observations on Aquatic Mollusks

The physical regime of the Colorado River has changed dramatically since the closure of Glen Canyon Dam in 1963; biological, sedimentological, and hydrological conditions have been altered. Sediment load normally carried by the river is impounded behind the dam, 24.8 km upstream from Lees Ferry. Operations of the hydroelectric powerplant create daily fluctuations in river level, in response to electrical demands in the Southwest. These daily fluctuations have been seen to have serious impact on the stability of beaches along the Colorado River through the Grand Canyon, beaches whose sediment supply has been largely cut off by the dam. The maximum normal discharge from the powerplant is 882 m^3/s due to turbine capacities, thus the Colorado River through the Grand Canyon no longer normally experiences large seasonal discharges from drainages in the upper part of the drainage basin (a historical maximum of 8400 m^3/s, in 1884, is recorded; Anderson & White 1979), and seasonal restructuring of sediment deposits is precluded. Flows exceeding the turbine capacity are in response to extraordinarily high reservoir levels, requiring the use of spillways that bypass the powerplant. This has been necessary only once since closure of the dam, in 1983, when peak flows reached approximately 2700 m^3/s.

The alteration of the riparian regime through the canyon has had impacts on the aquatic organisms of the river and tributaries, as well as the biotic community of the river banks. A baseline understanding of the conditions in the river and along its banks has been under investigation, mostly under the auspices of the Glen Canyon Environmental Studies (GCES, U.S. Bureau of Reclamation) (for summaries, see U.S. National Research Council 1987, U.S. Department of the Interior 1988, Carothers & Brown 1991, and Blinn et al. in press). These studies contribute toward management decisions regarding the operation of the powerplant, and toward decisions regarding resource usage and preservation of the ecosystem of the inner Grand Canyon.

In the Grand Canyon, aquatic mollusks are found in tributaries to the Colorado River; they have not been found in the river itself downstream from Lees Ferry. Their apparent failure to inhabit the river is due to the sediment input from several major tributaries (Paria River, Little Colorado River, and Kanab Creek), which similarly impacts productivity among other aquatic organisms (Carothers & Brown 1991). Their survival in the river reach between Glen Canyon Dam and Lees Ferry is because the river's natural sediment load is impounded behind the dam. Downstream from the dam—and upstream from the first significant input of sediment, the Paria River—the water is clear and cold. Fish, and invertebrate food sources for them, have been artificially stocked in the Lees Ferry fishery.

Below Lees Ferry, aquatic mollusks survive virtually only in wet tributaries, including the "tidal zone" at tributary mouths. The mechanism of dispersal of these animals is largely unknown, yet they proliferate in streams and at springs. In the Colorado River corridor, dispersal may be largely effected by downstream transport of eggs and individuals. Due to daily fluctuations of river level, tributary mouths are usually flooded daily. Such frequency, distinctly different from the seasonal floods of the predam river regime, elevates the probability of washing eggs and individuals out into the river. If then they survive to be washed during daily "flood" flows into tributary mouths further downstream, they are able to colonize these tributaries or interbreed with populations already living there. Empirical observations that suggest this mechanism of dispersal have been made at Nankoweap Creek. There, *Physella* (and a single specimen of *Fossaria*) were taken from pools in—and just upstream from—the delta of Nankoweap Creek, stranded by ebbing river waters. But it is evident that mollusks deposited here move up into the creek above the high water zone: mollusks were found in the lower ca. 200 m of the tributary. However, examinations along Nankoweap Creek for a distance of ca. 2 km from its mouth yielded no mollusks.

The impact of side-canyon flash floods is of unknown significance to molluscan colonization and productivity. Since the methods of molluscan distribution are not clearly known, it is difficult to evaluate the impact of habitat scouring and reestablishment of populations (either from upstream in the tributary, or from transplanted individuals transported by the Colorado River). It is clear, though, that flash floods can clear out established populations (as indicated by comparison of 1991 and 1992 observations at Bright Angel Creek and Elves Chasm, and by implications of the observations made at Crystal Creek and Havasu Creek).

To cite an extreme example of tributary flash flooding in historical times, we may look to December 1966, when a large winter storm dropped ca. 360 mm of rain on the Kaibab Plateau. Flash floods and debris flows cascaded down several major tributaries in eastern Grand Canyon. The study of the effects of this storm by Cooley et al. (1977) presents useful data on the physical alteration of stream channels and sedimentation in some of the tributaries mentioned in the present report. The floods were calculated to be on the order of a 100-year event by discharge rate, but the length of the time the streams were in flood, ca. 3 days, was determined to be unusually long. Calculated discharge rates from this storm have been noted in the appropriate locality descriptions in the present paper. Presumably, if molluscan populations were present in these tributaries in December 1966, the runoff eliminated or decimated them. The enlargement and reorganization of debris fans at the tributary mouths affects how the river will flood these tributary mouths, thus molluscan recolonization from river-transported individuals—if this is a viable mechanism of colonization—may be impossible until the river (or a later tributary flood) reorganizes the debris fan.

By far the most abundant and most diverse of aquatic mollusks in the Grand Canyon are the Physidae. Historically, they have been collected from spring areas within the eastern Grand Canyon (see previously in this paper). Along the Colorado River they are seen abundantly upstream from Lees Ferry, and in tributary mouths downstream from Lees Ferry. Within tributaries, their ranges are at this time unknown, although in the case of Garden Creek, a tributary of Pipe Creek, they are known from the source spring at Indian Gardens, along Bright Angel Trail, 5 km from the Colorado River.

The taxonomic diversity of physids is not clearly understood. Even though the collections in the Academy of Natural Sciences of Philadelphia contain specimens identified to many species, the understanding of systematics within the family is in a state of flux; the only recent work is the unpublished dissertation by Te (1978). It appears that many forms have been identified on shell characters alone, thus their identities are somewhat suspect. In the 1991 survey in the Colorado River corridor, nearly 1,000 specimens of *Physella* were collected, and as expected they show much variation in shell form. A preliminary anatomical examination of some of these specimens indicates that they are nonetheless a single species, but just which species is uncertain, depending upon the validity of the species of *Physella* and of taxonomic priority (S.-K. Wu pers. comm. 1992; and see remarks with the Family Physidae in the systematic list later in this paper).

Bivalve records are unavailable for the Colorado River or the immediate Grand Canyon region. The nearest record was that of Pilsbry & Ferris (1911), who reported *Pisidium* sp. in Kanab Creek north of Kanab, Utah. These specimens are ANSP 103316, identified as *P. casertanum* (Poli, 1791). But *Pisidium* was not seen at that locality in a 1991 survey by the U.S. Fish and Wildlife Service, conducted to evaluate the habitat of the proposed endangered Kanab ambersnail, *Oxyloma haydeni kanabensis* Pilsbry, 1948. However, what may be *Corbicula* (i.e. *C. fluminea* (Müller, 1774) (Corbiculidae), the introduced, now-cosmopolitan Asiatic bivalve) was found there (J. L. England pers. comm. 1992). *Corbicula* has not been reported from northern Arizona except for an occurrence near Temple Bar, Lake Mead, in the northwestern extremity of the state in the Basin and Range Province (Bequaert & Miller 1973, as *C. manilensis* (Philippi, 1844), with qualifications on the appropriate specific name; Counts 1991).

The authors were sent seven specimens of Sphaeriidae from samples taken from the Colorado River at Lees Ferry by a Glen Canyon Environmental Studies crew. An examination of the shells showed that at least two species are present, *Pisidium variabile* Prime, 1852, and *P. walkeri* Sterki, 1895. The provenance of the *Pisidium* species is unknown; if they were not naturally transported there, they were included with various species artificially stocked in the fishery below Glen Canyon Dam. At this time, the distribution and level of productivity of these animals within the fishery is unknown.

One shell of *Pisidium variabile* (ANSP 391073) was found gaping but still firmly attached at the hinge. Upon opening the shell, it was discovered that the body was absent, but inside it there were a juvenile of *Physella* sp. (ANSP 391074), a nematode (Nemata undet., ANSP WM4531 (General Invertebrates Collection in the care of the Department of Malacology)), and a small orange-colored seed to which was attached two tiny, but visible, bacterial colonies (ANSP ML4523 (General Invertebrates Collection), determination by H. M. Reiswig, pers. comm. 1992). This provides some insight on the relationship between various invertebrates in the biotic community of this stretch of river. In this case, the nematode apparently took refuge in the shell, capturing and consuming small organic items that passed by.

Observations on Terrestrial Mollusks

Terrestrial mollusks were not seen anywhere in the Colorado River corridor except in tributaries and at two riverside springs—Vasey's Paradise and Lava Falls Spring. A third locality, at Spring Canyon, yielded dead terrestrial shells near a spring a short distance up the tributary. A few localities between tributaries were examined, but limited time precluded expending any effort in quarrying talus for these animals; instead, indirect evidence of their existence (as dead shells) was sought, but none were found. The absence of terrestrial mollusks along the Colorado River may well be due to non-collection, and dedicated efforts will be necessary to search there for these animals. Pilsbry & Ferriss's (1911) records of *Sonorella* in the canyons of Shinumo and White Creeks serve as verification of the existence of these animals in areas conjoining the river corridor.

From the 1991 survey, terrestrial forms were found most abundantly at Vasey's Paradise and Thunder River. Both of these localities are of a kind infrequently met in the otherwise semi-arid interior of the Grand Canyon. Beside spring pour-outs and perennial streams there are richly diverse vegetational communities, producing food sources and protection for many animals. Vasey's Paradise (Fig. 4) is areally very restricted since the spring is in the canyon wall just above the Colorado River; only alongside the short cascades are there riparian plants, and outside of this small community the vegetation is that of the semi-arid desert inner canyon. Even though this beautiful community is at riverside and beckons every group of river travelers, presenting a potential for heavy human use of the area, access to it is discouraged by wet, slippery ledges and dense stands of poison ivy. Thunder River (Fig. 5), just 0.9 km long, is a tributary of Tapeats Creek 3 km from the Colorado River; it is accessible only by steep wilderness trails, either up from the Colorado River or down from the North Rim of the canyon.

In 1991, three species of terrestrial mollusk were found during a 1-1/2 hour collecting stop at Vasey's Paradise. Not all of the locality was accessible at the time it was visited, but a sizeable section of it was examined, in the zone between the Colorado River and the sheer wall at the base of the waterfalls (approximately the entire area shown in Fig. 4). The terrestrial mollusks were found above the Colorado River high water zone, but whether the daily fluctuations of the river have indirect impacts on these animals is unknown, for lack of previous data on molluscan distributions and needs for productivity. The only noticeable aspect of distribution of terrestrial mollusks at this locality, aside from relationship to vegetation, was that they favored the vegetation immediately adjacent to the sides of the several cascades, with less importance paid to exposure to the sun.

Among the molluscan species at Vasey's Paradise is the only known population of *Oxyloma haydeni kanabensis* Pilsbry, 1948, outside of the type locality (Kanab, Utah, 89 km to the northwest). Its identity was still unclear at the time Spamer & Bogan (in press) submitted their survey report on river corridor mollusks; it was identified therein as *Oxyloma* cf. *haydeni*. We are indebted to S.-K. Wu (pers. comm. 1992) for refining the identification. The presence of this snail at Vasey's Paradise is significant for two reasons. It is the first record of *Oxyloma* in the Recent of Arizona; previously it had been known in the state only in fossil deposits (Bequaert & Miller 1973, Mead 1991). Secondly, the subspecies has been proposed as endangered, by the U.S. Fish and Wildlife Service (England 1991a, b). The habitat at the type locality north of Kanab, Utah, has been cited as a candidate for designation as a "critical habitat," due to recent modifications of land use (England 1991b). Thus, at this time the Vasey's Paradise colony of *O. h. kanabensis* is the only one known in a natural setting. This locality is 12 km upstream from the formerly proposed Marble Canyon dam site.

The historical collections from the Grand Canyon region contain abundant terrestrial forms, mostly *Oreohelix* and *Sonorella*. The greater Grand Canyon region constitutes part of the southwestern range limit for *O. strigosa*, and it is the northern range limit for *Sonorella* (Bequaert & Miller 1973). The large expanses of limestone cliffs and talus provide ideal conditions for the survival of these groups throughout the Grand Canyon, although the hardy *Sonorella* can also be found in the talus even of metamorphic rocks (e.g. Pilsbry & Ferriss 1911; and see Appendix 1). Other terrestrial forms, like the succineids, have been observed throughout the canyon wherever appropriate conditions of moisture and vegetation occur.

The special biotic community at Thunder River survives as a direct result of its significant water supply. It is attractive to plants and animals both of the more temperate zones of the canyon rim and the more arid zones of the inner canyon. The biotic community at Thunder River is a special one in the Grand Canyon. While microcommunities of riparian and some temperate-zone plants occur at many springs in the semi-arid desert inner canyon, the community at Thunder River is more spread out. The waterfall and steeply cascading stream add spray to the air along the run of Thunder River. This seems to increase the water's benefit to area vegetation by reducing the rate of evapotranspiration, at a rate more than that enjoyed by the riparian communities found along less steeply inclined perennial streams. During the 1991 survey, only about an hour of actual collecting time was possible at Thunder River, divided between the confluence area with Tapeats Creek and the area near the base of the waterfall from Thunder Cave. But despite this limitation, several significant findings were made from the Thunder River collections.

Situated 1200-1500 m below the North Rim of the Grand Canyon, Thunder River's special riparian community of shady plants, and the presence of limestone walls and talus, make it an ideal habitat for many forms of terrestrial mollusk. Eight species (seven families) of terrestrial mollusk were found, all of them previously known from localities on the forested Kaibab Plateau, some 8 km distant. The species include the first record of the slug *Deroceras laeve* from inside the Grand Canyon, which also had before been unknown in Arizona from altitudes as low as the confluence of Thunder River and

Tapeats Creek, 762 m.

