Late Pleistocene(?) Land Snails (Mollusca: Gastropoda) in "Red Earth" Deposits of the Grand Canyon, Arizona

EARLE E. SPAMER
Academy of Natural Sciences of Philadelphia
1900 Benjamin Franklin Parkway
Philadelphia, Pennsylvania 19103-1195

ABSTRACT — The Late Pleistocene-Holocene (<40,000 yr B.P.) fauna and flora of the Grand Canyon, northwestern Arizona, are well documented. A malacofauna in this time and place, however, is conspicuously absent from the scientific literature. Some remarks in the literature on Recent mollusks pertain to gastropod shells (Pulmonata: Stylommatophora: Succineidae and Oreohelicidae) from the Grand Canyon that could be Late Pleistocene in age. The shells occur in colluvial deposits whose fine-sand and silt fractions are made up of oxidized iron minerals eroded from red-bed strata of shales and sandstones. The spackled, sediment-encrusted appearance of the shells, taken with considerations of slow erosional processes in this dry environment of the inner canyon, provide circumstantial evidence of significant age of the shells. The known data on occurrences of "red earth" shells are summarized here; illustrations of the fossil or subfossil specimens, and comparable Recent specimens from the Grand Canyon, are also provided. Aspects of the shells and matrix are discussed, and implications to paleoenvironmental conditions are made. Two additional taxa in the Oreohelicidae and Cochlicopidae are added to the list of shells from the Grand Canyon "red earths." More such deposits of shell-bearing "red earths" undoubtedly are to be found throughout the canyon; their discovery and study can provide additional data on Late Pleistocene-Holocene paleoclimates of the Grand Canyon.

Introduction

THE COMPOSITION and distribution of the Late Pleistocene-Holocene (<40,000 yr B.P.) fauna and flora of the Grand Canyon, northwestern Arizona (Fig. 1), is well studied (see extensive listings in Spamer, 1984, 1990, 1992b, 1993). Most of these fossil and subfossil remains occur in caves and rock shelters; they are frequently found in uriniferously indurated middens of packrats (*Neotoma* spp.). Other remains are the remnants of prey items left by mammalian and avian predators; many such remnants are preserved in the dung or pellets of these predators. Comparably, the dung of herbivores is a rich trove of floral remains of the immediate area. Together all of these fossils and subfossils preserve the record of changing climates in the Grand Canyon region before, during, and after the last glaciation of North America. Interpretations of this fossil record, coordinated by radiometric dating, show changes to the elevational distribution of plant communities in the Grand Canyon since Late Irvingtonian time. (For an especially well-documented study of paleoclimates and fossil assemblages at one Grand Canyon site, see Euler, 1984.)

Until recently, the fossil record of the Pleistocene-Holocene fauna of the Grand Canyon was restricted to vertebrates—mammals, birds, fish, reptiles, and amphibians. Invertebrates only recently have been reported from this portion of the Grand Canyon fossil record: Elias et al. (1992) have described arthropods—insects and arachnids mostly—from two caves in the eastern Grand Canyon.

Fossil mollusks—land snails specifically—have not been reported from the Grand Canyon Pleistocene-Holocene, despite the high degree of preservability of shell material and the generally taphonomically favorable environmental conditions in the usually warm, dry inner canyon. This is outwardly curious, as the modern land snail fauna of the Grand Canyon is abundant (Pilsbry and Ferriss, 1911, and Spamer and Bogan, 1993). The absence of these animals from cave deposits could be explained by the presumption that they would not wander far into dark caves, away from water and food. Even so, their remains also are conspicuously absent from reports on the contents of the dung and pellets of predators who did venture into the caves. Either the shell fragments have not been recognized in the dung, or, more probably, the sample size of dung has been insufficient to find the infrequently-eaten snails. The position of snails in the trophic food web of the canyon is unknown. They are herbivorous creatures, but what role their bodies and excreta play in the overall scheme of favored nutritional items is not documented. Generally speaking, the role of arid-climate land snails as prey items is presently poorly known (*e.g.*, Heller and Safriel, 1992).

Several reports between 1921 and 1939 have described or casually mentioned shells of the family Oreohelicidae found in "red earth" at a couple of locations in the Grand Canyon. These brief accounts nebulously defer pronouncement on the age of these specimens, only suggesting that they are "Pleistocene" and pragmatically group them as extirpated races of the modern malacofauna. The determinations of age were strictly by the outward appearance of the shells, and the fact that the shells were buried. Spamer (1992a, p. 83) first referred these earlier reports to the paleontological record, without comment. Spamer and Bogan (1993) briefly discussed these occurrences, and reported a newly found deposit containing shells of the family Succineidae. The opportunity is taken here to more fully describe all the known occurrences of Grand Canyon "red earth" shells, to introduce new records, and to provide illustrations of the Pleistocene(?) shells and comparable Recent forms from the canyon.

Repository abbreviations used in this paper are: ANSP—Department of Malacology, Academy of Natural Sciences of Philadelphia; USNM—Division of Mollusks, National Museum of Natural History, Smithsonian Institution. Common names and familial relationships referred to in this paper are as listed by Turgeon et al. (1988).

Reports of Shells in "Red Earth"

The literature on snail shells of the "red earth" in the Grand Canyon is sparse and based on relatively few specimens. Some of the early reports are so sketchy as to provide only general guidelines toward understanding the occurrences.

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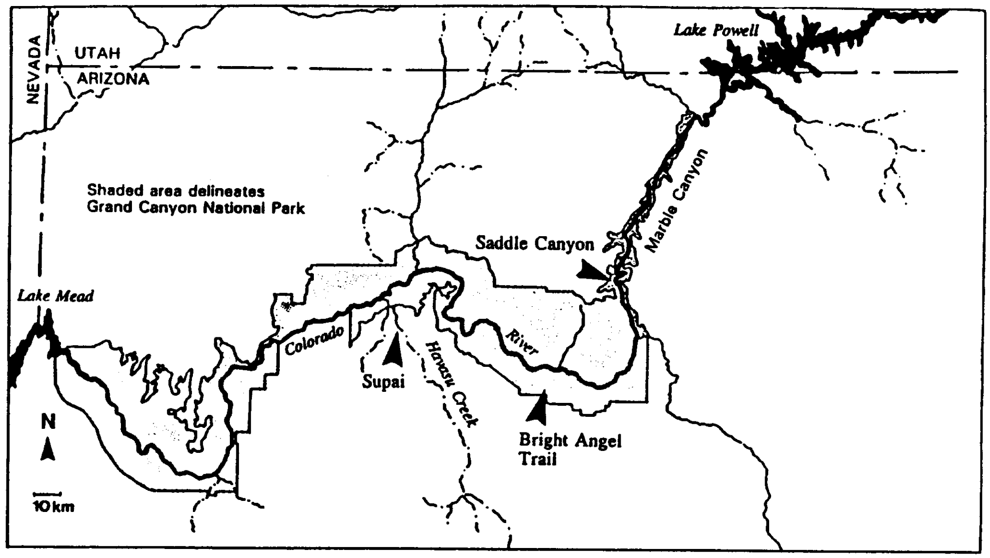

Figure 1. Map of the Grand Canyon area, northern Arizona, showing fossil localities mentioned in the text.

Oreohelix (Gastropoda: Oreohelicidae)

The first collection of shells from the "red earth" of the Grand Canyon were oreohelicids from upper Bright Angel Trail, found by James H. Ferriss in 1917. However, these specimens were not mentioned in the literature until Pilsbry (1934, p. 402) made passing reference to them.

Cockerell (1927, p. 101) named a new subspecies of *Oreohelix* from the Grand Canyon, *O. yavapai fortis* Cockerell, 1927. He systematically placed these shells under *O. yavapai* Pilsbry, 1905 based on shell characters and their geographic occurrence in an area (south of the Colorado River) in which the Oreohelicidae were at that time thought to be represented only by forms or subspecies of the Yavapai mountainsnail, *O. yavapai*. He reported:

> Last summer on the Bright Angel trail, in the Grand Canyon of Arizona, 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; but any one could doubtless collect a series, given longer time. The shells have in general the characters of *O. y. extremitatis* P. & F. but are much larger . . . .

