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The dung beetle fauna of the Big Bend region of Texas (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract. This paper reports the results of a 2001–2009 field study of the scarabaeine dung beetle fauna (Coleoptera: Scarabaeidae) of the Big Bend region of Texas, a three-county area of the Trans-Pecos portion of the Chihuahuan Desert. The observed fauna comprises 10 native species, *Canthon blumei* Halffter and Halffter, *C. imitator* Brown, *C. praticola* LeConte, and *C. mixtus* Robinson; *Onthophagus browni* Howden and Cartwright, *O. knausi* Brown, *O. velutinus* Horn and *O. brevifrons* Horn; *Copris arizonensis* Schaeffer and *Phanaeus texensis* Edmonds; as well as two exotic species introduced in the 1970s, *Digitonthophagus gazella* (Fabricius) and *Euoniticellus intermedius* (Reiche). The existing native fauna antedates the completion of desertification approximately 9,000 yrs BP and is similar ecologically and taxonomically to those in southeastern Arizona and northern Mexico. Ecological distribution follows three broad, overlapping habitat zones: desert montane forest, desert grassland and desert scrub. Species accounts include diagnoses, geographic distribution data, and information on collection method, habitat distribution and daily activity.

Key words. Trans-Pecos, Chihuahuan Desert, natural history.

Introduction

The Trans-Pecos area of Texas (Fig. 2A) has been recognized for many decades as one of seven natural regions of the state defined primarily by regional topography and vegetation (Cory and Parks 1937). It consists of the roughly 31,500 square miles (81,500 km^2) of mountains and basins lying west of the Pecos River. Covering almost all of the region is the northeastern portion of the Chihuahuan Desert (Fig. 1). As considered here, the Big Bend is that part of the Trans-Pecos centered in three contiguous west Texas counties: Jeff Davis, Presidio and Brewster (Fig. 2A). While a somewhat arbitrary area, the Big Bend nevertheless epitomizes the Trans-Pecos portion of the Chihuahuan Desert (see Schmidt 1979).

Over the years, the Trans-Pecos in general and Big Bend in particular have attracted many naturalists bent on observing the fauna and flora of this special part of the state (Burke 2003). The vertebrate fauna of the Big Bend has received intense scrutiny (see, for example, the numerous papers cited in Johnson et al. 1997). The invertebrate fauna has received far less attention. The subjects of some of these studies include grasshoppers (Tinkham 1948), dragonflies (Gloyd 1958), ants (Moody and Francke 1982; Cokendolpher 1990; Cokendolpher and Francke 1990), spiders (Broussard and Horner 2006), and species checklists (Quinn 2014; Van Pelt 1995). This paper expands coverage of Big Bend invertebrates to include the scarabaeine dung beetles of the area. Similar faunistic studies on dung beetles in other arid North American environments include Nealis (1977), Schoenly (1983), Howden and Scholtz (1986), Dajoz (1994), Lobo (1996, 2000), and Halffter et al. (2012).

As here reported, the Big Bend scarabaeine dung beetle fauna comprises the following 10 native and two introduced* species (Fig. 7): *Copris arizonensis* Robinson; *Phanaeus texensis* Edmonds; *Onthophagus brevifrons* Horn; *Onthophagus browni* Howden and Cartwright; *Onthophagus knausi* Brown; *Onthophagus velutinus* Horn; *Canthon mixtus* Robinson; *Canthon praticola* LeConte; *Canthon blumei* Halffter and Halffter; *Canthon imitator* Brown; **Euoniticellus intermedius* (Reiche); and **Digitonthophagus gazella* (Fabricius). Each species is treated below. Three other Trans-Pecos species not encountered by me in the Big Bend during this study are mentioned here to complete the picture for the subfamily inhabiting the region, but they are, so far, outliers to the study area: *Phanaeus difformis* LeConte, *Canthon melanus* Robinson and *C. probus* (Germar). *Phanaeus difformis*, a species widespread through much of the state (Edmonds 1994), has been collected near the Hueco Mountains, El Paso County (Schoenly 1983), as well as in Guadalupe Mountains National Park (park records) and nearby Black River (Eddy

Co., NM); the Marfa record cited by Edmonds (1994) is erroneous. *Canthon melanus* has been taken from sand dunes in El Paso Co. (Schoenly 1983; Riley and Wolfe 2003). Schoenly (1983) also reported *C. ebenus* (Say) from the Hueco Mountains area; but this record could refer to *C. praticola* or perhaps to *C. probus* (Germar), which is also reported from the Trans-Pecos by Riley and Wolfe (2003). Bill Warner (pers. comm.) reports *C. ebenus* to be common in the sand hills near Monahans (Ward Co.), Texas, just east of the Pecos River.

The desert landscape that defines the Trans-Pecos dates from the early Holocene roughly 9,000–10,000 years ago, when the Big Bend supported much the same vertebrate fauna and flora observed today (Wells 1977; Van Devender 1995). Due to insufficient fossil evidence, it is difficult to know exactly when the native dung beetle fauna became established, but it is not unreasonable to assume that its local history has paralleled that of, especially, the past and present resident mammals. In the case of the four contemporary inquilinous species associated with wood rats (*Copris arizonensis*, *Onthophagus brevifrons*, *O. velutinus* and *O. browni*) it is instructive to note that the main host species, *Neotoma albigula* Hartley and *N. micropus* Baird, have occupied the area since late Pleistocene, ca. 15,000 years ago (Stangl et al. 1994). Indeed, *O. brevifrons* and *O. browni* have been recovered from fossil wood rat (packrat) middens dating roughly 3,500 and 7,800 years ago, respectively, in southern New Mexico (Elias 1987), and *O. brevifrons* 13,000–17,500 years ago in the lower Big Bend (Elias and Van Devender 1990) and 3,000 years ago in the Bolsón de Mapimí of northern Mexico (Elias et al. 1995). The presence of the non-inquilinous species (*Canthon* spp., *Phanaeus texensis* and *O. knausi*) might well also have antedated the "completion" of the Chihuahuan Desert during the Pleistocene-Holocene interface, when the area was cooler and wetter and supported a rich megafauna that included, in addition to many present residents, ground sloths, mammoth, bison, horses, cameloids and proto-antelope (Stangl et al. 1994). When desertification had become far advanced, there is ample evidence of a surviving native megafauna that could have supported local dung beetle populations, including, among others, mule deer, elks, javelina, foxes, skunks, pronghorn and bison (Schmidly 1977). Elias and Van Devender (1990) discuss fossil insect evidence for climatic change in the Big Bend at the close of the Pleistocene. All in all, what is known about the climatological and ecological history of the Big Bend suggests that the current assemblage of native dung beetle species is largely attributable to surviving the effects of desertification in the region, rather than replacement of a pre-existing fauna by *in situ* speciation or by extensive immigration.

