Pleistocene Dung Beetles from MIS 5 at Ziegler Reservoir, Snowmass Village, Colorado (Coleoptera: Scarabaeidae: Aphodiinae)

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ABSTRACT—Nine aphodiine dung beetle species are recorded from Pleistocene sediments of the Ziegler Reservoir near Snowmass Village, Colorado, U.S.A. Insect remains from this deposit range from 125,000 to 77,000 yr BP, and are unique in their species richness and in their occurrence at high elevation (2720 meters). Three extant species occur: *Aphodius (Dialytodius) decipiens* Horn, *A. (Planolinellus) vittatus* Say, and *A. (Planolinoides) duplex* LeConte. Six unidentified species are also described, belonging to the genus *Aphodius*. All species are relatively small coprophagous dwellers known as endocoprids. The faunal richness of this site suggests a speciose dung beetle fauna existed at high elevations in this region, and intimates the importance of this site as one of the richest Pleistocene dung beetle sites in North America.

With mammals come feces, and with feces come dung beetles. When North America hosted an abundant mammal megafauna, the North American dung beetle fauna was supposedly, climate permitting, abundant and diverse, too. Sediments at the Ziegler Reservoir site near Snowmass Village in Colorado, U.S.A. (Johnson & Miller 2012; Johnson et al. 2014; Miller et al., in press), are richly fossiliferous and were deposited during such conditions, approximately 125,000 to 77,000 yr BP. Thus they offer an excellent opportunity to explore the dung beetle fauna of the Rocky Mountains before the Last Glacial Maximum. With bison, mammoth, mastodon, ground sloth, sheep, camels, horses, and a speciose small mammal fauna found at the site (Sertich et al., in prep.), a rich dung beetle fauna can be expected. Dung beetles (Coleoptera: Scarabaeidae) are a crucial element of most ecosystems with an abundant large herbivore fauna because they provide ecosystem services such as nutrient cycling and enhancement of plant growth, bioturbation, and suppression of parasites and dung breeding pests (Losey & Vaughan 2006; Kryger 2009). Here we examine this important element of the Pleistocene Snowmass ecosystems in detail.
**Site**
The Ziegler Reservoir is situated east of Snowmass Village, in Pitkin County, Colorado, at 39°12'28"N, 106°57'54"W, 2720 m asl. It is the only one of the few high elevation Pleistocene sites in the Rocky Mountains that preserved fossil insect faunas from before the Last Glacial Maximum, from the period between 125,000 and 77,000 yr BP. For geologic setting and stratigraphy see Pigati et al. (2014), for geochronologic framework Mahan et al. (2014).

**Methods**
Scott Elias and his team extracted beetle fragments as described in Elias (2014) from 25 samples (7.5 l each) taken from the Ziegler Reservoir site in June, 2011. Those fragments tentatively assigned to Scarabaeoidea were received from S. Elias for further identification. The specimens were identified by using published descriptions and extant material from the collections of the Denver Museum of Nature & Science and the Field Museum of Natural History, Chicago. All the scarab specimens, and all beetle samples from the Ziegler Reservoir site are deposited in the Entomology Collection, Department of Zoology, Denver Museum of Nature & Science (DMNS).

**Results**
From a sample volume of 287.5 l (Elias 2014), 32 fragments of scarab beetles were extracted. Twenty-nine fragments could be assigned to presumably 9 species. All species belong to the subfamily Aphodiinae, and to the tribe Aphodiini of the predominantly coprophagous dweller guild (endocoprids). The three other fragments, two front legs and one elytral part, likely belong to Aphodiinae also, but did not allow association with one of the established species. All specimens are from Marine Isotope Stage (MIS) 5 and range in age from 125,000 to 77,000 years (Elias 2014), covering the whole period from which fossil insects were obtained at the site. Although some Aphodiinae species are associated with rodent burrows, we can exclude modern contamination because of the condition of the disarticulated fragments, particularly their much reduced stiffness, small size, and the complete absence of setae.

**Systematic Paleontology**

**Family Scarabaeidae Latreille 1802**

**Subfamily Aphodiinae Leach 1815**

**Tribe Aphodiini Leach 1815**

**Aphodius Hellwig 1798**
Note: I do not follow the controversial upgrading of all *Aphodius* subgenera to genera as practiced by Gordon & Skelley (2007), because it lacks any phylogenetic foundation, hence being premature.