The depression of altitudinal occurrence for several mollusks of the Kaibab Plateau shows that they disperse into protective riparian communities inside environmental areas that are otherwise inhospitable. It is outwardly contrary to Pilsbry & Ferriss's (1910) observation that mollusks of higher Life Zones do not tend to distribute into lower zones (see also in the next section, on Life Zones). However, this does corroborate Pilsbry & Ferriss's (1910) deduction that molluscan habitation is more a function of protective cover than of conditions of temperature, humidity, and vegetational type: at Thunder River, the protection of shade and moist soil, as well as talus, encourages molluscan colonization when individuals are introduced from the Kaibab Plateau.

The molluscan community at Thunder River also is a model for (still undemonstrated) colonization of the banks of the Colorado River by terrestrial mollusks. Many habitats in the post-dam river regime provide adequate cover and resources for some terrestrial forms, particularly those that are calciphilous. The danger of flood scouring and drowning no longer is present due to moderated water flows from Glen Canyon Dam. Changes in vegetational cover also provide denser, more permanent protected areas.

LIFE ZONES, MOLLUSCAN DISTRIBUTIONS, AND COLLECTING BIASES IN THE GRAND CANYON

In 1889, C. Hart Merriam traveled through northern Arizona in the area around and north of the San Francisco Peaks, and into the Grand Canyon, where he studied the distribution of vegetation as a function of altitude and local climate. The distance between the Peaks (the highest altitude in Arizona, 3,554 m) and the bottom of the eastern part of the Grand Canyon (altitude ca. 780 m) is a linear distance of just 85 km. From these studies Merriam derived the concept of the Life Zone and published it in 1890.

Life Zones of the Grand Canyon Region

Four Life Zones occur in the Grand Canyon region: Lower Sonoran, Upper Sonoran, Transition, and Boreal. The Canadian Zone is barely represented on the summit of the Kaibab Plateau; pragmatically, the vegetation there is included in the Boreal Zone. This area has apparently not been investigated for mollusks, and for lack of data we do not include a Canadian Zone in discussions of molluscan distributions in the Grand Canyon region. Following, we briefly describe the ecological characteristics of the Life Zones of the Grand Canyon (data from Lowe 1964 and Brown et al. 1987). Altitudinal data are as given by Brown et al. (1987), but the boundaries between Life Zones, although distinct, occur at various altitudes due to slope aspects and localized climatological conditions.

LOWER SONORAN ZONE. <1200 m. Characterized by hot-desert plant species; winter nighttime temperature as low as 0° C (rarely lower), summer daytime temperature usually >32° C (occasionally >44° C); annual precipitation usually <254 mm, falling mostly as rain during summer thunderstorms. The records for Phantom Ranch (altitude 783 m, near the mouth of Bright Angel Creek), between 1935 and 1972, are -23° and 49° C, and greatest daily precipitation of 68.3 mm (Sellers & Hill 1974).

UPPER SONORAN ZONE. 1200-2100 m. Characterized regionally by different associations of vegetation that depend upon altitude, soil type, slope aspect, and localized climatological conditions: pinyon-juniper woodland (the dominant kind in the Grand Canyon region), mountain scrub and chaparral, sagebrush, blackbrush, and desert grassland; winter nighttime temperatures as low as -7° to 0° C, depending upon altitude; summer daytime temperatures 27° to >38° C; annual precipitation usually 254-381 mm, falling mostly as rain.

TRANSITION ZONE. 2100-2500 m. Dominated by *Pinus ponderosa*, the ponderosa or western yellow pine; slope aspect and localized climatological conditions permit Transition Zone species to grow at lower elevations in the canyon; winter nighttime temperatures are generally >7° C, and summer daytime temperatures are usually 18°-29° C; annual precipitation usually 381-635 mm, falling both as rain and snow. Records for three meteorological stations in the Transition Zone are as follows (Sellers 1960, Sellers & Hill 1974): Grand Canyon National Park (at Grand Canyon Village, altitude 2125 m, for records 1904-1972), -29° to 37° C, greatest daily precipitation 101 mm; Bright Angel Ranger Station (North Rim, altitude 2560 m, for records 1931-1972), -32° to 33° C, greatest daily precipitation 128 mm; Jacob Lake (altitude 2414 m, for records 1948-1972), -29° to 35° C, greatest daily precipitation 63.5 mm.

BOREAL ZONE. 2500-2800 m. Characterized chiefly by spruce and fir, with ponderosa pine occurring in favorable conditions on slopes with southern aspect; nighttime winter temperatures reach -29° C (with daytime high temperatures usually ~0°), and daytime summer temperatures usually 18°-24° C; annual precipitation is usually 635 to >762 mm, falling mostly as snow (snowpack accumulations usually 3.8 m) but with summer rains accounting for some of it.

Distributions and Biases in the Grand Canyon

Pilsbry & Ferriss (1910) first demonstrated that the distribution of molluscan faunas are not particularly well stratified, with respect to Life Zones. But there and in later publications, Pilsbry never actually itemized the distribution of molluscan faunas by Life Zone, only sometimes giving altitudinal information. In the Grand Canyon region, there are very well defined Life Zones, and the Grand Canyon collections of Pilsbry and colleagues provide precise information on the occurrences of mollusks in them. We have examined these collections and use them as empirical evidence of the conclusions of Pilsbry and others.

When Pilsbry & Ferriss (1911) published the results of their investigations in the Grand Canyon region, they took little notice of the remarkable contrasts between Life Zones. They had already addressed the relationships between mollusks and environment (Pilsbry & Ferriss 1910), as seen in the Chiricahua Mountains that rise above the desert of southeastern Arizona. Their observations are still held as valid interpretations of various external effects on molluscan distribution. They postulated that the mountainous "islands" are refugia, the snail populations being the descendants of populations that freely roamed in a more hospitable climate during late Cenozoic time. The larger kinds of snails were observed to be more restricted in distribution than smaller ones, probably because small forms are more easily transported by winds. The authors interpreted isolationism of colonies within a single mountain range as due to the ever-increasing erosion of canyon drainages, which act as barriers to migration. But they observed that aridity *per se* is not a determining factor in the distribution of the mollusks; rather, the lack of suitable cover, particularly rocks and especially limestone talus, is a distinctively determinate factor. They also specifically excluded environment (vegetational community, temperature, precipitation, etc.) as a primary effect on speciation; they instead referred speciation to the propagation of mutations within isolated colonies.

By inspection of Pilsbry's many publications, it is clear that he adopted the Life Zone concepts first presented by Merriam (1890). Pilsbry & Ferriss (1910) referred to molluscan distributions in Canadian, Alpine, Transition, Upper Sonoran, and Lower Sonoran zones; as noted, from studies in the Chiricahua Mountains of southern Arizona. They observed that the snails of higher zones are restricted to those zones, while snails of the lower zones range more freely into the higher zones. This was attributed to the distribution of plants, but floral distributions are responses to climatic conditions. It was to these initial observations that these authors referred in later studies of Southwestern molluscan distributions.

The Grand Canyon was seen by Pilsbry & Ferriss (1911) to be no barrier to the distribution of most molluscan species, and the present paper further documents this deduction. The exception of *Oreohelix strigosa depressa*, said by Pilsbry & Ferriss (1911) to occur only north of the canyon, has since been found on the southern side, too (Bequaert & Miller 1973). *Oreohelix yavapai* Pilsbry, 1905, however, is virtually restricted to the area south of the Colorado River, having been found only at one locality on the brink of the North Rim (see note below).

The Grand Canyon can also act as a corridor for molluscan distributions. Pilsbry & Ferriss (1911: 176) considered *Sonorella* "the sole Upper Austral genus" in the canyon, inhabiting "both sides of the river, up to and even upon the rim." The distribution of physids along the Colorado River also is an indication of the canyon as a corridor for distribution, although in this case due to aquatic transportation downstream. We can see the invasion of terrestrial mollusks into the Grand Canyon from lower elevations on the west, an advance of lower-Life Zone biota more toward a higher Life Zone; and a distribution of aquatic mollusks downstream between suitable side-canyon habitats.

Bequaert & Miller (1973) recognized four subspecies of *O. yavapai*, listing for the Grand Canyon area (on the south side only, citing Pilsbry & Ferriss 1911) *O. y. profundorum* Pilsbry

& Ferriss, 1911, and *O. y. extremitatis* Pilsbry & Ferriss, 1911. Bequaert & Miller synonymized *O. y. angelica* Pilsbry & Ferriss, 1911, with *O. y. extremitatis*. It should be noted that the sole record of *O. yavapai* on the North Rim, at Bright Angel Point (ANSP 143597, unpublished), was collected and identified by Pilsbry as *O. y. angelica*.

Pilsbry & Ferriss (1911: 176) considered the entire Grand Canyon malacofauna as characteristic of the Transition Zone, which occurs in the Grand Canyon area principally on the rims and uppermost parts of the canyon walls. They cited the occurrence in the Grand Canyon of "species inhabiting northern Arizona on one or both sides of the canyon or of forms evidently derived from such species." Being in the eastern part of the Grand Canyon in October, what Pilsbry and Ferriss may not have recognized was the incidence of extension of the desert environment from the Basin and Range eastward along the course of the Colorado River, into the heart of the Grand Canyon (see also in Appendix 1). Near the bottom of the Grand Canyon they were in the Lower Sonoran Life Zone, amply reflected by the vegetational community there. The Upper and Lower Sonoran Life Zones are widely distributed in the Basin and Range province of Nevada, southern Arizona and California, and adjacent areas. (The Lower Sonoran Life Zone in the western part of the Grand Canyon is where *Sonorella reederi* Miller, 1984, lives; this species' range upstream in the Colorado River corridor remains unknown (W. B. Miller pers. comm. 1989). It probably is more representative of the Basin and Range fauna than of the Grand Canyon fauna.)

The locations of collecting stations, too, affect interpretations of molluscan distribution. If collecting sites are a function of accessibility, many places inhabited by the small, slowly moving, cremnobate mollusk will be missed by the human collector; this is accentuated among the Grand Canyon's areas of dramatic topographic changes and slope conditions dangerous to people. The relatively arid inner canyon discourages heavy plant growth and the development of humus; the result also is that the erosion of the canyon walls is principally by rockfall and landslide, producing sheer cliffs in more resistant rock formations, and talus-covered slopes in rock formations more susceptible to erosion. The trails that Pilsbry, Ferriss, and Daniels followed in traversing the canyon follow geological faults that, due to preferential erosion along them, permit passage through usually impassable cliffs. In the upper reaches of the canyon walls, trails tend to follow easier grades along slope-forming talus, where collecting also is frequently productive. Further into the canyon, trails follow long, relatively gentle grades across expanses that are covered by scrubby vegetation and desert soils, far from steep talus slopes and protected areas that many land snails favor; and perennial water is never found on such expanses. The journey throughout is punctuated by steep inclines along which access to talus and secluded areas is not usually possible.

Pilsbry & Ferriss (1911: 176) observed that "The most productive horizons in the Grand Canyon are the Kaibab Limestone, which forms the slope immediately below the rim [i.e. the cliff-forming Kaibab Limestone and the talus slope covering the Toroweap Formation, also a limestone, beneath it], and the talus at the foot of the Cross-bed or Coconino Sandstone [beneath the Toroweap Formation], in sheltered recesses where a talus from the overlying limestone terrain has accumulated." This is seen by an examination of the distribution of Pilsbry's and colleagues' collecting stations. These stations are for the most part in the Transition Zone. With respect to geography, Pilsbry, Ferriss, and Daniels made frequent and profitable collections in two areas: 1) near the beginning of their trips, along the South Rim and in the upper part of the canyon in the vicinity of Bass Camp, and 2) in the more shallow, forested canyons incised in the Kaibab Plateau north of the Colorado River. However, collections also were made well inside the canyon, and in various publications where Pilsbry mentioned the Grand Canyon collections (as well as in his field notes; see Appendix 1) he remarked upon finding *Sonorella* in the talus of metamorphosed sandstone in the bottom of the canyon.

It must be pointed out that the "metamorphic rocks" cited by Pilsbry are not the Vishnu Schist and related rocks of the inner canyon; rather, these are the partly metamorphosed sandstones of the Shinumo Sandstone (or Shinumo Quartzite) of the Unkar Group. Rock fragments perhaps of partly metamorphosed Shinumo Sandstone, with epiphragm marks of *Sonorella coloradoensis*, are held in ANSP collections (ANSP 103341); the original label reads, "marks on metamorphic sandstone. White Creek." (Specimens of *S. coloradoensis* from White Creek are ANSP 103246 + A10381C and 103255 + A10381H; the latter dry lot, 103255, from 1.6 km above the confluence of White Creek with Shinumo Creek, contains specimens figured by Pilsbry & Ferriss (1911, pl. 12 figs. 26-28).) The degree of metamorphism of ANSP 103341 resembles the Shinumo, but the lithology also resembles the lower part of the Dox Formation, and the stated collecting locality is near the contact between these two strata.

The distribution of mollusks in Life Zones of the Grand Canyon region is empirically shown in Table 4; the data are combined from the historical collections in ANSP and from the 1991 survey. The point distribution indicates no stratification of mollusks by Life Zone. Only lower limits of distribution, as functions of inhospitable environments, are clearly shown. However, some of the lowest altitudinal occurrences of species are plotted from data provided by the 1991 survey along the Colorado River corridor and at Thunder River, from uncharacteristically low altitudes. Before these collections were available, the same plot would have shown for some species indications of restriction to higher altitudes, and more species with lower limits at higher altitudes. We have shown that skewed distributions, while reflecting natural conditions, are due to the presence of collecting sites within extraordinary conditions of cover for the mollusks (such as at Thunder River), which in turn is the direct effect of localized ecology. So, whereas the deduction of cover being more important to mollusks than ecological conditions is generally correct, as first published by Pilsbry & Ferriss (1910), we see that locally different ecological environments, in an otherwise inhospitable terrain, actually encourage colonization.

