

## Scarab beetles from pocket gopher burrows in the southeastern United States (Coleoptera: Scarabaeidae)

Paul E. Skelley

Florida State Collection of Arthropods  
Florida Department of Agriculture and Consumer Services  
P.O.Box 147100  
Gainesville, FL 32614-7100

Robert D. Gordon

Northern Plains Entomology  
P.O.Box 65  
Willow City, ND 58384

**Abstract:** This paper reports on the scarab beetles collected during a survey of nonparasitic arthropods living in burrows of the southeastern pocket gopher (*Geomys pinetus* Rafinesque, Geomyidae). Three new species are described: *Aphodius bakeri*, *A. baileyi* and *A. gambrinus*. A key to species of *Aphodius* occurring in these burrows is presented. Distributional data is provided for species of *Aphodius* and one species of *Euphoria* occurring in this microhabitat. Aspects of life histories of burrow inhabiting insects are speculated upon.

**Key Words:** *Aphodius*, *Euphoria*, *Geomys*, Pocket Gopher, Scarabaeidae.

### Introduction

The southeastern pocket gopher (*Geomys pinetus* Rafinesque) is a small burrowing rodent which comes to the surface only to make mounds (spoils of its digging), occasionally to forage, and rarely to disperse. It has been described as a "homely, belligerent sausage" (Avisé and Laerm 1982) which spends its life underground eating roots, tubers and occasional greens that it may pull down into its burrows. Gardeners have watched their plants sink into the ground because of these vegetarians (pers. comm. to PES). The gopher burrows, kept isolated from the surface by earthen plugs, resemble cave systems in which a keystone vertebrate brings nutrients that support a closed ecosystem of organisms.

More than 60 years ago entomologists in Florida studied various aspects of this fauna (Hubbell and Goff 1939, Hubbell 1940, Cartwright 1939, Ross 1940). This prompted research on the burrows of pocket gophers in Texas (Ross 1944a, 1944b, Cartwright 1944). Since then many papers have been published on ectoparasites of pocket gophers. Only five papers have been published regarding the burrow fauna in the US (Blume and Aga 1975, 1979, Blume and Summerlin 1988, Godwin 2000, Hardy 1980). Similarly, there are very few studies on pocket gopher burrow faunas in other countries.

In the mid-1980s, the first author started collecting beetles in burrows (Skelley and Kovarik 2001). This work led to discoveries of new species (Skelley and Woodruff 1991, Skelley and Gordon 1995) and caught the attention of other coleopterists. Eventually this interest developed into a systematic survey of the nonparasitic arthropods living in these burrows (see also Peck and Skelley 2001).

### Methods

Pocket gopher burrows were excavated on several occasions at several different sites before the survey was initiated. Total excavation of a burrow is time consuming (often taking 1-2 days), exhausting, frequently non-productive, and usually not appreciated by landowners. While excavation potentially yields data regarding the niche of a species, we chose to sample with dung and malt-baited pitfall traps placed in the burrow. Pitfall trapping allowed us to sample many sites with minimal effort and habitat disturbance. With the help of those listed in the acknowledgments, nearly 200 burrows were sampled across the range of the southeastern pocket gopher in the three main years of the survey.

Pocket gophers readily bury any disturbance in the burrow, including pitfall traps. So the gophers were removed and relocated. Once vacant, pitfall

traps were placed in the burrow. To finish the procedure, the holes containing the pitfall traps were covered with boards and buried to prevent surface animals from entering (Hubbell and Goff 1939, Ross 1944a, Skelley and Woodruff 1991).

Initial sampling of burrows at one site for an entire year indicated that burrow diversity peaks during the winter months in the Southeast. Some species are active year round, but all could be collected in the winter. Sampling efforts for the survey were focused between late November and April.

Voucher specimens of pocket gophers were collected in most areas to document their current distribution. The majority of these vouchers are deposited in the Field Museum of Natural History, Chicago, IL. Other specimens are deposited at Eastern Illinois University, University of Central Florida, Georgia Museum of Natural History, and Clemson University.

A total of 5837 specimens of scarabs was collected during this survey. The accumulated data are abbreviated to include only county localities for previously described species in order to conserve space. These data are available from the authors on request. Full data and analyses will be published in another paper covering various aspects of the pocket gopher and select members of the burrow fauna. Unless stated otherwise records are based on specimens collected in a pocket gopher burrow.

Full data are given only for the holotype and allotype of newly described species. Since all specimens were collected by persons listed in the acknowledgments, and in a "Geomys burrow," it is overly redundant to list these data for all of the paratypes. Therefore, paratype data are abbreviated to include only specific localities and dates of collection.

Scarab beetle specimens are deposited in numerous collections including: (FSCA) Florida State Collection of Arthropods, Gainesville, FL; (GDC) G. Dellacasa, Genova, Italy; (GMNH) Georgia Museum of Natural History, University of Georgia, Athens, GA; (HFHC) H. F. Howden, Ottawa, Canada; (NHML) Natural History Museum, London, United Kingdom; (OSUC) Museum of Biological Diversity, Ohio State University, Columbus, OH; (PBC) P. Bordat, Merrieres le Buisson, France; (PESC) P. E. Skelley, Gainesville, FL; (RHTC) R. H. Turnbow, Fort Rucker, AL; (TAMU) Texas A and M University, College Station, TX; (UNSM) University of Nebraska State Museum, Lincoln, NE; (USNM) United States National Museum of Natural History,

Washington, DC; (WBWC) W. B. Warner, Chandler, AZ.

### Biological Considerations of Pocket Gophers and Associates

**The Pocket Gopher.** Pocket gophers occur primarily west of the Mississippi River, where various genera and species are found from mountain tops to prairies and into the deserts. They occupy many different habitats and soil types. Accordingly, pocket gophers and the species inhabiting their burrows surely have wide ranging variations in behaviors.

The following discussions are focused on the gopher and insects occurring in the southeastern United States, with comments on western taxa. These conclusions may not apply to species in the western United States.

A pocket gopher burrow is a long set of tunnels which provides them shelter as well as access to food (typically roots and tubers). Pocket gophers live up to 5 years (Reid 1971) and continually dig new tunnels. These tunnels can be up to 165 meters long (Brown and Hickman 1973) and up to 3.5 meters deep (pers. obs. PES), although usually much shallower. Usually the burrow has a main run less than 0.75 meters (1-2 ft.) deep with shallower food runs, and deeper nest and dung chambers, usually only 1-2 meters (4-6 ft.) deep.

Regional variations occur in pocket gopher burrow structure. Dung chambers (the usual site for larval scarabs) are blind-end tunnels where the gopher defecates, then buries the dung. These chambers can be rather large, 0.25-0.75 meters long by 0.2 meters in diameter. In excavating 40 burrows near Tampa, FL, Brown and Hickman (1973) found no dung chambers. Instead they found widened tunnels with the dung lining the bottom in layers. The burrows excavated in north Florida and Alabama prior to the survey all had dung chambers.

Other variations in burrow structure are the winter mounds of pocket gophers in areas with high water tables (Davis 1960 and pers. obs. PES). These winter mounds contain the nest and dung chambers well above the main run. In some northern populations, pocket gophers are known to create burrows in snow banks (Turner *et al.* 1973). In the southeast, no winter mounds were observed, but in many areas the main tunnels varied dramatically in depth, apparently depending on the soil structure and depth of the water table. When shallow, these burrows could be a problem to livestock.

Turner *et al.* (1973) give a good review of pocket gopher biology and their relationships with human activity.

While excavating burrows, we frequently found closed off and abandoned sections with nests and dung chambers. As gophers excavate new tunnels, they apparently backfill old burrows to create new ones. This may bury larvae or pupae of insects in the old chambers and create a potential survival problem for insects left behind.

Pocket gopher's main surface activities are making mounds, occasional foraging close to the burrow, and dispersal. Miller and Bond (1960) discuss burrowing versus mounding activity. Mound production is nearly continuous throughout the year. General timing of mound production is apparently correlated with soil moisture and the concentrations of oxygen and carbon dioxide in the burrow (Kennerly 1964). However, mound production in the Southeast and in many other areas is dramatically increased in the fall (Hickman and Brown 1973) or during the rainy season in dry areas (Miller 1946, 1957). The reason for this dramatic increase in mounding is a matter of debate and probably differs from taxon to taxon and from area to area. Some theories for the dramatic annual increase in mounding include breeding season, soil moisture, dispersal, and provisioning food caches for the winter.

**Insect Adaptations to Burrows.** Some pocket gopher-associated insects display characters similar to true cavernicolous insects: reduced eyes, reduced wings, pale body color, long appendages. At present the only burrow-associated insect that shows the full range of cave adaptations is the camel cricket, *Typhloceuthophilus floridanus* Hubbell (Gryllacrididae), with its complete loss of eyes, long legs, and white body. Other species show some of these characters: reduced eyes, pale body and long legs (*Ptomophagus* spp., Leiodidae; *Ceuthophilus* spp., Gryllacrididae); long legs (*Onthophilus* spp. and *Geomysaprinus* spp., Histeridae) and paler body (*Aphodius* spp.).

Many of the species present in rodent burrow insects have long legs or tarsi. While long appendages are apparently an advantage in caves, many burrowing scarabs have elongated appendages that apparently have nothing to do with living in a "cave" (pers. obs. PES). A loss of cuticular pigment could simply be an adaptation to life beneath ground, as expressed in numerous psammophilous burrowing aphodiines and detritivores. When considering

characters of *Aphodius* inhabiting burrows, they may be adapted for a burrowing, and not a cavernicolous life as was speculated (Skelley and Woodruff 1991).

**Insect Dispersal.** True cave systems do not move and resources enter it in several ways (animal or other). True cave insects have no need to disperse, and allocation of resources to develop unneeded structures for life above ground could be a physiological detriment. This is one hypothesis why cave species have a tendency to lose eyes, wings, and pigment. A pocket gopher burrow is, in essence, a moving cave. However, insects living in a burrow need to move with it, or to be able to disperse. This need to disperse could create an advantage to maintain eyes and wings. Burrow species show varying amounts of structure reduction, which make any generalization about their dispersal abilities tenuous. Instead, there appear to be different strategies for dispersal.