**Aphodius (Dialytodius) decipiens Horn 1887**
(Figs 1–5)

**Material.** MIS 5a: 2 elytral fragments: DMNS ZE.15259 (Fig. 1; 49.16/15–20 cm; 84–77ka), DMNS ZE.15260 (Fig. 2; 49.16/20–25 cm; 84–77ka). MIS 5c: 1 elytral fragment: DMNS ZE.15261 (Fig. 3; 49.11/30–35 cm; 103–101ka); 2 presumably associated heads: DMNS ZE.15262 (Fig. 4; 49.11/20–25 cm; 103–101ka), width 1.1 mm; DMNS ZE.15263 (Fig. 5; 49.11/15–20 cm; 103–101ka).

**Description.** The elytral sculpture of *Aphodius decipiens* with deeply impressed, largely punctured striae and tectiform intervals is unique, at least amongst North American species. The shape of the two heads with slightly denticulate, margined, laterally convex clypeus, only slightly protruding lateral lobes (“genae”), densely punctured surface, and distinct frontal suture without tubercles fits this species (cf. Gordon & Skelley 2007: fig. 447).

**Discussion.** *Aphodius decipiens* is an extant species currently known from Alberta, Idaho, Montana, Oregon, and Wyoming (Gordon & Skelley 2007), and in Colorado from Mineral and San Juan Counties (Krell 2010). It is associated with rodents, having been
found in burrows of the Columbian ground squirrel (*Urocitellus columbianus* (Ord)), marmot (*Marmota* sp.), and pocket gopher (*Geomyidae* sp.) (Gordon & Skelley 2007). The Wyoming ground squirrel (*Urocitellus elegans* (Kennicott)) found at the site in layers of similar age as the *A. decipiens* fragments (Sertich et al., in press; Mahan et al. 2014) was likely one of several possible hosts available to this species.

*Aphodius (Planolinellus) vittatus* Say 1825
(Figs 6–12)

**Material.** MIS 5a: 1 elytral fragment: DMNS ZE.15286 (Fig. 6; 49.16/15–20 cm; 84–77ka). MIS 5b: 3 heads: DMNS ZE.15264 (Fig. 7; 49.14/78–83 cm; 93–87ka), width 1.2 mm; DMNS ZE.15265 (Fig. 8) and DMNS ZE.15266 (Fig. 9; 49.14/83–90 cm; 93–87ka), width 1.15 mm and 1.0 mm, respectively. 1 presumably associated pronotum: DMNS ZE.15284 (Fig. 10; 49.14/83–90 cm; 93–87ka). 1 presumably associated elytron: DMNS ZE.15283 (Fig. 11; 49.14/83–90 cm; 93–87ka), with humeral and apical red spot. MIS 5c: 1 head: DMNS ZE.15267 (Fig. 12; 49.11/30–35 cm; 103–101ka), width 1.2 mm.

**Description.** The following head characters correspond to the extant species *Aphodius vittatus*: head uniformly finely punctured, alutaceous, frontal suture with three tubercles, clypeus laterally slightly longitudinally wrinkled, medially very slightly emarginated, sides broadly rounded, lateral lobes rounded and slightly protruding. The elytral intervals of this species are finely, but distinctly punctured and alutaceous; punctures notch the thin striae; the color varies from reddish to dark, normally being two-tone. One elytron and one elytral fragment of the right size show these characters and probably belong to this species. One pronotum of the fitting size shows double punctation of the right density and is basally and laterally marginated, corresponding to *A. vittatus*.

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**Figures 1–5. Aphodius (Dialytodius) decipiens** Horn 1887 from MIS 5 of the Ziegler Reservoir site, Snowmass Village, Colorado. **Fig. 1.** Elytral fragment DMNS ZE.15259, 49.16, 84–77ka. **Fig. 2.** Elytral fragment DMNS ZE.15260, 49.16, 84–77ka. **Fig. 3.** Elytral fragment DMNS ZE.15261, 49.11, 103–101ka. **Fig. 4.** Head DMNS ZE.15262, 49.11, 103–101ka. **Fig. 5.** Head DMNS ZE.15263, 49.11, 103–101ka.
Discussion. *Aphodius vittatus* is a currently widespread and common species, occurring from southern Canada to northern Mexico, and from eastern Europe to central Asia (Gordon & Skelley 2007). In Colorado it has been recorded from several western counties, eastward up to Weld and El Paso Counties (Krell 2010). It is a generalist dung feeder occurring in a variety of habitats (Gordon & Skelley 2007).