UPDATED SYSTEMATIC LISTING OF MOLLUSKS OF THE GRAND CANYON REGION

In the following systematically organized lists of molluscan distributions, we treat mollusks of aquatic and terrestrial ecology separately. All localities cited are from Pilsbry & Ferriss's (1911) paper, various brief reports as itemized in the "Previous Work" section of the present paper and supplemented by Bequaert & Miller (1973), the 1991 survey (initially reported in Spamer & Bogan in press) and 1992 supplementary observations, and unpublished specimens in ANSP collections. We indicate previous identifications where they apply to cited references for the Grand Canyon region, and we do not present these lists as comprehensive synonymies. All stations (except Hance Trail, type locality of *Sonorella coloradoensis* and a few localities acknowledged to cited references) are represented by specimens in ANSP collections. The reference to "P. & F. stations" in the locality lists refer to the stations published by Pilsbry & Ferriss (1911), as further refined in the present paper (Table 1). We segregate the localities into occurrence by north or south side of the canyon and, when appropriate, to the Colorado River corridor. Updated catalog numbers for type specimens from the Grand Canyon region are included, since ANSP Department of Malacology cataloging procedures now call for paratype and paralectotype specimens to be split from the holotype or lectotype and receive new numbers; and alcohol-preserved materials receive new numbers in a separate catalog of lots preserved in alcohol.

Virtually all of the historical ANSP material was originally identified by H. A. Pilsbry. Identifications herein reflect later systematic updates of the ANSP collections and largely follow the standards established by Turgeon et al. (1988). We do not present these lists as systematic revisions, should they conflict with various workers' perpectives. Colorado River corridor material was identified by the authors (principally Bogan) or by researchers cited elsewhere in this paper. Comparative material from ANSP collections, used to make the identifications, has been cited by Spamer & Bogan (in press), and a revised listing of voucher material for the GCES-sponsored survey is provided in Appendix 2 herein. All species from the 1991 GCES survey were live collected except *Cionella lubrica, Gastrocopta pellucida, Discus cronkhitei, Hawaiia minuscula,* and *Sonorella coloradoensis*. All mollusks from the Grand Canyon region, held at ANSP, have been cataloged into the computerized database in the Department of Malacology.

Aquatic Mollusks

Aquatic mollusks are represented in the Grand Canyon region by sphaeriid bivalves and, among the gastropods, by planorbids,

Table 4. Altitudinal and Life Zone distributions of terrestrial mollusks of the Grand Canyon region.

Life Zone	Boreal	Transition		Upper Sonoran		Lower Sonoran	
Altitude range (m)[1]	>2438	2134-2438	1829-2134	1524-1829	1219-1524	914-1219	<914
Cochlicopidae							
Cionella lubrica (Müller, 1774)		•	•	•	•	•	•
Pupillidae							
Gastrocopta ashmuni (Sterki, 1898)		•	•				
G. pellucida (Pfeiffer, 1841)		•	•	•		•	
G. pilsbryana (Sterki, 1890)		•	•	•	•		
Pupoides hordacea (Gabb, 1866)				•			
P. nitidulus (Pfeiffer, 1859)				•			
Pupilla hebes (Ancey, 1881)		•	•		•		
P. syngenes (Pilsbry, 1890)		•	•	•	•		
Valloniidae							
Vallonia cyclophorella Sterki, 1892		•	•	•	•	•	•
V. perspectiva Sterki, 1893		•	•	•	•	•	•
Discidae							
Discus cronkhitei (Newcomb, 1865)		•	•			•	•
Succineidae							
Catinella avara (Say, 1824)		•	•	•	•	•	•
Oxyloma haydeni kanabensis Pilsbry, 1948							•
Succinea grosvenorii (Lea, 1864)		•				•	
Helicarionidae							
Euconulus fulvus (Müller, 1774)		•	•	•		•	
Zonitidae							
Hawaiia minuscula (Binney, 1841)		•	•		•		•
Zonitoides arboreus (Say, 1817)		•	•			•	•
Glyphyalinia indentata (Say, 1823)		•	•	•	•	•	•
Vitrinidae							
Vitrina alaskana Dall, 1905		•	•	•			
Limacidae							
Deroceras laeve (Müller, 1774)		•					•
Thysanophoridae							
Thysanophora hornii (Gabb, 1866)						•	•
Microphysula ingersollii (Bland, 1875)		•					
Oreohelicidae							
Oreohelix strigosa depressa (Cockerell, 1890)	•	•	•	•		•	•
O. yavapai Pilsbry, 1905		•		•	•		
Helminthoglyptidae							
Sonorella coloradoensis (Stearns, 1890)		•	•	•	•	•	•
S. reederi Miller, 1984							•

[1]Converted from original plots grouped in 1,000-foot intervals, from <3,000 ft to >8,000 ft, respectively.

physids, and lymnaeids. Many promising localities within the canyon are difficult to reach and remain unexplored malacologically. The absence of records of the Hydrobiidae (Gastropoda) is notable; Hershler & Landye (1988) report this group's occurrence at springs around the Grand Canyon area, but their study area did not include the Grand Canyon itself. The nearest occurrences of hydrobiids to the Grand Canyon are at Grapevine Spring, Mohave County, just west of the Grand Wash Cliffs and north of the Colorado River, and in Washington County, Utah (Landye 1980, Hershler & Landye 1988). Logistical problems of travel to ecologically appropriate locales within the Grand Canyon have thusfar discouraged such explorations of the Grand Canyon. Hydrobiids were not found during the brief reconnaissances conducted at stations on the 1991 survey. A more concerted effort is required to ascertain the existence or absence of these animals in the Grand Canyon.

Class GASTROPODA
Family LYMNAEIDAE

Genus **Fossaria** Westerlund, 1885

Fossaria obrussa (Say, 1825)

LOCALITIES. Colorado River corridor: Vasey's Paradise, Nankoweap Creek. New record of occurrence for the Grand Canyon.

REMARKS. Only two specimens were found during the 1991 survey. Widespread in United States, southern Canada, and northern Mexico (Bequaert & Miller 1973).

Fossaria parva (Lea, 1841)

LOCALITIES. North side: Pipe Spring.

REMARKS. Widespread in Nearctic North America (Bequaert & Miller 1973).

Family PHYSIDAE

REMARKS. The systematic understanding of physids is in a state of flux. Variability of shell characters, and an inadequate understanding of anatomical differences between some taxa within the family, lend uncertainty to the identification of these taxa. The most recent work on physid systematics is the unpublished dissertation by Te (1978), but it does not provide a key to the various taxa.

The following specifically identified specimens of *Physella* are listed from Grand Canyon occurrences as they appear in ANSP collections. The specific identifications mostly are those made by H. A. Pilsbry; they are retained pending future systematic revisions of the family. According to Bequaert & Miller (1973), *Physella* (or *Physa* sensu lato of some authors) is represented in Arizona by *Physella virgata virgata* (Gould, 1855), *Physella virgata bottimeri* (Clench, 1924), and *Physella humerosa* (Gould, 1855); however, the relationship between these species-level taxa remains unclear. Of the species listed below as Grand Canyon regional occurrences, Bequaert & Miller (1973: 202) regard *P. humerosa* as a possible misidentification of *P. virgata*, but neither *P. osculans* nor *P. squalida* are cited; and *P. osculans* also was not cited by Pilsbry & Ferriss (1911). *P. humerosa* is apparently founded upon subfossil specimens (fide S.-K. Wu). (The lectotype of *P. humerosa*, selected by Baker 1964: 155 but not noted by Bequaert & Miller 1973, is ANSP 17279; it is from "Gran Jornado and Pecos River," and see comments in Bequaert & Miller 1973: 203.) But the absence of preserved type bodies precludes a modern definition—thus recognition—of the species. And on the other hand, *P. virgata* is not a recognizable species to still other workers (S.-K. Wu, pers. comm., 1992).

Genus **Physella** Haldeman, 1843

Physella humerosa (Gould, 1855)

LOCALITIES. South side: Indian Gardens.

REMARKS. Bequaert & Miller (1973: 203) comment: "The supposed *P. humerosa* recorded by Pilsbry and Ferriss (1911:198) from Coconino Co. (Indian Gardens on Bright Angel Trail, Grand Canyon of Colorado Riv[.]), should be revised or collected again; they might have been what we are calling *P. virgata bottimeri*."

Physella osculans (Haldeman, 1841)

LOCALITIES. South side: Indian Gardens.

Physella squalida (Morelet, 1851)

LOCALITIES. South side: Indian Gardens.

Physella virgata virgata (Gould, 1855)

LOCALITIES. North side: Pipe Spring.

Physella sp.

LOCALITIES. Colorado River: Lees Ferry. North side: Phantom Creek. Colorado River corridor: Vasey's Paradise, Nankoweap Creek, Bright Angel Creek, Hermit Creek, Elves Chasm, Tapeats Creek, Kanab Creek, Lava Falls Spring, Spring Canyon.

REMARKS. A single species is suggested for the specimens collected during the 1991 survey, based on anatomical characters (S.-K. Wu pers. comm. 1992). However, since some confusion exists with the modern systematic description of physids (see above), these specimens are identified only to genus.

Family PLANORBIDAE

Genus **Gyraulus** Agassiz, 1837

Gyraulus parvus (Say, 1817)

Reported by Pilsbry & Ferriss (1911) as *Planorbis deflectus* (Say *in* Keating, 1824) (= *Gyraulus deflectus*).

LOCALITIES. North side: Fredonia.

REMARKS. Bequaert & Miller (1973: 210) cite Pilsbry & Ferriss's (1911) record in remarks on fossil *Gyraulus deflectus*, a species known in Arizona only from fossils. These specimens (ANSP 103346) are reidentified in ANSP collections as *G. parvus*; Bequaert & Miller (1973: 204-205) do not cite this species from north of the Colorado River.

Class BIVALVIA
Family SPHAERIIDAE

Genus **Pisidium** Pfeiffer, 1821

REMARKS. Specimens were found in fine, black, anaerobic clay near the Lees Ferry cobble bar. These species favor muddy bottoms and can be found in widely different stands of water (Burch 1975). The provenance of the Lees Ferry specimens is unknown; if they are not naturally occurring, they may have been introduced during the development of the fishery between Lees Ferry and Glen Canyon Dam, when a variety of aquatic invertebrates were introduced as fish food, in the late 1960s (Stone & Queenan 1967; Stone & Rathbun 1968, 1969).

Pisidium variabile Prime, 1852

LOCALITIES. Colorado River: Lees Ferry.

REMARKS. This is the first record of the species in the state of Arizona, even though it is cosmopolitan in North America (Burch 1975).

Pisidium walkeri Sterki, 1895

LOCALITIES. Colorado River: Lees Ferry.

REMARKS. This is the first record of the species in this part of Arizona (cf. Bequaert & Miller 1973). It is cosmopolitan in North America (Burch 1975) but is said to be "scarce and usually not abundant in any one place" (Herrington 1962: 51, and quoted by Burch 1975: 41), usually occurring in small lakes and ponds.

Terrestrial Mollusks

Class GASTROPODA
Family COCHLICOPIDAE

Genus **Cionella** Jeffreys, 1830

Cionella lubrica (Müller, 1774)

Reported by Pilsbry & Ferriss (1911) as *Cochlicopa lubrica* (Müller).

LOCALITIES. South side: Seep spring west of Bass Trail; Bright Angel Trail; Indian Gardens; P. & F. station A. North side: Thunder River; P. & F. station 3.

REMARKS. Bequaert & Miller (1973) note that this species is "widespread, 5,700 to 6,000 ft" (1737-1829 m). The Thunder River occurrence, however, places this species also in the special biotic community there at 762 m. No living specimens were collected from the 1991 survey at Thunder River; they were found in soil with dead shells of *Oreohelix*.

Family PUPILLIDAE

Genus **Gastrocopta** Wollaston, 1878

Gastrocopta ashmuni (Sterki, 1898)

Reported by Pilsbry & Ferriss (1911) as *Bifidaria ashmuni* Sterki.

LOCALITIES. South side: Bright Angel Trail. North side: Mount Trumbull; P. & F. station 100.

REMARKS. The Mount Trumbull locality is the northwesternmost occurrence of the species (Bequaert & Miller 1973).

Gastrocopta pellucida (Pfeiffer, 1841)

Reported by Pilsbry & Ferriss (1911) as *Bifidaria pellucida hordacella* (Pilsbry, 1890).

LOCALITIES. South side: P. & F. station A. North side: Mount Trumbull. Colorado River corridor (north side): Spring Canyon.

REMARKS. A single, broken shell with intact aperture was collected from the 1991 survey at Spring Canyon.

Gastrocopta pilsbryana (Sterki, 1890)

Reported by Pilsbry & Ferriss (1911) as *Bifidaria pilsbryana* Sterki.

LOCALITIES. South side: Bright Angel Trail; P. & F. station A. North side: Bright Angel Point; Mount Trumbull; P. & F. stations 7, 12, 100.

Genus **Pupoides** Pfeiffer, 1854

Pupoides hordacea (Gabb, 1866)

LOCALITIES. North side: Antelope Valley, Mount Trumbull.

REMARKS. The Mount Trumbull locality is the westernmost occurrence of this Rocky Mountain species (Bequaert & Miller 1973).