Burrow inhabiting camel crickets (Orthoptera: Rhaphidophoridae) are ancestrally wingless and have long legs. In the burrow they are very active, running and hiding in crevices to avoid a pocket gopher as it plunges down the burrow (Hubbell 1940). Hubbell and Goff (1939) expand on the idea that camel crickets disperse below ground as a gopher enters another burrow for mating, occupies an abandoned burrow, or leaves its mother to create its own burrow. This hypothesis of below ground dispersal for burrow-inhabiting camel crickets is supported by several observations: they have not been collected above ground, indicating they may never come to the surface; multiple life stages are found at the same time, indicating a loss of timing with any outside influences; and species with the most reduced characters (eyes, pigmentation) have restricted distributions (T. Cohn, pers. comm. to PES).

Hubbell and Goff (1939) disregard the possibility of above ground dispersal for all burrow insects based on the observation that they are not collected on the surface. While this appears to be true for camel crickets (Hubbell's speciality group) it does not appear to be the case for beetles. Hubbell and Goff saw no evidence of other groups (flies, beetles, crickets) leaving the burrows (with the exception of *Aphodius aegrotus* Horn at light) and used this to support their theory of subterranean dispersal. Studying the collection records published in their paper, all of the work done by these pioneers was primarily in warm summer months (April to Au-

gust). During our fall and winter surveys, we observed numerous flies and staphylinids exiting freshly opened burrows, as well as diurnal flights of burrow-inhabiting *Aphodius*.

Pocket gopher burrows are considered to be closed systems that are rarely open to the surface. Under what situations would a beetle need to risk coming to the surface? Larval and pupal stages of beetles are relatively immobile. As a pocket gopher digs it frequently backfills old burrows, nests and dung chambers. Immature beetles left behind will need to find an active system for the species to survive. All burrow scarabs have normal eyes and fully developed wings. Skelley and Woodruff (1991) speculated that scarabs come to the surface and disperse above ground, searching for an active burrow.

Numerous observations have been made supporting the above-ground dispersal hypothesis for gopher associated beetles: one *Euphoria aestuosa* Horn was collected on top of the board that covered a burrow; one *Aphodius dyspistus* Skelley and Woodruff was collected in a flight intercept trap; one *Aphodius hubbelli* Skelley and Woodruff and the holotype of *Onthophilus giganteus* Helava (Histeridae) were collected in surface pitfall traps; one *Aphodius tanytarsus* and two *Aphodius pholetus* Skelley and Woodruff were collected under fresh mounds; numerous *Aphodius laevigatus* Haldeman and *A. aegrotus* have been collected at light; several *Spilodiscus floridanus* Ross (Histeridae) have been collected on mounds or actually observed flying into them (pers. obs. PES); B. Warner (pers. comm.) collected burrow inhabitants in Arizona using unbaited pitfall traps that resembled open burrows; small diurnal flights of *Aphodius iowensis* Wickham and *Aphodius criddlei* Brown are routinely observed from late September to mid-October in North Dakota (pers. obs. RDG); a massive flight of *Aphodius haldemani* Horn was observed in early October 1966, in Clay County, Minnesota (pers. obs. RDG); diurnal dispersal flights of burrow-associated *Aphodius* have been observed from September to December (pers. comm., W. J. Brown, Ottawa Canada, deceased, and pers. obs. RDG), and numerous other observations by numerous other coleopterists (pers. comm.).

If burrow inhabiting beetles are dispersing above ground they could be using two possible methods to enter an active burrow. The first is to find a temporary opening to the surface. Pocket gophers are known to leave the burrow open after heavy rains, to forage, or to disperse. The second

way to gain access is to locate a fresh mound and follow the backfilled tunnel to the burrow. While it would be easiest enter an open burrow, pocket gophers do not leave them open for long. A few observations mentioned above indicate some beetles search out mounds. How they find a mound is under study. Some hypotheses on how they find mounds include: chemical (odor of fresh turned soil, or of pocket gopher), visual (seeing a hole or mound), thermal (mounds heat and cool at different rates compared to the surrounding ground, unpublished data PES), water content in fresh mounds, and others.

Having accepted that beetles gain access to burrows in two possible ways, why do most of the collection records indicate a fall or winter activity period? A beetle's survival depends on its ability to find and enter a new burrow system. Dispersal should be timed to allow the best chance for finding a new burrow. Possible answers to the timing come from behaviors of the pocket gopher. As mentioned before, pocket gophers have a dramatic increase in mounding activity in the fall. This increase in mounding activity would increase a beetle's chance to find an active burrow temporarily open, or a fresh mound.

Either method of burrow entry would allow for some beetle activity year round, with an increase in the fall and winter to coincide with increased pocket gopher activity. Based on our collecting records and the apparent seasonality of species, the strategy and timing of dispersal differs among taxa. Further study is needed to confirm these dispersal hypotheses.

**Dung Feeding Specialization.** Gordon (1983) presented data on food and habits of *Aphodius* species in the eastern United States. These data were used to group the species into five categories:

- Category I - Species associated with deer dung.
- Category II - Species associated with rodent burrows or nests, or burrows of gopher tortoise.
- Category III - Native generalists.
- Category IV - Native detritivores.
- Category V - Native species with unknown habits.

For Category I species, Gordon (1983) presents convincing evidence that the type of dung and microenvironmental placement in the surface environment is important as it relates to water content and potential utilization of dung. Surface dung beetles could have evolved adaptations that would

allow them to locate better dung types (i.e. pellet vs pat) and specific conditions as relate to various abiotic factors (i.e., water content, temperature and size).

Burrow dung beetles only have one type of dung (pellet) and one condition (under ground with relatively constant temperature, humidity and size). If these beetles have "specialized" on this type of dung then any behavior with adaptive advantages would relate to their ability to find the situation in which the dung resides. The advantage may be that beetles spend as little time as possible on the surface by focusing on finding a structure, not dung. Once in the active structure of a suitable host, dung is plentiful and only a short distance away. The best evidence for this is that Category II beetles are not collected in surface traps, unless they are in or very close to the structure. Pocket gopher beetles are not collected in surface dung traps, but readily come to the same bait and trap when placed in the burrow.

Expanding a little more on this idea, in the western US, there are many species of *Aphodius* which have close associations with certain types of rodents (pack rats, ground squirrels, kangaroo rats, pocket gophers, etc.), all of which produce recognizable structures. The associated *Aphodius* may show a niche specialization (to structure type or location) more than a dung condition specialization as seen with surface species of Gordon's Category I. Following on these ideas, Gordon's (1983) category descriptions are expanded as follows:

Category I - Deer dung feeders, specializing in dung of specific conditions on the surface.

Category II - Dung feeders specializing in dung of specific structures (burrows, nests, or tree holes) and host (rodent, tortoise).

Category III - Native generalists, possibly specializing in dung of a specific habitat.

Category IV - Native detritivore

Category V - Native species of unknown habits or specializations.

As Gordon (1983) did for Category I, the species in Category II can also be broken into temporal sets. Most of the *Aphodius* in the southeast pocket gopher burrows are active in the winter months, while *A. laevigatus* is a warm weather species (active year round in many parts of Florida) and *A. aegrotus* is active year round with a peak of activity in the early Fall (August to November) (Skelley and

Woodruff 1991). These data will be analyzed in subsequent studies.

Biologies of these insects and how they relate to the life cycles of a "belligerent sausage" are worth further study. It is hoped that current efforts will encourage more studies into this intriguing system.

### Key to *Aphodius* Inhabiting Southeastern Pocket Gopher Burrows

Recent papers (Skelley and Woodruff 1991, Skelley and Gordon 1995) described several species of *Aphodius* occurring in southeastern pocket gopher burrows and comment on how the species fit into existing keys. The most notable keys being Gordon's (1983) key to the *Aphodius* of the eastern United States, and Woodruff's (1973) key to *Aphodius* of Florida. With the addition of three new species, it becomes problematic to adequately modify those keys without creating confusion.

Species considered in this paper are rarely, if ever, collected outside of burrow systems. Exceptions being *A. aegrotus* and *A. laevigatus* which are frequently encountered at lights. Conversely, species of *Aphodius* found outside burrows are rarely collected in burrows. Those that have are a result of accidental entry or improper sampling technique.

The following key is presented to enable those working in southeastern pocket gopher burrows to identify *Aphodius* known to occur in these systems. If a specimen collected in a burrow is not in this key, the previously mentioned keys need to be consulted for identification.