The type locality of *O. y. fortis* is not known with any more precision than the greater portion of the upper half of Bright Angel Trail, which extends over an elevational change of about 3,000 ft [914 m], immediately north of Grand Canyon Village (see Figs. 2 and 3) in Grand Canyon National Park. The living oreohelicid of this area, from higher up on Bright Angel Trail, was originally named *O. y. angelica* by Pilsbry and Ferriss (1911), which Pilsbry (1939) later synonymized with *O. y. extremitatis* Pilsbry and Ferriss, 1911, another Grand Canyon subspecies whose type locality is also in the national park, at the head of Bass Trail about 16 miles [25.7 km] to the northwest of Bright Angel Trail. Pilsbry's synonymization of these two subspecies is corroborated by Bequaert and Miller (1973).

Marshall (1929, pp. 1-2) described another subspecies of *O. yavapai* from the Grand Canyon, *O. y. vauxae* Marshall, 1929, like *O. y. fortis* based on shell characters and geographic occurrence:

> The study of a collection of *Oreohelix* made by Mrs. Mary Vaux Walcott in the canyon at Supai, Coconino County, Ariz., in 1928, and presented by her to the United States National Museum, not only proved that they belonged to a new subspecies, but their examination entailed a close scrutiny of forms long since contained in our collection but not previously studied.
>
> * * *
>
> The specimens appear to be fossil or subfossil, because of the reddish mineral matter coating them in spots. This shell is evidently a subspecies of *Oreohelix yavapai* Pilsbry, the type of which comes from Yavapai County, which adjoins Oconino [*sic*] County. It is much larger than *Oreohelix yavapai* but has essentially the same sculpture.

Mrs. Mary Vaux Walcott was the second wife of the preeminent paleontologist and pioneer Grand Canyon geologist, Charles D. Walcott. The type locality of *O. y. vauxae* is near the village of Supai, on the Havasupai Indian Reservation in the lower reaches of Cataract Canyon, 35 miles [56.3 km] northwest of Grand Canyon Village and Bright Angel Trail. Unfortunately, data about the precise location of the occurrence are not available. We can assume that it was not far from Topocoba Trail, the sole access route to Supai either from the canyon rim or from the Colorado River.

It should be noted that Marshall's reference to the adjoining Yavapai County is somewhat misleading. The type locality of the nominate *O. y. yavapai* is along Oak Creek, which is a tributary to the Verde River more than 100 miles [161 km] to the southeast of Supai.

Pilsbry (1939, pp. 523-524) reidentified *Oreohelix* specimens from Bright Angel Trail that he earlier (Pilsbry, 1921) had called *O. strigosa depressa* (Cockerell, 1890), now calling them *O. yavapai fortis* Cockerell, 1927. Pilsbry's (1921) original report mostly quoted a letter from Hawaiian malacologist C. Montague Cooke, Jr., who collected the specimens:

> *Oreohelix s. depressa* (Ckll.). '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

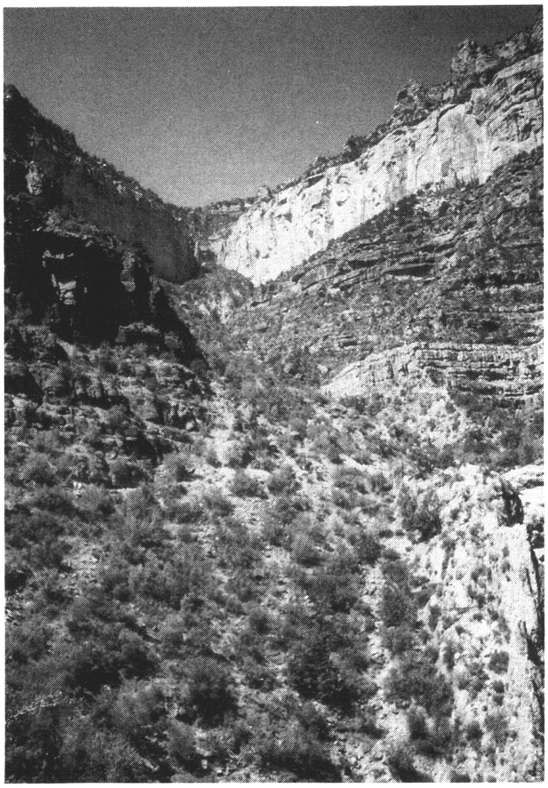

Figure 2. View southwestward on upper part of Bright Angel Trail, up the canyon of Garden Creek (which has no perennial water in this reach). The perspective is from a point in the lower part of the Supai Group, not far above Jacob's Ladder (see map in Fig. 3). This point is about 2000 feet (610 m) below the rim of the canyon; the altitude is about 4800 feet (1463 m). The type locality of *Oreohelix yavapai fortis* Cockerell, 1927 covers most of this view, up to the prominent light-colored cliff which is the Coconino Sandstone. The "red earth" colluvial sediments accumulate in the taluses and landslide deposits that lie across the Hermit Shale and Supai Group (the alternating slopes and cliffs in this view, below the Coconino). The true rim of the canyon is visible as the distant skyline through the center notch; the dipping appearance of the strata is an illusion of perspective due to the outcrops of horizontal strata following the topographic contour of Garden Creek. Garden Creek has developed in the fault zone of Bright Angel fault (down to the east, on left side of this photo, running through the notch). The trail bypasses the sheer cliffs by following landslides and rock falls in the fault zone. (Photo by Spamer, 4 June 1992.)

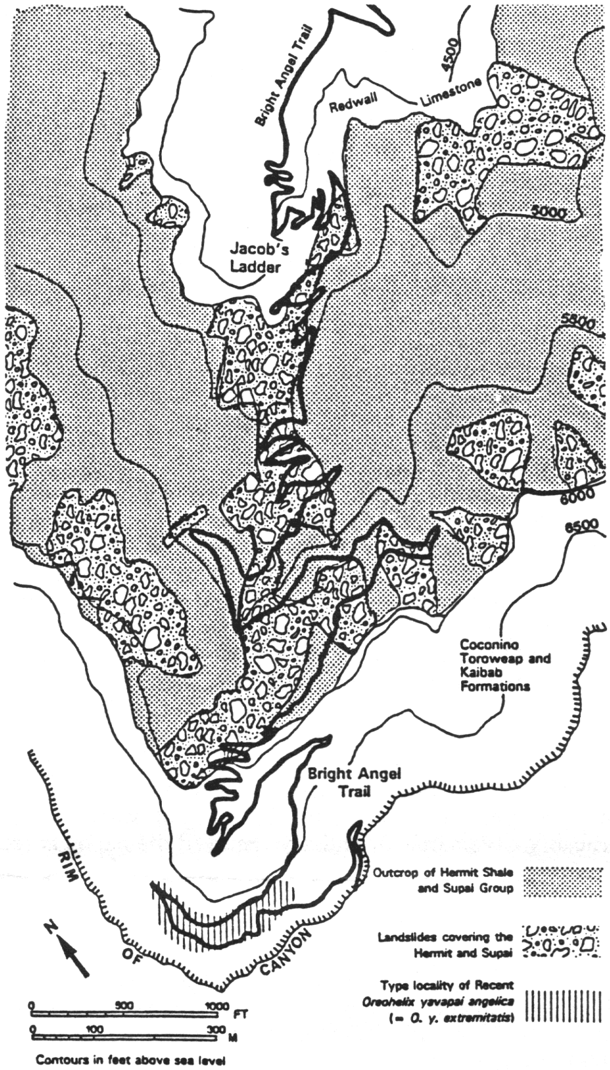

Figure 3. Map of upper Bright Angel Trail, showing the topographic expression of the area and the outcrop of the Hermit Shale (Permian) and Supai Group (Permian-Pennsylvanian) (after Washburn, 1981, and Billingsley and Breed, 1986). It is at the level of the Hermit-Supai strata where the "red earth" colluvial deposits have accumulated, mostly in landslide deposits that interrupt the outcrop pattern; these include limestone talus fallen from the Toroweap and Kaibab Formations near the canyon rim. The Redwall Limestone (Mississippian) crops out below the Supai (Jacob's Ladder). Immediately above the Hermit is the Coconino Sandstone, in turn overlain by the Toroweap and Kaibab Formations (all Permian). Most of the known specimens of *Oreohelix yavapai fortis* Cockerell, 1927 were found along the trail at the level of the Hermit and Supai. Subfossil specimens of *Oreohelix yavapai extremitatis* Pilsbry and Ferriss, 1911 came from the type locality of this subspecies' synonym, *O. y. angelica* Pilsbry and Ferriss, 1911, where the Kaibab and Toroweap crop out.