Pupoides nitidulus (Pfeiffer, 1859)

Reported by Pilsbry & Ferriss (1911) as *Pupoides marginata* (Say, 1821) (= *P. albilabris* (C.B. Adams, 1841)).

LOCALITIES. North side: Mount Trumbull.

REMARKS. Bequaert & Miller (1973) identify the Mount Trumbull occurrence as *Pupoides albilabris*.

Genus **Pupilla** Fleming, 1828

Pupilla blandii (Morse, 1865)

LOCALITIES. North side: Mount Logan and "Grand Canyon" (Bequaert & Miller 1973). Localities not represented by specimens in ANSP.

Pupilla hebes (Ancey, 1881)

Reported by Pilsbry & Ferriss (1911) as *Pupilla hebes* and *P. h. kaibabensis* Pilsbry & Ferriss, 1911.

LOCALITIES. North side: P. & F. stations 100 (type locality of *P. h. kaibabensis*), 105.

TYPES. *Pupilla hebes kaibabensis* Pilsbry & Ferriss, 1911: lectotype ANSP 103283 (selected by Baker 1962: 11, as ANSP 103283a); 120 paralectotypes ANSP 371700.

REMARKS. Pilsbry (1948: 938) regarded the subspecies as possibly "a stunted or hunger form" of *P. hebes*.

Pupilla syngenes (Pilsbry, 1890)

Reported by Pilsbry & Ferriss (1911) as: *Pupilla syngenes* (Pilsbry), *Pupilla syngenes* form *dextroversa* (Pilsbry & Vanatta, 1900), and *Pupilla syngenes avus* Pilsbry & Ferriss, 1911.

LOCALITIES. South side: Bright Angel Trail; P. & F. stations A, C, 2 (type locality of *P. s. avus*). North side: P. & F. stations 5, 7, 12, 25, 100; also from Mount Logan (cf. Bequaert & Miller 1973).

REMARKS. The Mount Logan locality (36°20' N, 113°10' W) is the westernmost occurrence of the species (Bequaert & Miller 1973). Bequaert & Miller also present some remarks on the forms of this species and its evolution.

Pupilla sp.

LOCALITIES. South side: P. & F. station A.

Family VALLONIIDAE

Genus **Vallonia** Risso, 1826

Vallonia cyclophorella "Ancey" Sterki, 1892

LOCALITIES. South side: Grandview Point; Bright Angel Trail; Indian Gardens; P. & F. stations A, 2. North side: Bright Angel Point; P. & F. stations 5, 12, 27, 64, 82, 85, 106.

Vallonia perspectiva Sterki, 1893

LOCALITIES. South side: Indian Gardens, P. & F. station A. North side: Bright Angel Point.

Superfamily PUPILLACEA: Family Indeterminate

LOCALITIES. South side: P. & F. station A.

Family DISCIDAE

Genus **Discus** Haldeman, 1840

Discus cronkhitei (Newcomb, 1865)

Reported by Pilsbry & Ferriss (1911) as *Pyramdula (Goniodiscus) cronkhitei* (Newcomb, 1865).

LOCALITIES. North side: Thunder River, Mount Trumbull.

REMARKS. The Thunder River occurrence of this species at 762 m is slightly below the stated Recent altitudinal range for this species in Arizona (838-3658 m; Bequaert & Miller 1973). The Thunder River specimens, from the 1991 survey, were dead collected.

Family SUCCINEIDAE

Genus **Catinella** Pease, 1870

Catinella avara (Say, 1824)

Reported by Pilsbry & Ferriss (1911) as *Succinea avara* Say.

LOCALITIES. South side: Bass Station; Indian Gardens; P. & F. stations A, C, D, 2. North side: P. & F. stations F, G, 3, 9; Phantom Creek; Tapeats Creek; Thunder River. Colorado River corridor (south side): Hermit Creek, Lava Falls Spring. Colorado River corridor (north side): Vasey's Paradise, Saddle Canyon, Bright Angel Creek, Shinumo Creek.

REMARKS. Shells of this species can be confused with *Succinea grosvenorii* Lea, 1864. Spamer & Bogan (in press) initially reported *S. grosvenorii* from several localities of the 1991 Grand Canyon survey (Vasey's Paradise, Saddle Canyon, Hermit Creek, Tapeats Creek, Lava Falls Spring, and Thunder River). Upon reevaluation of life habits and appearance (e.g. Pilsbry & Ferriss 1911, Pilsbry 1948, field observations in 1991 and 1992), and after examination of some specimens by S.-K Wu (pers. comm. 1992), we believe that our records of *S. grosvenorii* cannot be certainly ascribed to that species, but to *C. avara* instead. We believe that this is a more conservative evaluation than to have records of both species, and further field studies and anatomical examinations are necessary.

Genus **Succinea** Draparnaud, 1801

Succinea grosvenorii Lea, 1864

LOCALITIES. South side: P. & F. station 2. North side: Mount Trumbull; Antelope Valley; P. & F. station 78; also from Trail Canyon between Jacob Lake and House Rock Ranch (ca.2134 m), and from ca.18 km west of Jacob Lake (Bequaert & Miller 1973).

REMARKS. These records are as cited in the literature. See also remarks with *Catinella avara*.

Genus **Oxyloma** Westerlund, 1885

Oxyloma haydeni kanabensis Pilsbry, 1948

Reported by Spamer & Bogan (in press) as *Oxyloma* cf. *haydeni* (Binney, 1858).

LOCALITIES. Colorado River corridor (north side): Vasey's Paradise.

REMARKS. The species was erected based on specimens collected by J. H. Ferriss in 1909 from a locality identified as "The Greens," near Kanab Creek ca.9.6 km north of Kanab, Utah (holotype ANSP 103166, 15 paratypes ANSP 391101; alcohol-preserved component of types not located). The species *O. haydeni* is known from Nebraska. Some workers believe that the subspecies is sufficiently distinct, anatomically, to treat it as a separate species (S.-K. Wu pers. comm. 1992, and Clarke 1991); this evaluation awaits proper systematic treatment. This subspecies has been proposed as an endangered animal by the U.S. Fish and Wildlife Service (England 1991a, b). It is known only from the type locality and Vasey's Paradise. The type locality is environmentally altered and has been proposed as a critical habitat (England 1991b). The Vasey's Paradise colony, discovered during the 1991 Grand Canyon survey, is the only known one surviving in a wilderness setting, and the only known living colony of this genus in Arizona. Identification of the Vasey's Paradise specimens was corroborated by S.-K. Wu (pers. comm. 1992), based on anatomical dissections. A record of *O. h. kanabensis* in fossil deposits in Provo, Utah (Baily & Baily 1952: 91), is without any remark or subsequent reference to it; and based only on shell characters, the identification is suspect.

Family HELICARIONIDAE

Genus **Euconulus** Reinhardt, 1883

Euconulus fulvus (Müller, 1774)

Reported by Pilsbry & Ferriss (1911) as *Euconulus fulvus alaskensis* (Pilsbry, 1899).

LOCALITIES. South side: Grandview Point; Bright Angel Trail; Indian Gardens; P. & F. stations A, C, 2. North side: Mount Trumbull; P. & F. stations 5, 7, 18, 64, 79, 82.

Family ZONITIDAE

Genus **Hawaiia** Gude, 1911

Hawaiia minuscula (Binney, 1841)

Reported by Pilsbry & Ferriss (1911) as *Zonitoides minuscula* (Binney).

LOCALITIES. South side: Grandview Point. North side: Mount Trumbull. Colorado River corridor (north side): Vasey's Paradise, Spring Canyon.

REMARKS. Bequaert & Miller (1973: 145) suggested that this is Arizona's most common snail. They listed an altitudinal range of 762-2591 m, with additional occurrences in "irrigated artificial habitats of towns." The occurrences at Vasey's Paradise (884 m) and Spring Canyon (458 m) are near the minimum altitude given for this species, but both are in natural springhead vegetational communities outside of which is inhospitable to these animals. The specimens from Vasey's Paradise and Spring Canyon were dead collected from silt accumulated in the bottoms of small pools, but they were placed in alcohol to preserve whatever body tissues remain.

Genus **Zonitoides** Lehmann, 1862

Zonitoides arboreus (Say, 1817)

LOCALITIES. South side: Grandview Point. North side: Thunder River; P. & F. station G.

REMARKS. Bequaert & Miller (1973: 146) indicate that this species is found in Arizona between 1524-3658 m, "below 5,000 ft [1524 m] only as introductions by man under artificial conditions of moisture and shelter." The Thunder River occurrence at 762 m is in sheltered natural conditions. The single specimen from this locality was dead collected.

Genus **Glyphyalinia** Martens, 1892

Glyphyalinia indentata (Say, 1823)

Reported by Pilsbry & Ferriss (1911) as *Vitrea indentata umbilicata* Cockerell, 1899.

LOCALITIES. South side: Bass Station, Bright Angel Trail, Indian Gardens, Grandview Point. North side: Bright Angel Point; Thunder River; P. & F. stations H, 4.

REMARKS. Bequaert & Miller (1973) recognize only *G. indentata paucilirata* (Morelet, 1851) as occurring in Arizona, intergrading in the mid-Atlantic states with the nominate *G. i. indentata*. ANSP collections do not recognize the subspecies.

Family VITRINIDAE

Genus **Vitrina** Draparnaud, 1801

Vitrina alaskana Dall, 1905

LOCALITIES. South side: Seep spring west of South Bass Trail. North side: Bright Angel Point; Warm Spring Canyon (no station number); P. & F. station 12.

REMARKS. Bequaert & Miller 1973) regard *V. alaskana* as the American subspecies of the Old World *V. pellucida* (Müller, 1774), based on shells and genitalia of specimens taken at the San Francisco Peaks.

Family LIMACIDAE

Genus **Deroceras** Rafinesque, 1820

Deroceras laeve (Müller, 1774)

Reported by Pilsbry & Ferriss (1911) as *Agriolimax hemphilli ashmuni* Pilsbry & Vanatta *in* Pilsbry & Ferriss, 1910.

LOCALITIES. North side: Thunder River; P. & F. station 78.

REMARKS. The Thunder River occurrence is the first record of this genus from inside the Grand Canyon. Specimens were first seen and brought to the senior author's attention by Dennis Silva. Bequaert

& Miller (1973: 149) regard the species as native in Arizona, "normally at 4,500 to 8,000 ft [1372-2438 m]; at lower elevations in cultivated areas." At Thunder River it was found at 762 m in sheltered natural conditions.

Family THYSANOPHORIDAE

Genus **Thysanophora** Strebel & Pfeffer, 1880

Thysanophora hornii (Gabb, 1866)

LOCALITIES. North side: P. & F. station F; also reported from Mount Logan (Bequaert & Miller 1973).

REMARKS. Bequaert & Miller (1973) indicate that this species is typical in the Lower Sonoran Life Zone.

Genus **Microphysula** Cockerell *in* Pilsbry, 1926

Microphysula ingersollii (Bland, 1875)

Reported by Pilsbry & Ferriss (1911) as *Thysanophora ingersolli* (Bland).

LOCALITIES. North side: P. & F. stations 26, 100.

REMARKS. Bequaert & Miller (1973) indicate that this is mostly a high-altitude species.

Family OREOHELICIDAE

Genus **Oreohelix** Pilsbry, 1904

REMARKS. This is the most common and widely dispersed terrestrial mollusk in the Grand Canyon. Although both *O. strigosa depressa* and *O. yavapai* are identified from specimens on both sides of the canyon, the chasm is a virtual barrier to dispersal; *O. s. depressa* is restricted mostly northward of the canyon, while *O. yavapai* is restricted mostly southward of the canyon. Both species are not very restricted by altitude, but *O. yavapai* is restricted in its upper range to the Transition Zone. Although *O. yavapai* has been found on the North Rim (Bright Angel Point, uppermost Transition Zone), it has not been found in higher altitudes of the Kaibab Plateau, away from the canyon rim where *O. s. depressa* is found into the Boreal Zone. The apparent absence of *O. yavapai* from the Boreal Zone may indicate a true ecological upper limit (Transition Zone) for the species.

Three alcohol-preserved lots in ANSP collections (ANSP A12347-A12349) are identified only as *Oreohelix* sp. They were collected during the 1906/1909 expeditions along Bright Angel Trail (A12347 and A12349) and South Bass Trail (A12348). Corresponding dry lots for these specimens are unknown, and specific identifications await anatomical dissection. Presumably, these lots correspond to what Pilsbry & Ferriss (1911) were identifying as forms of *O. yavapai*, but they are mentioned here also because they could represent South Rim *O. strigosa depressa*.

Oreohelix strigosa depressa (Cockerell, 1890)

LOCALITIES. South side: reported by Bequaert & Miller (1973: 126) in Coconino County; South Rim localities not represented in ANSP collections. North side: Thunder River; P. & F. stations 8, 10-22, 24-27, 32-35, 37, 49-57, 59-62, 64-71, 73-100, 103, 105.

REMARKS. The ANSP collection does not systematically separate the subspecies of *O. strigosa* (Gould, 1846). However, Bequaert & Miller (1973) indicate that the nominate *O. s. strigosa* occurs neither in Arizona nor in the Southwestern Molluscan Province, and Pilsbry & Ferriss's (1911) identifications were to the subspecies *O. s. depressa*, thus we retain the identification in this paper. In terms of altitudinal distribution, this is the most cosmopolitan of Grand Canyon terrestrial snails.

Daniels (1912, pl. 5 fig. 16) illustrated a scalariform shell from Jacob Canyon, and a sinistral shell from the Powell Plateau (pl. 5 fig. 17), without discussion.

