# Pleistocene Mammals from the Rock Springs Local Fauna, Central Florida

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*ABSTRACT.*— Although several of the interesting fossil mammals from Rock Springs, Orange County, Florida, have been mentioned in scientific papers, this is the first comprehensive report of its mammalian fauna. The fauna, which evidently accumulated during several intervals of late Pleistocene deposition, consists of at least 27 species, including both marine and terrestrial forms. The faunal composition, coupled with modes of preservation (e.g., a barnacle-encrusted specimen of a terrestrial species), provides direct evidence of at least one marine transgression (probably corresponding to the Pamlico shoreline) into central peninsular Florida. Two extralimital taxa characterize the Rock Springs fauna: (1) current affinities of *Thomomys* sp. (pocket gophers) are with western North America, and (2) *Mormoops* sp. (leaf-chinned bats) now occur in western North America and the Neotropics.

## INTRODUCTION

The Rock Springs site in central Florida has yielded an interesting sample of late Pleistocene vetebrate fossils. Although the first collections were made in the 1920s, the first mention of fossil vertebrates from Rock Springs was a list of seven taxa (Gut 1939). Of the five vertebrate classes represented in this fauna, only the avifauna has been comprehensively reported (Woolfenden 1959). Auffenberg (1963) included two serpent species— *Drymarchon corais,* an indigo snake, and *Crotalus giganteus,* a large rattlesnake— from Rock Springs in his review of the fossil snakes of Florida. Ray et al. (1963) discussed the presence of *Mormoops megalophylla,* a leaf-chinned bat, and Ray (1964) and Gillette (1976) studied a species of small cat, *Felis amnicola,* from this site. Webb (1974) listed some 17 mammalian species from the Rock Springs site.

This paper presents the first comprehensive compilation of the Rock Springs mammalian fauna. Re-examination of all available fossil material, including a new collection made in 1982, reveals 27 mammalian taxa, some 14 of which are extinct (Table 1). Ten species in the Rock Springs local fauna presently occur in Florida. Because one species was not identifiable to genus (i.e., the large felid), its current status

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Table 1. Mammalian fauna of the late Pleistocene Rock Springs site, Orange County, Florida.

| Species | Extinct | Extant in Florida | Extant, not in Florida |
|---|---|---|---|
| *Blarina* cf. *carolinensis* | | X | |
| *Mormoops megalophylla* | | | X |
| *Myotis austroriparius* | | X | |
| *Holmesina septentrionalis* | X | | |
| *Dasypus bellus* | X | | |
| cf. *Glossotherium* | X | | |
| *Sylvilagus* sp. | | X | |
| *Geomys pinetis* | | X | |
| *Thomomys* cf. *orientalis* | X | | |
| *Castor canadensis* | | X | |
| cf. *Sigmodon* | | X | |
| cf. *Tursiops* | | X | |
| *Urocyon cinereoargenteus* | | X | |
| cf. *Canis dirus* | X | | |
| *Tremarctos floridanus* | X | | |
| *Ursus americanus* | | X | |
| *Felis amnicola* | X | | |
| cf. Felidae gen. et sp. indet. | | | |
| *Mammut americanum* | X | | |
| *Mammuthus* sp. | X | | |
| *Trichechus manatus* | | X | |
| *Tapirus veroensis* | X | | |
| *Equus* sp. | X | | |
| *Mylohyus nasutus* | X | | |
| *Paleolama mirifica* | X | | |
| *Odocoileus virginianus* | | X | |
| *Bison* sp. | X | | |

is uncertain. The one extant species in the Rock Springs fauna not now occurring in Florida is *Mormoops megalophylla.* The other extralimital genus in the Rock Springs fauna is *Thomomys,* the smooth-toothed pocket gophers. General affinities of *Mormoops* and *Thomomys* lie in western North America and the Neotropics.

Rock Springs is located in Kelly Park about 10 km (6 mi.) north of Apopka, Orange County, Florida (Sorrento quad. NE1/4, NE1/4, NW1/4, Sec. 15, T20S, R28E). Its elevation is about 7 m above present sealevel. The spring is one of many flowing into the Wekiva River, a tributary of the St. Johns River. The spring discharges at a mean rate of 1.83 cubic m/second (64.6 cubic ft./second) from a partially-submerged

cavern in a 5 m high limestone bluff of the early Miocene Hawthorne Formation (Rosenau et al. 1977). The mouth of the cavern is about 1.5 m in diameter. The Rock Springs fauna has been collected along the initial 200 m of the spring run, and the underlying Crystal River Formation of the Ocala Group (late Eocene age) is exposed in places along the run. Present habitats in the surrounding region are the longleaf pine-turkey oak sandhill ecosystem and the live oak xeric hammock association, as is common in the upland karst regions of peninsular Florida. Mesic hardwoods and other floodplain and freshwater marsh species occupy the adjacent riparian corridor.