Studies of Chihuahuan Desert dung beetle faunas are few. Besides Schoenly (1983), mentioned above, only two other works provide useful comparison with that at hand. Lobo (1996) reported three species of Scarabaeinae in the Bolsón de Mapimí of extreme northeastern Durango and adjacent areas of Chihuahua and Coahuila, Mexico (about 400 air km S of Marfa), where the climate and terrain are similar to the lower (< 950 m) portions of the Big Bend. Here Lobo found three species, all shared with the Big Bend fauna: *Canthon mixtus* (reported as *C. puncticollis*) as well as the introduced species *Digitonthophagus gazella* and *Euoniticellus intermedius*. Since the original study, Lobo (2000) also confirmed the presence at Mapimí of two additional species, likewise shared with the Big Bend fauna: *Canthon imitator* and *C. praticola*. A striking difference between Mapimí and Big Bend faunas is the reported overwhelming dominance of the two exotic species in Mapimí, which together outnumbered the native species nearly 100:1. In the second study, Dajoz (1994) surveyed the scarabaeine fauna of southwestern Arizona at several sites in the broader region of the Chiricahua Mountains, an area of the Chihuahuan Desert comparable in size and complexity to the Big Bend. As reported by Dajoz, the southwestern Arizona fauna comprised 18 species, only three of which (*C. imitator*, *C. praticola* and *Onthophagus browni* [presumably reported as *O. hecate* (*Panzer*)]) are shared with the Big Bend. Bill Warner (pers. comm.) reports that the southeastern Arizona fauna is considerably richer than reported by Dajoz, especially in the number of species of *Onthophagus* and smaller *Canthon* (*Boreocanthon*). Besides its significantly greater diversity, the southeastern Arizona fauna exhibits a significant difference from that of the Big Bend: the presence of at least six Mexican species whose northern range reaches southwestern Arizona via the Sierra Madre Occidental corridor (*Canthon indigaceus* LeConte, *Dichotomius colonicus* [Say], *Copris lecontei* Matthews, *C. macclevei* Warner, *Phanaeus quadridens* [Say] and *Onthophagus hopfneri* Harold). Dung beetle communities of other Mexican arid zones have received some recent attention, a notable example of which is Halffter et al. (2012).

The life cycles and adult activity cycles of Big Bend dung beetles are inextricably correlated with the timing, amount and distribution of rainfall in the region. Annual rainfall varies from about 380+

mm at higher elevations (> 1250 m) to roughly one-half of that amount in desert scrub areas (< 1250 m). Roughly 75% of the precipitation in any given year falls as often intense, afternoon and evening thunderstorms during the summer monsoon months of June through September. The rains during this period are far from evenly distributed, either spatially or temporally, such that favorable conditions for adult activity on the surface are continually in flux. The resulting local unpredictability of favorable conditions is a challenge for these beetles (as well as many other insect groups) clearly reflected by short term environmental patchiness in abundance and local distribution of populations. Thus, a given locale may be the site of a population explosion while, at the same time, another locale a short distance away is devoid of active adults. Thus, the environmental context for dung beetles in the Big Bend is a mosaic over distance and time that bespeaks the need for these animals to be adapted for coarse patchiness in resources and opportunity. Local extinction and repopulation is an on-going dynamic of Chihuahuan Desert dung beetle populations as they respond over time to the changing mosaic of local climate.

The habitat distribution of Big Bend dung beetles correlates loosely with three, not mutually exclusive vegetation zones in the area: a) desert grassland (Fig. 9–14); b) desert scrub (Fig. 15–18); and c) montane woodland/parkland (Fig. 19–25). These correspond closely with habitat zones observed for mammals of the area (Blair 1940; Blair and Miller 1949; Stangl et al. 1994). The main defining character of each is ground cover, which is affected not only by altitude but also by local edaphic, physiographic and microclimatic factors. The montane woodland zone occurs above 1500 m, where rainfall is higher and rainy season temperatures are less extreme, and where the local landscape is highly fractured by arroyos, small canyons, and intermittent creeks. The dominant vegetation formation here features low (< 6 m) oak, pinyon pine and juniper trees on grassy substrate. Grasslands exist mainly above 1250 m as vast, virtually treeless, open areas, such as the Marfa and Valentine plains, surrounded by the main mountainous areas of the region, as well as small meadowlands amidst montane habitat. The dominant vegetational features are bunch grasses and scattered yucca, except along intermittent streams and fractured hillsides where mesquite and native black walnut may maintain precarious holds. Desert scrub generally occurs below 1075 m where conditions are drier and temperature extremes most accentuated. Numerous cacti, mesquite, and creosote bush are signature plants along with cottonwood and hackberry trees in favorable spots near springs and creeks. Soils are thin and rocky. These three vegetation zones are far from homogenous, with many intermediate ecotones where they contact or interdigitate with each other. Habitat distributions in given cases are included in the species accounts below.

My field observations allow me to speculate only tentatively about population dynamics of Big Bend dung beetles. Generation cycles during the rainy season are probably dependent upon the timing and amount of rainfall in a given area. Spring and early summer precipitation sufficient to trigger early emergence of adults (May/June) can set the stage for a second annual generation if sufficient rain continues through the summer months. An instance of such a midsummer explosive emergence occurred in early August 2004 (a wet year) at the Miller Ranch "catclaw" grassland community near headquarters. This site was sampled by two 48-hour, human-feces baited pitfall traps that yielded the following specimen counts: *Canthon imitator*, 527; *C. praticola*, 211; *C. mixtus*, 489; *Digitonthophagus gazella*, 31; and *Phanaeus texensis*, 6. Of interest is the notable lack in the trapfall of *C. blumei* as well as either of the two inquilinous *Onthophagus* species known to occur in the same community, *O. velutinus* and *O. browni*. Similar populations explosions were also observed at other sites: [1] > 450 *O. knausi* in a 48-hr pitfall at Pinto Canyon Ranch (August 2004); [2] pooled results over two days at the Chihuahuan Desert Research Institute (August 2008): *Canthon blumei*, 528; *C. imitator*, 33. These results are in stark contrast to Whitford et al. (1995), whose analysis of invertebrates of the Chihuahuan Desert grasslands of the Jornada del Muerto Basin near Las Cruces, NM, led to the conclusion that "Scarab beetles, which feed on dung, are not abundant in desert grasslands."

Besides habitat parameters, ecological partitioning among Big Bend species is partly a function of feeding and reproductive behaviors. The four species of *Canthon* are ball-rolling beetles ("tumblebugs") that garner provision by separating and forming a ball of food, which is rolled away and buried at a distance from the source. All four *Canthon* occur on the Hip-O Ranch (Presidio Co.), an ideal potential venue for a future study dedicated to resource partitioning among these congeners. All remaining species are burrowers that remove portions of the food source to tunnels dug beneath or near the source. Dung beetle feeding and reproductive strategies are discussed at length by Halffter and Edmonds (1982).

Hanksi and Cambefort (1991) and Simmons and Ridsdill-Smith (2011) provide a broad look at dung beetle ecology and ecological/behavioral evolution.

Materials and Methods

This paper is based on my field notes and specimens collected in the Big Bend over the nine-year period 2001–2009. The specimen base, approximately 1500 individuals, is deposited in the insect collection of the Department of Entomology, Texas A&M University, College Station, Texas. Field work was largely confined to the months of summer rains (May–October), with most work concentrated in the wetter summer months of July–September. Principal collection sites were the following (Fig. 2B; numbering there corresponds to that below):