Pilsbry & Ferriss (1911: 190) took note that at several Kaibab Plateau stations they had collected forms of *Oreohelix* referable to *O. strigosa cooperi* (Binney, 1858) (= *O. s. depressa*). Although they stated that two shells were in fact this form, they were uncertain whether all the shells resembling *O. s. cooperi* were truly distinguishable from *O. s. depressa*, so they described them as *O. s. depressa*.

Oreohelix yavapai Pilsbry, 1905

Reported by Pilsbry & Ferriss (1911) as: *O. y. profundorum* Pilsbry & Ferriss, 1911; *O. y. extremitatis* Pilsbry & Ferriss, 1911; and *O. y. angelica* Pilsbry & Ferriss, 1911.

LOCALITIES. South side: Hermit's Rest; Bright Angel Trail (type locality of *O. y. angelica*); Yavapai Point; P. & F. stations A (type locality of *O. y. profundorum*), C, 2 (type locality of *O. y. extremitatis*). North side: Bright Angel Point.

TYPES. *Oreohelix yavapai yavapai* Pilsbry, 1905 (from Purtyman's Ranch, Oak Creek Canyon, Yavapai County, Arizona, south of the study area of the present paper): lectotype ANSP 79415 (selected by Pilsbry 1939: 518, fig. 339a, as "type" (= Pilsbry 1905, pl. 25 fig. 53)), paralectotype ANSP 371490; also alcohol-preserved lot ANSP A12351 containing one mature body and six or more embryonic shells (but whether the body corresponds to the lectotype or paralectotype is uncertain). *Oreohelix yavapai angelica* Pilsbry & Ferriss, 1911: lectotype ANSP 103239 (Pilsbry & Ferriss 1911, pl. 12 fig. 23, designated by Baker 1962: 3, as ANSP 103239a), 38 paralectotypes ANSP 371707. Pilsbry (1939: 527) mentioned "Lectotype and paratypes," with figures (figs. 343.22-25), but nowhere was the lectotype specimen uniquely indicated, thus Baker's designation constitutes first indication of the lectotype. *Oreohelix yavapai extremitatis* Pilsbry & Ferriss, 1911: lectotype ANSP

103236 (Pilsbry & Ferriss 1911, pl. 12 fig. 18, designated by Baker 1962: 8, as ANSP 103236a), 267 paralectotypes ANSP 371709. Pilsbry (1939: 526) mentioned "Type and paratypes," with figures (figs. 343.15-21), but nowhere was the type (= lectotype) uniquely indicated, thus Baker's designation constitutes first indication of the lectotype. *Oreohelix yavapai profundorum* Pilsbry & Ferriss, 1911: lectotype ANSP 103234 (designated by Pilsbry 1939: 524, fig. 343.4; = Pilsbry & Ferriss 1911, pl. 12 fig. 4), 78 paralectotypes ANSP 371710.

REMARKS. The ANSP collections do not systematically recognize subspecies of *Oreohelix yavapai*. From within the bounds of the study area of this paper, Bequaert & Miller (1973) do recognize the subspecies *O. y. profundorum* and *O. y. extremitatis*, but they place *O. y. angelica* in synonymy with the latter, as did Pilsbry (1939: 526).

Two more subspecies from the Grand Canyon were erected based on subfossil or fossil shells: *O. y. fortis* Cockerell, 1927 (Bright Angel Trail), and *O. y. vauxae* Marshall, 1929 (Supai, Havasu Canyon). Pilsbry (1934: 402-403) synonymized *O. y. vauxae* with *O. y. fortis*. These are discussed separately in the present paper, in the section, "Pleistocene-Holocene Mollusks of the Grand Canyon."

Family HELMINTHOGLYPTIDAE

Genus **Sonorella** Pilsbry, 1900

Sonorella coloradoensis (Stearns, 1890)

LOCALITIES. South side: Near Hance Trail (type locality); Bass Station; Bright Angel Trail; P. & F. stations A, B, C, D, E. North side: Thunder River; P. & F. stations F, G, H, 3, 4, 5, 23, 25, 100, 101, 104, 109.

REMARKS. The Thunder River specimens were dead collected. The shells were compared to other specimens of this species in ANSP collections, as well as to specimens of *Oreohelix* from Thunder River and other Grand Canyon localities.

Bequaert & Miller (1973) note that this is the northernmost species of *Sonorella*. Daniels (1912: 39) cited a scalariform specimen of this species from the Powell Plateau, without discussion.

Sonorella reederi Miller, 1984

LOCALITIES. South side: Just west of and below Rampart Cave, westernmost Grand Canyon (type locality).

TYPES. Holotype USNM 792406, 7 paratypes in five institutions and Miller's personal collection, including ANSP 356004.

REMARKS. This may be the species noted by Bequaert & Miller (1973: 120) as an undescribed form "closely related" to *S. c. mohaveana* Miller, 1968.

Sonorella "betheli" Henderson, 1914

TYPES. Holotype in University of Colorado Museum (UCM); a paratype is ANSP 109733.

REMARKS. This species was erected based on specimens said to be from Bright Angel Trail (type locality). According to Pilsbry (1939: 174), the locality is in error; the specimens were probably collected near Los Angeles, California. Pilsbry synonymized the species with *Helminthoglypta traski* (Newcomb, 1861).

CONCLUDING REMARKS ON THE RECENT MALACOFAUNA

The diversity and distribution of the malacofauna of the Grand Canyon region is characteristic of the Southwestern Molluscan Province. Aquatic forms are restricted to habitats that have perennial water and suitable substrata, regardless of the extralocal environment. Where canyons are cut into the plateaus, over short linear distances there are dramatic changes in altitude and ecological conditions. Infrequent occurrences of springs, and virtually no surface runoff from the limestone-capped plateaus that surround the Grand Canyon, produce conditions of aridity in the inner canyon; but where water does occur, rich riparian communities are found. On the plateaus, altitude has a direct bearing on temperature and precipitation potential; biotic communities correspond to this relationship accordingly, as well as to the effects of slope aspect. In higher altitudes, cooler temperatures prevail, precipitation is greater, and vegetation is more diverse and abundant.

The Grand Canyon is not a significant barrier to the dispersal of molluscan species. Aquatic forms are found in tributaries along the entire course of the Colorado River, and their historic records of occurrence at springs indicate that they are probably well distributed between suitable locales in the upper reaches of the canyon, too. The effects of sedimentation have an impact only on the establishment of colonies, perhaps not so much on transport and dispersal. A tolerance to sedimentation benefits short-term survival in such generally inhospitable conditions, until redeposition in a suitable habitat is achieved. Many terrestrial mollusks are found on both rims of the canyon, as well as at sites within the canyon. The Grand Canyon, alone or in concert with the higher plateaus north of the canyon, serves as an ultimate barrier to only some terrestrial forms.

In the post-dam Colorado River corridor, the altered riparian regime has provided conditions for the survival of terrestrial mollusks that are more satisfactory than conditions that existed there before closure of the dam. More stable conditions of shelter, and the development of heavier stands of vegetation, combine with the omnipresent slopes of talus and the reduced danger of high river flows and seasonal floods, to provide a more reliably undisturbed environment. Future investigations will have to prospect for terrestrial mollusks in the river corridor between tributaries.

The molluscan communities of the region occupy areas of shelter. Their distribution between environmental Life Zones is more a function of that shelter, rather than the overall conditions of temperature and precipitation (as first indicated by Pilsbry & Ferriss 1910, and as shown by Grand Canyon molluscan distributions published by Pilsbry & Ferriss 1911 and supplemented by the present study). The downward distribution of mollusks that normally inhabit higher (cooler, wetter) Life Zones, however, is not necessarily restricted by the lack of shelter characteristic of lower (warmer, drier) Life Zones, as Pilsbry & Ferriss (1910) indicated. Significant translation downward of Transition Zone and Boreal Zone mollusks of the Kaibab Plateau, into the Lower Sonoran Zone is possible when outstanding conditions of shelter are present, as in the case of Thunder River. Vasey's Paradise also is a model of this downward translation, although areally and altitudinally of much more limited extent. Dispersal mechanisms from higher to lower zones can be effected by usual natural means such as transport by animals or by wind. Gravity thus also is seen to be a factor in dispersal mechanisms in the canyon lands.

The position of aquatic and terrestrial mollusks in the trophic food web of the Grand Canyon is virtually unknown. Brief reports of mollusks in the guts of fish and lizards (see Previous Work section) are known, but an understanding both of the importance and preferences of mollusks in the diets of the canyon's animal community is completely unknown. Likewise, the productivity levels of the Grand Canyon mollusks is unknown. It is lamentable that no data are available from the pre-dam river environment. The 1991 survey and any surveys in the near future will serve as a baseline against which to compare later surveys of molluscan diversity and distribution in the river corridor. The historical collections of terrestrial mollusks from the canyon and Kaibab Plateau, however, will be a help toward studies of possible changes in diversity and distribution in the canyon overall since around 1900. A resurvey of the areas collected by Pilsbry, Ferriss, and Daniels is a logical beginning for such a study.

PLEISTOCENE-HOLOCENE MOLLUSKS OF THE GRAND CANYON

The late Pleistocene and Holocene (<40,000 yr B.P.) fossil record of the Grand Canyon is richly represented by plant and vertebrate species. The faunal and floral diversity and distributions, as well as interpretations of paleoclimates, have been well researched by many investigators (see references listed in Spamer 1990, Part 3). Published data on the fossil record of invertebrates from this time and place is presently restricted to a single publication (Elias et al. 1992) that includes data on 42 taxa of Pleistocene and Holocene Arthropoda from Bida and Kaetan Caves, in eastern Grand Canyon. Radiometric (^{14}C) dates for these remains are reported as ranging from 30,600±1800 to 2960±200 yr B.P. A corresponding record for Mollusca has not been mentioned anywhere in the Grand Canyon literature (Spamer 1990, and in press). This is remarkable when one considers that the semi-arid climate of the inner canyon has preserved wood and the dung (containing pollen and plant fragments) and soft tissues of vertebrates that lived in the area.

Here, we refer to the paleontological record three published reports of molluscan material (Oreohelicidae) from the Grand Canyon. We also report a new record of similarly found shells of the family Succineidae.

Family SUCCINEIDAE

Genus **Catinella** Pease, 1870

Catinella cf. avara (Say, 1824)

Specimens: ANSP 391070, 391086, 391095.

During the 1991 Grand Canyon molluscan survey, specimens of fossil or subfossil succineids were collected along the trail at Saddle Canyon (Colorado River Mile 47.0, Km 75.6). They were first observed during a trip in May 1991 (brought to the senior author's attention by David Lyle), and the locality was revisited in July 1991 to more accurately establish the record of occurrence.

Based on an examination of shell characters, S.-K. Wu (pers. comm. 1992) has referred these shells to *Catinella* (and not to *Succinea*), a genus which incidentally is found alive (*C. avara*) along the shaded portion of the perennial Saddle Canyon creek (as reported in the present paper). There is no noticeable difference between the shells of living and fossil *Catinella* from the Grand Canyon, thus we refer these specimens to *C. avara*.

LOCALITY AND OCCURRENCE. Saddle Canyon, below the Redwall Limestone-Muav Limestone contact, along trail on south side of Saddle Canyon ca.100 m above and ca.0.5 km from the Colorado River, on talus slopes that are completely exposed to the sun; approximate coordinates 36°22'00" N, 111°53'30" W; 3200 ft, 976 m.

The shells were found in "red earth," apparently in conditions similar to those under which were found the oreohelicids mentioned below. The Supai Group overlying the Redwall Limestone is not visible above the Redwall here; it has eroded back from the canyon rim. However, the red staining on the Redwall indicates that sheet wash during storms delivers sediment over the local rim to the localities below.

Poorly-defined drainages shallowly exhume part of the talus slope, and in these drainages were found accumulations of rocks, some twigs, and shells. The surrounding rocks were covered with thin layers of blackened, dead moss of limited extent. Some cryptogamic soil development was noticed in the area. No discernable water source, intermittent or otherwise, was seen anywhere near or above the trail. The Muav Limestone is a major aquifer in the Grand Canyon region, and most of the canyon's large springs occur in it, above the impermeable Bright Angel Shale. Similar springs also occur at the contact between the Redwall and Muav Limestones.

The occurrence of succineids so far from a perennial water source, in such an exposed locale, seems to indicate that a failed spring source is nearby. The scenario is plausible. Huge travertine mantles originating in the Muav Limestone at many places in the Grand Canyon—areas now without spring activity—indicate widespread distribution of springs during wetter periods sometime in the past (Billingsley & Elston 1989, Szabo 1990).

Family OREOHELICIDAE

Genus **Oreohelix** Pilsbry, 1904

Oreohelix yavapai Pilsbry, 1905

Synonymy for Grand Canyon fossil forms only:
Oreohelix strigosa depressa (Cockerell, 1890), Pilsbry (1921: 48), Pilsbry (1939: 523). ANSP 128624 (5 specimens, collected by C. M. Cooke, Jr., 1921, Bright Angel Trail).
Oreohelix yavapai fortis Cockerell, 1927: 101; Pilsbry (1934: 402-403, pl. 15 figs. 1-6, 14); Pilsbry (1939: 523-524, figs. 338.1-6, 14 (pp. 518-519)); Spamer (1992: 83). Type locality: upper half of Bright Angel Trail. Holotype ANSP 141875, 1 paratype ANSP 371711; figured specimens (Pilsbry 1934, 1939) ANSP 143691 (figs. 1-6) with 40 unfigured specimens, collected by J. H. Ferriss, 1917, Bright Angel Trail; and ANSP 158169 (fig. 14) with 17 unfigured specimens, collected by J. H. Ferriss, 1921, Bright Angel Trail. Baker (1962: 9) apparently mistook Pilsbry's (1939, fig. 338.1) illustration of the holotype as a lectotype designation; but since the species was described by Cockerell (1927) on the "type and an immature specimen," this is clearly what today can be called a holotype and paratype.
Oreohelix yavapai vauxae Marshall, 1929: 1-2, pl. 1 figs. 1-3, 11; Pilsbry (1934: 402-403); Pilsbry (1939: 523-524); Spamer (1992: 83). Type locality: near Supai, Havasu Canyon. Holotype USNM 380687, 14 paratypes USNM 380688.