The material comprising the Rock Springs mammal fauna represents the efforts of many amateurs and professionals, including J. Bauer, R. and J. Franz, L. F. Lovell, Mrs. C. A. Meyer, G. S. Morgan, J. W. Pierce, G. M. Ponton, A. E. Pratt, R. Savage, C. Simpson, J. R. Todd, K. T. Wilkins and G. E. Woolfenden. Additional Rock Springs fossils are contained in the private collection of H. James Gut, which is now in the custody of his son, Robert M. Gut of Jacksonville, Florida. Specimen numbers cited in the following annotated species list refer to the catalogue of the Florida State Museum Vertebrate Paleontology Collection at the University of Florida (UF). Catalogue numbers preceded by "V" are part of the Florida Geological Survey collection which is also housed with the UF collection.

## ANNOTATED SPECIES LIST

### Order Insectivora

### Family Soricidae

*Blarina* cf. *carolinensis* (Bachman) 1837

*Material.*— Partial right mandible with $I\overline{1}$, $P\overline{4}$-$M\overline{2}$, (UF 48997); partial left mandible with $M\overline{1}$, (UF 48998).

*Remarks.*— Short-tailed shrews in Pleistocene deposits in Florida have previously been referred to *B. brevicauda,* the name formerly applied to most living populations of *Blarina* in eastern North America. Recent morphometric and karyotypic study of modern populations indicates that northern, southeastern and southwestern populations are separate species, with southeastern populations referred to *Blarina carolinensis* (Genoways and Choate 1972; George et al. 1982). I apply *carolinensis* to the Rock Springs *Blarina* solely on geographic grounds. Statistical comparisons of later Pleistocene material from Florida with modern *B. brevicauda, B. hylophaga* and *B. carolinensis* are necessary to establish species identification.

Order Chiroptera

Family Mormoopidae

*Mormoops megalophylla* (Peters) 1864

*Material.*— Cranial and post-cranial material (UF 3860-3866) as described by Ray et al. (1963).

*Remarks.*— Identification was established by Ray et al. (1963), who compared Rock Springs *Mormoops* with samples of the two living species of the genus. Kurtén and Anderson (1980) noted Rock Springs as the only Pleistocene occurrence of the species in continental North America.

Family Vespertilionidae

*Myotis austroriparius* (Rhoads) 1897

*Material.*— Skull with partial maxillary dentition (UF 8925); rostrum with partial maxillary dentition (UF 8926); 6 dentaries with partial dentitions and 1 edentulous dentary (UF 8927); 20 humeri (UF 8928); 25 radii (UF 8929); 30 metacarpals (UF 8930); 4 femora (UF 8931).

*Remarks.*— This material is assigned to *M. austroriparius* rather than to *M. grisescens* Howell 1909 because of its relatively small size. *M. austroriparius* is a very common cave-dwelling bat of the karst regions of present-day Florida (Rice 1957).

Order Edentata

Family Dasypodidae

*Holmesina septentrionalis* (Leidy) 1889

*Material.*— 2 movable scutes (UF 24845); 4 fixed scutes (UF 24846).

*Dasypus bellus* (Simpson) 1930

*Material.*— 1 fixed scute (V-4455).

*Family Mylodontidae*

cf. *Glossotherium* (Owen) 1840

*Material.*— Distal phalanx (V-4394).

*Remarks.*— Poorly ossified epiphyses indicate that this claw is that of a juvenile. The small size (greatest length = 51 mm) and roundness of the claw suggest *Glossotherium*. Measurements taken midway between proximal and distal ends are: mediolateral width 15 mm; dorsoventral depth 22 mm. Claws of other ground sloth genera are more mediolaterally compressed than in *Glossotherium*.

Order Lagomorpha

Family Leporidae

*Sylvilagus* sp. Gray 1867

*Material.*— Left dentary with $P\overline{3}$-$P\overline{4}$, $M\overline{2}$-$M\overline{3}$ (V-4467); proximal femur (UF 49201); distal femur (UF 49202).