> the last pine on the trail, just below the foot of the high yellow cliffs. Dead specimens were seen along the trail to just below the part of the trail called Jacob's Ladder. Unfortunately, we were with a rather large party and I had a mule that wouldn't stop. I collected six specimens, which I am sending you, and saw 15 or 20 additional along the trail.'
>
> This species has been found high on the northern side of the Canyon, but not until now on the southern side.

The "yellow cliffs" are the upper cliff-forming rock formations, the lowest one of which is the Coconino Sandstone some 600-800 feet [183-244 m] below the rim (see Fig. 2). Pines, however, routinely occur along Bright Angel Trail down as far as the 4900-foot elevational contour [1494 m], 1900 feet [579 m] below the rim; and a few isolated trees can be found along the trail at elevations as low as 4250 feet [1295 m] (Washburn, 1981). Jacob's Ladder is where the trail descends through the sheer Redwall Limestone and accumulated talus 2100-2500 feet [640-762 m] below the rim.

Even though *O. strigosa depressa* is virtually restricted to the north of the Grand Canyon (Pilsbry and Ferriss, 1911; Bequaert and Miller, 1973; and see discussions in Spamer and Bogan, 1993), it has been identified anatomically from specimens collected south of the Grand Canyon (Bequaert and Miller, 1973). But it is apparent that Pilsbry (1939), by his reidentification of the Bright Angel Trail specimens, may have been unwilling to recognize *O. strigosa depressa* on the south side of the canyon, the area considered to be the realm of *O. yavapai*. To place the Bright Angel Trail shells in a taxon systematically related to a species known to occur on the south side (*O. yavapai*) would of course have been a more conservative pronouncement, one more in line with traditional systematic concepts of forms and subspecies of the time (*e.g.*, Cockerell, 1906).

The Cooke specimens from Bright Angel Trail also were mentioned in Hand's (1922, p. 127) travelogue of a malacological trip taken just a year after Cooke:

> Where he [Cooke] saw his fifteen or twenty we found several hundred, all dead. There is an immense dike of limestone here in the midst of the sandstone and snails must have recently flourished.

The "immense dike of limestone" may refer to the Redwall Limestone; otherwise it may refer to the abundance of limestone talus that litter the broad slopes below the Coconino Sandstone. The limestone component of this talus is derived from the Kaibab and Toroweap Formations that form the rim of the canyon.

In 1990 and 1992, I travelled down Bright Angel Trail and in 1992 particularly kept watch for shells eroding out of colluvium alongside the trail. None were seen by this cursory examination, which probably is no less thorough than were Cooke's and Hand's observations 70 years previously. Natural erosion along the trail, as well as trail maintenance and the great increase in traffic along it since the 1920s, probably have partly or entirely removed the deposits seen by Cooke and Hand.

Catinella (Gastropoda: Succineidae)

On 27 May 1991, while on a trip down the Colorado River I stopped at Saddle Canyon, a tributary on the western side of the Colorado River in the Marble Canyon section of Grand Canyon National Park. This is at Colorado River Mile 47.0 [Km 75.6], River Right, as measured by convention from Lees Ferry. This is a popular stop for river travelers, who ascend a trail to reach a shady, tree-lined narrows and a small waterfall about a mile [1.6 km] from the river. The trail climbs steeply from the river to a talus slope ca. 200-300 ft [61-91 m] higher, which it then follows until the grade of the creek in Saddle Canyon is met. In the first stretch there is no shelter and it can be quite hot in the sun. It is dry there, and a cryptogamic crust is seen on flat surfaces away from the much-used footpath.

During this visit, Mr. David Lyle reported that he had seen shells in the sediment at trailside, and I returned with him to investigate (see Fig. 4 for view at site). A few whole, somewhat weathered succineid shells were seen, and the area was noted for closer examination on a return trip in late July during the first malacological reconnaissance of the river corridor (Spamer and Bogan, 1993).

The shells occur in a reddish silt-like deposit that is a part of poorly sorted colluvium that fills a very weakly incised drainage in talus on the south side of the mouth of Saddle Canyon about 0.3 mile [0.5 km] from the Colorado River. The incision appears to be adjacent to the weakly developed drainage depicted by a small indentation seen in the 4000-foot [1219 m] contour on the 15′ topographic sheet of the area (Fig. 5). The reddish fine sand is intermixed with angular stones and pebbles and some dried vegetational debris, mostly twigs. The talus has accumulated below the Redwall Lime-

Figure 4. View at the discovery site of succineid shells in a "red earth" deposit at Saddle Canyon, Marble Canyon section of the Colorado River (see pointer in map, Fig. 5). The view is to the northeast, out of the mouth of Saddle Canyon toward the opposite wall of Marble Canyon. The Colorado River is visible as a dark line below the center of photo. The elevation here is about 200 feet (61 m) above river level, about 0.3 mile (0.5 km) from the river; the altitude of the locality is about 3200 feet (975 m). In the opposite wall is seen the contact between the Redwall (more massive, upper cliff) and Muav (more ledge-like, lower cliff) limestones. The talus along the trail in foreground overlies the Muav, and the large stones on this slope are mostly debris from the Redwall. Note the aridity of the locale and the scrubby desert vegetation. (Photo by D. Lyle, 27 May 1991; Spamer collection.)

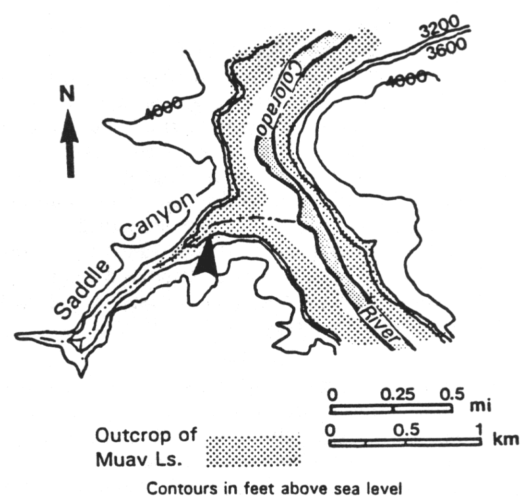

Figure 5. Map of the vicinity of the mouth of Saddle Canyon, showing the general topographic expression and (shaded) the outcrop pattern of the Muav Limestone (after USGS Nankoweap 15′ quadrangle, and Huntoon et al., 1986). The position of the fossil/subfossil succineid locality cited herein is indicated by the large pointer. The Redwall Limestone (Mississippian) overlies the Muav Limestone (Cambrian). The unshaded area at riverside shows where river gravels and the Saddle Canyon debris fan cover the Muav. Just downstream from Saddle Canyon is the contact between the Muav Limestone and Bright Angel Shale (Cambrian) beneath it. The major regional aquifer in the Muav is the result of impermeable beds in the lower Muav and in the Bright Angel.

stone, the principal formation of the walls of Marble Canyon along this reach of the Colorado River.

Blackened, dry moss covers some of the rocks in the area. However, there is no discernible water source in the area—intermittent or perennial—either beside the trail or on the cliff above it; yet the old, weathered shells are those of snails that depend on water being very close by. For further discussion of the age of these specimens, see the next section, on "Age."

Paleontology

The fossil-to-subfossil paleontological record for Mollusca of the Grand Canyon is updated here. For discussion of the age of these specimens, see the next section, on "Age."

Class Gastropoda
Subclass Pulmonata
Order Stylommatophora
Family Cochlicopidae
Genus *Cochlicopa* Férussac, 1821

Cochlicopa lubrica (Müller, 1774)

Discussion—A single specimen of this species was discovered on cleaning matrix from the aperture of a fossil or subfossil shell of *Oreohelix yavapai extremitatis* Pilsbry and Ferriss, 1911 (ANSP 158168, collected on uppermost Bright Angel Trail by J. H. Ferriss in 1921; Pl. 1, fig. K_2). (See also the discussion under *O. y. extremitatis*, below.) *C. lubrica* is widespread today in the Grand Canyon region (see Pilsbry and Ferriss, 1911; Pilsbry, 1948; Spamer and Bogan, 1993), and specimens were taken at this same locale (uppermost Bright Angel Trail; see Fig. 3) by H. A. Pilsbry and J. H. Ferriss in 1906 (ANSP 94082).

Family Succineidae
Genus *Catinella* Pease, 1870

Catinella cf. avara (Say, 1824). (Pl. 1, fig. M)
Catinella cf. *avara* (Say). Spamer (1992b, p. 1008).
Catinella cf. *avara* (Say). Spamer and Bogan (1993, pp. 59-60).