Three published records of fossil or subfossil molluscan shells (Oreohelicidae) from the Grand Canyon have appeared in the malacological literature, but they have never been mentioned in the paleontological literature. Both records name new subspecies of *Oreohelix yavapai*: *O. y. fortis* Cockerell, 1927, and *O. y. vauxae* Marshall, 1929. Pilsbry (1939: 523) also indicated that specimens he (Pilsbry 1921) had described as *O. strigosa depressa* also belonged to the fossil subspecies *O. y. fortis*. These forms were described on shell characters alone; their larger size was the principal diagnostic characteristic used to distinguish them from *O. y. yavapai*. In the ANSP collections, no subspecies of Recent *O. yavapai*, such as those named by Pilsbry & Ferriss (1911) from different populations in the Grand Canyon, are recognized as systematically distinct. Because the fossil taxa were based on variable shell characters alone, there is no practical basis by which to distinguish subspecific characters between them, thus they are simply referred to as *O. yavapai*.

LOCALITIES AND OCCURRENCES. *Oreohelix yavapai fortis*. The original description cites the locality as on Bright Angel Trail, "halfway up" (i.e. above the top of the Redwall Limestone, perhaps somewhere in the Supai Group). Cockerell (1927: 101) described the occurrence: "Last summer on the Bright Angel trail . . . I noticed about halfway up that the bright red earth contained shells of *Oreohelix*, to all appearances fossil, and presumably of pleistocene age. Nearly all those exposed were broken, and in the short time at my disposal I only obtained one perfect adult . . . ." He added, "The larger size is possibly correlated with a moister climate in past times . . . ." However, Pilsbry & Ferriss (1911: 187) observed that environmental constraints, including moisture, do not necessarily correlate with shell size of oreohelicids of the Grand Canyon.

C. M. Cooke's description of occurrence of what Pilsbry (1939) reidentified as *Oreohelix yavapai fortis*, quoted by Pilsbry (1921), is: "Collected along the Bright Angel Trail, from about 1000 to 3400 ft. [305-1036 m] below the rim. I found the first specimen very close to the last pine on the trail, just below the foot of the high yellow cliffs [Coconino Sandstone and overlying strata, which places the locality in the Hermit Shale, a red, very easily eroded formation]. Dead specimens were seen along the trail to just below the part of the trail called Jacob's Ladder [through the red sandstones and shales of the Supai Group, then the steep descent through the Redwall Limestone]."

Hand (1922: 127), in a malacological travelogue, also reported seeing these shells along Bright Angel Trail: "Where he [Cooke] saw his fifteen or twenty we found several hundred, all dead. There is an immense dike [bed] of limestone here in the midst of the sandstone and snails must have recently flourished."

The senior author descended Bright Angel Trail in June 1992 and watched for dead mollusk shells. None were seen by casual examination of slopes, especially where "red earth" is exposed. This area constantly erodes, the trail is continually maintained by the National Park Service, and human and mule traffic is much more frequent today than it was when the early reports were made, so these trailside deposits may have been obliterated. However, a careful survey is necessary to establish whether deposits are present, here and elsewhere in the canyon.

Oreohelix yavapai vauxae. Supai, Havasu Canyon (village of Supai, Havasupai Indian Reservation, which is situated on the lower part of the Supai Group). "The specimens appear to be fossil or subfossil, because of the reddish mineral matter coating them in spots" (Marshall 1929: 2).

Mode of Occurrence Indicating Age

Pilsbry (1934: 403) grouped the Grand Canyon oreohelicid fossils together both with respect to taxonomic synonymy and age: "The Grand Canyon and the Supai shells occur fossil [sic] in a red earth deposit very likely of the same age, probably Pleistocene." Of course, his determination of age was simply based on the silt-encrusted, somewhat pitted, "old" appearance of the shells. He may also have been influenced by the preservational qualities of the semi-arid climate of the inner canyon. And indeed, an examination of lots held in ANSP collections (cited in the synonymy, above) does tempt one to infer great age of the specimens. The succineid specimens recovered in 1991 have a similarly silt-encrusted, pitted, "old" appearance.

The "red earth" in the Grand Canyon is found in pockets on talus slopes, usually as a mixture of red silt, finely broken talus (stones and gravel), and vegetational debris. Some deposits are within poorly defined, shallow drainages. The red silt is derived from weathered material washed from the Hermit Formation and strata of the Supai Group, all of which immediately overlie the prominent cliff of the Redwall Limestone half-way down the canyon wall, and which stain red the surface of the otherwise bluish-gray Redwall Limestone. Talus from the easily eroded Hermit-Supai strata accumulates with blocks of Redwall at the foot of the Redwall cliff.

Citations of the snails found in these "red earth" taluses as "fossils" are based on relative appearances of age, thus a similarly inferred age for the deposits. Whether the shells actually are of Pleistocene age (>10,000 yr B.P.) is unknown, lacking corroboration by radiometric techniques or associated palynological indications of age. Are these deposits only thin veneers, which would suggest short-period accumulation followed by easy erodability (thus possibly young age); or are they part of thicker (and older?) deposits, protected by the accumulation of talus, which are just now being cut into by precipitation runoff?

The deposits on Bright Angel Trail are likely to be eroded very easily; the area traditionally experiences frequent slides and rockfalls. The precise location of the Havasu Canyon locality is not known, thus no opinion of relative age of the slopes can be rendered here. The Saddle Canyon locality is somewhat stabilized by vegetation and has some appearances of slope armoring and desert soil development that indicate slow erosional processes now. In each case, however, the snail shells appear to have been buried for some time, based on their weathered appearance.

It may be possible to establish either advanced or very young ages for these shells, if more can be collected. Conventional radiometric techniques could determine ages of thousands of years, while new methods such as measurements of aspartic acid racemization (Goodfriend 1992) could indicate ages of a few centuries.

ACKNOWLEDGMENTS

The senior author thanks Lawrence E. Stevens (U.S. National Park Service) and Dean W. Blinn (Northern Arizona University) for the opportunity to join a Glen Canyon Environmental Studies research trip on the Colorado River; funding was provided through GCES. Special thanks are extended to Dave Wegner of the GCES office for his personal attention to travel arrangements. Specimens were contributed by Todd Goodman, Tom Martin, Clay Runck, Joe Shannon, Mike Shaver, and Dennis Silva, who, with the rest of the GCES and boat crews, also provided enthusiastic companionship in the field. We are grateful to Shi-Kuei Wu (University of Colorado Museum), Kenneth C. Emberton (ANSP), and Henry M. Reiswig (Redpath Museum, McGill University) for providing identifications of material. Larry England (U.S. Fish and Wildlife Service) was helpful in providing information on the Kanab ambersnail and its habitat at the type locality. Lawrence E. Stevens and H. Lee Fairbanks (Pennsylvania State University) reviewed the manuscript and provided useful remarks on its content and organization. Gary Rosenberg kindly made available the resources of the ANSP Department of Malacology. Curation of specimens was made possible partly under NSF collection support grant BSR-8911074, to the ANSP Department of Malacology. Thanks are also extended to Edward Daeschler, for locating the mice collected by H. A. Pilsbry; and John Cadle and Ned Gilmore, for providing the data on frogs and toads collected by Pilsbry.

LITERATURE CITED

Anderson, T. W. and N. D. White. 1979. Statistical summaries of Arizona streamflow data. U.S. Geological Survey Water-Resources Investigations 79-5.

Babbitt, J. E. and S. Thybony. 1991. A guide to the South and North Bass Trails. Grand Canyon Natural History Association.

Baily, J. L., Jr., and R. I. Baily. 1952. Further observations on the Mollusca of the relict lakes in the Great Basin [Part 2]. Nautilus 65(3): 85-93 (with pl. 4 published with [Part 1] in Nautilus, 65(2), 1951).

Baker, H. B. 1962. Type land snails in the Academy of Natural Sciences of Philadelphia. I. North America, north of Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 114: 1-21.

Baker, H. B. 1964. Type land snails in the Academy of Natural Sciences of Philadelphia. Part III. Limnophile and thalassophile Pulmonata. Part IV. Land and fresh-water Prosobranchia. Proceedings of the Academy of Natural Sciences of Philadelphia 116: 149-193.

Bequaert, J. C. and W. B. Miller. 1973. The mollusks of the arid Southwest; with an Arizona checklist. University of Arizona Press, Tucson.

Billingsley, G. H. and D. P. Elston. 1989. Geologic log of the Colorado River from Lees Ferry to Temple Bar, Lake Mead, Arizona. Pages 1-36 *in* D. P. Elston, G. H. Billingsley, and R. A. Young, eds. Geology of the Grand Canyon, northern Arizona (with Colorado River guides). 28th International Geological Congress, Field Trip Guidebook T115/315. American Geophysical Union, Washington, D.C.

Blinn, D. W., L. E. Stevens, and J. P. Shannon. In press. The effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. U.S. National Park Service report (NPS Cooperative Agreement No. CA-8009-8-0002).

Brown, B. T., S. W. Carothers, and R. R. Johnson. 1986. Grand Canyon birds; historical notes, natural history, and ecology. University of Arizona Press, Tucson.

Burch, J. B. 1975. Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America (rev. ed.). Malacological Publications, Hamburg, Michigan.

Carothers, S. W. and B. T. Brown. 1991. The Colorado River through Grand Canyon; natural history and human change. Tucson: University of Arizona Press.

Carothers, S. W. and C. O. Minckley. 1981. A survey of the fishes, aquatic invertebrates and aquatic plants of the Colorado River and selected tributaries from Lee [sic] Ferry to Separation Rapids. U.S. Department of the Interior, Water and Power Resources Service, Lower Colorado Region, Boulder City, Nevada. [Cover title: A survey of the aquatic flora and fauna of the Grand Canyon. Final Report.]

Clarke, A. H. 1991. *Oxyloma haydeni kanabensis* Pilsbry, 1948. Kanab Amber Snail. Pages 23-36 *in* Ecosearch, Inc. Status survey of selected land and freshwater gastropods in Utah. Final report. Contract no. 14-16-0006-89-021 (revised) (prepared for U.S. Fish and Wildlife Service). Ecosearch, Inc., Portland, Texas.

Cockerell, T. D. A. 1927. A large form of Oreohelix yavapai in the Grand Canyon. Nautilus 40(3): 101.

Cole, G. and D. M. Kubly. 1976. Limnologic studies on the Colorado River and its main tributaries from Lee's Ferry to Diamond creek including its course in Grand Canyon National Park. Colorado River Research Program, Report Series, Grand Canyon National Park, Technical Report 8.

Cooley, M. E., B. N. Aldridge, and R. C. Euler. 1977. Effects of the catastrophic flood of December 1966, North Rim area, eastern Grand Canyon, Arizona. U.S. Geological Survey Professional Paper 980.

Counts, C. L. 1991. *Corbicula* (Bivalvia: Corbiculidae).

Part 1. Catalog of fossil and recent nominal species. Part 2. A compendium of zoogeographic records of North America and Hawaii, 1924-1984. Tryonia, 21.

Cox, N. I. 1982. A harsh land and proud; saga of the Arizona Strip. Cox Printing Co., Las Vegas.

Dall, W. H. 1897. Report of the mollusks collected by the International Boundary Commission of the United States and Mexico, 1892-1984. Proceedings of the U.S. National Museum 19(1111): 333-379.

Daniels, L. E. 1911. Notes on Oreohelix. Nautilus 25(2): 18-19.

Daniels, L. E. 1912. Abnormal shells. Nautilus 26(4): 38-42.

Elias, S. A., J. I. Mead, and L. D. Agenbroad. 1992. Late Quaternary arthropods from the Colorado Plateau, Arizona and Utah. Great Basin Naturalist 52: 59-67.

England, J. L. 1991a. Endangered and threatened wildlife and plants; emergency rule to list the Kanab ambersnail as endangered. Federal Register 56(153): 37668-37671.

England, J. L. 1991b. Endangered and threatened wildlife and plants; proposal to list the Kanab ambersnail as endangered and designate critical habitat. Federal Register 56(221): 58020-58026.

[Ferriss, J. H.] 1910. A collecting excursion north of the Grand Canyon of the Colorado [letter to H. A. Pilsbry, with an unsigned introductory paragraph by Pilsbry]. Nautilus 23(9): 109-112.

Goodfriend, G. A. 1992. Rapid racemization of aspartic acid in mollusc shells and potential for dating over recent centuries. Nature 357: 399-401.

Hand, E. E. 1922. Sonorellas and scenery. Nautilus 35(4): 123-129.

Henderson, J. 1914. A new Sonorella from the Grand Canyon, Arizona. Nautilus 27(11): 122-124.

Herrington, H. B. 1962. A revision of the Sphaeriidae of North America. Publications of the Museum of Zoology, University of Michigan, 118.

Hershler, R. and J. J. Landye. 1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). Smithsonian Contributions to Zoology 459.

Hughes, J. D. 1978. In the house of stone and light; a human history of the Grand Canyon. Grand Canyon Natural History Association.

Huntoon, P. W. 1970. The hydro-mechanics of the ground water system in the southern portion of the Kaibab Plateau, Arizona. Ph.D. dissertation, University of Arizona.