1. Miller Ranch (~16 km W Valentine): The Miller Ranch of Presidio and Jeff Davis Counties has been the site of a series of faunistic and floristic studies over many years and its vertebrate fauna is among the best known in the Big Bend. Most of the founding studies appeared in 1949: Blair and Miller 1949 (mammals); Phillips and Thornton 1949 (birds); Jameson and Flury 1949 (reptiles and amphibians); and York 1949 (vegetation). Davis and LaDuc (2018) have recently revisited the reptile and amphibian fauna of the ranch. Sites sampled for my study were mainly grassland habitats near headquarters and the Camp Holland area at the mouth of ZH Canyon. The ranch includes all habitat types found in the Big Bend except montane park/forest land.
2. Davis Mountains Preserve (~35 km NW Fort Davis, Jeff Davis Co.): The DMP comprises roughly 13,500 ha in the heart of the Davis Mountains complex owned and operated by the Texas Nature Conservancy. This "sky island" is home to a unique mosaic of montane habitats between 1,500 and 2,400 m. Sites sampled in this study were woodland grasslands and arroyos below 2,000 m.
3. Chihuahuan Desert Research Institute (~8 km SE Fort Davis, Jeff Davis Co.): The CDRI embraces about 200 ha of mixed habitat. Sites sampled for this study were mainly located in the Quarry section, a much rockier and varied area than that surrounding the Visitors' Center to the northeast.
4. Davis Mountains State Park (~2 km W Fort Davis, Jeff Davis Co.): Field work in the park was restricted to the non-public research area along Limpia Creek and adjacent hills. Limpia Creek provides important riparian habitat within the park, which consists mainly of montane woodland associations.
5. Hip-O Ranch (~7 km W Marfa, Presidio Co.): At the time of this study, this working ranch was owned by the Nature Conservancy and covered ca. 8,000 ha of typical Marfa plain grassland habitat at an altitude varying little from 1400 m. Sample sites included pastureland as well as hillside habitat in the low escarpments west of headquarters.
6. Pinto Canyon Ranch (~56 km SSW Marfa, Presidio Co.): The principal PCR study site was the streambed/arroyo leading from Pinto Canyon Creek to headquarters, a riparian corridor through desert grassland/scrub in a highly fractured landscape.
7. Muerto Springs Ranch (~16 km E Valentine, Jeff Davis. Co): MSR embraces 10,000 ha of high grassland and montane habitat. The main study site was at Muerto Springs itself, about one mile east of headquarters.
8. Humphreys Ranch (~35 km S Marfa, Presidio Co.): This property comprises roughly 400 ha of disturbed desert scrub and grassland in the Alamito Creek drainage.
9. Chinati Hot Springs (~15 km ENE Ruidosa): CHS is a small area of desert scrub bisected by an intermittent stream at about 1075 m in far south Presidio Co.
10. Paisano Baptist Encampment (~17 km W Alpine, Brewster Co.): PBE is a 100 ha area of montane habitat in the southern portion of the Davis Mountains complex. Sampled areas were on the northern periphery of the property away from the developed area. The entire property lies above 1450 m.

Qualitative collection data are included for each species account; these include locality, altitude, and months of capture but, in the interest of brevity, neither numbers of specimens collected nor precise dates of capture. These omitted data are available from the reference collection deposited at Texas A&M University. In most cases, collection data are from label data, but they are often enhanced with coordinates and altitude derived from Google Earth. Data marked with an asterisk (*) were garnered from reliable

literature or other sources, cited herein. When necessary, label distance and altitude measurements were converted to metric units. Data are also included for material collected in July 2005 at Maderas del Carmen sites in the Sierra El Carmen range across the Rio Grande from Big Bend National Park in the Mexican state of Coahuila, a protected area administered by CEMEX and site of major ongoing environmental and wildlife conservation studies (see McKinney 2012). This area is essentially an extension of the study area and the data in question have not been published elsewhere.

A combination of collecting techniques was used: light traps (incandescent and UV), direct capture from food sources and pitfall traps. By far the most productive sampling technique was the use of lethal pitfall traps baited with human feces. The trap design is illustrated in Fig. 8 and is similar to those routinely employed in dung beetle studies (see Gou and Hashim 2018 and references therein). For this study, the trap body was a ~1.5-liter plastic receptacle buried to its rim and filled part way with a salt water solution to which was added a few drops of dishwashing detergent. Bait placed in a 30 ml (1-ounce) paper condiment cup is suspended over the solution in a three-armed, wire hanger and the mouth of the trap was then covered with a "hat" fashioned from the bottom of a plastic plant nursery pot. The "hat" serves to address two contradictory problems: rapid desiccation of the bait and flooding by rain. Traps were not deployed in accordance with any rigorous experimental design, but, rather, in an intuitive way aimed at maximizing coverage of a collection site in the interest of discovering resident species rather than assessing population characteristics.

The Big Bend Scarabaeine Dung Beetles

Canthon Hoffmannsegg

The genus *Canthon* includes over 200 species restricted to the New World, most of which inhabit tropical South and Middle America. The United States is home to 18 species, of which 16 occur in Texas. *Canthon* species are the "tumblebugs" universally familiar to naturalists, ranchers, farmers and others who have observed their remarkable habit or fashioning and rolling a ball of dung across the ground and ultimately burying it at some distance from the source. The Big Bend fauna includes four species, all widespread and closely associated with livestock and other grazing mammals, where they can be observed in large numbers jostling for position at a fresh dung pad (Fig. 3). All are dark colored, with evenly rounded bodies lacking any horns or other projections, and long, slender middle and hind legs. While they superficially closely resemble each other, the sexes can be distinguished by a combination of two external attributes: in the male, the protibial spur is bifurcate (usually asymmetrically so) and the last abdominal sternum is emarginate medially to receive the apex of the pygidium (Fig. 27); in the female, the protibial spur is acute (rounded in worn individuals) and the last abdominal sternum is not obviously emarginated medially (Fig. 28). The four Big Bend *Canthon* species are easily separated by the following key.

1. Clypeus bidentate medially (Fig. 26, 29). Larger beetles, length 10–20 mm. . . . . **[Subgenus *Canthon* s. str.] 2**
— Clypeus quadridentate, middle two teeth larger than outer ones (Fig. 33–34). Small beetles, length ≤ 8 mm. . . . . **[Subgenus *Boreocanthon*] 3**

2. Black, only rarely with hint of blue reflections (Fig. 29–30). Propleuron divided by sharp, transverse carina extending from lateral margin to coxa (Fig. 31, arrow) . . . . . ***Canthon* (*C.*) *blumei* Halffter and Halffter**
— Near black but almost always with blue reflections under strong light (Fig. 26). Propleuron not divided by a carina, smooth and continuous (Fig. 32) . . . . . ***Canthon* (*C.*) *imitator* Brown**

3. Pronotum punctate. Smaller, length 3–5 mm . . . . . ***Canthon* (*B.*) *mixtus* Robinson**
— Pronotum granulate. Larger, length 5–8 mm . . . . . ***Canthon* (*B.*) *praticola* LeConte**

***Canthon* (*Canthon*) *blumei* Halffter and Halffter**
Fig. 29–31

Diagnosis. Black, only rarely with even subtle hint of blue. Dorsum completely, densely covered by small granules on field of fine shagreening. Clypeus bidentate, teeth acute, separated by rounded emargination. Elytral striae fine, superficial, almost effaced posteriorly. Propleuron divided by sharp, transverse carina extending from procoxa to lateral margin (Fig. 31, arrow). A formal description of this species appears in Halffter and Halffter (2003; as *C. humectus blumei*; raised to species status in Halffter et al. 2015).

Big Bend collection sites (altitudinal range: 1480–1555 m).

Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul).

Jeff Davis Co.: **[1]** Davis Mountains State Park, Limpia Canyon Research Area, 30°36′5″N 103°55′34″W, 1525 m (Jun, Aug)**; [2]** 16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); **[3]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul); **[4]** Chihuahuan Desert Research Institute (Quarry Unit), 30°32’06”N 103°50′37″W, 1480 m (Aug–Sep); **[5]** ~8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Visitor Center area), 30°32′32″N 103°50′11″W, 1555 m (Aug).

Presidio Co.: **[1]** 6 km~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104°07′12″W, 1530 m (Aug–Sep).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung, carrion).

Surface activity. Diurnal.

Habitat. Primarily montane woodlands, occasionally open grassland.