Only specimens referred to the paleontological record are included here.

Distribution—Vicinity of the south side of the mouth of Saddle Canyon, in erosional debris below the contact between the Muav and Redwall Limestones, Marble Canyon section of Grand Canyon National Park, Coconino County, Arizona (Fig. 4). Recent specimens have been collected from many localities throughout the Grand Canyon area (see Spamer and Bogan, 1993, p. 55).

Referred Specimens—ANSP 391070, 391086.

Discussion—Based solely on shell characters, arguments could be made that these specimens are one of two succineid genera, *Catinella* or *Succinea* Draparnaud, 1801. The shells were examined and identified as *Catinella* sp. by Dr. Shi-Kuei Wu (personal communication, 1992). Spamer (1992b) and Spamer and Bogan (1993) reported these specimens as *Catinella* cf. *avara* (Say, 1824) based upon comparisons with shell characters of the living suboval ambersnail, *C. avara* (identified anatomically), from Saddle Canyon (ANSP 391085; Pl. 1, fig. N).

Family Oreohelicidae
Genus *Oreohelix* Pilsbry, 1904

Oreohelix yavapai Pilsbry, 1905 (Pl. 1, fig. A)

Oreohelix yavapai fortis Cockerell, 1927. (Pl. 1, figs. B-D, G-J)
Oreohelix strigosa depressa (Cockerell, 1892). Pilsbry (1921, p. 48).
Oreohelix yavapai fortis Cockerell (1927, p. 101).
Oreohelix yavapai vauxae Marshall (1929, pp. 1-2, pl. 1, figs. 1-3, 11).
Oreohelix yavapai fortis Cockerell. Pilsbry (1934, pp. 402-403, pl. 15, figs. 1-6, 14).
Oreohelix yavapai fortis Cockerell. Pilsbry (1939, pp. 523-524, figs. 338.1-6, 338.14).
Oreohelix yavapai fortis Cockerell. Bequaert and Miller (1973, pp. 35, 129).
Oreohelix yavapai fortis Cockerell. Spamer (1992a, pp. 16, 83).
Oreohelix yavapai vauxae Marshall. Spamer (1992a, pp. 47, 83).
Oreohelix yavapai fortis Cockerell. Spamer (1992b, pp. 62, 354, 531, 786, 830, 928, 950).
Oreohelix yavapai vauxae Marshall. Spamer (1992b, pp. 97, 399, 531, 812, 830, 928, 983).
Oreohelix yavapai Pilsbry. Spamer (1992b, p. 1008).
Oreohelix yavapai Pilsbry. Spamer and Bogan (1993, pp. 60-61).

With the exception of *O. s. depressa*, the listed taxa are known only as fossils (or subfossils); all citations are listed here. For *O. s. depressa*, only specimens referred to the paleontological record (= *O. y. fortis*) are included here.

Types—*Oreohelix yavapai fortis* — Holotype ANSP 141875 (Pl. 1, fig. C herein) and paratype ANSP 371711 (the immature specimen cited by Cockerell, 1927; Pl. 1, fig. D herein). The holotype was figured (as "type") by Pilsbry (1934, pl. 15, fig. 1), and again by Pilsbry (1939, fig. 338.1), which Baker (1962, p. 9) apparently mistook as a lectotype designation. Because the original description (Cockerell, 1927) was based upon the "type and an immature specimen," we can clearly refer to a holotype and paratype.

Oreohelix yavapai vauxae — Holotype USNM 380687 (Pl. 1, fig. B), 14 paratypes USNM 380688.

Referred Specimens—ANSP 143691, containing the specimens figured by Pilsbry (1934, pl. 15, figs. 2-6; 1939, figs. 338.2-6) (and see others in Pl. 1, figs. G, H herein); these are from Ferriss's original collection of this taxon 1917, not cited until Pilsbry (1934) mentioned them. ANSP 158169, containing the specimen figured by Pilsbry (1934, pl. 15, fig. 14; 1939, fig. 338.14) (and see another in Pl. 1, fig. J herein), from Ferriss's 1921 collection. ANSP 128624, the specimens collected by C. M. Cooke, Jr. in 1921 (Pl. 1, fig. I); only five of the six originally cited (Pilsbry, 1921) are accounted for.

Type Locality—Upper part of Bright Angel Trail, where the Hermit Shale and Supai Group crop out or are covered by landslide debris, Garden Creek (no perennial water in this part of the tributary), Grand Canyon National Park, Coconino County, Arizona.

Distribution—Type locality, and vicinity of Supai, Havasupai Indian Reservation, Cataract Canyon, Coconino County, Arizona.

Synonymy—Pilsbry (1934, pp. 402-403) synonymized *Oreohelix yavapai vauxae* Marshall, 1929 with *O. y. fortis* Cockerell, 1927, commenting (p. 402): "Assisted by Prof. Junius Henderson I made a careful comparison of this Grand Canyon *fortis* with the type lot of *O. yavapai vauxae* from Supai, about 30 miles west-southwest [*errore*] of Grand Canyon. We were unable to detect any constant difference . . . ." He also noted, "Specimens from [Ferriss, Cooke, and Cockerell] . . . in the collection of the Academy show a considerable range of variation," and later (Pilsbry, 1939, p. 523) counted "over 80" such specimens although 71 are accounted for today.

Discussion—Once again, systematic identifications were based solely on shell characters. The shell forms of oreohelicids are especially variable, and today systematically precise and reliable identifications can be made only from anatomical or molecular investigations. While competent investigators are often able to make some identifications based only on shell characters, shell-form identifications are pragmatically best reserved for field identifications, as informal guidelines to species potential at the collecting site,

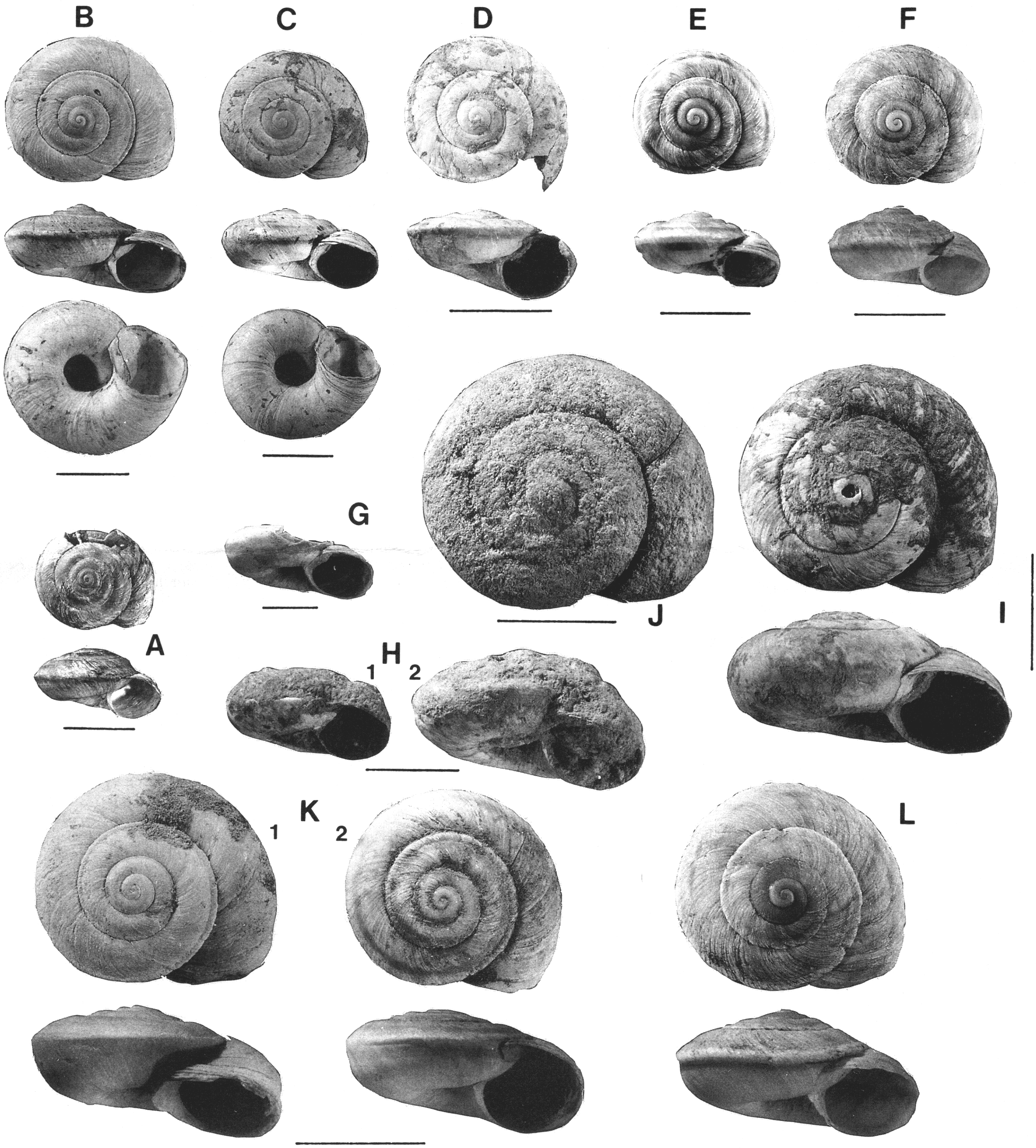
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Plate 1

Fossil or subfossil shells of the "red earth," and comparative Recent material from the Grand Canyon. Scale bars = 1 cm.