Huntoon, P. W., G. H. Billingsley, W. J. Breed, J. W. Sears, T. D. Ford, M. D. Clark, R. S. Babcock, E. H. Brown, et al. 1976. Geologic map of the Grand Canyon National Park, Arizona. Museum of Northern Arizona, and Grand Canyon Natural History Association.

Johnson, P. W., and R. B. Sanderson. 1968. Spring flow into the Colorado River, Lees Ferry to Lake Mead, Arizona. Arizona State Land Department, Water-Resources Report 34.

Landye, J. J. 1980. Rediscovery of *"Amnicola" deserta* Pilsbry (Mollusca: Gastropoda) and two new undescribed hydrobioid gastropods from the Virgin River drainage, Utah-Arizona [abstract]. Bulletin of the American Malacological Union 1980: 70-71.

Lowe, C. H. 1964. Arizona's natural environment; landscapes and habitats. University of Arizona Press, Tucson.

Maddux, H. R., D. M. Kubly, J. C. deVos, Jr., W. R. Persons, R. Staedicke, and R. L. Wright. 1987. Effects of varied flow regimes on aquatic resources of Glen and Grand canyons. Final report. Arizona Game and Fish Department.

Marshall, W. B. 1929. Three new land shells from the genus Oreohelix from Arizona. Proceedings of the U.S. National Museum 76 (art. 5) (no. 2802).

Mead, J. I. 1991. Late Pleistocene and Holocene molluscan faunas and environmental changes in southeastern Arizona. Pages 215-216 *in* J. R. Purdue, W. E. Klippel, and B. W. Styles, eds. Beamers, bobwhites, and blue-points; tributes to the career of Paul W. Parmalee. Illinois State Museum, Scientific Papers, vol. 23 (and University of Tennessee, Department of Anthropology, Report of Investigations, no. 52).

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. U.S. Department of Agriculture, North American fauna, no. 3.

Miller, W. B. 1968. New Sonorella from Arizona. Nautilus 82(2): 50-52, 59-63.

Miller, W. B. 1984. Three new species of Sonorella (Gastropoda: Pulmonata: Helminthoglyptidae) from Arizona. Proceedings of the Biological Society of Washington 97(4): 681-687.

Pilsbry, H. A. 1892. Manual of conchology, 2nd Series: Pulmonata, Vol. 8 (Helicidae, Vol. 6). Conchological Section, Academy of Natural Sciences of Philadelphia.

Pilsbry, H. A. 1894. Manual of conchology, 2nd Series: Pulmonata, Vol. 9 (Helicidae, Vol. 7). Guide to the study of Helices. Conchological Section, Academy of Natural Sciences of Philadelphia.

Pilsbry H. A. 1897. A classified catalogue of American land shells, with localities [part 2]. Nautilus 11(5): 59-60.

Pilsbry, H. A. 1900. Sonorella, a new genus of helices. Proceedings of the Academy of Natural Sciences of Philadelphia 52: 556-560.

Pilsbry, H. A. 1905. Mollusca of the southwestern states. I: Urocoptidae; Helicidae of Arizona and New Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 57: 211-290.

Pilsbry, H. A. 1921. Land shells from Palm Canyon, California, and the Grand Canyon. Nautilus 35(2): 48.

Pilsbry, H. A. 1934. Notes on the anatomy of

Oreohelix,—III, with descriptions of new species and subspecies. Proceedings of the Academy of Natural Sciences of Philadelphia 85: 383-410.

Pilsbry, H. A. 1939, 1940, 1946, 1948. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, Vol. 1, Pt. 1, pp. 1-573 [1939]; Vol. 1, Pt. 2, pp. 575-994 [1940]; Vol. 2, Pt. 1, pp. 1-520 [1946]; Vol. 2, Pt. 2, pp. i-xlvii, 521-1113 [1948].

Pilsbry, H. A. and J. H. Ferriss. 1910. Mollusca of the southwestern states: IV. The Chiricahua Mountains, Arizona. Proceedings of the Academy of Natural Sciences of Philadelphia 62: 44-147.

Pilsbry, H. A., and J. H. Ferriss. 1911. Mollusca of the southwestern states, V: The Grand Canyon and northern Arizona. Proceedings of the Academy of Natural Sciences of Philadelphia 63: 174-199.

Pilsbry, H. A., and J. H. Ferriss. 1918. Mollusca of the southwestern states—IX, The Santa Catalina, Rincon, Tortillita and Galiuro Mountains. X, The Mountains of the Gila headwaters. Proceedings of the Academy of Natural Sciences of Philadelphia 70: 282-333.

Pilsbry, H. A. and C. W. Johnson. 1898. A classified catalogue with localities of the land shells of America north of Mexico. Henry A. Pilsbry and Charles W. Johnson, Editors of The Nautilus, Philadelphia. [Reprinting of Pilsbry's list published in parts in The Nautilus, 1897-1898, with corrections.]

Randle, T. 1992. EIS update. Colorado River Studies Office Newsletter 5: 5.

Sellers, W. D. 1960. (ed.) Arizona climate. Institute of Atmospheric Physics, University of Arizona, Tucson.

Sellers, W. D. and R. H. Hill. 1974. (eds.) Arizona climate, 1931-1972 (rev., 2nd ed.). University of Arizona Press, Tucson.

Spamer, E. E. 1990. Bibliography of the Grand Canyon and the lower Colorado River; from 1540. Grand Canyon Natural History Association Monograph 8.

Spamer, E. E. 1992. Geology of the Grand Canyon: An annotated bibliography with an annotated catalogue of Grand Canyon type fossils. Vol. 5. Geological Society of America Microform Publication 23.

Spamer, E. E. In press. The Grand Canyon fossil record; a source book in paleontology of the Grand Canyon and vicinity, northwestern Arizona and southeastern Nevada. Geological Society of America Microform Publication 24.

Spamer, E. E. and A. E. Bogan. In press. Mollusks of the Colorado River corridor, Grand Canyon, Arizona; with an overview of mollusks of the Grand Canyon region. *In* D. W. Blinn, L. E. Stevens, and J. P. Shannon. The effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. U.S. National Park Service report (NPS Cooperative Agreement No. CA-8009-8-0002).

Stearns, R. E. C. 1890. Scientific results of explorations by the U.S. Fish Commissions steamer Albatross. No. XVII.—Descriptions of new West American land, fresh-water, and marine shells, with notes and comments. Proceedings of the U.S. National Museum 13: 205-225.

Stevens, L. 1987. The Colorado River in Grand Canyon; a guide (3rd ed.). Red Lake Books, Flagstaff, Arizona.

Stone, J. L. and A. B. Queenan. 1967. Tailwater fisheries investigations; creel census and limnological study of the Colorado River below Glen Canyon Dam; July 1, 1966-June 30, 1967. Arizona Game and Fish Department report.

Stone, J. L. and N. L. Rathbun. 1968. Tailwater fishery investigation; creel census and limnological study of the Colorado River below Glen Canyon Dam; July 1, 1967-June 30, 1968. Arizona Game and Fish Department report.

Stone, J. L., and N. L. Rathbun. 1969. Tailwater fisheries investigations; creel census and limnological study of the Colorado River below Glen Canyon Dam; July 1, 1968-June 30, 1969. Arizona Game and Fish Department report.

Szabo, B. J. 1990. Age of travertine deposits in eastern Grand Canyon National Park, Arizona. Quaternary Research 34: 24-32.

Tainter, S. L. 1947. Apex Copper property, Coconino County, Arizona. U.S. Bureau of Mines, Report of Investigations RI 4013.

Te, G. A. 1978. A systematic study of the family Physidae (Basommatophora: Pulmonata). Unpublished Ph.D. dissertation, University of Michigan.

Tomko, D. S. 1976. Dietary characteristics of some amphibians and reptiles. Pages 45-60 *in* S. W. Carothers and S. W. Aitchison, eds. An ecological survey of the riparian zone of the Colorado River between Lees Ferry and the Grand Wash Cliffs, Arizona. Colorado River Research Program, Report Series, Grand Canyon National Park, Technical Report 10.

Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson, and J. D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. American Fisheries Society Special Publication 16.

U.S. Department of the Interior. 1988. Glen Canyon Environmental Studies Final Report, January 1988. U.S. Department of the Interior.

U.S. Geological Survey. 1987. The national gazetteer of the United States of America—Arizona 1986. U.S. Geological Survey Professional Paper 1200-AZ.

U.S. National Research Council, Commission on Physical Sciences, Mathematics, and Resources, Water Science and Technology Board, Committee to Review the Glen Canyon Environmental Studies. 1987. River and dam management: a review of the Bureau of Reclamation's Glen Canyon Environmental Studies. National Academy Press, Washington, D.C.

APPENDIX 1

Field Notes of Henry A. Pilsbry Grand Canyon, 13-30 October 1906

The Department of Malacology, Academy of Natural Sciences of Philadelphia, holds many volumes of field notes by Henry A. Pilsbry. While sometimes wanting in precise information, these are valuable records of his itineraries, activities and observations of conditions at some collecting sites. One volume, written in pencil, contains the record of his trip across the Grand Canyon with James H. Ferriss, in October 1906; it has never been quoted. Editorial remarks appear within square brackets, and numbered notes appear at the end of this appendix. Rules are as drawn across the page by Pilsbry. Bars (I) indicate page breaks.

The back page of this notebook includes a labelled sketch showing the geologic cross-section of the Grand Canyon as known to Pilsbry. The geologic formations of the canyon are central to travel and identification of location within the canyon; so much so that even hikers learn the stratigraphic terminology. The stratigraphic terminology in Pilsbry's notebook is typical for the turn of the 19th-20th centuries, but not very precise even in contemporary perspective. Perhaps the data were as given by William Wallace Bass, who as a miner had a modest but nontechnical working knowledge of the relationships of the Grand Canyon's strata. A transcription of unit names as presented in Pilsbry's notebook, and their modern equivalents, follows:

"Cherty limestone" [~Kaibab Formation].

"Upper Aubrey limestone" [~Toroweap Formation].

"Crossbedded sandstone" [Coconino Sandstone].

"Lower Aubrey Sandstones (red)" [Hermit Formation and Supai Group].

"Redwall limestone" ["sandstone" originally written] [Redwall Limestone, Temple Butte Limestone, and(?) Muav Limestone].

"Lower Carboniferous Sandstone" [perhaps the Muav Limestone; Bright Angel Shale and Tapeats Sandstone].

"Quartzite base of Carboniferous" [Unkar Group?]. [No direct mention is made in Pilsbry's field notes, or by Pilsbry & Ferriss (1911), of the middle Proterozoic Unkar Group, a series of block-faulted strata that dip to the northeast and are unconformably beneath the Paleozoic Tapeats Sandstone and unconformably above the early Proterozoic Vishnu Schist. The lower part of the Unkar Group composes the walls of most of lower Shinumo Creek, and it is in these strata that W. W. Bass had his mines. A prominent stratum of this group is the Shinumo Sandstone, marginally a sandstone or a quartzite. Reference to these strata as the "base of the Carboniferous" is a geologically unappropriate generalization; the term is based upon the observation that they are mostly sedimentary units, like the horizontally-bedded Paleozoic strata that comprise the greater part of the Grand Canyon's walls, and contrary to the metamorphic basement beneath these strata. (See also note 6 of this appendix.)

"Archaean" [Vishnu Schist and related rocks].

Field Notes

Sat. Oct. 13 /06.

Arrived at Williams after Canyon train had left. Sunday went up Bill Williams mountain. Just below in in [sic] Aspens found Vitrina alaskana under damp stones, somewhat numerous. Higher up, + up to within 1/2 mile of summit found Vallonia, Thys. ingersolli?, Pupilla blandiana Pyr. striatella etc. No trace of Oreohelix or larger shells. Rock is a sort of hard conglomerate. not stratified, + probably volcanic or Cambrian. At top there seems to be some stratified rock.[1]

Vitrina is much less voluminous than V. limpida. the only shell lobe is a I small one at suture

[sketch] thus

Tail does not project behind the shell. Many composites still in bloom, but flowers mostly frost killed. Thin ice formed Sunday morning, but soon warms up in the sun.

Arrived at Bass Camp, at rim of Canyon Oct. 16. Found Sonorella under low white sandstone rocks at Bass Sta. At Camp, we coll. Pupilla etc., Sonorella + Oreohelix on talus ca 200 ft below rim.

Oct 17 went down around 1st I Amphitheatre of trail, + at S.E. side of its head, under the great white ["cross-bed" inserted here in ink] lime + <u>sandstone</u> cliff,[2] the talus runs over the sandstone, covering it rather thickly. It is covered with humus + shrubs (deciduous), one like currant bush, others very thorny, like osage orange. here among moss + grass, + under + around stones, found <u>Oreohelix y profundorum</u>[3] very common. Very few Sonorella, but Cochlicopa, Pupilla etc. Got a lot of dist. This place is 800-1000 ft below rim.. Then crossed over the Leconte plateau [LeConte Plateau] to Huethawalee Butte [Mount Huethawali], which is whitish sandstone over red sandstone of the plateau.[4] Found it very dry. No shells whatever. I

Oct. 18. Cleaned up in morning. p.m. went to small amphitheatre W of Bass Camp, + about 1/2 to 3/4 mile W. of top of trail. Here found Succinea, Euconulus, a few dead Pupilla, Sonorella + Oreo. All on upper talus, 1-300 ft. below rim.

Oct. 19. to Springs about 2 miles W of Bass trail. They seep out at base of crossbedded sandstones On talus below, found Sonorella, Vitrina, Cochlicopa etc.

Oct 20 Went down trail to River. At about 5000 ft found Sonorella bones [dead shells] under slabs of red sandstone.