Comments. *Canthon blumei* was originally described as a subspecies of *C. humectus* occupying the southern and western parts of Texas; it was raised to species status by Halffter et al. 2015. The remaining populations of *C. humectus* comprise a widely distributed Mexican species complex whose range covers most of the Mexican Altiplano (Halffter and Halffter 2003; Halffter et al. 2015) and which are the subject of ongoing evolutionary studies by Gonzalo Halffter and his associates. *Canthon blumei* is similar morphologically and ecologically to *C. imitator*, both of which are common in the Big Bend area. In contrast to *C. imitator*, which is abundant in the open grasslands, this species displays a distinct preference for montane wooded habitat. They can be captured together, but the relative frequencies of the two are strikingly different depending upon habitat. In the Quarry section of the Chihuahuan Desert Research Institute property near Fort Davis, a typical wooded montane habitat (Fig. 21), an August 2008 48-hr baited pitfall trap captured 192 *C. blumei* and only two *C. imitator*, and a contemporary trap in somewhat higher and more open montane habitat near the visitors' center yielded 336 *C. blumei* and 31 *C. imitator*. In lower, open grassland, these ratios switch to strongly favor *C. imitator*, often in the absence of *C. blumei* (see Introduction).

***Canthon* (*Canthon*) *imitator* Brown**
Fig. 26–28, 32

Diagnosis. Black with subtle, but persistent blue/blue-green reflections easily seen under strong light (especially ventrally). Dorsum completely, densely covered by small granules on field of fine shagreening. Clypeus bidentate, teeth rounded, separated by acute emargination. Elytral striae fine, superficial, almost effaced posteriorly. Propleuron smooth, not divided by transverse carina (Fig. 32). A formal description of this species appears in Halffter (1961).

Big Bend collection sites (altitudinal range: 1055–1630 m).

Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul); **[2]** ~25 km S Alpine (on TX 118), Woodward Ranch, 30° 09′07″N 103°36′51″W, 1475 m (Sep); **[3]** 8 km SW Marathon (Fort Peña Colorado Park), 30°09′08″N 103°17′15″W, 1200 m [Aug].

Jeff Davis Co.: **[1]** Davis Mountains State Park, 30°35′43″N 103°56′05″W, 1540 m [Jun, Aug]; **[2]** ~12 km W Balmorhea (Madera Canyon Ranch), 30°54′37″N 103°53′16.04″W, 1140 m (May); **[3]** 16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); **[4]** ~16 km NE Valentine, Muerto Springs

Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul); **[5]** ~8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Visitor Center area), 30°32′32″N 103°50′11″W, 1555 m (Aug).

Presidio Co.: **[1]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug); **[2]** Dalquest Research Site, 29°33′30″N 103°47′30″, 1110 m [Sep]; **[3]** 37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); **[4]** 20–26 km SSE Marfa (along FM 169), 1355–1415 m (Jun); **[5]** 27 km SSE Marfa (along FM 169), 30°08′42″N 104°02′13″W, 1325 m (Jul); **[6]** ~72 km SSW Marfa (along FM 2810), 29°59′48″N 104°35′51″W, 1075 m [Sep]; **[7]** 3 km NE Marfa (along FM 1112), Marfa Golf Course, 30°19′40″N 103°59′41″W, 1470 m (Jul, Sep); **[8]** ~96 km SSE Marfa (Old Alazan Ranch, headquarters), 29°33′01″N 103°53′25″W, 1275 m (Mar); **[9]** ~30 km SSE Marfa (along FM 169), Humphreys Ranch, 30°02′30″N 104°01′00″W, 1285 m (Jul); **[10]** 60 kmSSE Marfa (along FM 169), Casa Piedra, 29°44′07″N 104°03′03″W, 1055 m (Sep); **[11]** 12 kmNE Ruidosa (via Chinati Hot Springs road), Chinati Hot Springs, 30°02′17″N 104°36′02″W, 1090 m (Aug); **[12]** ~13 km E Marfa (via US 90/67), 30°16′07″N 103°48′44″W, 1565 m (Jul); [**13]** 20–26 km SSE Marfa (multiple sites along FM 169), 1355–1415 m (Jun–Jul); **[14]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); **[15]** Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug); **[16]** ~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104°07′12″W, 1530 m (Aug–Sep); **[17]** near Plata (FM 169/Alamito Creek bridge) Kennedy Ranch (headquarters), 29°52′16″ N 103°59′28″ W, 1200 m (Jun); **[18]** Pinto Canyon Ranch (~65 km SSW Marfa on FM 2810), 29°59′54″N 104°30′48″W (Pinto Canyon Creek), 1460 m (Aug); **[19]** 8 km8km W La Viuda Peak, 29°42′30″N 103°54′30″, 1200 m (Sep).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung; horse dung).

Surface activity. Diurnal.

Habitat. Usually in association with livestock, strong preference for open grassland.

Comments. This species is common and widely distributed in Texas and the southwestern United States. François Génier (pers. comm.) has suggested that the appropriate name for Big Bend populations of this taxon should be *Canthon floridanus* Brown, as yet an open question pending formal taxonomic action. In the interest of following current usage, I here conserve the name *C. imitator*.

Canthon (*Boreocanthon*) *mixtus* Robinson

Fig. 33

Diagnosis. Black with strong blue highlights revealed under strong light. Small, length 3–5 mm. Clypeus strongly quadridentate. Pronotum finely but not densely punctate, elytral interstriae with shining spots in place of punctures. Subhumeral stria usually carinulate; tip of pygidium usually more convex than remainder of surface. A formal discussion of this species appears in Halffter (1958).

Big Bend collection sites (altitudinal range: 1010–1630 m [2310 m in Sierra El Carmen]).

Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul);

Jeff Davis Co.: **[1]** 16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); **[2]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs, near headquarters), 30°40′28″N 104°24′07″W, 1475 m (Jul); **[3]** 8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Visitor Center area), 30°32′32″N 103°50′11″W, 1555 m (Aug); **[4]** Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Aug–Sep);

Presidio Co.: **[1]** C.E. Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug); **[2]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); **[3]** ~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m (Aug–Sep); **[4]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug); **[5]** Dalquest Research Site, 29°33′30″N 103°47′30″, 1010 m [Sep]; **[6]** 37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); **[7]** 20–26 km SSE Marfa (along FM 169), 1355–1415 m (Jun); **[8]** 3 km NE Marfa (along FM 1112), Marfa Golf Course, 30°19′40″N 103°59′41″W, 1470 m (Jul, Sep); **[9]** ~30 km SSE Marfa (along

FM 169), Humphreys Ranch, 30°02′30″N 104°01′00″W, 1285 m (Jul); **[10]** ~8km W La Viuda Peak, 29°42′30″N 103°54′30″, 1200 m (Sep); **[11]** ~19 km E Marfa (via US 90/67), 30°16′07″N 103°48′44″W, 1565 m (Jul); **[12]** ~3 km N Marfa (along TX 17), 30°20′27″N 104°01′7″W, 1500 m (Jul); **[13]** near Plata (FM 169/Alamito Creek bridge) Kennedy Ranch (headquarters), 29°52′16″ N 103°59′28″ W, 1200 m (Jun); **[14]** Pinto Canyon Ranch (~65 km SSW Marfa on FM 2810), 29°59′54″N 104°30′48″W (Pinto Canyon Creek), 1460 m (Aug).

MEXICO: Coahuila, Sierra El Carmen (Maderas del Carmen), 28°59′54″N 102°36′ 42″ W, 2310 m. (Jul).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung).

Surface activity. Diurnal.

Habitat. Grasslands and open areas in desert scrub.