A. *Oreohelix yavapai* Pilsbry, 1905, LECTOTYPE (ANSP 79415); the nominate species for Grand Canyon subspecies, including the fossil or subfossil specimens discussed in this paper. RECENT. Purtyman's Ranch, Oak Creek, Yavapai County, Arizona; collected by E. H. Ashmun, 1900. Originally figured by Pilsbry (1905, pl. 25, fig. 53). The figured syntype was designated the lectotype by Pilsbry (1939, p. 518, fig. 339a). The shell is slightly damaged, but the hole reveals the desiccated remnants of the (incomplete?) body inside the final whorl. (The alcohol-preserved component of the original syntypic suite, a single body, is ANSP A12351; whether it belongs to the lectotype shell or one of the paralectotypes is not recorded.) × 1.30

B. *Oreohelix yavapai vauxae* Marshall, 1929, HOLOTYPE (USNM 380687) (= *O. y. fortis* Cockerell, 1927). FOSSIL OR SUBFOSSIL. Originally figured by Marshall (1929, pl. 1, figs. 1-3, 11. Vicinity of Supai, Havasupai Indian Reservation, Cataract Canyon, Coconino County, Arizona; collected by Mrs. Mary Vaux Walcott, 1928. × 1.32

C, D. *Oreohelix yavapai fortis* Cockerell, 1927, HOLOTYPE and PARATYPE. FOSSIL OR SUBFOSSIL. Upper part of Bright Angel Trail, in the outcrop belt of the Hermit Shale and Supai Group, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; types collected by T. D. A. Cockerell, Summer 1926. **C.** HOLOTYPE (ANSP 141875), originally figured by Pilsbry (1934, pl. 15, fig. 1; 1939, fig. 338.1). × 1.29 **D.** PARATYPE (ANSP 371711), an immature specimen not previously figured. × 1.86

E. *Oreohelix yavapai extremitatis* Pilsbry and Ferriss, 1911, LECTOTYPE (ANSP 103236). RECENT. Near Bass Trail, ca. 200 feet below canyon rim, Grand Canyon National Park, Coconino County, Arizona; collected by H. A. Pilsbry and J. H. Ferriss, 16 October 1906. Originally figured by Pilsbry and Ferriss (1911, pl. 12, fig. 18). Lectotype designated by Baker (1962, p. 8), based on syntype figured by Pilsbry and Ferriss (1911, pl. 12, fig. 18). × 1.65

F. *Oreohelix yavapai angelica* Pilsbry and Ferriss, 1911, LECTOTYPE (ANSP 103239) (= *O. y. extremitatis* Pilsbry and Ferriss, 1911). RECENT. Uppermost Bright Angel Trail, "100 to 400 feet below canyon rim," Garden Creek, Grand Canyon National Park, Coconino County, Arizona; collected by H. A. Pilsbry and J. H. Ferriss 29 October 1906. Originally figured by Pilsbry and Ferriss (1911, pl. 12, fig. 23). Lectotype designated by Baker (1962, p. 3), based on the syntype figured by Pilsbry and Ferriss (1911, pl. 12, fig. 23). × 1.68

G. *Oreohelix yavapai fortis* Cockerell, 1927. FOSSIL OR SUBFOSSIL. ANSP 143691. The largest surviving specimen in ANSP collections; a shell 25.8 mm in diameter (apertural view only; spire is missing). Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; part of the first collection of "red earth" shells in the Grand Canyon, by J. H. Ferriss, 1917. Mentioned by Pilsbry (1934, 1939) but neither figured nor cited by lot number, nor noted to be broken. × 1.0

H. *Oreohelix yavapai fortis* Cockerell, 1927. FOSSIL OR SUBFOSSIL. Two sediment-encrusted specimens from lot ANSP 143691; part of the first collection of "red earth" shells in the Grand Canyon, by J. H. Ferriss, 1917. Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona. Apertural views only, showing heavy encrustation mostly on upper surfaces of whorls. × 1.70

I. *Oreohelix yavapai fortis* Cockerell, 1927. FOSSIL OR SUBFOSSIL. The largest surviving specimen received from C. M. Cooke, Jr. (ANSP 128624). Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; collected by Cooke in 1921. Note also style of sediment encrustation. × 2.10

J. *Oreohelix yavapai fortis* Cockerell, 1927. FOSSIL OR SUBFOSSIL. ANSP 158169. A specimen illustrating heavy encrustation of top shell surface with carbonate cement. Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; collected by J. H. Ferriss, 1921. × 2.17

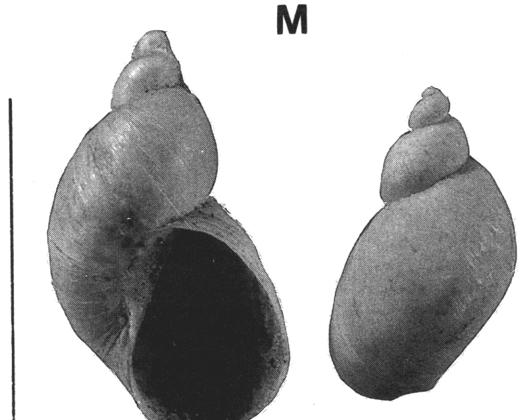
K. *Oreohelix yavapai extremitatis* Pilsbry and Ferriss, 1911 (originally identified as *O. y. angelica* Pilsbry and Ferriss, 1911). FOSSIL OR SUBFOSSIL. Two specimens (ANSP 158168). Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; collected by J. H. Ferriss, 1921. × 2.35

L. *Oreohelix yavapai extremitatis* Pilsbry and Ferriss, 1911 (originally identified as *O. y. angelica* Pilsbry and Ferriss, 1911). RECENT. ANSP 139110. Upper part of Bright Angel Trail, Garden Creek, Grand Canyon National Park, Coconino County, Arizona; collected by D. L. Emery, August 1925. × 2.35

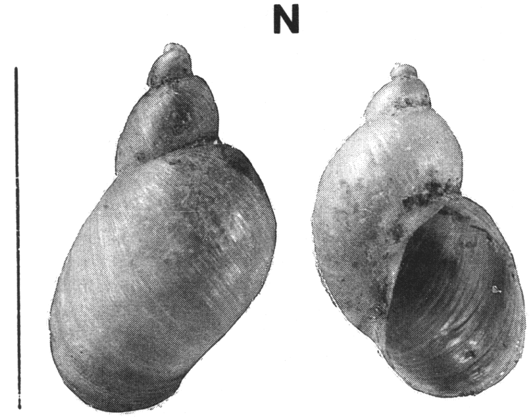
M. *Catinella* cf. *avara* (Say, 1824). FOSSIL OR SUBFOSSIL. ANSP 391086. Saddle Canyon Trail, Saddle Canyon, Grand Canyon National Park, Coconino County, Arizona; collected by E. E. Spamer, 25 July 1991. Apertural and reverse view of two different specimens. × 4.44

N. *Catinella avara* (Say, 1824). RECENT. ANSP 391085. Saddle Canyon, Grand Canyon National Park, Coconino County, Arizona; collected by E. E. Spamer, 25 July 1991. Apertural and reverse view of two different uncleaned specimens. × 4.52

M



N



until adequate studies can be made of the animal body. However, when one is presented only with shells, as with those from the "red earth" deposits, some satisfactory middle ground on identifications has to be acknowledged between the the paleontological and modern zoological communities. Since the populations that produced the Grand Canyon shells are extinct, no animal bodies will ever be forthcoming. It may be quite satisfactory, then, to describe the local Late Pleistocene(?)-Holocene oreohelicid fauna according to paleontological criteria and reserve the name *O. y. fortis* solely for these populations of large-shelled oreohelicids, and possibly for similar shells that may be in undiscovered deposits in the canyon. However, when exercising these paleontological criteria there will be subjective factors in the taxonomy that will require an arbitrary division between *O. y. fortis* and the dead shells of subspecies that are extant. I discuss one such example under *O. y. extremitatis*, below.