*Remarks.*— Two species of similar-sized cottontails, *Sylvilagus palustris* and *S. floridanus,* presently range throughout most of Florida. The distribution of a third, much larger species, *S. aquaticus,* closely approaches the Florida panhandle in Alabama; quite possibly the species has recently extended its range into extreme western Florida. Left mandibular toothrow lengths were measured in five specimens each (mixed sex) of modern *S. palustris* and *S. floridanus* from Alachua County, Florida, in efforts to assign specific identity to the Rock Springs rabbit material. The sample mean for toothrow length for *S. floridanus* is 15.20 mm (s = 0.29 mm) and for *S. palustris* is 15.24 mm (s = 0.45 mm). Toothrow length in the Rock Springs specimen is 14.9 mm. Lack of mensural differences between these three samples dictates referral of the Rock Springs rabbit to *Sylvilagus* sp.

Order Rodentia

Family Geomyidae

*Geomys pinetis* Rafinesque 1817

*Material.*— Isolated upper $P\underline{4}$, (UF 49205).

*Remarks.*— *Geomys pinetis* is the only extant pocket gopher in the eastern United States. The southeastern pocket gopher is presently abundant in the vicinity of Rock Springs, and in other parts of the southeastern United States characterized by the longleaf pine-turkey oak sandhill ecosystem. Despite the limited referred material, its generic identity is certain. Extant *Geomys* species possess an enamel band on the posterior surface of the fourth upper premolar. This posterior enamel investment on upper $P\underline{4}$ is absent in *Thomomys* species and in the early-to-middle Irvingtonian species of *Geomys* in Florida (Wilkins 1984).

*Thomomys* cf. *orientalis* Simpson 1928

*Material.*— Six mandibles with partial to complete dentitions (UF 46571-46576).

*Remarks.*— Generic assignment of these specimens is indicated by the presence of both anterior and posterior enamel bands on the lower molars; anterior bands are absent in *Geomys* species. The genus *Thomomys* presently occurs in western North America (Hall 1981). The only

other *Thomomys* material reported from the southeastern United States is from Sabertooth Cave (Rancholabrean, Citrus Co., Florida). Simpson's (1928) description of the species referred only to skull material, none of which is available in the Rock Springs deposit. Pending further study, the Rock Springs *Thomomys* is tentatively referred to *orientalis.*

The Rock Springs site has yielded additional geomyid material for which generic assignment cannot be made on qualitative grounds. Similarity in size and preservation to the *Thomomys* material listed above suggests that four mandibles lacking cheekteeth (UF 46577-46580) are referable to *Thomomys*. No effort has been made to identify isolated lower $P\overline{4}$'s (UF 46581) and molars (UF 46582) beyond the family level.

## Family Castoridae

### *Castor canadensis* Kuhl 1820

*Material.*— Lower molar (V-4399).

*Remarks.*— The presence of beaver in the Rock Springs fauna was previously noted by Johns (1958), who argued that its present distribution (restricted in Florida to the panhandle and northern peninsula) is less extensive than it was in historic and Pleistocene times. The Rock Springs specimen, coupled with two nearly complete mandibles with $P\overline{4}$-$M\overline{3}$ (V-5403) from the shores of nearby Lake Monroe, Volusia County, comprises the species' southernmost Pleistocene record in Florida. Post-Wisconsinan records include specimens from middens in Seminole, Volusia and Brevard counties (Furgeson 1951) and along the Indian River (Allen 1942).

## Family Cricetidae

### cf. *Sigmodon* Say and Ord 1825

*Material.*— Two isolated upper incisors (UF 48999).

*Remarks.*— Comparison of these incisors with modern *Sigmodon hispidus* and other rodents from Florida suggests this generic assignment. Martin (1974) recognized the occurrence of two species of cotton rats, *S. bakeri* and *S. hispidus,* in the United States and Mexico during the late Irvingtonian and Rancholabrean. Identification to species requires molar teeth.

Order Cetacea

Family Delphinidae

cf. *Tursiops*

*Material.*— Vertebra (UF 48976).

*Remarks.*— The specimen is a complete centrum (diameter = ca. 38 mm) with one complete transverse process (length = ca. 75 mm). The paired portion of the neural arch ventral to its fusion into the spine is present. Comparison with modern small odontocetes from Florida suggests *Tursiops.* The relatively intact nature of this specimen, and the lack of water-wear, suggests *in situ* deposition and comprises further evidence of marine transgression above the Rock Springs elevation.