Comments. *Canthon mixtus*, whose type locality is Marfa, appears to be a near-endemic to the Big Bend portion of the Chihuahuan Desert, but its occurrence in coniferous forest at high altitude in the Sierra El Carmen is quite unexpected. It is similar to *C. melanus*, reported from El Paso Co. (Riley and Wolfe 2003), which has a shallow, obtuse (rather than deep, acute) clypeo-genal notch; moreover, the tip of the pygidium is neither shinier nor more convex than the remainder of the surface. *Canthon melanus* is a common species in southwestern Arizona, where *C. mixtus* is absent.

Canthon (*Boreocanthon*) *praticola* LeConte

Fig. 34–35

Diagnosis. Dorsum black, lacking any hint of blue highlights. Small, length 5–8 mm. Clypeus strongly quadridentate. Upper surfaces densely granulate on finely shagreened background; no visible puncturing. Pygidial surface evenly curved, apex not distinctly more convex than basal area. A formal discussion of this species appears in Halffter (1958).

Big Bend collection sites (altitudinal range: 1200–1630 m).

Jeff Davis Co.: **[1]** 16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); **[2]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul); **[3]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs, near headquarters), 30°40′28″N 104°24′07″W, 1475 m (Jul).

Presidio Co.: **[1]** 37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); **[2]** 20–26 km SSE Marfa (along FM 169), 1355–1415 m (Jun); **[3]** 8 km8km8 km W La Viuda Peak, 29°42′30″N 103°54′30″, 1200 m (Sep); **[4]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); **[5]** ~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104°07′12″W, 1530 m (Aug–Sep).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung).

Surface activity. Diurnal.

Habitat. Grasslands.

Comments. *Canthon praticola* is a wide-ranging species in more open habitats of the northern Chihuahuan Desert, including southwestern Arizona, through the Great Plains into southern Canada. Bill Warner (pers. comm.) reports that this species will utilize prairie dog (*Cynomys*) dung encountered at the burrow entrance.

Onthophagus Latreille

The genus *Onthophagus* embraces about 2300 species distributed world-wide, of which about 70% occur in Africa and Asia. As one of the most species-rich genera of animals, it is increasingly the subject of taxonomic and phylogenetic scrutiny (Breeschoten et al. 2016, and references therein). The United States is home to about 30 species last reviewed by Howden and Cartwright (1963). The Big Bend fauna includes four widespread species, three of which are putative associates of wood rats. All four species

are small (2.5–7.5 mm long), and as tunneling (rather than ball-rolling) dung beetles, they are not likely to be observed on the surface. The nesting behavior of these beetles consists of packing the blind end of a tunnel with a "sausage" of food into which is laid a single egg, a process repeated several to many times in a single nest below the food source (Halffter and Edmonds 1982). Of interest is the fact that the three inquilinous Big Bend species are collected in pitfall traps baited with human feces. But while adults are not obligatory feeders on wood rat dung, the question remains whether or not they would use it to provision their nests.

The four smaller-size, dark colored Big Bend species can be similar to the naked eye, but each is easy to identify with the following key:

1. Pronotum evenly covered with small, shiny tubercles (Fig. 48) **2**
— Pronotum punctate, lacking distinct granules (Fig. 40, 53) **3**

2(1) Male (Fig. 44–45) — head with pair of erect, slightly inclined horns set between eyes; pronotum convex except for shallow anterior concavity receiving appressed head horns. Female (Fig. 46–47) — pronotum convex, almost always lacking any indication of anterior prominence . . . . . ***Onthophagus velutinus* Horn**
— Male (Fig. 41–42) — head lacking horns, with 2 transverse carinae, posterior one slightly raised medially; pronotum with large, flat, apically bifurcate prominence extending well over head. Female (Fig. 43) — pronotum with conspicuous low, transverse ridge above anterior margin . . . . . ***Onthophagus browni* Howden and Cartwright**

3(1) Pronotum densely covered with flat, umbilical, setose punctures (Fig. 53). Small, length ≤ 5 mm. Male — pronotum with small, triangular projection above anterior margin (Fig. 49), otherwise evenly convex; protibia narrow, elongate, apical third strongly curved inward (Fig. 52A). Female — pronotum more or less evenly convex (Fig. 50–51), lacking distinct anterior feature; protibia (Fig. 52B) proportionately shorter, wider and less curved than in male . . . . . ***Onthophagus knausi* Brown**
— Pronotum evenly covered with simple, impressed punctures (Fig. 40). Larger, length over 5 mm. Protibia similar in both sexes (Fig. 39). Male (Fig. 36–37) — pronotum strongly humped, anterior surface concave on either side of prominent midline. Female (Fig. 38) — pronotum humped anteriorly, anterior surface evenly concave, proportionately lower than in male . . . . . ***Onthophagus brevifrons* Horn**

Onthophagus velutinus Horn

Fig, 44–48

Diagnosis. Dorsum black to brownish black, often with greenish reflections. Length 4–6.5 mm. Pronotum evenly but not densely covered by small shining granules, each with associated short seta, on field of extremely fine shagreening (Fig. 48); elytral interstriae with two longitudinal rows of small, setose granules on field of fine shagreening; pygidium evenly punctate, punctures setose. Front legs similar in both sexes. Male (Fig. 44–45) – Clypeus weakly upturned medially. Clypeal carina weak, frontal carina replaced by pair of slender, nearly parallel horns (reduced in small individuals). Pronotum convex except for shallowly concave, vertical anterior surface; concavity partially divided by weak, median, vertical carina extending partway down from upper margin. Female (Fig. 46–47) – Clypeus not upturned. Head with two transverse carinae, clypeal carina weak, frontal carina stronger, ends often distinctly raised higher than middle. Pronotum evenly convex, rarely with slightest hint of anteromedian process. A formal description of this species appears in Howden and Cartwright (1963).

Big Bend collection sites (altitudinal range: 555–1540 m).

Brewster Co.: **[1]** *Big Bend National Park, Panther Junction, 29°19′28″N 103°12′21″W, 1170 m (May); **[2]** *Big Bend National Park, Boquillas Ranger Station, 29°10′59″N 102°57′37″W, 555 m (May); **[3]** *Big Bend National Park, Oak Spring, 29°16′55″N 103°20′13″W, 1325 m (May); **[4]** Stillwell RV Park, FM 2627, 29°38′40″N 103° 04′47″W, 770 m (Jun).

Jeff Davis Co.: **[1]** ~8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Aug); **[2]** Davis Mountains State Park, 30°35′43″N 103°56′05″W, 1540 m.

Presidio Co.: **[1]** C.E. Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug); **[2]** ~16 kmW Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350m (Jul–Aug); **[3]** ~7 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m (Aug–Sep);– **[4]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug).

Collection method(s). a) baited pitfall trap (human, laboratory rat feces); (b) incandescent and UV light trap; (c)*direct capture in nest of *Neotoma albigula.*

Surface activity. Nocturnal.

Habitat. In association with wood rats (*Neotoma*) in all zones, but more common in montane and grassland zones.

Comments. *Onthophagus velutinus* is a common species in southern Arizona and is recorded also from Colorado. It is a close relative of *O. cartwrighti* Howden, which occurs in southern California and Baja California, of *O. arnetti* Howden and Cartwright (southern Arizona), as well as of *O. browni* (Howden 1973). (See also comments below concerning *O. browni*.)