1. Pronotum laterally explanate, shelf-like, explanate border broader than gena is long; lateral margin noticeably thickened at middle (Fig. 12); body dark brown ..... *A. platypleurus* S&W
- Pronotum narrowly explanate laterally, explanate border narrower than gena is long, or not explanate; lateral margin of uniform thickness; body pale reddish or dark brown ..... 2
- 2(1). Pronotal disc with distinct, coarse punctures that are relatively evenly spaced across entire surface, (Figs. 2-6) ..... 3
- Pronotal disc without coarse punctures (may be densely punctate laterally), or with few, indistinct, irregularly spaced punctures (Figs. 10, 11) ..... 6

- 3(2). Pronotum and elytra setose (Figs. 2-4), possibly rubbed off in places; elytra frequently dull or encrusted with dirt ..... 4  
 — Pronotum and elytra glabrous (Figs. 5-6), rarely with fine setae at apical declivity of elytra; elytra smooth, glossy ..... 5
- 4(3). Elytral striae deep, as broad as or broader than intervals; pronotal punctures nearly contiguous (Fig. 3) ..... *A. dyspistus* S&W  
 — Elytral striae fine, not deep, much narrower than the intervals; pronotal punctures well separated (Fig. 2) ..... *A. baileyi* S&G, n.sp.
- 5(3). Coarse pronotal punctures 8-10 times diameter of fine punctures; coarse punctures widely spaced at posterior angle (Fig. 6) .....  
 ..... *A. tanytarsus* S&W  
 — Coarse pronotal punctures 3-5 times diameter of the fine punctures; coarse pronotal punctures nearly contiguous at posterior angle (Fig. 5) ..  
 ..... *A. bakeri* S&G, n.sp.
- 6(2). Pronotum margined at base (Figs. 10, 11), not laterally explanate ..... 7  
 — Pronotum not margined medially at base, lateral edge explanate ..... 9
- 7(6). Pronotum with widely scattered coarse punctures on disc; pronotum lacking lateral marginal line in anterior half (Fig. 11) ..... *A. alabama* S&G  
 — Pronotum lacking coarse punctures on disc; lateral marginal line of pronotum complete (Fig. 10) ..... 8
- 8(7). Small species, length less than 6 mm; clypeal margin lacking setae (Fig. 10); lateral pronotal disc with coarse punctures, often contiguous .  
 ..... *A. aegrotus* Horn  
 — Large species, length more than 7 mm; clypeal margin distinctly fimbriate (Fig. 13); lateral pronotal disc impunctate .....  
 ..... *A. laevigatus* Haldeman
- 9(6). Clypeus near anterior margin rugose-granulate; coarse pronotal punctures present laterally and basally; dorsal color primarily dark brown .....  
 ..... *A. pholetus* S&W  
 — Clypeus near anterior margin smooth; coarse pronotal punctures present laterally, not basally; dorsal color reddish brown to dark brown .  
 ..... 10
- 10(9). Coarse pronotal punctures distinct laterally; ventral body color reddish-brown; male metatibia notched on ventral edge, with patch of setae on inner surface restricted to extreme apex (Fig. 7) .....  
 ..... *A. hubbelli* S&W



Figure 1. *Euphoria aestuosa* Horn, 2 color forms. Lengths = 13 and 15 mm.

- Coarse pronotal punctures weak laterally; ventral body color primarily dark brown; male metatibia with smooth ventral edge, and apical patch of setae occupying 1/3-1/2 of inner surface (Figs. 8, 9) ..... *A. gambrinus* S&G, n.sp.

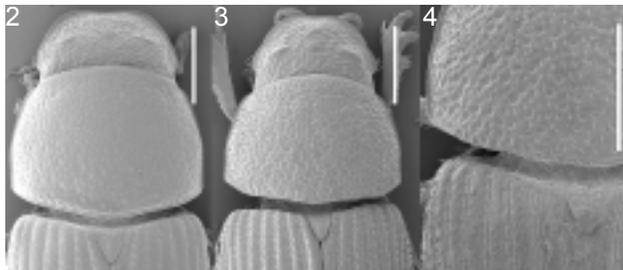
### Systematics

The scarabs in *G. pinetus* burrows are all dung feeding species belonging to the genus *Aphodius* (11 spp.) or *Euphoria* (1 sp.). Occasionally other scarabs fell into the traps or were attracted to the bait because of a poorly sealed board covering the hole. These accidentals were infrequently collected in the burrows, but are abundant surface dwelling species. They are not considered a normal part of the burrow fauna and have been omitted for that reason. Some species collected accidentally are *Aphodius stupidus* Horn, *Aphodius distinctus* (Müller), *Aphodius campestris* Blatchley, *Onthophagus tuberculifrons* Harold, *Phaneus igneus* MacLeay, and *Copris minutus* (Drury). The following accounts are for species that appear to be obligate *Geomys* burrow associates.

#### *Euphoria aestuosa* Horn (Fig. 1)

*Euphoria aestuosa* Horn 1880: 400.

**Diagnosis:** Length 10.5 to 17.0 mm, width 6.0 to 10.0 mm. Body dull, color pattern with two distinct forms: entirely black; or with orange pronotum

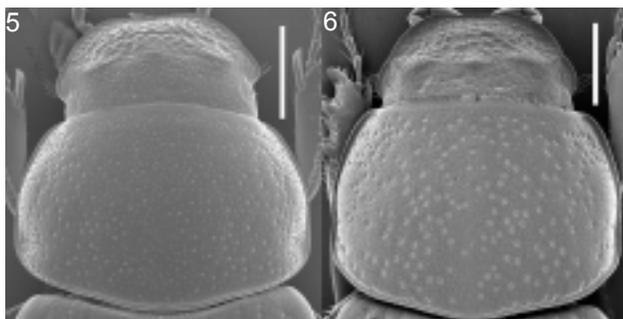


Figures 2-4. Pronota and elytral bases of 2.) *Aphodius baileyi* Skelley and Gordon, 3.) *A. dyspistus* Skelley and Woodruff, 4.) *A. sepultus* Cartwright. Line = 0.2 mm.

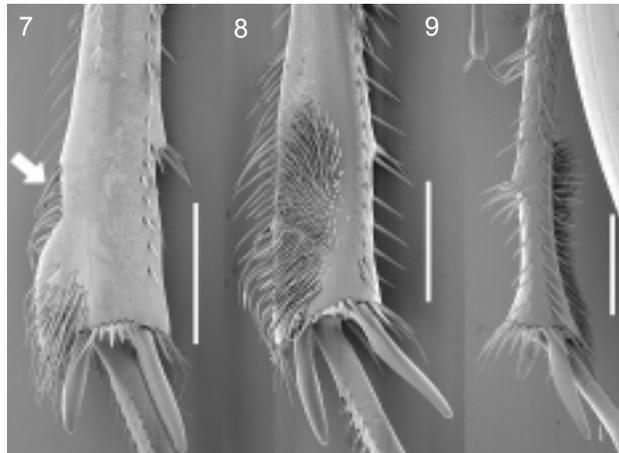
bearing an inverted central heart-shape black mark and orange elytra with black sutural margin (Fig. 1). Clypeus with smooth anterior margin. Pronotum with basal margin rounded, not distinctly concave around scutellum. Elytra dull, lacking any tomentose markings.

**Remarks:** This is the only southeastern *Euphoria* with the basal margin of the pronotum rounded and a color pattern of orange with black, or entirely black. Members of this species from southern prairie states can also be intermediate in color pattern, having varying amounts of orange (pers. comm. A. Hardy). This species may be confused with *Stephanucha thoracica* Casey which is known to live in pocket gopher mounds (Skelley 1991) and is also known to have similar variations in color pattern. The genus *Stephanucha* is distinguished by a dentate clypeal margin.

Hardy (1980) reported that *E. aestuosa* was reared from the dung chamber of a pocket gopher in northern Louisiana. He gave additional records from eastern Kansas, Oklahoma, and Texas. Godwin (2000) reports on another rearing of *E. aestuosa* from pocket gopher burrows in east Texas, gives additional distributional data for specimens



Figures 5-6. Heads and pronota of 5.) *Aphodius bakeri* Skelley and Gordon, 6.) *A. tanytarsus* Skelley and Woodruff. Line = 0.5 mm.



Figures 7-9. Metatibiae of 7.) *Aphodius hubbelli* Skelley and Woodruff inner surface (arrow indicates notch on ventral edge), 8-9.) *A. gambrinus* Skelley and Gordon 8.) inner surface, 9.) dorsal view. Line = 0.5 mm.

studied, and discusses color pattern variations in the prairie populations.

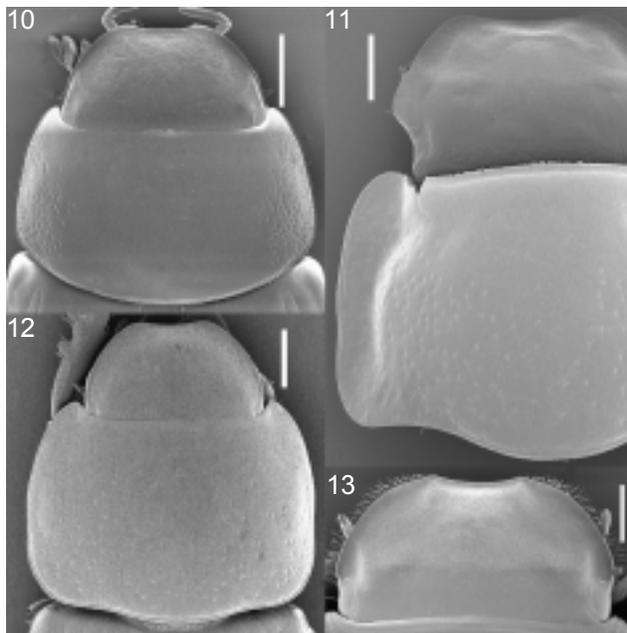
We were unable to distinguish southeastern specimens from those collected in eastern Texas and presently consider them to be conspecific. This is the only scarab in southeastern pocket gopher burrows which is found on both sides of the Mississippi River. All other scarabs (*Aphodius* spp.) are distinct with sister species occurring west of the Mississippi River. Further research may reveal that these *Euphoria* are also distinct.

Peck and Thomas (1998) refer to a specimen from Florida as "sp. nr. *discicollis* Thomson." According to A. Hardy (pers. comm.) the genus *Euphoria* is in need of revision. The correct name for those occurring in east Texas and, as presently considered, those occurring in the Southeast is *E. aestuosa*.

**Specimens studied:** A total of 54 specimens of *E. aestuosa* was examined from the following counties: **FLORIDA:** Okaloosa, Calhoun, Santa Rosa. **GEORGIA:** Baker, Dodge.

### *Aphodius aegrotus* Horn (Fig. 10)

*Aphodius aegrotus* Horn 1870: 127-128.  
*Aphodius geomysi* Cartwright 1939: 356-357; Woodruff 1973: 83 (synonymy).



**Figures 10-13.** Heads and pronota of 10.) *Aphodius aegrotus* Horn, 11.) *A. alabama* Skelley and Gordon, 12.) *A. platypleurus* Skelley and Woodruff, 13.) *A. laevigatus* Haldeman. Line = 0.5 mm.

**Diagnosis:** Length 4.0 to 5.3 mm, width 2.0 to 2.5 mm. Body entirely pale red. Pronotal disc lacking punctation, laterally with coarse punctures frequently contiguous (Fig. 10). Protibia dorsally punctate. Elytron lacking setae on disc and marginal bead.