*Aphodius (Planolinoides) duplex* LeConte 1878  
(Figs 13–19)

**Material.** **MIS 5a:** 1 head: DMNS ZE.15268 (Fig. 13; 49.16/10–15 cm; 84–77ka), width 1.55 mm. 1 possibly associated elytral fragment (rolled up; not photographed): DMNS ZE.15276 (49.16/20–25 cm; 84–77ka). **MIS 5b/5a:** 1 elytral fragment: DMNS ZE.15285 (Fig. 14; 49.16/5–10 cm; 84–77ka). **MIS 5b:**

**Figures 6–12.** *Aphodius (Planolinellus) vittatus* Say 1825 from MIS 5 of the Ziegler Reservoir site, Snowmass Village, Colorado. **Fig. 6.** Elytral fragment DMNS ZE.15286, 49.16, 84–77ka.  **Fig. 7.** Head. DMNS ZE.15264, 49.14, 93–87ka.  **Fig. 8.** Head DMNS ZE.15265, 49.14, 93–87ka.  **Fig. 9.** Head DMNS ZE.15266, 49.14, 93–87ka.  **Fig. 10.** Pronotum DMNS ZE.15284, 49.14, 93–87ka.  **Fig. 11.** Elytron DMNS ZE.15283, 49.14, 93–87ka.  **Fig. 12.** Head DMNS ZE.15267, 49.11, 103–101ka.
1 head: DMNS ZE.15269 (Fig. 15; 49.14/83–90 cm; 93–87ka), width 1.5 mm. 3 possibly associated elytral fragments: DMNS ZE.15270 (Fig. 16) and DMNS ZE.15271 (Fig. 17; 49.14/78–83 cm; 93–87ka); DMNS ZE.15272 (Fig. 18; 49.14/83-90 cm; 93–87ka). **MIS 5e**: 1 head: DMNS ZE.15273 (Fig. 19; 66.7; 125ka), width 1.1 mm.

**Description.** The head of *Aphodius duplex* has a transverse clypeal ridge, the frontal suture tuberculated in males, clypeus and frons (except the middle) strongly punctured, vertex with finer, irregular punctuation, and lateral lobes only slightly protruding. As Horn (1887) already realized, “The presence of a transverse clypeal carina is less of a peculiar character than supposed by Dr. LeConte” [the author of the species] but taking the other characters mentioned above into consideration, the identification is likely. The size difference between the two heads is remarkable, but *Aphodius* species

**Figures 13–19.** *Aphodius (Planolinoides) duplex* LeConte 1878 from MIS 5 of the Ziegler Reservoir site, Snowmass Village, Colorado. **Fig. 13.** Head DMNS ZE.15268, 49.16, 84–77ka. **Fig. 14.** Elytral fragment DMNS ZE.15276, 49.16, 84–77ka. **Fig. 15.** Head DMNS ZE.15269, 49.14, 93–87ka. **Fig. 16.** Elytral fragment DMNS ZE.15270, 49.14, 93–87ka. **Fig. 17.** Elytral fragment DMNS ZE.15271, 49.14, 93–87ka. **Fig. 18.** Elytral fragment DMNS ZE.15272, 49.14, 93–87ka. **Fig. 19.** Head DMNS ZE.15273, 66.7, 125ka.
are known for intraspecific size variation. The frontal suture of the smaller head has no tubercles, indicating that it belonged to a female. The larger heads are male.

Four elytral fragments show characters similar to *A. duplex* elytra (Gordon & Skelley 2007: fig. 170) with thin striae the punctures of which notch the borders of the striae, and with obsolete punctation on the smooth, slightly convex intervals. Those fragments could belong to this species.

**Discussion.** *Aphodius duplex* is a rodent associate having been collected from burrows of Richardson’s ground squirrel (*Urocitellus richardsonii*) in Alberta and Wyoming. The species is currently distributed from southern Manitoba to Alberta and eastern Washington, south to Montana and Colorado (Gordon & Skelley 2007). In Colorado, it has been recorded from Fremont and Larimer Counties (Krell 2010). The Wyoming ground squirrel (*Urocitellus elegans*) found at the site in layers of similar age as the *A. duplex* fragments (Sertich et al., in prep.; Mahan et al., 2014) was likely one of several possible hosts available to this species.