Onthophagus browni Howden and Cartwright

Fig. 41–43

Diagnosis. Dorsum black, occasionally showing weak greenish reflections; legs coffee brown. Length 5–7.5 mm. Pronotum evenly but not densely covered by small shining granules, each with associated short seta, on field of extremely fine shagreening (as in Fig. 48); elytral interstriae with two longitudinal rows of small, setose granules on field of fine shagreening; pygidium evenly punctate, punctures setose. Front legs similar in the two sexes. Male (Fig. 41–42) – Head lacking horns, bearing two transverse carinae; clypeus slightly upturned medially. Pronotum with large, flattened, apically widened, emarginate process extending over posterior portion of head (reduced in small individuals). Female (Fig. 43) – Head bearing two simple, transverse carinae; clypeal margin not upturned. Pronotum convex except for low, transverse ridge rising above anterior margin. Complete formal description given by Howden and Cartwright (1963).

Big Bend collection sites (altitudinal range: 725–1785 m).

Presidio Co.: **[1]** C.E. Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug); **[2]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); **[3]** ~6 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m (Aug–Sep); **[4]** Fort Leaton, 29°32′31″N 104°19′28″W, 770 m (Jun); **[5]** ~40km E Redford via Hwy 170, Grassy Banks Rest Area, 725 m, ~29°17′01″N 103°53′12″W (nd).

Jeff Davis Co.: **[1]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul); **[2]** Davis Mountains Preserve, 31°37′42″N 104°05′01″W, 1785 m (May).

Collection method(s). a) baited pitfall trap (human feces); (b) incandescent light trap; (c) flight intercept trap; (d) *soil beneath wood rat nest.

Surface activity. Nocturnal.

Habitat. All zones in association with wood rats (*Neotoma*).

Comments. This species is closely related to *O. velutinus*; and while males and larger females are easily distinguished, small or worn females can be difficult to identify if not associated with larger specimens or conspecific males. While they are attracted to human feces, they are collected in significantly larger numbers from soil beneath the living area of wood rat nests (Halffter and Matthews 1966; Howden and Cartwright 1963). *Onthophagus browni* is also common in southeastern Arizona, where it was apparently referred to as *O. hecate* by Dajoz (1994). Bill Warner (pers. comm.) reports that *O. browni* and *O. velutinus* are separated by altitude/habitat in southeastern Arizona, the former species higher in the

mountains and the latter at lower elevations in the flats and bajadas, a distribution pattern paralleled by *Copris arizonensis* and *C. macclevei*.

Onthophagus knausi Brown

Fig. 49–53

Diagnosis. Dull black, occasional reddish-brown highlights on head. Small, length 2–5 mm. Pronotum densely punctate, punctures flat, annular, often with central seta (Fig. 53), more crowded anteriorly and laterally; elytral interstriae each with irregular row(s) of small, setose tubercles; apex of pygidium distinctly shinier, more convex and coarsely punctate apically than basally. Male (Fig. 49) – Clypeal carina absent, frontal carina absent except in smallest individuals; clypeal margin reflexed upward, truncate to broadly bidentate; front legs (Fig. 52A) slender, elongate, apex of femur extending beyond lateral pronotal margin, tibia narrowed, elongate, apical third noticeably curved inward, apex (above spur) with pencil of yellow hairs; anterior margin of pronotum produced as triangular (sometimes tab-like) protuberance overhanging anterior margin (Fig. 49). Female (Fig. 51) – Clypeal carina present, usually sharp and broadly curved anteriorly, frontal carina present, thickened and raised medially; clypeus bidentate, not upturned medially; front legs (Fig. 52B) not elongate, femora not extending beyond pronotal margin, tibia evenly bowed, apical third not abruptly curved inward, lacking hair pencil; pronotum evenly convex, only rarely with slightest hint of anteromedian protuberance. This species is described by Howden and Cartwright (1963).

Big Bend collection sites (altitudinal range: 1475–1555 m [2490 m in Sierra El Carmen]).

Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul).

Jeff Davis Co: **[1]** Davis Mountains Preserve, 31°41′40″N 104°07′30″W, 1850 m (Jul–Aug); **[2]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul–Aug); **[3]** ~8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Aug).

Presidio Co.: **[1]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug).

MEXICO: Coahuila, Sierra El Carmen, 28°59′30″N 102°32′54″W, 28°59′54″N 102°36′42″W, 29°00′06″ N 102°35′48″ W, 1815–2490 m (Jul).

Collection method(s). a) baited pitfall trap (human feces).

Habitat. Montane and grassland riparian corridors.

Surface activity. Unknown.

Comments. My identification of Big Bend populations as *O. knausi* was provisionally corroborated by the late Henry F. Howden (pers. comm.). However, definitive identification of Big Bend populations of this species must await a re-examination of the taxonomic status of this as well as a small group of closely related species (*O. mextexus* Howden and Cartwright; *O. alluvius* Howden and Cartwright and *O. knulli* Howden and Cartwright). The type series of *O. mextexus* (originally described as *O. monticolus*) includes a single specimen from Boot Springs, in the Chisos Mountains of Big Bend National Park; the remainder were collected in the Sierra Madre Oriental south of Monterrey, Nuevo Leon, about 500 km SSE of the park. According to details provided by Serge Laplante of the Canadian National Collection in Ottawa, who kindly examined it on my behalf, the Boot Springs specimen is similar to *O. knausi* from elsewhere in the Big Bend as well as material collected by me in Sierra El Carmen, Coahuila, across the Rio Grande from Big Bend National Park. For now, I regard the Boot Springs specimen as conspecific with other Big Bend populations of *O. knausi*, and not a putative fifth Big Bend species of *Onthophagus*.

With an average length of about 4 mm, *O. knausi* is the smallest of the Big Bend dung beetles. It prefers riparian areas, where it can occur in high numbers. Creekside traps at Pinto Canyon Ranch and the Quarry section of the Chihuahuan Desert Research Institute commonly yielded 100 or more (up to 250) individuals in 48-hour lethal pitfall traps. I never collected it from either cattle or horse droppings. It probably survives on the droppings of deer, javelina and other animals frequenting intermittent creek

and streambeds. Ratcliffe and Paulsen (2008) report *O. knausi* from human feces baited traps in wooded areas of southeastern Nebraska. *Onthophagus knausi* is a wide-ranging species. Riley and Wolfe (2003) report it from the Trans-Pecos, Edwards Plateau and south Texas plains/lower Rio Grande vegetational areas of the state; it undoubtedly occurs widely to the south of the Rio Grande in adjacent areas of northern Mexico. Howden and Cartwright (1963) report it also from Kansas, Nebraska and Illinois.

***Onthophagus brevifrons* Horn**
Fig. 36–40

Diagnosis. Weakly shining black, often with bluish or greenish reflections. Length 7–10 mm. Pronotum (Fig. 40) bearing sharply defined, sometimes setose, deep punctures interspersed with much smaller, shallower punctures, puncturing densest on anterior face and disk. Front legs similar in both sexes, not elongate in male (Fig. 39). Elytral interstriae tuberculate. Male (Fig. 36–37) – Clypeus reflexed, anterior edge truncate, transverse carina absent or only weakly indicated; frontal carina with median tubercle; pronotum strongly humped anteriorly, hump rounded (seen from above), presenting a near-vertical, bilaterally weakly concave anterior surface. Female (Fig. 38) – Clypeus rounded, scarcely reflexed, clypeal carina strong, raised medially; frontal carina strongly developed, extending between eyes; pronotum convex, broadly tumid anteriorly, but never as strongly as in male. This species was re-described by Howden and Cartwright (1963).

Big Bend collection sites (altitudinal range: 1410–1785 m).

Presidio Co.: **[1]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug); **[2]** C.E. Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug).

Jeff Davis Co.: **[1]** *Davis Mountains Preserve, 31°37′42″N 104°05′01″W, 1785 m (May).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture on ground surface; (c) soil beneath *Neotoma* nest.