**Remarks:** *Aphodius aegrotus* belongs to a group of species which has punctures on the dorsal surface of the protibia. *Aphodius aegrotus* can be distinguished by its unique pronotal puncture pattern and broadened body. *Aphodius troglodytes* Hubbard differs by having long setae on its elytral margin. *Aphodius campestris* Blatchley and *A. rubeolus* Beauvois differ by having pubescence on the apical 1/3 of the elytra, near the lateral margin. *Aphodius stercorosus* Melsheimer differs by having fine punctures on the pronotal disc, being darker in color, and has a narrower, more parallel sided body.

*Aphodius aegrotus* is commonly collected at light. Woodruff (1973) lists many of these records. Most of these records will not be included in the larger analysis of the pocket gopher burrow fauna because beetles were not collected in association with a burrow. County records based on specimens not collected in pocket gopher burrows are presented separately below for a more complete distribu-

tional record. All of these counties have (or had) populations of pocket gopher.

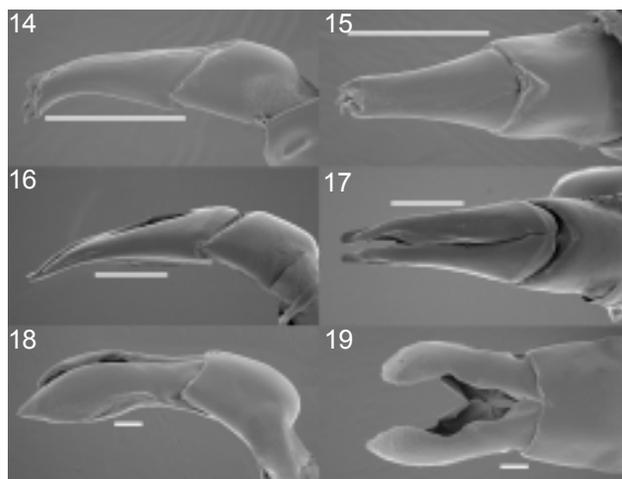
Second only to *A. laevigatus*, *A. aegrotus* was the most commonly collected *Aphodius* during this survey. Possible reasons for their abundance are discussed under "Remarks" for *A. laevigatus*. *Aphodius aegrotus* is listed in Woodruff and Deyrup (1994) as a "Species of Special Concern" because of its strict association with pocket gophers.

**Specimens studied:** A total of 902 specimens of *A. aegrotus* was examined from the following counties: **ALABAMA:** Autauga, Baldwin, Bullock. **FLORIDA:** Alachua, Bay, Brevard, Calhoun, Columbia, Dixie, Duval, Gilchrist, Hernando, Hillsborough, Jackson, Lafayette, Levy, Liberty, Madison, Nassau, Okaloosa, Pasco, Pinellas, Polk, Putnam, Santa Rosa, St. Johns, Suwannee, Taylor, Volusia, Walton, **GEORGIA:** Baker, Burke, Charlton, Decatur, Dodge, Richmond, Taylor, Thomas. Additional county records, mainly collected at light traps (Woodruff 1973): **FLORIDA:** Escambia, Highlands, Jefferson, Lake, Orange, Seminole.

#### *Aphodius alabama* Skelley and Gordon (Fig. 11)

*Aphodius alabama* Skelley and Gordon 1995: 217-219

**Diagnosis:** Length 4.9 to 6.7 mm, width 2.2 to 3.0 mm. Body broad, widest across pronotum, some-



**Figures 14-19.** Male genitalia of 14-15.) *Aphodius baileyi* Skelley and Gordon, 16-17) *A. bakeri* Skelley and Gordon, 18-19.) *A. gambrinus* Skelley and Gordon; 15,17,19) dorsal view, 14,16,18) lateral view. Line = 0.2 mm.

what flattened; dark reddish brown. Pronotum broad, lacking lateral depressions and "shelves"; lateral margin absent on anterior half; basal margin complete; pronotal punctures irregularly scattered over surface (Fig. 11).

**Remarks:** This species is easily distinguished from other southeastern US species by its unusually broad pronotum with the characteristics described above. *Aphodius alabama* appears to inhabit only two small portions of the pocket gopher range. Limiting factors for this restricted range are not known.

**Specimens studied:** Including the type series, a total of 128 specimens of *A. alabama* was examined from the following counties: **ALABAMA:** Coffee, Dale. **GEORGIA:** Baker, Jenkins, Richmond.

***Aphodius baileyi* Skelley and Gordon**  
new species  
(Figs. 2, 14, 15)

**Description:** Holotype male, length 3.0 mm, width 1.4 mm. Body elongate, convex, not flattened, widest across middle of pronotum. Color yellowish brown except apical 1/2 of head, lateral 1/4 of pronotum, and legs paler yellowish brown, anterior femur yellow. Head slightly convex; surface shining, polished, strongly granulate throughout, lacking pubescence except vertex with short, decumbent hairs. Clypeal apex broadly, faintly emarginate medially with broadly rounded anterior angle. Gena well developed, fimbriate. Pronotum (Fig. 2) convex, somewhat explanate laterally, surface glossy, faintly alutaceous, punctures separated by 1 to 3 times a diameter medially, punctures coarser and denser laterally, each puncture with short, decumbent seta; lateral margin weakly curved, anterior angle abruptly rounded, with small, distinct depression, posterior angle and pronotal base forming abrupt, oblique angle lacking depression, base distinctly margined. Elytron (Fig. 2) glossy, surface faintly alutaceous; striae narrow, flat, interval broad, slightly convex, bearing a row of distinct punctures on each side near stria, each puncture bearing a single, short, decumbent seta. Mesosternum dull, strongly alutaceous, faintly carinate between coxae. Metasternum dull, strongly alutaceous laterally, weakly glossy medially, coarsely punctate on each side of midline. Abdominal sternites dull, alutaceous, each with 3 irregular transverse rows of long, decumbent setae. Protibial

spur as long as basal 2 tarsomeres, slightly curved ventrally, slightly sinuate. Profemur ventral surface alutaceous, weakly shining, impunctate; posterior surface impunctate. Mesotibial apical fringe composed of irregularly alternating long and short setae, long setae separated by one short seta laterally, separated by 2 or 3 short setae medially, long setae distinctly longer than inferior mesotibial spur. Inferior mesotibial spur less than half length of superior spur, slender, apex obliquely truncate, inner and outer angles slightly dentate. Meso- and metafemur sparsely punctate, each bearing long setae in an irregular row along posterior margin, some additional seta bearing punctures present near apical femoral margin in outer half of femur. Meso- and metatrochanter each with a single long seta. Metatibia slender, rounded; metatibial apical fringe composed of irregularly alternating long and short setae, long setae separated by a single short seta at outer angle, then progressively separated by 2 short setae, then 5 short setae medially, long setae 0.6 times length of inferior metatibial spur; metatibial spurs unequal in length, inferior spur slightly shorter, superior spur as long as tarsomere I. Protarsomeres I-IV subequal in length, protarsomere V as long as protarsomeres III-IV combined. Meso- and metatarsomere I as long as II-III combined; meso- and metatarsomere V as long as III-IV combined; meso- and metatarsal claws 0.6 times length of tarsomere V. Paramere apex nearly truncate, slightly emarginate medially, with small, apical, membranous appendage (Fig. 14, 15).

**Female:** Similar to male except pronotum slightly more convex, less explanate laterally; protibial spur slightly less robust; inferior mesotibial spur straight, apically acute.

**Variation:** Length 2.9. to 3.8 mm, width 1.4 to 1.7 mm. Pubescence on body surface can be rubbed off, particularly on vertex; male pronotum often with trace of posterolateral depression.

**Type material:** Label data for holotype male and allotype female of *Aphodius baileyi*: **GEORGIA: Thomas Co.**, NE of Metcalf, 2.7 mi. S. jct. Rt. 19 on New Hope Rd. (Sedgefield Plantation), 10-24-I-1999, Kovarik, Turnbow & Baker, *Geomys* burrow pitfall (FSCA).

Paratypes (715): same data as holotype (6); same data as holotype except 24-I-21-III-1998 (6); **ALABAMA: Russell Co.**, 9 mi. NW. Seale, jct. CR-22 & CR-65, 17-30-I-1999 (1). **FLORIDA: Jackson**