Spamer's (1992b) and Spamer and Bogan's (1993) identification of the Grand Canyon fossil oreohelicids as simply the specific *O. yavapai* was based on the systematic arrangement of the ANSP collections, which do not systematically recognize subspecies in the genus *Oreohelix* (see Richardson, 1984).

Oreohelix yavapai extremitatis Pilsbry and Ferriss, 1911 (Pl. 1, figs. E, F, K, L)

Oreohelix yavapai extremitatis Pilsbry and Ferriss (1911, pp. 184-185, pl. 12, figs. 15-21); Pilsbry (1939, pp. 526-528, figs. 343.15-25). (Recent.)

Oreohelix yavapai angelica Pilsbry and Ferriss (1911, pp. 185-186, pl. 12, figs. 22-25). (Recent.)

This taxon is founded on Recent specimens, but only specimens referred to the paleontological record are included here. No previous note of fossil or subfossil specimens of this taxon appears in the literature.

Distribution—Uppermost portion of Bright Angel Trail, where the Kaibab and Toroweap Formations crop out and in associated landslide debris, Garden Creek (no perennial water in this part of the tributary), Grand Canyon National Park, Coconino County, Arizona (see Fig. 3).

Referred Specimens—ANSP 158168 (originally identified by H. A. Pilsbry [original label] as *O. y. angelica* Pilsbry and Ferriss, 1911).

Synonymy—Pilsbry (1939, pp. 526-527) synonymized *O. y. angelica* with *O. y. extremitatis*, commenting (p. 526): "The snail described as *O. y. angelica* . . . is merely a local form of *extremitatis*, not deserving racial distinction, as I view it now." His reference to a "Lectotype and paratypes of *angelica*" (p. 527) fails to uniquely identify the lectotype, thus Baker (1962, p. 3) is credited with the selection of the lectotype. Similarly, Pilsbry's (1939, p. 526) reference to a "Type and paratypes" for *O. y. extremitatis* also fails to uniquely identify the lectotype, and Baker (1962, p. 8) is credited with selecting this primary type as well.

Discussion—Although buried specimens have been referred to *O. y. fortis*, a lot of 216 specimens originally identified as *O. y. angelica* (= *O. y. extremitatis*) (ANSP 158168, collected by Ferriss in 1921 from uppermost Bright Angel Trail), is composed of specimens stained red and encrusted or filled with "red earth" sediment (Pl. 1, fig. K). Pilsbry nowhere mentioned the unusual reddish sediment-stained characteristic of these shells, which is unlike any other lot of Grand Canyon shells in ANSP collections.

The shell surfaces of individuals in ANSP 158168 do not appear to be as encrusted or weathered as the shell surfaces of *O. y. fortis* (compare Pl. 1, figs. H-J). H. A. Pilsbry has added an emendation in pencil on the original label: "extreme extrematis" (presumably a lapsus for *extremitatis*), which is an early indication of Pilsbry's (1939) synonymization of *O. y. angelica* with *O. y. extremitatis*. Almost all of the specimens in this lot are smaller than those usually referred to *O. y. fortis*, but their mode of occurrence is remarkably similar. Furthermore, many of the specimens in this lot resemble the immature specimen that is the paratype of *O. y. fortis* (ANSP 371711), and variations in size of adult specimens of some *O. y. fortis* and *O. y. extremitatis* do overlap. The *O. y. extremitatis* specimens clearly can be referred to as subfossil specimens, but, as with the others that are under discussion in this paper, whether they are Late Pleistocene or early- to mid-Holocene age is conjectural.

A remarkable constituent of the matrix filling these shells is the presence of some embryonic oreohelicids. Several matrix-filled shells were cleaned out, yielding in addition to the mineral matter some delicate vegetational fragments and three embryos—two single whorls 0.8 mm in diameter and a nuclear whorl ~0.2 mm in diameter. It cannot be positively determined whether the embryonic shells belonged to the individuals from which they were cleaned. However, their presence in the outermost part of the last whorl, where the oreohelicid uterus would be, together with their extreme fragility, is evidence for their not having been transported with sand grains that are of comparable size. In addition, the shell of the "glossy pillar," *Cochlicopa lubrica*, cited above, also was found in the matrix of one shell (Pl. 1, fig. K_1).

I have mentioned that paleontological criteria should be used to identify the buried shells of the Grand Canyon "red earth" deposits, and that these shells may satisfactorily be called *O. y. fortis*. I also mentioned that somewhat arbitrary criteria may have to separate this subspecies from relic shells of living subspecies. The buried shells of *O. y. extremitatis*, are smaller, less-weathered, and found much higher on Bright Angel Trail than the specimens of *O. y. fortis*. The *O. y. extremitatis* specimens are in the domain of living members of this subspecies, in terms both of morphological similarity and geographic occurrence—in fact, they are from the type locality of one of its synonymous subspecies, *O. y. angelica*. They are more closely the forebearers of living *O. y. extremitatis* than are *O. y. fortis*, thus it would be unwise even under the constraints of paleontological criteria to rename them based solely on their mode of occurrence.

Age

Conclusions as to the age of the fossil or subfossil oreohelicids of the Grand Canyon are based solely upon the fact that they were buried and are weathered, often broken. The comparisons could have been made by previous authors with the view toward similar occurrences of mollusk shells in the so-called "drift" of river sediments and glacial-outwash deposits of Pleistocene age.

Cockerell's (1927, p. 101) original description of *Oreohelix yavapai fortis* casually suggests that the shells were ". . . to all appearances fossil, and presumably of pleistocene age."

In the description of *Oreohelix yavapai vauxae*, Marshall (1929, p. 2) stated simply: "The specimens appear to be fossil or subfossil, because of the reddish mineral matter coating them in spots."

Pilsbry (1934, p. 403) compared the two oreohelicid occurrences in the Grand Canyon and suggested a similar age for them: "The Grand Canyon and the Supai shells occur fossil [*sic*] in a red earth deposit very likely of the same age, probably Pleistocene." On p. 407 of that paper Pilsbry listed *O. y. fortis* as extinct, with an age simply "Pleistocene." And later, Pilsbry (1939, p. 523) commented: "The red earth in which the [Bright Angel Trail] shells are found is presumed to be Pleistocene. Those from Supai Canyon were in a similar red earth deposit."

Bequaert and Miller (1973, p. 129) reiterated the noncomittal consensus of earlier authors, stating that the two taxa under consideration here "were based on Pleistocene or sub-Recent fossils." These statements are all the remarks about the age of the Grand Canyon buried oreohelicids.

The determination of age of these shells has been based solely on relative factors of physical appearance and mode of occurrence. Whether the shells are in fact Pleistocene in age

(> 10,000 yr B.P.) is unknown, in the absence of corroborative data from radiometric techniques or palynological indicators that are well worked out for the Late Pleistocene and Holocene of the Grand Canyon. Conventional radiometric techniques could determine ages of thousands of years for the Grand Canyon "red earth" snails. Ages of hundreds of years might be obtained through new techniques such as measurements of aspartic acid racemization (Goodfriend, 1992).

Geological Considerations of the "Red Earth"

Several geological aspects of the "red earth" deposits must be addressed to comprehend the implications that these deposits may be as old as the Late Pleistocene.

Stratigraphy and Erosion

Five stratigraphically contiguous geologic formations in the Grand Canyon erode into a long slope—in descending order, the Hermit Shale, Esplanade Sandstone, Wescogame Formation, Manakacha Formation, and Watahomigi Formation; the latter four comprise the Supai Group. These units immediately overlie the sheer cliff of the Redwall Limestone (see Fig. 2). Most of these formations are easily eroded sands and red shales that generally are described by geologists as "red beds." The iron minerals of the red shales oxidize, and the rain-washed fine sand and silt that flows down over all the beds below stains those layers a red color. Even the normally blue-gray Redwall Limestone is almost everywhere completely stained red on its surface, hence its name. It is this oxidized eroded material that accumulates as colluvium on the slopes and in drainages of the Grand Canyon.