**Aphodius sp. 1, subgenus Agoliinus, aleutus-group**

(Fig. 20)

**Material.** MIS 5c: 1 head: DMNS ZE.15274 (Fig. 20; 49.11/30–35 cm; 103–101ka), width 1.3 mm.

**Description.** A punctured head with an emarginated clypeus, obtusely angled at the sides of the emargination, straight towards the well pronounced, rounded triangular lateral lobes, with a relatively flat frons, and without tubercles on the frontal suture is present in several extant species of the subgenus *Agoliinus* of the *aleutus*-group. It also resembles heads of *Dialytes*, but the relatively flat frons and the shape of the lateral lobes do not fit extant *Dialytes* species.

**Discussion.** Overall, the *aleutus*-group contains 18 species in North America. All species are surface dung feeders, mostly generalists (Gordon & Skelley 2007) which would have been readily supported by the large mammal fauna of the site (Sertich et al., in prep.).

**Aphodius sp. 2, subgenus Agoliinus**

(Figs 21–22)

**Material.** MIS 5a: 1 head: DMNS ZE.15275 (Fig. 21; 49.16/20–25 cm; 84–77ka), width 1.5 mm. **MIS 5b:** 1 head: DMNS ZE.15277 (Fig. 22; 49.14/83–90 cm; 93–87ka), width 1.35 mm.

**Description.** The following combination of characters points to the subgenus *Agoliinus*: Head alutaceous, punctures of clypeus and frons moderately strong, finer at the margin of the clypeus, punctures on vertex of different sizes, frontal suture without tubercles (ZE.15277; female) or with three weak tubercles (ZE.15275; male), clypeus emarginated, sides broadly rounded, lateral lobes slightly protruding, narrow, rounded, sinuated close to the eye (resembling more *Agoliinus* than the somewhat similar *Planolinoides*).

**Discussion.** *Agoliinus* species generally inhabit higher elevations or higher latitudes and are either surface dung feeders or associated with rodents (Gordon & Skelley 2007).
Aphodius sp. 3, subgenus Agoliinus/Planolinoides
(Figs 23–24)

Material. MIS 5a: 2 heads: DMNS ZE.15278 (Fig. 23), DMNS ZE.15279 (Fig. 24; 49.16/15–20 cm; 84–77ka), right side damaged, but ca. 1.9 and almost 2 mm wide, respectively.

Description. The following combination of characters points to the subgenera Agoliinus or Planolinoides: Vertex with dense fine punctation, frons and clypeus with larger, moderately dense punctures, frontal suture with strong central tubercle and weaker lateral tubercles, clypeus not emarginated, lateral lobes slightly protruding, narrow, rounded, sinuated close to the eye (more of the Agoliinus type).

Aphodius sp. 4
(Fig. 25)

Material. MIS 5b/5a: 1 head: DMNS ZE.15280 (Fig. 25; 49.16/5–10 cm; 84–77ka), width 1.3 mm.

Description. The characters of the head do not allow the assignment to a subgenus (head orange brown, frons and vertex finely and sparsely punctured, clypeus more strongly, but equally sparsely punctured, frontal suture with three weak tubercles, rounded lateral lobe well pronounced on left side, clypeus not emarginated).
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Aphodius sp. 5

(Fig. 26)

Material. MIS 5a: 1 head: DMNS ZE.15281 (Fig. 26; 49.16/15–20 cm; 84–77ka), width 1.1 mm.

Description. The characters of the head do not allow the assignment to a subgenus (moderately strong, deep punctures, interspersed with finer punctures, frontal suture visible, without tubercles, lateral lobes weak, broadly rounded, hardly any angle between lobes and clypeus, clypeus weakly emarginated, sides broadly rounded).

Aphodius sp. 6

(Fig. 27)

Material. MIS 5a: anterior half of 1 head: DMNS ZE.15282 (Fig. 27; 49.16/30–35 cm; 84–77ka), fragment width ca. 1.1 mm.

Description. The characters of the head do not allow the assignment to a subgenus (alutaceous, clypeus with fine, dense punctures, slightly wrinkled anterolaterally, clypeus hardly emarginated, sides broadly rounded, frontal suture with a central tubercle and weak lateral tubercles).

Unidentified Aphodiinae fragments

(Fig. 28–30)

A front leg (DMNS ZE.15291; MIS 5b, 49.14/83–90 cm; 93–87ka; Fig. 28), a front tibia (DMNS ZE.15292; MIS 5b, 49.14/78–83 cm; 93–87ka; Fig. 29) and an elytral fragment (DMNS ZE.15293; MIS 5c, 49.11/20–25 ka).
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cm; 103–101ka; Fig. 30) belong to Aphodiinae, but could not be assigned to one of the species above.