Order Carnivora

Family Canidae

*Urocyon cinereoargenteus* (Schreber) 1775

*Material.*— Distal humerus (UF 49000).

*Remarks.*— This specimen resembles humeri of modern individuals of the gray fox from central Florida.

cf. *Canis dirus* Leidy 1858

*Material.*— Canine fragment (V-4397).

*Remarks.*— This identification follows Webb (1974).

Family Ursidae

*Tremarctos floridanus* (Gidley) 1928

*Material.*— Molar fragment (UF 8946); 2 upper M3's (UF 8947-8948).

*Remarks.*— The genus is extinct in North America, with the sole living species restricted to the South American Andes. *Tremarctos floridanus,* the Florida spectacled bear, was a common member of many of Florida's Pleistocene faunas; *Ursus* and *Tremarctos* remains are often found in the same deposits. Ecological differences of the two species apparently allowed coexistence (Kurtén 1966). Adaptation of *T. floridanus* to a highly herbivorous lifestyle is evident from its relatively broad molars, which allowed for increased occlusal surface areas. The relatively narrow and elongate molars of *U. americanus* indicate more omnivorous adaptation.

*Ursus americanus*

*Material.*— Two upper M3's (UF 8951-8952); femur (UF 8953).

*Remarks.*— The black bear presently occurs throughout much of Florida. An unfossilized femur attests to its relatively recent occurrence in the Rock Springs vicinity. Generic identity of other ursid material is uncertain: distal humerus (UF 49203); canine fragment (UF 49204).

Family Felidae

*Felis amnicola* Gillette 1976

*Material.*— Right dentary with $P\overline{3}$-$M\overline{1}$ (UF 4522)

*Remarks.*— This specimen was originally recognized and illustrated by Ray (1964) as a jaguarundi, *Felis yagouaroundi.* Subsequently, Gillette (1976) described a new species of small river cat, *F. amnicola,* to which he referred this Rock Springs dentary.

cf. Felidae

gen. et sp. indet.

*Material.*— Phalanx (UF 8954)

*Remarks.*— Webb's (1974) tabulation of "*Felis* sp." at Rock Springs probably refers to this specimen, which compares favorably in size with the modern Florida panther, *Felis concolor coryi* Bangs 1899.

Order Proboscidea

Family Mammutidae

*Mammut americanum* (Kerr) 1791

*Material.*— Right dentary fragment (V-4378); molar fragments (UF 48986, V-4385, V-4464); molar enamel fragment (V-4465).

Family Elephantidae

*Mammuthus* sp. (Falconer) 1857

*Material.*— Molar (V-4473); molar plates (UF 48987, V-4383); tusk fragments (V-4384).

*Remarks.*— In accordance with Kurtén and Anderson (1980), mammoth material is provisionally referred to *Mammuthus* sp. pending comprehensive study of the genus.

Order Sirenia

*Trichechus manatus* Linnaeus 1758

*Material.*— Cheektooth (UF 48981); cheektooth fragment (UF 48982); edentulous maxillary fragment (V-4451); ear ossicle (UF 48983);

tympanic (UF 48984); vertebrae material (UF 48979-48980, V-4469); ribs (UF 48977-48978, V-4380).

*Remarks.*— Various states of preservation are evident in this manatee material. Some is well permineralized, whereas other specimens are only slightly fossilized. The material was probably deposited during several different intervals, including times when the site was marine or estuarine, or when it comprised a freshwater system occupied by manatees much as are many other river systems in Florida today.

Order Perissodactyla

Family Tapiridae

*Tapirus veroensis* Sellards 1918

*Material.*— Palate with left $\underline{I1}$, $\underline{I3}$, $\underline{P1}$, $\underline{M3}$ and right $\underline{P1}$-$\underline{M3}$ (UF 18702); left maxilla with $\underline{M1}$-$\underline{M3}$ (V-4389); upper molar fragment (UF 48970); left dentary and symphysis with $\overline{P4}$-$\overline{M3}$ (V-4390/4391); partial right dentary with $\overline{P4}$-$\overline{M3}$ (UF 12485); left $\overline{I2}$ (UF 48971); deciduous $\overline{P2}$ (UF 8945); left $\overline{P2}$ (V-4396); lower molar (UF 48969); 5 isolated teeth (V-4454).

*Remarks.*— All referred material resembles *T. veroensis* rather than the larger *T. copei* Simpson 1945.