Surface activity. Presumed nocturnal.

Habitat. All zones in association with wood rats (*Neotoma*).

Comments. *Onthophagus brevifrons* is the scarcest and largest species of Big Bend *Onthophagus*, always collected in low numbers (one to four individuals in lethal pitfalls) in creek beds and arroyos where wood rats are known to occur. The low numbers undoubtedly reflect a strong preference for wood rat feces such that significant numbers are more likely to result by excavating the soil beneath the rodent′s nest quarters. It is similar to *O. coproides* Horn, an inquiline in pocket gopher nests in Arizona, New Mexico and northern Mexico and to other species of mountainous Mexico with broadly humped male pronotum (the chevrolati group), many of which are associated with mammal nests. This species is one of a triplet of closely related US species, all with specialized microhabitats: *O. brevifrons* in wood rat nests; *O. subtropicus* Howden and Cartwright in wood rat nests of east Texas; and *O. cavernicollis* Howden and Cartwright with cave-dwelling bats in Arkansas (Halffter and Matthews 1966). Slay et al. (2012) speculate that this latter species, while collected in bat guano, actually utilizes wood rat dung in the caves for breeding. Small males of *O. brevifrons* can closely resemble the female, from which they can be distinguished by having a medially emarginate last abdominal sternum (as in Fig. 27). Riley and Wolfe (2003) reported *O. brevifrons* also from south Texas and the Panhandle plains regions of the state. Cokendolpher and Polyak (1996) collected a specimen from Milliped Cave, Sinkhole Flat, Eddy Co., NM (~35 km NW Carlsbad ~3700 ft). Howden and Cartwright (1963) report collecting it along with *O. browni* from a single *Neotoma* nest in Portal, Arizona.

***Copris* Müller**

The genus *Copris* occurs world-wide, with most of its 225 or so species occurring in Africa and Asia. Tropical Africa alone is home to about 100 species (Cambefort and Nguyen-Phung 1996). They are absent from Australia and all but the northwestern corner of South America. McCleve and Kohlmann (2005)

reported 32 species (some of which include recognized subspecies) in the Western Hemisphere. Of these, only one (*C. incertus* Say) reaches South America, nine inhabit the United States, while the remaining occur in Mexico and Central America. Four species (*C. arizonensis* Schaeffer*, C. remotus* LeConte, *C. lecontei* Matthews and *C. macclevei* Warner) are shared between Mexico and the United States. The likely closest relative of *C. arizonensis* is *C. warneri* McCleve and Kohlmann, a Mexican species from the mountains of Chihuahua and Sonora likely also associated with *Neotoma* (McCleve and Kohlmann 2005). The genus in the Western Hemisphere was revised by Matthews (1961).

The nesting behavior of the genus is described by Halffter and Matthews (1966) and Halffter and Edmonds (1982); it is unusual among dung beetles in that it exhibits active parental care of the brood. Most *Copris* species for which habits are known are nocturnal and exploit the excrement of surface mammals. Four Mexico–US species have known relationships with nesting vertebrates: *C. arizonensis* and *C. macclevei* with wood rats [*Neotoma*], *C. megasoma* with gophers [*Thomomys*] and *C. gopheri* with the gopher tortoise [*Gopherus polyphemus* Daudin]. In these cases, the adults utilize the feces of their vertebrate host for feeding and nesting in the soil beneath nest chambers and tunnels; only rarely are they attracted to feces-baited pitfall traps.

Copris arizonensis Schaeffer

Fig. 64–69

Diagnosis. Black, surface lustrous, sides of body more-or-less parallel. Length 13–22 mm. Male (Fig. 64–66) – Head of large individuals bearing posteriorly curved horn, tip of which approaches bifurcated median process of pronotum; flanks of pronotum each with large, acute, forward-directed, blade-like process separated from apically bifurcated median process by broad, declivitous concavity (in smaller individuals horn and processes progressively attenuated, Fig. 65). Female Fig. 67–69) – Head with short, erect horn, apex widened, scoop-like; pronotum convex except for pair of blunt tubercles, one on each side near anterior angle and separated by thick transverse ridge. Matthews (1961) provides a full re-description of this species.

Big Bend collection sites (altitudinal range: 1375–1800 m).

Brewster Co.: **[1]** Alpine, Sul Ross State University campus, 30°22′04″N 103°38′52″W, 1375 m; **[2]** *Big Bend National Park, Basin area, 29°16′04″N 103°17′39″W, 1660 m (May); **[3]** *Alpine, Sunny Glen, 30°22′41″N 103°45′06″W, 1445 m (Jun).

Jeff Davis Co.: **[1]** *Davis Mountains State Park, 30°35′43″N 103°56′5″W, 1540 m (Jun, Aug)**; [2] ***Davis Mountains Resort, 30°37′30″N 104°05′30″W, 1800 m (Jun–Aug).

Collection method(s). a) UV light trap; b) *direct capture beneath nests of *Neotoma*.

Surface activity. Nocturnal.

Habitat. Montane, juniper-pinyon woodlands and arroyos in association with the wood rat, *Neotoma albigula* (and possibly also *N. mexicana* Baird).

Comments. This is by far the rarest dung beetle in the Big Bend. All examined specimens from the region were collected at lights. *Copris arizonensis* is also known from various locations in the mountains of southeastern Arizona and adjacent areas of southwestern New Mexico and northern Chihuahua, Mexico [Matthews 1961; McCleve and Kohlmann 2005; Warner 1990].) Figure 64 depicts a specimen from southeastern Arizona (Dragoon Mts., Cochise Co.) exhibiting maximum expression of male armament, which I have not observed in Big Bend specimens (Fig. 65). The occurrence of *C. arizonensis* in scattered higher mountainous areas of northern Chihuahua and the desert southwest is doubtless the result of shrinking and vertical isolation of suitable, high-elevation habitat during post-Pleistocene desertification of the region.

Phanaeus MacLeay

The genus *Phanaeus* embraces about 55 species distributed from the United States southward through Mexico and Central America into all but the southern cone of South America; of these, the 35

or so species included in the subgenus *Phanaeus* comprise a phyletic group virtually confined to North and Central America (Edmonds 1994; Edmonds and Zidek 2012). The United States is home to six species, four of which reside in Texas, one in the Big Bend. The nesting behavior of *Phanaeus* is described by Halffter and Matthews (1966) and Halffter and Edmonds (1982). It involves the elaborate subterranean construction of a pear-shaped brood ball consisting of a spherical core of larval food (usually dung) encased in a thick casement of compressed soil. The large majority of the members of the genus are diurnal coprophages; many are quite common in pasture ecosystems.

***Phanaeus texensis* Edmonds**
Fig. 70–73

Diagnosis. Black, often with blue-violet highlights; upper surface dull. Length 12–22 mm. Male (Fig. 70–72) – Head of large individuals bearing long horn curved posteriorly over the pronotum; pronotum roughened by irregular granular sculpturing, strongly flattened, with salient, laterally curved posterior angles; in smaller males head horn shorter and triangular area of pronotum reduced in size and prominence. Female (Fig. 73) – Head with anteriorly bowed ridge between and in front of eyes; pronotum granulate, convex, with transverse, weakly bowed ridge near anterior margin. Elytral interstriae flat, densely roughened. Edmonds (1994) provides a formal description of this species (as *P. triangularis texensis*; raised to species status in Edmonds and Zidek 2012).

Big Bend collection sites (altitudinal range: 1325–1850 m).