Co., N. of Dellwood, 2.5 mi. S. jct. Rt. 271 on Rt. 164 at Brenson Pond, 21-28-XII-1997 (1); **Jefferson Co.**, 3.5 mi. NW. Monticello, 2.5 mi. W. Rt-259 on W. Lake Rd., 18-27-I-1999 (3), 2.1 mi. NW. Waukeenu, "El Destino" Plantation, 10-25-I-1998 (4), 3.4 mi. W. Waukeenu on St-27, 20-26-I-1997 (2); **Leon Co.**, Tallahassee, 0.8 mi. E. US-27 on Old Bainbridge Rd., 11-20-I-1998 (1), 5.3 mi. W. of Miccosukee, 26-I-16-III-1999 (2); **Madison Co.**, 3.8 mi. W. Madison on US-90 [8.9 mi. E. Rt. 221 on US-90], 18-20-I-1999 (3); **Taylor Co.**, Perry airport; jct. Rt. 362 & 361A, 20-XII-1997 to 8-I-1998 (3) and 19-21-XII-1997 (2). **GEORGIA: Baker Co.**, N. Newton, 4.3 mi. N. jct. Coolewahee Creek on Rt. 91, 10-31-I-1999 (15) and 31-I-13-III-1999 (47); **Decatur Co.**, NW. Bainbridge, 3.5 mi. N. jct. Rt. 27/84 on Rt. 352, 29-XII-1997 to 11-I-1998 (4), Bainbridge, 3.6 mi. N. jct. Rt. 84 on Rt. 253, 1-I-14-IV-1998 (4); **Dodge Co.**, Gresston, 1 mi. NE. on Wilson Woodard Rd., 2-8-III-1997 (1) and 8-30-III-1997 (86), 1.1 mi. NE. Gresston, 30-III-22-V-1997 (2); **Grady Co.**, N. Beachton, 0.2 mi. W. jct. Rt. 319 on Blackshear Rd., 10-23-I-1999 (15), N. Beachton, 0.3 mi. W. jct. Rt. 319 on Blackshear Rd., 10-I-1999 (39) and 10-23-I-1999 (171), N. Beachton, 0.6 mi. W. jct. Rt. 319 on Blackshear Rd., 10-23-I-1999 (1) and 23-I-21-III-1999 (12), 7 mi. W. Metcalf on Metcalf-Beachton Rd., 1-15-XII-1996 (1), S. Thomasville; 0.3 mi. E. SR 319 on Metcalf Rd., 10-17-XII-1996 (1) and 17-23-XI-1996 (1); **Thomas Co.**, W. Metcalf, 1.8 mi. S. Metcalf Rd. on Springhill Rd., 17-23-XI-1996 (1), 4.4 mi. N. Metcalf on SR.59, 12-14-I-1996 (4) and 13-21-I-1996 (52) and 21-28-I-1996 (154) and 28-I-3-II-1996 (1), 2 mi. SW. Metcalf on SR.59, 15-I-1996 (1) and 21-28-I-1996 (1), 2.5 mi. W. Metcalf on Beachton Rd., 3-10-II-1996 (1) and 1-22-II-1997 (3) 5.8 mi. N. Metcalf on SR.59 at Magnolia Rd., 13-21-I-1996 (1) and 21-28-I-1996 (4) and 28-I-3-II-1996 (4) and 16-22-III-1996 (33) and 22-31-III-1996 (9). Paratypes are deposited in the following collections: FSCA, GDC, GMNH, HFHC, NHML, OSUC, PBC, PESC, RHTC, UNSM, USNM, WBWC.

**Remarks:** *Aphodius baileyi* is similar to both *A. sepultus* Cartwright and *A. dyspistus* Skelley and Woodruff. From both species it is differentiated by the glossy dorsal surface; convex elytral intervals, and smaller, distinctly separated pronotal punctures (Fig. 2). *Aphodius sepultus* (Fig. 4) and *A. dyspistus* (Fig. 3) have a dull dorsal surface; flat elytral intervals, and very large, nearly contiguous pronotal punctures. In addition, *A. sepultus* is known only from Texas and Louisiana. *Aphodius*

*baileyi* shares part of the range of *A. dyspistus* and they are frequently found together in the same burrow system.

**Etymology:** This species is named for Mark Bailey who provided several unpublished records of pocket gophers in Alabama, and helped us trap beetles in several remote localities.

***Aphodius bakeri* Skelley and Gordon  
new species  
(Figs. 5, 16, 17)**

**Description:** Holotype male, length 4.5 mm, width 2.0 mm. Body elongate, normally convex, not flattened, widest across middle of elytra. Color dark reddish brown except anterior 1/2 of head, lateral 1/4 of pronotum, sutural interval, humeral angle and apical 1/3 of elytron, and legs paler yellowish to reddish brown. Head slightly convex, surface glossy, strongly granulate throughout except on finely punctate vertex. Clypeal apex broadly, distinctly emarginate medially with broadly rounded anterior angles. Gena well developed, fimbriate. Pronotum (Fig. 5) strongly convex, narrowly, weakly explanate laterally, surface shining, faintly alutaceous, with intermixed fine and coarse punctures, punctures dense, large punctures separated a diameter or less, becoming nearly contiguous on anterior and posterior angles; lateral margin distinctly curved, anterior angle abruptly rounded with small, indistinct depression, posterior angle broadly rounded with large, distinct depression, pronotal base completely margined. Elytron glossy, surface faintly alutaceous, stria narrow with coarse, punctures separated by a diameter, interval convex with row of fine punctures on each side. Mesosternum dull, strongly alutaceous, flat between coxae. Metasternum dull, strongly alutaceous laterally, with coarse, setigerous punctures, medially shining, moderately coarsely punctate, punctures separated by a diameter or less. Abdominal sternites dull, with indistinct, coarse, setigerous punctures throughout, setae long in lateral 1/3, short medially. Protibia with apical spur large, as long as basal 2 tarsomeres combined, strongly curved downward, slightly sinuate. Profemur alutaceous, nearly impunctate, posterior surface with indistinct, coarse punctures throughout. Mesotibial apical fringe composed of irregularly alternating long and short setae, long setae as long as inferior tibial spur separated by one short seta laterally, separated by 2 or 3 short setae medially. Inferior mesotibial spur less than half length of superior spur, slender,

tapered to truncate apex, outer angle of apex rounded, inner angle dentate. Meso- and metafemur sparsely punctate throughout, sparse, anterior margin and posterior 1/3 bearing long setae. Meso- and metatrochanter each with single long seta and 3 short setae. Metatibia slender, rounded, strongly flared apically; metatibial apical fringe like mesotibia; metatibial spurs unequal in length, inferior spur 2/3 length of superior spur, superior spur slightly longer than tarsomere I. Protarsomeres I-IV subequal in length, protarsomere V as long as previous 2.5 tarsomeres combined. Meso- and metatarsomere I as long as subsequent 2.5 tarsomeres combined; meso- and metatarsomere V as long as III-IV combined; meso- and metatarsal claws 0.6 x length of tarsomere V. Parameres simple, lacking membranous appendages, apex slender, flattened before apex in lateral view (Figs. 16, 17).

**Female:** Similar to male except protibial spur shorter, slender; inferior mesotibial spur slender, apically acute.

**Variation:** Length 3.5 to 4.7 mm, width 1.6 to 2.2 mm. Dorsal color varies from dark reddish brown to pale yellowish brown.

**Type material:** Label data for holotype male of *Aphodius bakeri*: **GEORGIA: Grady Co.**, Beachton, N., 0.3 mi. W. jct. Rt. 319 on Blackshear Rd. (Pebblehill Plantation), 10-23-I-1999, Kovarik, Turnbow & Baker, *Geomys* burrow pitfall (FSCA). Allotype female label data: **GEORGIA: Thomas Co.**, Metcalf, NE, 2.7 mi. S. jct. Rt. 19 on New Hope Rd. (Sedgefield Plantation), 10-24-I-1999, Kovarik, Turnbow & Baker, *Geomys* burrow pitfall (FSCA).

Paratypes (55): same data as holotype (4); same data as allotype (4); **ALABAMA: Covington Co.**, 1.5 mi. NW. Wing, 18-19-I-1998 (1). **FLORIDA: Calhoun Co.**, 1.7-2.6 mi. E. jct. Bay CR-167 on Calhoun CR-274, 20-30-I-1999 (1); **Okaloosa Co.**, Deerland, 2.8mi. W. Co. line on US 90, 17-31-XII-1991 (3) and 29-XII-1992 (1) and 30-XII-1992 to 5-I-1993 (1); **Santa Rosa Co.**, 2.5 mi. NW. Munson [0.2 mi. S. Big Juniper Ck], 3-18-I-1999 (3), 2 mi. NW. Munson, 0.5 mi. N. Amos Cabrnis Rd. 20-XII-1998 (2), 6.9 mi. N. Harold, 0.3 mi. W. Bryant Bridge Rd. & Bud Bass Rd., 20-XII-1998 to 2-I-1999 (1), 5.2 mi. S. Munson, Bryant Bridge Rd. N. of Alligator Creek, 20-XII-1998 to 2-I-1999 (1), S. edge Blackwater River St. Pk., 2.7 mi. N. Harold & 1mi.E., 20-XII-1998 to 2-I-1999 (1), S. Munson; 4.7mi.S.jct.Rt-4 & Rt-191 on Sandy Landing Rd.,

19-XII-1998 to 3-I-1999 (2), N. Harold, 0.8 mi. N. on Deaton Bridge Rd., 28-XII-1997 to 19-I-1998 (4), 2.2 mi. N. Munson, 0.45 mi. E. Rt.191 on Green Rd., 20-XII-1998 (1), 2.2 mi. N. Munson, 0.7 mi. E. Rt.191 on Green Rd., 20-XII-1998 to 2-I-1999 (1), 2.2 mi. N. Munson, 1 mi. E. Rt.191 on Green Rd., 3-19-I-1999 (17) and 20-XII-1998 to 2-I-1999 (2); **WALTON Co.**, DeFuniak Springs airport, 21-26-I-1990 (1). **GEORGIA: Baker Co.**, 8 mi. SW. Newton, J. W. Jones Ecol. Ctr., xeric area, 14-21-III-1997 (1), N. Newton, 4.3 mi. N. jct. Coolewahee Creek on Rt.91, 10-31-I-1999 (1); **Early Co.**, 3.2 mi. NW. Cedar Springs, Shackelford Williams Bluff Preserve, 6-21-II-2001 (1); **Grady Co.**, N. Beachton, 0.3 mi. W. jct. Rt.319 on Blackshear Rd., 10-23-I-1999 (5); **Thomas Co.**, NE. Metcalf, 2.7 mi. S. jct. Rt.19 on New Hope Rd., 10-24-I-1999 (5) and 24-I-21-III-1999 (1). Paratypes are deposited in the following collections: FSCA, GDC, GMNH, HFHC, NHML, OSUC, PBC, PESC, RHTC, UNSM, USNM, WBWC.

Five other specimens (PESC) not designated as paratypes but considered this species have the following data: **FLORIDA: Walton Co.**, DeFuniak Springs Airport, 8-22-XI-1996 (1); **Santa Rosa Co.**, 0.8 mi. N. Harold on Deaton Bridge Rd., 5-20-XII-1998 (1) and 1-III-10-IV-1999 (1); **Santa Rosa Co.**, 2.2 mi. N. Harold; S. boundary of Blackwater R. St. For. WMA, 6-20-XII-1998 (1) and 1-III-10-IV-1999 (1).