That the shells are stained red and are encrusted with cement is an indication that they have been buried in the "red earth" deposits for some time. The environment of the inner canyon is dry, so the distribution of eroded iron-oxide minerals is accomplished by sheet wash from precipitation usually only during seasonal thunderstorms. At higher elevations, snowpacks do accumulate in winter months, the melting of which also helps to distribute these oxidized sediments.

Where colluvium accumulates as red silt, it is almost always mixed with broken stones and dry vegetational debris. One may argue that the shells, particularly as occurring in colluvium, may have been transported from higher levels. However, even though many of the shells are broken, indicating some sort of post-mortem impact, enough of them are whole or nearly whole to infer that these fragile shells have not been transported far. The breakage of shells could also be attributed to crushing by shifting sediment or even to trampling by indigenous animals such as mountain sheep or people.

In comparing the oreohelicid occurrences of Supai and the Bright Angel Trail, we are at a disadvantage by not knowing the precise locality of the Supai occurrence, thus its gross sedimentary constituents; but it is completely reasonable to expect that the mode of occurrence was similar to that of the Bright Angel Trail specimens. The village of Supai itself is situated at the foot of the Supai Group, atop the Redwall Limestone. Mrs. Walcott's collecting station could have been anywhere near Supai, including the narrower, scenic, travertine-mantled gorge in the Redwall Limestone downstream from Supai, where Cataract Canyon is known as Havasu Canyon.

The succineid mode of occurrence in Saddle Canyon is apparently very similar to those of the oreohelicids. The only difference between them is that the succineids occur in a talus that has accumulated below the Redwall Limestone.

This brings us to consider the depth and longevity of the colluvial deposits. Are they thin veneers, which would suggest short-period accumulation and quick erosion (thus possibly young age), or are they exposures of thicker (older?) deposits that are just now being cut into by precipitation runoff?

The deposits along Bright Angel Trail tend to be eroded very easily; the area experiences frequent slides and rockfalls, and, as noted, the trail is maintained. Quick obliteration of the snail-bearing silty colluvial deposits would point to their being but thin veneers covering bedrock and larger accumulations of rock-fall talus. No opinions can be expressed about the Supai occurrences since we have no precise information on the collecting site. The Saddle Canyon locality is partly stabilized by vegetation, and it has appearances of slope-armoring by cobbles and small boulders (see Fig. 4). There also has been the formation of aridisols such as the cryptogamic soil crust seen in the area; these point to slow erosional processes now because of the long period of time required to build and maintain these fragile crusts (*e.g.*, Hendricks, 1985; Cole, 1990; Beymer and Klopatek, 1992). Regardless of the age of the deposits, the shells have the outward appearance of long-term burial and chemical weathering, the oreohelicids more so than the succineids (compare figures in Pl. 1); thus the original suggestions of Pleistocene age cannot be invalidated by the available evidence.

Constituents and Coloration of the "Red Earth"

Most of the specimens mentioned in this paper are stained by the "red earth" in which they were deposited; many are encrusted or filled with sediment (see illustrations in Pl. 1) that is predominantly fine-grained quartz sand with a reddish siltier fraction that occurs in clumps and adheres to many of the sand grains. Since the precise collecting stations for all of the oreohelicids are unknown, the remanants of matrix in and on them are all we know of the physical aspects of the individual deposits. It is clear, too, that the specimens contained in a single lot in the ANSP collections, although collected by a single collector on a single day, appear to have come from different "red earth" deposits along Bright Angel Trail. This is evident from the visible differences in sediment coloration and types of sand grains. The weathering of these sediments also certainly has affected the colors, but without careful field examinations all that can be reported here are the many hues seen in the scant amount of matrix on and in the shells in hand. Color nomenclature used in this section conforms to the Geological Society of America Rock-Color Chart.

Matrix with *Catinella* cf. *avara*, Saddle Canyon. The sand grains are fine (<0.25 mm), moderately sorted, moderately rounded to subangular, clear to amber-colored quartz. They are slightly coated by a carbonate cement, and they are mixed with very finely ground vegetational debris. The overall appearance of the scant amount of sediment on the shells is pale reddish brown (10 R 5/4) to light brown (5 YR 6/4).

Matrix with *Oreohelix yavapai vauxae*, near Supai. The shell is very clean, but some matrix remains inside the last whorl. The sand grains are fine (≤0.25 mm), mostly subangular to subrounded quartz, slightly coated by a carbonate cement. Colors are variable, including moderate red (5 R 5/4) to grayish red (5 R 4/2), dusky red (5 R 3/4), and pale reddish brown (10 R 5/4).

Matrix with *Oreohelix yavapai fortis*, Bright Angel Trail. All sands, except where otherwise noted, are fine (≤0.25 mm), subangular to subrounded quartz. *ANSP 141875* (holotype): Pale reddish brown (10 R 5/4) to dark reddish brown (10 R 3/4). *ANSP 371711* (paratype): Pale reddish brown (10 R 5/4) and moderate reddish orange (10 R 6/6). *ANSP 143691* (Ferriss's 1917 specimens): pale reddish brown (10 R 5/4) to grayish red (10 R 4/2), with some pale red (5 R 6/2 and 10 R 6/2) and moderate yellowish brown (10 YR 5/4). *ANSP 158169* (Ferriss's 1921 specimens): angular quartz grains to 0.5 mm are present together with tiny pieces of limestone (very light gray, N8), the smallest ones of which are reduced to powder when touched with a probe; overall appearance of matrix is mostly moderate brown (5 YR 4/4) with moderate reddish orange (10 R 6/6), pale yellowish brown (10 YR 6/2), and nearly grayish red (10 R 4/2). *ANSP 128624* (Cooke's 1921 specimens): grayish red (10 R 4/2), pale yellowish brown (10 YR 6/2), and pale reddish brown (10 R 5/4).

Matrix with *Oreohelix yavapai angelica*, Bright Angel Trail. The coloration of the *O. y. angelica* subfossils is quite varied, generally pale reddish brown (10 R 5/4) and moderate brown (5 YR 4/4) to grayish red (10 R 4/2). However, one shell in the lot is decidedly different; it is coated with sediment that is very light gray (N8), very pale orange (10 YR 8/2) to pale yellowish brown (10 YR 6/2); but on a fresh surface it is grayish orange (10 YR 7/4). The overall grayish appearance of the sediment of this shell resembles the limestone and dolomite of the uppermost formations of the Grand Canyon's walls, the Kaibab and Toroweap Formations.

Comparison with Recent Burials

Buried Recent shells of *Oreohelix strigosa depressa* (Cockerell, 1892) (Oreohelicidae; ANSP 391091, 391092) and *Sonorella coloradoensis* (Stearns, 1890) (Helminthoglyptidae; ANSP 391088, 391089) were collected during the Colorado River malacological reconnaissance in 1991 (Spamer and Bogan, 1993). They were found in grayish, sandy humic soils in the riparian vegetation along Thunder River, a perennial cave-spring outlet some 3 km from the Colorado River in Grand Canyon National Park, a tributary to Tapeats Creek. Many of the shell apertures were packed with sediment, but few of them are very stained or otherwise discolored. One shell of *S. coloradoensis* contains sediment that is somewhat reddish, although not as ruddy as the sediments of the fossil or subfossil shells from Supai and the Bright Angel Trail. Most of the specimens were dug out of the sediment, but the shell surfaces are unmarred and exhibit none of the mineral encrustation and weathering that is characteristic of the more fossiliferous shells.

Paleoclimatic Considerations

Late Pleistocene Climate. It has been suggested by previous authors that the *Oreohelix yavapai fortis* race lived under ecological conditions much more favorable than those present today in the Grand Canyon; *i.e.*, conditions of greater shelter and therefore, by implication, cooler and/or wetter climate. In turn, this implies a vegetational gradient that is different from that present today. If true, this would be only a circumstantial correlation between shell size and local environment; in fact there is no demonstrated correlation between these aspects (see the section below on "Shell Size and Composition"). And of course it further supposes that the *O. y. fortis* shells are indeed Late Pleistocene in age.