Family Equidae

*Equus* sp.

*Material.*— Upper cheektooth (UF 48975); lower molar (UF 48974); incisors (UF 48972-48973); radius (V-4471).

*Remarks.*— The material represents several states of preservation. The unfossilized radius, that of an immature individual, probably represents the domestic *Equus caballus*. The dental material is fossilized and is provisionally referred to *Equus* sp.

Order Artiodactyla

Family Tayassuidae

*Mylohyus nasutus* (Leidy) 1869

*Material.*— Partial right mandible with $\overline{P3}$-$\overline{M3}$(UF 17720).

*Remarks.*— This specimen is particularly interesting because of its preservation. Overall coloration of the specimen is black, in contrast to buff or chalky colors of most other Rock Springs material. The ventral surface of the dentary is broken away to expose the mandibular canal. External surfaces of the jaw, as well as the internal surfaces of the mandibular canal, are encrusted with growths of various marine organisms, including barnacles. Assuming *in situ* deposition, this specimen further

documents marine transgression of the Rock Springs site. The most recent occurrence of a transgression sufficient to cover the Rock Springs site probably corresponds to the Pamlico marine terrace (Healy 1975). Hence, the minimum age estimate for this specimen is about 125,000 years (see Discussion).

Family Camelidae

*Paleolama mirifica* (Simpson) 1929

*Material.*— Deciduous P4 (V-4398); P4 (V-4453); M3 (UF 12491).

*Remarks.*— Webb (1974:183) recorded this stout-legged llama as a member of the Rock Springs fauna in his study of Florida Pleistocene Lamini.

Family Cervidae

*Odocoileus virginianus* (Zimmermann) 1780

*Material.*— Right dentary with P3-M3 (V-4395); isolated cheekteeth (UF 48988-48989, V-4462); distal tibia (UF 48990); distal metatarsal (UF 48991).

*Remarks.*— The white-tailed deer presently occurs throughout Florida. Because of differential preservation, deer material in the Rock Springs fauna appears to have been deposited during several intervals.

Family Bovidae

*Bison* sp.

*Material.*— Upper cheektooth (UF 10037); M3 (UF 52184); lower cheektooth (UF 15065).

*Remarks.*— Robertson (1974) stated that unequivocal species determination for the three species of *Bison* in Florida can be made only from horn core material. He was unable to identify diagnostic dental characters, although he noted that, by its smaller size, *Bison bison* (Linnaeus) 1758 could sometimes be distinguished from the two larger species, *Bison latifrons* (Harlan) 1825 and *Bison antiquus* Leidy 1852. Mesurements of the nearly unworn lower M3(UF 52184) are: greatest alveolar length = 47.7 mm, greatest alveolar width = 21.2 mm, and greatest crown height = 69.1 mm. The large size of the Rock Springs M3 suggests the presence of one of the larger *Bison* species rather than *B. bison.*

## DISCUSSION

### Chronology

As with many late Pleistocene fluvial sites in Florida, the Rock Springs local fauna accumulated during several intervals. Some material

is Recent or even unfossilized (e.g., some of the *Equus* and *Odocoileus*). In addition, some Miocene fossils of marine invertebrates and sharks have eroded from the limestone bedrock through which the stream flows. The late Pleistocene fossilized materials represent accumulation in two types of situations: one of higher sealevels and another of much lower sealevels. The cetacean vertebra, the barnacle-covered *Mylohyus* dentary, and the *Trichechus* material comprise evidence of marine intrusion. The last time seas could have covered the Rock Springs locale (elevation 7 m above present sealevel) was some 125,000 years before present (ybp). According to eustatic studies, 125,000 ybp was the most recent occasion that seas have been higher than at present (Shackleton and Opdyke 1973; Bloom et al. 1974; Chappell 1974). In Florida, this late Sangamonian interglacial transgression corresponds to the Pamlico shoreline at about 9 m (Healy 1975). It is possible, yet unlikely, that some earlier transgressions of similar or greater extent introduced the marine influence. Thus, the cetacean, the barnacles encrusting the previously-deposited peccary jaw, and at least some of the sirenian material are probably of Sangamonian age.