**Remarks:** *Aphodius bakeri* resembles *A. tanytarsus* Skelley and Woodruff but is easily differentiated by having metatarsal claws half as long as tarsomere V, and moderately coarse pronotal punctures intermixed with distinct fine punctures (Fig. 5). *Aphodius tanytarsus* has metatarsal claws nearly as long as metatarsomere V, and extremely coarse pronotal punctures intermixed with faint, very fine punctures (Fig. 6). In addition the male genitalia of these two species are distinctly different in gross structure, especially in a lateral view.

Five specimens are excluded from the paratype series because they possess the following atypical characters. Clypeus and epistome with rugose sculpture reduced, nearly absent; pronotum broad, distinctly explanate laterally, lateral border nearly straight; and elytral interval with dense, confused fine punctures not arranged in rows on each side of interval. In all other respects, including male genitalia, these specimens do not differ from the typical form and are considered slightly aberrant examples of *A. bakeri*.

**Etymology:** This species is named for Wilson Baker who helped us gain access to many privately owned plantations in the Red Hills region of south-west Georgia and north Florida. Without his assistance, we would not have been able to collect in many of the most interesting sites sampled.

***Aphodius dyspistus* Skelley and Woodruff  
(Fig. 3)**

*Aphodius dyspistus* Skelley and Woodruff 1991:  
518-521

**Diagnosis:** Length 2.8 to 3.9 mm, width 1.3 to 1.9 mm. Body dark brown, deeply densely punctate, each dorsal puncture with distinct seta; elytral intervals appearing raised; elytral striae deep, appearing broader than intervals, punctures very large and paired (Fig. 3); body frequently coated with dirt.

**Remarks:** *Aphodius dyspistus* is the only *Aphodius* in the SE with dorsal body setae and heavy sculpturing. It is most closely related to *A. sepultus* and *A. baileyi*; see "Remarks" under *A. baileyi*. These small species seem to be extremely abundant in burrows, yet their size and propensity to be covered with dirt make them difficult to find.

**Specimens studied:** Including the type series, a total of 771 specimens of *A. dyspistus* was examined from the following counties: **ALABAMA:** Autauga, Baldwin, Bullock, Coffee, Dale, Escambia, Houston, Macon, Montgomery, Russell. **FLORIDA:** Alachua, Calhoun, Dixie, Flagler, Gilchrist, Jackson, Jefferson, Lafayette, Leon, Levy, Nassau, Okaloosa, Putnam, Santa Rosa, St. Johns, Taylor, Walton. **GEORGIA:** Baker, Burke, Charlton, Decatur, Dodge, Early, Grady, Jenkins, Marion, Richmond, Thomas.

***Aphodius gambrinus* Skelley and Gordon  
new species  
(Figs. 8, 9, 18, 19)**

**Description:** Holotype male, length 9.5 mm, width 4.4 mm. Body elongate, moderately flattened, widest across base of pronotum. Color yellowish brown except head, pronotum, and anterior leg darker reddish brown, meso- and metasternum black. Head feebly convex, surface glossy, polished, finely, almost imperceptibly punctate, faintly alutaceous. Clypeus without pubescence, apex broadly, weakly

emarginate medially, anterior angle broadly rounded. Gena nearly obsolete, laterally fimbriate. Pronotum broad, weakly convex, surface glossy, finely, almost imperceptibly punctate medially, lateral 1/5 coarsely sparsely punctate, broadly explanate, with depression extended from base to apex, less strongly depressed near anterior angle, anterior angle abrupt, posterior angle broadly rounded, lateral margin straight medially, base not margined. Elytron glossy, faintly alutaceous; striae weakly impressed, finely punctate; interval impunctate, slightly alutaceous, nearly flat. Mesosternum dull, strongly alutaceous, densely, coarsely punctate, flat between coxae. Metasternum alutaceous, coarsely, densely punctate laterally, shining, impunctate medially. Abdominal sternites dull, alutaceous, with fine, short pubescence medially, short pubescence intermixed with long sparse pubescence laterally. Protibial spur as long as basal 2 tarsomeres, curved down, evenly, gradually tapered from base to apex, widest at apex, apex truncate. Profemur ventral surface alutaceous, densely, coarsely punctate, with long pubescence; posterior surface alutaceous, somewhat shining, finely punctate. Mesotibia curved, apical 3/4 of inner surface covered with long, dense golden setae, apical fringe composed of alternating long and short setae, long setae separated by one short seta, long setae shorter than inferior mesotibial spur; inferior mesotibial spur half length of superior spur, broad, robust, tapered to blunt apex in apical 1/4, apical 1/4 slightly bent toward mesotarsus. Meso- and metafemur sparsely coarsely punctate, anterior 1/4 bearing long setae, posterior margin with an oblique row of coarse, outer 1/4 with contiguous punctures bearing long setae, posterior margin with large clump of long, decumbent, golden setae extended from base of oblique row of setae nearly to trochanter. Meso- and metatrochanter with small clump of moderately long setae on posterior margin. Metatibia laterally flattened, inner surface with clump of long, dense golden setae in apical 1/2 to 1/3, ventral edge straight (Figs. 8, 9), apical fringe like mesotibia fringe, metatibial spurs unequal in length, inferior spur 3/4 length of superior spur, sinuate, curved toward metatarsus in apical 1/4, superior spur flattened in apical 3/4, shorter than tarsomere I. Protarsomeres I-IV subequal in length, protarsomere V slightly longer than protarsomeres III-IV combined. Meso- and metatarsomere I as long as metatarsomere II-IV combined; meso- and metatarsomere V as long as III-IV combined; meso- and metatarsal claws half length of tarsomere V. Paramere highly mod-

ified with apical portion broad, membranous, base in dorsal view with short, sclerotized structure bearing an apical "brush" of setae, base in ventral view with another short sclerotized projection bearing an apical "brush" (brushes not visible in Figs. 18, 19).

**Female:** Similar to male except pronotum less broadly explanate with curved lateral margin; meso and metafemur lacking patches of setae; protibial spur slender, distinctly curved, apex acute; inferior mesotibial spur straight, slender; mesotibia lacking dense setae on inner surface; metatibia lacking patch of dense setae in apical 1/2.

**Variation:** Length 8.5 to 9.8 mm, width 4.0 to 4.4 mm.

**Type material:** Label data for holotype male and allotype female of *Aphodius gambrinus*: GEORGIA: Grady Co., S. Thomasville, 0.3 mi. E. jct. SR-319 on Metcalf Rd., 10-17-XII-1996, P. Skelley & P. Kovarik, *Geomys* pitfall (FSCA).

Paratypes (82): same data as holotype (5); **ALABAMA: Escambia Co.**, 8 mi. ESE. Brewton, 0.5 mi. W. CR-19 on Nalty Rd., 20-XII-1998 (1). **FLORIDA: Leon Co.**, vic. Woodville, 0.9 mi. E. Rt.363 on Natural Wells Rd., 10-22-I-1998 (2); **Santa Rosa Co.**, 2.2 mi. N. Munson, 1 mi. E. Rt.191 on Green Rd., 3-19-I-1999 (9), 2 mi. NW. Munson, 0.5 mi. N. Amos Cabrnis Rd on Rt-191, 21-XI-6-XII-1998 (1), 2.5 mi. NW. Munson [0.4 mi. S. Big Juniper Ck.], 6-20-XII-1998 (1), 2.5 mi. NW. Munson [0.2 mi. S. Big Juniper Ck], 3-18-I-1999 (4), S. of Munson, 2.8 mi. S. jct. Rt-4 & Rt-191 on Sandy Landing Rd., 17-XII-1998 to 3-I-1999 (7) and 3-18-I-1999 (1), S. of Munson, 4.3 mi. S. jct. Rt-4 & Rt-191 on Sandy Landing Rd., 19-XII-1998 to 3-I-1999 (6), S. of Munson, 4.9 mi. S. jct. Rt-4 & Rt-191 on Sandy Landing Rd., 20-XII-1998 to 2-I-1999 (2), 0.8 mi. N. of Harold on Deaton Bridge Rd., 19-I-5-IV-1998 (1), 2.2 mi. N. Harold, S. boundary of Blackwater R. St. For. WMA, 6-20-XII-1998 (2) and 19-XII-1998 to 3-I-1999 (1). **GEORGIA: Baker Co.**, N. of Newton, 4.3 mi. N. jct. Coolewahee Creek on Rt.91, 10-31-I-1999 (2) and 31-I-3-III-1999 (1); **Grady Co.**, S. of Thomasville, 0.3 mi. E. SR 319 on Metcalf Rd., 17-23-XI-1996 (1), N. of Beachton, 0.2 mi. W. jct. Rt.319 on Blackshear Rd., 10-23-I-1999 (1), N. of Beachton, 0.3 mi. W. jct. Rt.319 on Blackshear Rd., 10-23-I-1999 (2), N. of Beachton, 0.6 mi. W. jct. Rt.319 on Blackshear Rd., 10-23-I-1999 (1); **Thomas Co.**, W. of Metcalf, 1.8 mi. S. Metcalf Rd. on Springhill Rd.,

10-17-XII-1996 (3) and 17-23-XI-1996 (2) and 23-XI-1-XII-1996 (1), NE. of Metcalf, 2.7 mi. S. jct. Rt.19 on New Hope Rd., 10-24-I-1999 (11) and 24-I-21-II-1999 (3), 4.4 mi. N. Metcalf on SR.59, 12-14-I-1996 (1), 5.8 mi. N. Metcalf on SR.59 at Magnolia Rd., 13-21-I-1996 (1), 2 mi. SW. Metcalf on SR.59, 16-22-III-1996 (2) and 22-31-III-1996 (1), 2.5 mi. W. Metcalf on Beachton Rd., 3-10-II-1996 (7). Paratypes are deposited in the following collections: FSCA, GDC, GMNH, HFHC, NHML, OSUC, PBC, PES, RHTC, UNSM, USNM, WBWC.