Paleobotanical evidence from Grand Canyon deposits has shown that floristic elevational gradients were depressed into the canyon during cooler and wetter(?) times in the Late Pleistocene. At the elevational level of the Hermit Shale and Supai Group, at which is situated the type locality of *O. y. fortis*, a fir and limber pine forest was present during the regional maximum of the last continental glaciation (see diagrammatic illustration in Spamer, 1984, fig. 2, and literature citations in Spamer, 1990, 1993). Together the heavier vegetation, the northerly aspect of the slopes here, and the limestone talus, produced an environment that was one of considerable shelter, ideal for oreohelicids. This does not corroborate a Late Pleistocene age for *O. y. fortis*, but the data do not invalidate the hypothesis.

Proximity to Water. Although the localities of the colluvium-buried oreohelicids and succineids are dry today, the presence of these snails there indicates that there were once more favorable conditions for snails at these sites. The oreohelicids are easier to accommodate in a dry environment, for even though they do require water they are calciphilous animals whose dependence is on calcium such as that in the calcium carbonate of limestones. An adequate water supply presumably would be available from sporadic precipitation, just as it is for the proliferate modern oreohelicid fauna of the canyon.

On the other hand, succineids require close proximity to perennial water as well as to shelter, so the Saddle Canyon fossil locality, in so dry and exposed an area, requires some thought as to the implications of the presence of snails there. As noted, there is no evidence of a spring anywhere near or above the locality which is high above the creek in Saddle Canyon (see Fig. 4); yet at one time there must have been water there. This points to a wetter time in the inner canyon, when more springheads were active due to higher aquifer levels (Szabo, 1990).

The empirical evidence for a wetter period in the Grand Canyon region can be seen in the huge travertine mantles that in some areas blanket parts of the canyon wall. Since travertine, composed principally of calcium carbonate, accumulates from evaporating mineralized water, it is clear that where these mantles are found there were some long-lived springs in the canyon walls. These processes are active today along Havasu Creek downstream from Supai. The processes of travertine accumulation do not imply any significance to the support of molluscan communities or to the accumulation of snail-filled colluvial deposits; they are mentioned here only as documentation of the presence of failed springs in the Grand Canyon.

Ages of the large travertine mantles are in the range of 15,000 to 338,000 yr B.P., based on uranium-series dating, and specific date ranges correspond well to periods known to be wetter than present in the Southwest (Szabo, 1990). Because of the great age of the older dated travertines, they are not likely to be contemporaneous with the colluvial deposits under consideration here because uncemented colluvium is far more susceptible to erosion than strongly cemented travertine; to expect such unconsolidated deposits to survive for tens to hundreds of thousands of years is incredible.

It is possible that shells can be found in the travertines, too; specimens in ANSP collections (not from the Grand Canyon), as well as notes in the literature (*e.g.*, Vanatta, 1921), corroborate this mode of occurrence. Nevertheless, I have thusfar unsuccessfully searched for land snails enrobed by travertine at two locales only: inactive travertine deposits at Elves Chasm (Colorado River Mile 116.6, Km 187.6) and modern travertine accumulations in lower Havasu Creek (Mile 156.8, Km 252.3). But caution should be had when interpreting climatically-influenced diversity of molluscan populations of the travertine spring areas. Exceptional conditions of riparian vegetative cover can exist alongside water sources deep inside the canyon, in very localized areas outside of which are inhospitable to most mollusks. Spamer and Bogan (1993) have shown that molluscan diversity in such geographically confined areas can promote cohabitation of mollusks that normally are confined to more suitable ecological life zones higher or further away from the specialized area.

At Saddle Canyon, no travertine is seen on the slopes, but it must be pointed out that the beds at the base of the Redwall Limestone and the formation that lies beneath it here, the Muav Limestone (see Fig. 4), comprise a major regional aquifer (Huntoon, 1974), in which many of the Grand Canyon's springs are found. It is quite probable that a failed Muav spring is nearby the Saddle Canyon succineid locality, perhaps now buried beneath the talus slope that is accumulating at the foot of the Redwall cliff.

Shell Size and Composition Indicating Local Ecological Conditions. Cockerell (1927), in the original description of *Oreohelix yavapai fortis*, compared the shells to those of the living subspecies *O. y. extremitatis* Pilsbry and Ferriss, 1911 and *O. y. angelica* Pilsbry and Ferriss, 1911. Both of these subspecies were named based on specimens from the Grand Canyon. Cockerell supposed that the large size of *O. y. fortis* was environmentally controlled:

> The larger size is possibly correlated with a moister climate in past times, and the form may be regarded as a race or subspecies *fortis*, closely related to the much smaller *O. yavapai angelica* P. & F. which occurs living higher up on the Bright Angel trail.

Pilsbry (1934, 1939) repeated Cockerell's comment on the possible correlation with a moister climate.

The primary types of *O. y. extremitatis* and *O. y. angelica* are shown in Pl. 1, figs. E and F, respectively. It can be readily seen upon comparing the types with other specimens from the Grand Canyon that, aside from the differences in size, there are no morphological characters that can be used to define a unique systematic separation of the two subspecies.

The identification of oreohelicids and succineids is particularly independent of shell characteristics, and anatomical and molecular techniques of identification are increasingly the necessary means for providing names for new occurrences of these animals (*e.g.*, Hoagland and Davis, 1987; Fairbanks, 1989).

Pilsbry and Ferriss (1910) provided a seminal discussion of the influence of environment on land snail shells in the arid Southwest. Many of their observations are valid even today. These same authors, in their 1911 paper on the Grand Canyon malacofauna, concluded that no particular exclusion of land snails is detectable in the ecologically highly zoned walls of the canyon, save only that species less tolerant of harsher arid conditions were restricted to higher altitudes of the forested canyon rims and adjacent plateaus. Ferriss (in Pilsbry and Ferriss, 1911, p. 187, footnote 6) made observations of local environment—altitude, humidity, and slope aspect—on oreohelicids on the North Rim of the Grand Canyon, finding no clear correlation of shell size and coloration with these factors.

Goodfriend (1986), although not mentioning oreohelicids or succineids, has provided a worthwhile review of the causes of variation in shell form and size among land snails, based on work done in the arid Middle East. Among his observations, contrary to Ferriss's observations cited above, is a relationship between available moisture and shell size (but not shell thickness), although the biological mechanism behind this relationship is not clear. These observations of course have direct application to arid-climate terrestrial molluscan faunas generally, including those which inhabit the Grand Canyon. The malacological community is still in need of experimental and systematic work of these molluscan relationships as they apply to the malacofauna of the Southwest. For these reasons it would be premature at this stage of scientific investigation to invoke a direct correlation between shell size and paleoclimate, especially regarding specific forms that may be extinct.

The ratio of oxygen isotopes ($^{18}O/^{16}O$) in the carbonate fraction of land mollusk shells may be useful, when conjoined with radiometric data on age, in indirectly identifying the isotopic composition of precipitation. In this way these values can provide a measure of $\delta^{18}O$ in times of different climate (Goodfriend and Magaritz, 1989).

Continued Work

It is likely that many occurrences of snails in "red earth" are to be found throughout the Grand Canyon. Particularly promising locations are in the colluvial deposits in the broad slopes of eroded red-beds that are littered with limestone talus derived from formations higher in the canyon wall. Studying these deposits and their contained shells, and testing samples of the shells and matrix, might give researchers the means by which to determine the age of these deposits. This information can add to existing data on the greater assemblage of Late Pleistocene-Holocene faunas and climates of the Grand Canyon, as well as to extend the record of the modern Grand Canyon malacofauna back into the Pleistocene. Similarly, mollusks enrobed in travertine deposits, which could yield ages older than those of the colluvial deposits, may also provide additional clues into the distribution and diversity of snails of even earlier periods of the Pleistocene that predate the fossil and paleoclimatic record of the packrat middens and cave deposits.

If future workers discover deposits of buried shells in the Grand Canyon, they may find different forms of shells than those described herein. At that time, a more critical look at the systematic characters of the modern and fossil specimens will have to be made. Caution is called for when applying names to paleontological material of taxonomic groups that have been described based on the anatomical features of Recent material. Taxonomists could wind up with the taxonomically weak and systematically devalued situation of having mollusks whose distributions are restricted to their type localities, and whose systematic interrelationships are effectively unknown. It may therefore be more worthwhile to utilize the "red earth" snail shells as indicators of geomorphic processes and, perhaps, paleoclimatic conditions in the Grand Canyon.

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