Most of the terrestrial vertebrates presumably were deposited during one or more phases of reduced sealevel. During at least one such interval, sealevel and the piezometric surface dropped sufficiently to produce habitats suitable to vertebrates that do not now occur in eastern North America. Woolfenden (1959) noted a western contingent in the Rock Springs avifauna. A portion of the Rock Springs mammal fauna also exhibits noneastern United States affinities. Smooth-toothed pocket gophers (genus *Thomomys*) are known from the Rock Springs deposit, but the genus now occurs only in Mexico and western North America (Hall 1981). The range of *Mormoops megalophylla* is now restricted to the southwestern United States, southward through much of Central America and into northern South America (Smith 1972). *Mormoops blainvilli,* the only other extant species of the genus, occurs in the West Indies (Hall 1981).

## Paleoenvironmental Interpretations

The genus *Mormoops* (as well as the species *M. megalophylla* itself) is neotropical and temperate in distribution and occupies humid to semiarid to arid situations at elevations generally less than 3000 m (Smith 1972). Similarly, *Thomomys* pocket gophers occupy habitats including deserts, prairies, montane meadows and forests ranging over some 35 degrees of latitude and 3000 m of elevation. It is apparent that no single temperature or rainfall regime characterizes the entire range of either genus. Therefore, because of their broad habitat and environmental tolerances, the presence of *M. megalophylla* or *Thomomys* at Rock Springs need not be directly indicative of any particular habitat types.

Yet, their presence does offer clues in reconstructing certain aspects of the paleoenvironment.

*Bats.*— The two species of bats recorded as fossils at Rock Springs are usually considered obligate cave-dwellers, although alternate roosts are also used (Barbour and Davis 1969). Their presence suggests a reduced piezometric surface. No modern records of *M. austroriparius* are known from the Rock Springs cavern, although the species is reported from various northwestern Orange County caverns in the immediate vicinity (Rice 1957). The present water level in the Rock Springs cavern is probably too high to accomodate sizable colonies of bats. Additionally, bat bones are quite delicate; that most of the fossilized bat material is intact suggests the absence of flowing water in the cavern during the depositional intervals. Yet, some water was probably on the cave floor during occupation by *Myotis austroriparius.* This is perhaps the most abundant extant bat species in Florida and it resides in caves with either still or flowing water beneath roosting sites. Avian remains from Rock Springs also showed little evidence of water-wear (Woolfenden 1959). As with many other stream deposits, the context and associations of fossil specimens is unknown and cannot be reconstructed. However, the similarity of preservation of both *Mormoops* and *Myotis* fossils indirectly suggests that occupation of the cave could have been contemporaneous.

*Pocket gophers.*— The contemporaneous occurrence of two contrageneric pocket gopher species in a fossil deposit was previously reported by Dalquest and Kilpatrick (1973). They interpreted their cave deposit (Shulze Cave, early Holocene, Edwards County, Texas) as the roost of barn owls that foraged over a broad area, including the different habitats occupied by *Thomomys bottae* and *Geomys bursarius,* which had mutually exclusive microgeographic distributions. It is quite possible that the Rock Springs cavern served as an owl roost during times of reduced water table levels. Fossil barred owls, *Strix varia*, are known from Rock Springs (Woolfenden 1959). Lack of stratigraphic context disallows determination of whether *Geomys* and *Thomomys* occurred contemporaneously in the Rock Springs vicinity rather than being members of faunas of different time intervals. Nevertheless, the mere presence in the fauna of the two species of pocket gophers allows inferences regarding soil characteristics. Miller (1964) examined soil preferences and competitive interactions of three genera of pocket gophers in Colorado. He found that *Geomys* species required deeper, sandier and more friable soils than either *Pappogeomys* species (including *Cratogeomys* species) or *Thomomys* species. *Thomomys,* in contrast, was well suited to shallow, gravelly, less friable soils, although *Thomomys* could and would inhabit deeper soils where available. Requirements of *Pappogeomys* were intermediate to the other genera.

Miller found in competition experiments that, in its preferred deeper soils, *Geomys* excluded species of other genera, whereas *Thomomys* was the superior competitor in shallow soils. Hence, presence of *Geomys* and *Thomomys* in the Rock Springs deposit suggests local occurrence of two markedly different substrates. The deep, sandy soils predominating the vicinity today favor *Geomys* and generally represent sediments of marine terraces of interglacial periods. Shallower, gravelly soils often occupied by *Thomomys* in western North America are uncommon in Florida today. However, such soils could be developed via erosion of deep sands overlying limestone. Shallow sands mixed with gravel formed of eroding limestone could form a substrate inhabitable by *Thomomys* but not by *Geomys.*

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