**Remarks:** *Aphodius gambrinus* belongs to a small group of species that includes *A. hubbelli* Skelley and Woodruff, *A. haldemani* Horn, and *A. magnificens* Robinson. Of this group, only *A. hubbelli* occurs in the southeastern United States and *A. gambrinus* is differentiated from that species by the black meso- and metasternum, head and pronotum darker in color than elytra, broader pronotum, and male with dense patch of metatibial setae (Figs. 8, 9). *Aphodius hubbelli* has reddish brown meso- and metasterna, concolorous dorsal surface, relatively narrower pronotum, and patch of metatibial setae confined to small apical area in the male (Fig. 7). *Aphodius hubbelli* and *A. gambrinus* are often collected in the same burrow.

**Etymology:** This name was chosen to represent the amount of excitement experienced in discovering so many new species during this pocket gopher survey. A successful collecting trip was often toasted with a beer. When *A. gambrinus* was first recognized as different (by a unique female), the fact that it is beer-colored was the most obvious character. Again, a toast was made to the newly discovered species. To continue celebrating, it seems a fitting honor to name this species after "Gambrianus," the mythical Flemish king attributed with inventing beer.

***Aphodius hubbelli* Skelley and Woodruff  
(Fig. 7)**

*Aphodius hubbelli* Skelley and Woodruff 1991: 524-527.

*Aphodius haldemani* Horn in Woodruff 1973: 92, Woodruff 1982: 90; Gordon 1983: 647.

**Diagnosis:** Length 7.8 to 9.3 mm, width 3.5 to 4.2 mm. Body glossy, uniformly reddish brown, somewhat flattened. Head smooth at anterior margin. Pronotum with lateral depressions distinctly punctate; laterally explanate, "shelf" narrower than

gena is long; lacking margin at base. Male protibial spur broadened, parallel sided, apex truncate; metatibial inner surface flattened with small patch of setae at extreme inner apex, and ventral margin weakly notched (see arrow in Fig. 7).

**Remarks:** *Aphodius gambrinus*, *A. laevigatus*, and *A. hubbelli* are the largest species of *Aphodius* in southeastern pocket gopher burrows. They are most easily recognized by their body color and pronotal shape. In the southeast, *A. laevigatus* and *A. hubbelli* have similar red color and body size. *Aphodius laevigatus* has a simple pronotum which lacks a lateral explanate margin and has a fimbriate clypeus. *Aphodius gambrinus* has a dark body color and the characteristic patch of setae on the male metatibia.

*Aphodius hubbelli* appears most closely related to *A. haldemani*. Except for being found in different geographic areas, females of these species are nearly indistinguishable. Slight differences in pronotal punctation can be useful for recognition, but not reliable due to frequent variations in density. Males are easily distinguished by sexual dimorphism. *Aphodius haldemani* has a triangular protibial spur and has unmodified metatibiae. Further remarks are made under *A. gambrinus* regarding relationships with other species. *Aphodius hubbelli* is listed in Woodruff and Deyrup (1994) as a "Species of Special Concern" because of its strict association with pocket gophers.

**Specimens studied:** Including the type series, a total of 616 specimens of *A. hubbelli* was examined from the following counties: **ALABAMA:** Autauga, Baldwin, Bullock, Coffee, Covington, Dale, Escambia, Houston, Macon, Montgomery, Russell. **FLORIDA:** Alachua, Bay, Calhoun, Columbia, Flagler, Jackson, Jefferson, Leon, Liberty, Madison, Nassau, Okaloosa, Putnam, Santa Rosa, Taylor, Walton. **GEORGIA:** Baker, Burke, Charlton, Decatur, Dodge, Early, Grady, Jenkins, Marion, Richmond, Screven, Talbot, Taylor, Thomas.

***Aphodius laevigatus* Haldeman  
(Fig. 13)**

*Aphodius laevigatus* Haldeman 1848: 103

*Aphodius concavus* Haldeman; Blatchley 1928: 23  
(misidentification)

*Aphodius goffi* Cartwright 1939: 354; Cartwright  
1951: 29 (synonymy)

**Diagnosis:** Length 7.4 to 9.3 mm, width 3.4 to 4.3 mm. Body glossy, reddish, cylindrical. Clypeus fimbriate (Fig. 13). Pronotal surface impunctate.

**Remarks:** *Aphodius laevigatus* is distinguished from other species of southeastern *Aphodius* by large body size, reddish color, and fimbriate clypeus (Fig. 13). It is related to a western group of species whose members occupy rodent burrows. Two of these, *A. concavus* Say and *A. kirni* Cartwright, inhabit pocket gopher burrows, as do most other species of the *A. concavus* group.

*Aphodius laevigatus* is commonly collected at light and rarely in surface pitfall traps. Woodruff (1973) lists many additional records. As with *A. aegrotus*, these records will not be included in the larger analysis of pocket gopher burrow fauna because the beetles were not collected in association with a burrow. These records are presented separately below to give a more complete distribution.

*Aphodius laevigatus* and *A. aegrotus* are the most common and widespread species of *Aphodius* inhabiting pocket gopher burrows in the southeast. Both species are listed by Woodruff (1982) and Woodruff and Deyrup (1994) as a "Species of Special Concern" because of their strict association with pocket gophers. Our data would indicate less of a concern for these two species than for other species with more restricted ranges.

**Specimens studied:** A total of 1893 specimens of *A. laevigatus* was examined from the following counties: **ALABAMA:** Baldwin, Covington, Escambia, Macon, Montgomery, Russell. **FLORIDA:** Alachua, Bay, Brevard, Calhoun, Columbia, Dixie, Duval, Flagler, Gilchrist, Hernando, Hillsborough, Jefferson, Lafayette, Lake, Leon, Levy, Liberty, Madison, Nassau, Pasco, Pinellas, Polk, Putnam, Santa Rosa, St. Johns, Suwannee, Taylor, Volusia, Walton. **GEORGIA:** Baker, Burke, Charlton, Decatur, Dodge, Jenkins, Richmond, Taylor, Thomas. Additional county records from Woodruff (1973): **FLORIDA:** Orange, Seminole.

***Aphodius pholetus* Skelley and Woodruff**

*Aphodius pholetus* Skelley and Woodruff 1991:  
531-532

**Diagnosis:** Length 6.5 to 7.5 mm, width 3.2 to 3.6 mm. Body glossy, brown. Anterior clypeal surface

with narrow rugose-granulate area. Pronotum lacking basal margin; punctures of disc restricted to base and lateral margins; lateral pronotum narrowly explanate with weak depressions.

**Remarks:** *Aphodius pholetus* is the only southeastern *Aphodius* with a narrowly explanate pronotum and a narrowly rugose-granulate clypeus. It is closely related to *A. atwateri* Cartwright and *A. oklahomensis* Brown that live in pocket gopher burrows in the southern Great Plains.

This is the rarest species of southeastern pocket gopher *Aphodius*. Reasons for its infrequent collections are unknown. They could be due to behavior, sampling biases in technique or location, or simply by having very localized demes.

**Specimens studied:** Including the holotype, a total of 15 specimens of *A. pholetus* was examined from the following counties: **FLORIDA:** Okaloosa, Santa Rosa. **GEORGIA:** Baker.

***Aphodius platypleurus* Skelley and  
Woodruff  
(Fig. 12)**

*Aphodius platypleurus* Skelley and Woodruff 1991: 528-530.

**Diagnosis:** Length 6.5 to 8.0 mm, width 3.2 to 3.8 mm. Body dark brown. Pronotum explanate laterally, broadly shelf-like, "shelf" as broad as or broader than the gena is long (Fig. 12); lateral pronotal margin thickened medially.

**Remarks:** *Aphodius platypleurus* is the only southeastern species with a highly modified pronotum. It resembles *A. acuminatus* Cartwright, a species that inhabits pocket gopher burrows in east Texas and Louisiana.

This species is relatively common throughout its range, with one interesting aberration. If the habitat has been heavily, or frequently, disturbed, this species is not present. The disturbances often relate to livestock, plowing, or other human activities. Preliminary collecting in an abandoned pasture over a 3 year period, produced no specimens of this species. A single attempt one mile away in "natural" open woodlands produced the type series. In reviewing sites where this species was collected, it was noticed that all sites were relatively undisturbed or managed for wildlife. The exact factors limiting this species are not known. Some of the

other, less common, species of *Aphodius* in this study could exhibit similar patterns within their small ranges, but the lack of adequate collection localities prevents similar comparisons at this point. A detailed look at this phenomenon is needed before any definitive conclusions are drawn.

**Specimens studied:** Including the type series, a total of 233 specimens of *A. platypleurus* were examined from the following counties: **ALABAMA:** Covington, Dale, Macon, Russell. **FLORIDA:** Bay, Calhoun, Gilchrist, Leon, Levy, Okaloosa, Putnam, Santa Rosa. **GEORGIA:** Baker, Talbot.

***Aphodius tanytarsus* Skelley and Woodruff  
(Fig. 6)**

*Aphodius tanytarsus* Skelley and Woodruff 1991: 521-524.

**Diagnosis:** Length 3.9 to 5.4 mm, width 1.8 to 2.4 mm. Body brown, glossy. Head strongly rugose-granulate. Pronotum with irregular coarse and fine punctures; coarse puncture 8 to 10 times larger than the fine punctures; posterior pronotal angles with coarse punctures widely spaced (Fig. 6). Elytra smooth, lacking setae, or rarely with fine setae on apical declivity. Metatarsal claws extremely long, nearly as long as metatarsomere V.

**Remarks:** *Aphodius tanytarsus* is unique in the Southeast by its long tarsal claws, otherwise it is similar only to *A. bakeri*. These two can be distinguished by the pattern and size of pronotal punctures: *A. tanytarsus* has very large punctures that are widely spaced in the posterior pronotal angles (Fig. 6); *A. bakeri* has smaller punctures that nearly coalesce in the posterior pronotal angles (Fig. 5).

**Specimens studied:** Including the type series, a total of 373 specimens of *A. tanytarsus* was examined from the following counties: **ALABAMA:** Baldwin, Bullock, Coffee, Dale, Escambia, Macon, Russell, **FLORIDA:** Alachua, Bay, Calhoun, Gilchrist, Jackson, Leon, Liberty, Okaloosa, Santa Rosa, Walton. **GEORGIA:** Baker, Early, Marion, Talbot, Taylor, Thomas.