	~~3824~~
top of red wall limestone	4364. ft
base (little below of do.	3824

| found Sonorella again, few bones, below redwall limestone in talus of do. about 3000 ft.

River here 260 ft across at waters edge—a sullen turbid yellow stream, in a canyon of dull purplish rock, perhaps 200 ft deep + 3-400 ft wide. There is a little sand in places, + some much-worn rounded drift-wood, lodged in crevices

Bench-mark	US Geol Surv.	low water—	2200 ft
"		high "	2230 ft
"		to bottom of river	2147 "

Vegetation here, except for a few cacti, the mesquite + larger Opintias [sic], is about the same as on upper taluses, but sparser.[5] |

Oct 21. Crossed to camp on Shinumo Creek.

Oct 22. Went up Shinumo Cr. found banded Sonorella in talus of angular granite stones[6] on S. side of Cr., not far above camp. Further up got stone-colored gray frog[7] + tadpoles. Frogs rather stupid + easily caught. do. tadpoles. Followed left tributary to Creek—a small stream—about 1 mile up. It zigzags in granite walls, with here + there a talus. Found bandless Sonorella in taluses on S. side—flatter + larger apert. than banded one from the large creek. All day we found Thys. horni + a few Succinea.

[On reverse of this page is the following:]

Very cold here last night—could not have been much above freezing but warmer today. Canyon so deep the sun does not get in except a few hours a day. |

[Here was found a photograph between leaves of the notebook; legend on reverse reads, "White Creek Grand Cn." It illustrates a view upstream in the cobble-strewn dry creekbed. An unidentified figure appears in the middle ground.]

Oct. 23. Went down creek to mouth, + Ferriss fished without success. Creek enters the granite iron-colored like river gorge. Camp is about one mile from the river. No snails but Succinea + a few Thys. horni. Found cat tails + rushes near creek, also Fireweed. The erect, large-leaved Opuntia is particularly fine. Returned to camp to lunch, + in pm. went up to junction of left branch with Creek. This is fully a mile above camp. Here we took minnows from a pool near the creek. Also got 1 small red-wasted [sic] frog or toad near the creek + several of the gray frog. The latter varies in tint | + distinctiveness of markings. It is bright yellow along sides where belly joins the sides. They cling close to vertical rocks + are easily caught thereon, but take to water freely if alarmed. All rocks we have found snails in along creek here are the steeply tilted granitic with veins of quartz + often porphyretic [sic] or conglomerate, with strata of pebbles. Taluses are apparticularly angular hard rock, sharp to handle. Camp is probably 2-300 ft above river level. Left branch of creek may be 100 ft higher. It is very narrow, with iron-like, subvertical sides + few steep ~~terraces~~ taluses. |

This morning it was	44° F.
noon, in tent	54°
7 pm.	62°

Oct 24. Went up left branch (= White Creek) to amphitheatre. It passes out of granite //// into level bedded sandstone. then opens into a grand amphitheatre bounded by the Red Wall. We spent night on talus of latter, + coll thin, hardly lipped Sonorella there. Also V. indentata. The veg. is quite diff—oaks + manzanita etc found maidenhairs in canyon of cr. Returned evg. of Oct 25 Caught mice + skinned 6.[8] Plenty of frogs on White Creek. | Got letters from Adeline.

Oct 26: Returned to Bass Camp.

" 27. Collected in cove to the right of trail below crossbed sandstone "head of Starvation Tank wash.["] Talus is overgrown with shrubbery, but no pinions [piñon trees], though below it is covered with them. There is an oak of the white oak group here, mostly very scrubby. Found Sonorella in abundance, not deep.

Returned to trail cove. I went up on talus about 4-500 yd. W. of head of cove, where pinions abound. Found Sonorella where pinon [sic] thins out, in abundance. Oreohelix was found about 200 yds W. of head of canyon. Only one or two. This is near mouth of the bay |

[sketch map][9]

Thus. The dead ones increase in quantity eastward, but I could find no live ones until last segment of talus, which is ca 30-40' high + about 100 long, with a great rock in middle [see Note 9]. This is nearly opposite the zigzag stairs by which trail descnds [sic] the crossbed sandstone. |

These taluses of crossbed overlie red sandstone + cover it where we worked, thus —

[sketch]

In Mojave Canyon [Muav Canyon]—amphitheatre above head of White Creek—there is much greasewood + holly-leaved oak, no white oak. This is at base of the Redwall, on its talus. ~~which~~ |

[sketch][10] |

Oct 28 Feathery shrub is called buck brush or Forget your troubles. Said to have properties of cinchona. Went from Camp to Bass Station, + later to Grand Canyon [Grand Canyon Village].

Oct 29 Monday. [On Bright Angel Trail.] Worked on cherty limestone talus [Kaibab and Toroweap Formations], from about 75 to 350 ft below rim, which is here 6866 ft above sea level Above found sinistral Pupilla + Oreohelix, V. indentata + Euconulus at 300 ft the Oreo. are scarce but Sonorella sets in, + V. indentata is common, Pupilla rare. The talus is very steep but well covered with vegetation. Our work was in area covered by zigzags of the BA Trail [sketch] thus. I

to the right of trail, along the crossbed sandstone the Oreo. have a tendency to descending last whorl. This near base of the X bed sandstone. Along cliff talus to the right there are dead Oreo + Sonor., the former not descending, but could find no live ones.

Trail runs down a rift in X-bed, filled with talus of limestone + at sides, esp. below, some sandstone

[sketch] Thus.

Oct 30 Tuesday. Returned to Williams. Collected above large dam (left) this p.m. found Conulus [sic], V. indentata Z. arborea + one minute Pupa. at low altitude, under + around walpai rock, chiefly among aspens. Enroute now for Albuquerque.

Notes:

[1]Bill Williams Mountain is a volcanic peak. The reference to stratified rock near the top may refer to stratified deposits of ash or pumice. Pilsbry had no geological training.

[2]The cross-bedded sandstone referred to throughout the journal is the Coconino Sandstone, a cliff-forming formation. Overlying it are the Toroweap and Kaibab Formations (ascending) that are limestones, generally. Talus from the Kaibab and Toroweap accumulates on slopes of the slightly more easily eroded Toroweap, and beneath the Coconino cliff.

[3]Pilsbry had written *y. profundorum* in ink over the original pencilled text, which had read *Oreohelix s. bassiana*. He clearly had originally believed this to be a form of *O. strigosa* and had intended to name a taxon for William Wallace Bass, but that name is in manuscript form only.

[4]Mount Huethawali is capped by the light-colored Kaibab, Toroweap, and Coconino Formations.

[5]Here was evidence for Pilsbry of being in the Lower Sonoran Life Zone.

[6]The "granite" referred to by Pilsbry here and later in his field notes is a curious term. Colloquial Grand Canyon terminology, particularly at the turn of the 19th-20th centuries, sometimes referred to the metamorphic rocks and associated intrusives of parts of the inner gorges of the canyon as "granite," although in fact these rocks are schist, gneiss, granodiorites, and pegmatites mostly. In the Shinumo Creek area, only minor amounts of granitic rocks are exposed, then only near the Colorado River near Bass Rapids, where travelers saw them when they crossed the Colorado on Bass's cable car. Pilsbry's references to granites further up Shinumo and White Creeks is an uncertain term; there are none of these rocks there. He may have referred to the Unkar Group of strata, which dip to the northeast. Exposed in this group are are (stratigraphically ascending) the Bass Limestone, a diabase sill (an intrusive igneous rock), Hakatai Shale, Shinumo Sandstone, and Dox Formation. None of these formations are particularly metamorphic in gross appearance; in fact they are quickly recognizable as sedimentary units (except for the massive diabase sill). Pilsbry may have used a generalized term, incorporating all of the rock formations beneath the Great Unconformity (the stratigraphic break at the base of the horizontal, Paleozoic Tapeats Sandstone) in the undifferentiated term, "granite." This supposition is substantiated by his entry of 24 October, where he observed that he had passed from the "granite" into "level bedded" sandstone in lower White Creek; here one does pass across the Great Unconformity, from the Dox Formation into the Tapeats Sandstone, as one ascends the creek. (Geologic map of eastern Grand Canyon, Huntoon et al. 1976.)

[7]Frogs are noted in several places in Pilsbry's field notes; however, he did not indicate that he had collected any specimens. ANSP holds several lots of alcohol-preserved frogs and toads given by Pilsbry; they all are indicated to be from Shinumo Creek, but the locality could have been generalized for the purposes of convenience. These specimens are in the ANSP collections as *Bufo punctatus* Baird & Girard, the Red Spotted Toad, a cosmopolitan species in the Grand Canyon region (ANSP 17532, Department of Herpetology), and *Hyla arenicolor* Cope, the Canyon treefrog, a species restricted to the inner canyon in this part of Arizona (ANSP 17533-17564).

[8]This probably refers also to the "thousand mouse camp" mentioned in Ferriss's (1910) letter to Pilsbry. Six skulls are present in ANSP collections (ANSP 21758-21763, Department of Mammalogy); the accompanying label reads, "Skulls of skinned *Peromyscus*, Shinumo Creek, Grand Canyon, Ariz[.]; H. A. Pilsbry!". One skull, labelled "mouse 1," is dated "Oct 21," and the others are not dated. Despite the discrepancy between this date and the date of his field notes entry, note that Pilsbry had crossed the river to the Shinumo Creek camp on 21 October. There also are alcohol-preserved specimens of *Peromyscus* sp., ANSP 12324-12333 (Department of Mammalogy); the accompanying label reads, "*Peromyscus*; Shinumo Creek, north side of Grand Canyon, opp. Mystic Spring Trail [i.e. on opposite side of river from South Bass Trail], Coconino Co., Arizona. Oct-Nov. 1906; H. A. Pilsbry!"

[9]This sketch map delineates the relative locations of South Bass Trail, the contour of the local cliff face,

and the following observations: "live Oreohelix," "all dead," "last dead ones," and, in so-called Starvation Tank Wash, "Sonorella terrace."

[10]This sketch was redrawn and printed by Pilsbry & Ferriss (1911, fig. 5) to illustrate the type locality of *Oreohelix yavapai profundorum*. The sketch appears in Pilsbry's field notes two pages after mentioning it in the text. The field notes include labels that were not reproduced, including "Oreohelix alive" (at mound on left), "no pinions. Brush Oreo dead" (from left-hand mound to second less well-defined mound along base of cliff of Coconino Sandstone), "Oreo to about here" (at right-hand side of the second less well-defined mound), "a few pinions" (to left of boulders in middle of talus slope), and "pinions" (to right of same boulders). The little trees drawn by Pilsbry on the published illustration appear in the notebook only on the smaller talus slope on top of the Coconino cliff.

APPENDIX 2

Voucher Specimens for Survey Conducted for Glen Canyon Environmental Studies Grand Canyon National Park

All specimens were collected as part of the Glen Canyon Environmental Studies. Data for all lots have been entered into the computerized database in the Department of Malacology, ANSP. Six-digit numbers are specimens in the dry collection; numbers with the prefix "A" are in the alcohol-preserved collection. Selected specimens from several lots are retained in the collections of the University of Colorado Museum (UCM), at Boulder, as voucher specimens for anatomically-based identifications provided to the authors; these lots are preserved as alcohol-preserved and corresponding dry lots (S.-K. Wu, pers. comm. 1992). Non-molluscan specimens cited in this paper are retained in the ANSP General Invertebrates Collection, in the care of the Department of Malacology.

BIVALVIA: VENEROIDA

SPHAERIIDAE. *Pisidium variabile* Prime: 391072, 391073. *P. walkeri* Sterki: A16155, A16156.

GASTROPODA: BASSOMATOPHORA

LYMNAEIDAE. *Fossaria obrussa* (Say): A16162, A16163; 391079. PHYSIDAE. *Physella* sp.: A16148-A16151, A16153, A16154, A16178-A16210, A16212, A17370, A17372, A17375; 391066, 391071, 391074, 391075, 391084; UCM 37253 (ex ANSP A16187), 37256-37258 (ex ANSP A16196, A16199, A16203, respectively). BASSOMATOPHORA indet. (protoconchs only, ?Physidae): A16160.

GASTROPODA: STYLOMMATOPHORA

COCHLICOPIDAE. *Cionella lubrica* (Müller): A16161; 391076. PUPILLIDAE. *Gastrocopta pellucida* (Pfeiffer): 391080. DISCIDAE. *Discus cronkhitei* (Newcomb): 391081, 391082. SUCCINEIDAE. *Catinella avara* (Say): A16152, A16172-A16177, A16211, A17371, A17373, A17374; 391068, 391085, 391087, 391096-391099; fossil or subfossil shells: 391070, 391086, 391095. *Oxyloma haydeni kanabensis* Pilsbry: A16168-A16171; 391067, 391069, 391083, 391093, 391094; UCM 37254 (ex ANSP A16169), 37255 (ex ANSP A16171). ZONITIDAE. *Glyphyalinia indentata* (Say): 391078. *Hawaiia minuscula* (Binney): A16164-A16167. *Zonitoides arboreus* (Say): 391077. LIMACIDAE. *Deroceras laeve* (Müller): A16158, A16159, A16767. OREOHELICIDAE. *Oreohelix strigosa* (Gould) [as cataloged; cited as *O. s. depressa* (Cockerell) in the present paper]: A16157; 391090-391092. HELMINTHOGLYPTIDAE. *Sonorella coloradoensis* (Stearns): 391088, 391089.

POSTSCRIPT

The final ruling designating *Oxyloma haydeni kanabensis* Pilsbry, 1948, as endangered has been published (J. L. England, 1992, Federal Register 57(75): 13657-13661).