Note. Elias (2014 and pers. comm.) mentioned Aegialia (Psammoporus) opaca Brown 1931 (Tribe Aegialiini Laporte 1840) from MIS 5a, represented by a fragment of a right elytron from sample 49.16/20–25 cm (84–77ka). I could not find this specimen in any of the samples and cannot confirm this species from the Ziegler Reservoir fauna.

Discussion

While beetles are generally abundant in Pleistocene deposits (Buckland & Coope 1991), Scarabaeidae are represented less frequently and are rarely species rich (Kiselev and Nazarov 2009). Other Colorado Pleistocene sites revealed only one to four dung beetle species (Short & Elias 1987; Elias & Nelson 1989), being a usual number for the North American and Eurasian Pleistocene (Kiselev & Nazarov 2009; Zinovyev 2011). In a few Pleistocene sites in Europe, 10 to 15 dung beetle species were found (Cooke et al. 1961; Coope & Angus 1975; Bidashko & Proskurin 1987). With nine dung beetle species of the genus Aphodius, the Ziegler Reservoir site is one of the most speciose sites for dung beetles in the North American Pleistocene.

Most Pleistocene scarab specimens can be assigned to extant species (Krell 2006). With 79 extant species of aphodiine dung beetles recorded from Colorado (Krell 2010) and over 430 in the Nearctics (Smith 2009), many having a rather uniform appearance, we need unique structures or sculptures to reliably identify fossil fragments to species. Only a portion of the specimens from Ziegler Reservoir provides us with species-specific characters. Even then, as with all fossil fragments, the identification is very likely to be correct, but not absolutely certain since we do not know possible extinct

Figures 28–30. Unassigned fragments of Aphodiinae from MIS 5 of the Ziegler Reservoir site, Snowmass Village, Colorado. Fig. 28. Front leg DMNS ZE.15291, 49.14/83–90 cm; 93–87ka. Fig. 29. Front tibia DMNS ZE.15292, 49.14/78–83 cm; 93–87ka. Fig. 30. Elytral fragment DMNS ZE.15293, 49.11/20–25 cm; 103–101ka.
similar species, recent speciation events, extensive range shifts, or a possibly different morphological variation of the species a hundred thousand or more generations ago. A third of the beetle species identified from the Ziegler Reservoir fauna no longer occurs in Colorado (Elias 2014), but the three identified _Aphodius_ species of dung beetles still do, or occur here again. Colorado is outside the current range of the here unconfirmed _Aegialia opaca_ (reported by Elias 2014) which has its southernmost limits in northern California and Montana.

Not all sites with recorded megafauna bear a diverse dung beetle fauna (Barnosky et al. 1988; Coope 2007), sometimes not containing any dung beetles at all (Medvedev and Voronova 1977; Kiselev et al. 1982); but some reveal them in abundance such as the Trafalgar Square site (Franks et al. 1958; Coope 2000), the late-glacial woolly mammoth discoveries at Condover, Shropshire (Allen et al. 2009), and the mammoth channel at Lynford, Norfolk (Coope 2012), as we would expect. The Ziegler Reservoir fauna also met our expectations and adds to our deficient knowledge of Pleistocene North American dung beetles. Despite numerous megafaunal sites, the only dung beetle having been found associated with Pleistocene mammoth dung is the large, Holarctic _Aphodius fossor_ (Elias 2010: 190). Although this species is currently widespread in Colorado (Krell 2010), it is not represented in the Snowmass samples. The only insects having been found associated with ground sloth dung are Diptera larvae and pupae of the family Sciaridae. No beetle was found (Waage 1976).

**Conclusion**
The dung beetle specimens represented in Pleistocene samples of the Ziegler Reservoir site contain both rodent associates and general surface feeders. All of them belong to the smaller species of the dung beetle communities, and to the dweller guild. Rollers and tunnelers which form a significant part of extant temperate dung beetle faunas were not found. Despite the relative richness for a Pleistocene site, the nine aphodine species are likely to represent only a small portion of the Pleistocene dung beetle fauna of Colorado. This fauna is unlikely to be much poorer than the over 90 currently occurring dung beetle species in Colorado (Krell 2010) because of the plentiful food supplied by a more diverse Pleistocene mammal fauna. Nevertheless the higher-than-average number of dung beetle species found at the site indicates a higher-than-average dung beetle diversity of the Pleistocene dung beetle communities in this high elevation part of the Rocky Mountains.

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