**Acknowledgments**

Scientific collecting permits for pocket gophers were obtained from the Alabama Department of Conservation and Natural Resources; the Florida

Game and Fresh Water Fish Commission, Division of Wildlife; and the Georgia Department of Natural Resources.

Some travel funding was provided through T. Cohn from the University of Michigan, Ann Arbor, MI. We thank A. Hardy, California Department of Food and Agriculture, Plant Pest Diagnostic Center, Sacramento, CA, for providing information on the taxonomy of the genus *Euphoria*.

We thank the following for unpublished pocket gopher locality data and for access to sites: R. Franz and C. McCaffery, Florida Museum of Natural History, Gainesville, FL; R. Studeman, Nature Conservancy, Tallahassee, FL; W. Baker, Tall Timbers Research Station, Tallahassee, FL; J. Laerm, Georgia Museum of Natural History, Athens, GA; G. Folkerts, Auburn University, AL; M. Bailey, Conservation Services Southeast, Shorter, AL.

For collecting specimens, we thank: M. Bailey, Conservation Services Southeast, Shorter, AL; E. Cronin, Gainesville, FL; S. Fullerton, University of Central Florida, Orlando, FL; R. Jarrett, Florida Department of Agriculture and Consumer Services, Daytona, FL; M. A. Goodrich, Eastern Illinois University, Charleston, IL; P. Harpootlian, Simpsonville, SC; P. W. Kovarik, Ohio State University, Columbus, OH; R.W. Lundgren, Archer, FL; R. F. Morris, Lakeland, FL; F. Skillman, Sunsites, AZ; C. Smith, Georgia Museum of Natural History, Athens, GA; M. C. Thomas, Gainesville, FL; R. H. Turnbow, Fort Rucker, AL; W. F. Michener, D. Fussel, and R. Birkhead, J. W. Jones Ecological Research Center, Newton, GA.

We thank the following for reviewing the manuscript: W. Godwin, Texas A & M University, College Station, TX; W. B. Warner, Chandler, AZ; and M. C. Thomas and W. N. Dixon, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL. This is Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Contribution No. 908.

#### Literature Cited

- Avisé, J. and J. Laerm** 1982. The pocket gopher. Florida Naturalist, April-June 1982: 7-10.
- Blatchley, W. S.** 1928. The Scarabaeidae of Florida. Florida Entomologist 12(2): 22-30.
- Blume, R. R. and A. Aga.** 1975. *Aphodius* from burrows of a pocket gopher in Brazos County, Texas (Coleoptera: Scarabaeidae). Coleopterists Bulletin 29(3): 161-162.
- Blume, R. R. and A. Aga.** 1979. Additional records of *Aphodius* from pocket gopher burrows in Texas (Coleoptera: Scarabaeidae). Coleopterists Bulletin 33(1): 131-132.
- Blume, R. R. and J. W. Summerlin.** 1988. Histeridae (Coleoptera) from pocket gopher burrows (Geomyidae) in east central Texas. Coleopterists Bulletin 42(2): 202-204.
- Brown, L. N. and G. C. Hickman.** 1973. Tunnel system structure of the southeastern pocket gopher. Florida Scientist 36(2-4): 978-103.
- Cartwright, O. L.** 1939. Eleven new American Coleoptera (Scarabaeidae, Cicindelidae). Annals of the Entomological Society of America 32(2): 353-364.
- Cartwright, O. L.** 1944. New *Aphodius* from Texas gopher burrows. Entomological News 55: 129-135, 146-150.
- Cartwright, O. L.** 1951. New synonymy in the Aphodiini of the United States. Coleopterists Bulletin 5(2): 29-30.
- Davis, W. B.** 1960. Pocket gophers. Pp. 143-151. In: W. B. Davis. The mammals of Texas. Bulletin 27. Texas Game and Fish Commission, Austin, Texas.
- Godwin, W. B.** 2000. Second record of *Euphoria aestuosa* Horn 1880 reared from dung chambers of *Geomys breviceps* Baird. Scientific Note. Southwestern Entomologist 25(2): 145-147.
- Gordon, R. D.** 1983. Studies on the genus *Aphodius* of the United States and Canada (Coleoptera: Scarabaeidae). VII. Food and habits; distribution; key to eastern species. Proceedings of the Entomological Society of Washington 85(4): 633-652.
- Haldeman, S. S.** 1848. Descriptions of North American Coleoptera, chiefly in the cabinet of J. L. LeConte, M.D., with references to described species. Journal of the Academy of Natural Sciences Philadelphia 1: 95-110.
- Hardy, A. R.** 1980. The rarest U. S. *Euphoria*. Scarabaeus 1: 4-5. [Scarabaeus was a short lived "Newsletter for those interested in the Scarabaeidae." Because of the valuable information presented, this paper needed to be cited. Copies of this newsletter may exist in the personal or institutional libraries of scarab researchers active in the early 1980s.]
- Hickman, G. C. and L. N. Brown.** 1973. Pattern and rate of mound production in the southeastern pocket gopher (*Geomys pinetus*). Journal of Mammalogy 54(4): 971-975.

- Horn, G. H.** 1870. Description of the species of *Aphodius* and *Dialytes* of the United States. Transactions of the American Entomological Society 3 (Sept. 1870): 110-134, pl.3.
- Horn, G. H.** 1880. Synopsis of the *Euphoriae* of the United States. Proceedings of the American Philosophical Society 18: 397-408.
- Hubbell, T. H.** 1940. A blind cricket-locust (*Typhlocyathophilus floridanus* n. gen. et sp.) inhabiting *Geomys* burrows in peninsular Florida (Orthoptera, Gryllacrididae, Rhaphidophorinae). Annals of the Entomological Society of America 33: 10-32
- Hubbell, T. H. and C. C. Goff.** 1939. Florida pocket gopher burrows and their arthropod inhabitants. Proceedings of the Florida Academy of Science 4: 127-166, 2 figs. [often cited as 1940]
- Kennerly, T. E., Jr.** 1964. Microenvironmental conditions of the pocket gopher burrow. Texas Journal of Science 16(4): 395-441.
- Miller, M. A.** 1946. Reproductive rates and cycles in the pocket gopher. Journal of Mammalogy 27: 335-358.
- Miller, M. A.** 1957. Burrows of the Sacramento Valley pocket gopher in floor-irrigated alfalfa fields. Hilgardia 26: 431-452.
- Miller, R. S. and H. E. Bond.** 1960. The summer burrowing activity of pocket gophers. Journal of Mammalogy 41(4): 469-475.
- Peck, S. B. and M. C. Thomas.** 1998. A distributional checklist of the beetles (Coleoptera) of Florida. Arthropods of Florida and Neighboring Land Areas 16: i-viii, 1-180.
- Peck, S. B. and P. E. Skelley.** 2002. Small carrion beetles (Coleoptera: Leiodidae: Cholevinae) from burrows of *Geomys* and *Thomomys* pocket gophers (Rodentia: Geomyidae) in the United States. Insecta Mundi (in press).
- Reid, V. H.** 1971. Population dynamics of northern pocket gophers on rangeland in western Colorado. Unpublished. 35 pp. [cited in Turner *et al.* 1973.]
- Ross, E. S.** 1940. New Histeridae (Coleoptera) from the burrows of the Florida pocket gopher. Annals of the Entomological Society of America 33: 1-9.
- Ross, E. S.** 1944a. Arthropod collecting in the burrows of a Texas pocket-gopher. Entomological News 55: 57-61.
- Ross, E. S.** 1944b. *Onthophilus kirni* new species, and two other noteworthy histeridae from burrows of a Texas pocket-gopher. Entomological News 55: 115-118.
- Skelley, P. E.** 1991. Observations on the biology of *Stephanucha thoracica* Casey (Coleoptera: Scarabaeidae: Cetoniinae). Coleopterists Bulletin 45(2): 176-188.
- Skelley, P. E. and R. D. Gordon.** 1995. A new species of *Aphodius* (Coleoptera: Scarabaeidae) from Alabama pocket gopher burrows. Insecta Mundi 9(3-4): 217-219.
- Skelley, P. E. and P. W. Kovarik.** [2001]. Insect surveys in the Southeast: investigating relictual entomofaunas. 2000 Symposium on Insect Behavioral Ecology and Systematics. Florida Entomologist [in press]
- Skelley, P. E. and R. E. Woodruff.** 1991. Five new species of *Aphodius* (Coleoptera: Scarabaeidae) from Florida pocket gopher burrows. Florida Entomologist 64(4): 517-536.
- Turner, G. T., R. M. Hansen, V. H. Reid, H. P. Tietjen, and A. L. Ward.** 1973. Pocket gophers and Colorado mountain rangeland. Colorado State University Experiment Station, Fort Collins, Bulletin 554S. ix + 90 pp.
- Woodruff, R. E.** 1973. The scarab beetles of Florida (Coleoptera: Scarabaeidae). Part I. Arthropods of Florida and Neighboring Land Areas 8: 1-220.
- Woodruff, R. E.** 1982. Rare and endangered Scarabaeidae of Florida, pp. 84-102. In: R. Franz [ed.], Rare and endangered biota of Florida. Invertebrates. Vol. 6. University of Florida Press, Gainesville, 131 pp.
- Woodruff, R. E. and M. Deyrup.** 1994. Order Coleoptera, Family Scarabaeidae. Pp. 368-455. In: M. Deyrup and R. Franz [eds]. Rare and Endangered Biota of Florida, Volume IV. Invertebrates. University of Florida Press, Gainesville, 798 pp.
- Addendum:** While this paper was in press, *Euphoria aestuosa* Horn was officially synonymized under *Euphoria discicollis* Thompson 1878, now the correct name for this species.
- Hardy, A. R.** 2001. Studies in the Euphorina of the Americas (Coleoptera: Scarabaeidae) II. Status of names in *Euphoria*, types and synonymies, with notes on South American Species. Pan-Pacific Entomologist 77(3):127-143.