Jeff Davis Co: **[1]** Davis Mountains Preserve, 31°41′40″N 104°07′30″W, 1850 m (Jul–Aug); **[2]** Davis Mountains Preserve (Madera Canyon Unit), 1845 m (Sep); **[3]** 16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); **[4]** 8 km 8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Sep); **[5]** ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul).

Presidio Co.: **[1]** 37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); **[2]** 20–26 km SSE Marfa (along FM 169), 1355–1415 m (Jun); **[3]** 27 km SSE Marfa (along FM 169), 30°08′42″N 104°02′13″W, 1325 m (Jul); **[4]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33′30″N 104°38′44″W, 1350 m (Jul–Aug); **[5]** Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug); **[6]** 3 km NE Marfa (along FM 1112), Marfa Golf Course, 30°19′40″N 103°59′41″W, 1470 m (Jul, Sep).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cowdung; pronghorn dung; horse dung; *deer carcass).

Surface activity. Diurnal.

Habitat. Montane woodlands and grasslands throughout the Big Bend area.

Comments. *Phanaeus texensis* is not common in the Big Bend, but it is widespread there. It is a burrowing species that searches for food (usually dung) on the surface that, once located, is buried by bits in tunnels underneath or to the side of its find. Often the only sign that it is present is a small mound of soil pushed to the surface during excavation of the tunnel. Because it passes most of its adult life underground, this species is, in spite of its size and conspicuousness, largely unknown to ranchers, hunters and others who frequent pasturelands in the area. While it prefers montane habitats, it can be found in other grassland and scrub habitats as well, but usually above 1380 m. Big Bend specimens of this species are always darkly colored, but scarce individuals can occasionally assume metallic green/coppery coloration in eastern parts of the state. In 1994, I considered *P. texensis* (as *P. triangularis texensis*) essentially absent from the Big Bend, an error corrected here. A peripheral record in Pecos Co. about 32 km northwest of Marathon on U.S. Hwy 385 (Brewster Co.), reports *P. texensis* from a deer carcass.

While *P. texensis* occurs throughout much of the western two-thirds of the state, including the Big Bend, another species occurs at the periphery of the Trans-Pecos and could be regarded as an incipient (or perhaps previous) member of the Big Bend fauna. This second *Phanaeus* is *P. difformis* LeConte (Fig. 74–75), which is broadly distributed in the south-central United States and has penetrated western areas into the northern limit of the Trans-Pecos via river drainage systems into southeastern New

Mexico and eastern Colorado (Edmonds 1994). A few isolated specimens have been collected in the Hueco Mountains east of El Paso (Schoenly 1983) as well as in Guadalupe Mountains National Park and near Malaga, New Mexico (personal records). Another common *Phanaeus*, *P. vindex* MacLeay, occurs widely in the Texas plains, New Mexico and Arizona; I agree with Bill Warner (pers. comm.) that its apparent absence from the Trans-Pecos is surprising.

The Exotic Species

Digitonthophagus gazella and *Euoniticellus intermedius* are two of fifteen exotic species introduced into Texas (most unsuccessfully) between 1972 and 1987 as biological controls of the horn fly, *Haematobia irritans* (Linné) (Fincher 1990), via intense competition with the flies for a common food source, dung. Since their release in eastern and central parts of the state in 1972 (*D. gazella*) and 1979 (*E. intermedius*), they have become virtually ubiquitous members of dung beetle communities associated with livestock across the state, including in the Trans-Pecos (where *D. gazella* was reported by 1979!). Both are highly opportunistic and combine high reproductive potential, ecological plasticity and high vagility that have resulted in their spread throughout much of the state and southward well into Mexico and beyond. Analysis of the dispersal of these two species from Texas into Mexico, Central and South America in provided by Kohlmann (1994), Montes de Oca and Halffter (1998) and Noriega et al. (2017). Both species are common in the Big Bend and occur in all habitats supporting livestock; they are often collected together.

Digitonthophagus gazella (Fabricius)

Fig. 54–59

Diagnosis. Elytra yellow to mottled yellowish brown; pronotum blackish-brown except for continuous yellow band following lateral and posterior borders. Length 6–8 mm. Male (Fig. 54–55) – Head of larger individuals with pair of widely spaced, vertical, slightly curved, acute horns set just inside eyes; carina separating frons and clypeus bowed anteriorly; pronotum with narrow, bilobate central tumosity near anterior margin; protibia (Fig. 56) tridentate, slender and rather strongly curved medially, inner apical angle extended as digit-like spur projecting beyond spur (Fig. 59B, arrow). Female (Fig. 57–58) – Head with strongly elevated ridge extending between eyes; carina separating frons and clypeus bowed anteriorly; pronotum with wide, bilobate prominence; protibia tridentate, wider, only slightly curved medially, inner apical angle simple, not digitiform (Fig. 59A). This species was re-described by Génier and Moretto (2017) and the correct usage of the species epithet 'gazella' was considered by Génier and Davis (2017).

Big Bend collection sites (altitudinal range: 1010–1850 m).

Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul); **[2]** *Big Bend National Park, North Rosillos Mountains Preserve, 29°28′48″N 103°11′16″W, 1010 m (Jul).

Jeff Davis Co.: **[1]** 8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Aug); **[2]** Davis Mountains State Park, 30°35′43″N 103°56′05″W, 1540 m (Jun, Aug); **[3]** Davis Mountains Preserve, 31°41′40″N 104°07′30″W, 1850 m (Jul–Aug); **[4]** 8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Visitor Center area), 30°32′32″N 103°50′11″W, 1555 m (Aug).

Presidio Co.: **[1]** ~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m (Aug–Sep); **[2]** ~30 km SSE Marfa (along FM 169), Humphreys Ranch, 30°02′30″N 104°01′00″W, 1285 m (Jul); **[3]** 27 kmSSE Marfa (along FM 169), 30°08′42″N 104°02′13″W, 1335 m (Jun); **[4]** 60 kmSSE Marfa (along FM 169), Casa Piedra, 29°44′07″N 104°03′03″W, 1055 m (Sep); **[5]** ~1 km E Marfa (along FM 1112), 30°18′56″N 104° 00′08″W, 1490 m(Aug); **[6]** ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); **[7]** 12 kmNE Ruidosa (via Chinati Hot Springs road), Chinati Hot Springs, 30°02′17″N 104°36′02″W, 1090 m (Aug); **[8]** ~13 km E Marfa (via US 90/67), 30°16′07″N 103°48′44″W, 1565 m (Jul); **[9]** 20–26 km SSE Marfa (multiple sites along FM 169), 1355–1415 m (Jun–Jul); **[10]** ~3 km N Marfa (along TX 17), 30°20′27″N 104°01′7″W, 1500 m (Jul); **[11]** 37 km SSW Marfa (along FM 2810), 1630 m (Jun); **[12]** Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m (Aug).

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung; horse dung); c) UV and incandescent light trap.

Surface activity. Nocturnal.

Habitat. Generally distributed throughout the region in all habitats, although more common in open pasturelands and desert scrub.

Comments. The generic name derives from the finger-like projection of the tibial apex of the male (Fig. 56, 59B). *Digitonthophagus gazella* was originally placed in *Onthophagus*, where it is often still found in the literature. Recent molecular studies (Breeschoten et al. 2016), however, show *Digitonthophagus* to be somewhat distantly related to *Onthophagus*. The scientific literature on this species, especially in the context of the livestock industry, is extensive.

***Euoniticellus intermedius* (Reiche)**
Fig. 60–63

Diagnosis. Dorsum mottled yellowish brown, usually with distinct dark, angular area extending along midline of pronotum. Pronotum evenly punctate; body elongate. Male (Fig. 62–63) – Head with large, blunt, slightly curved, cylindrical horn (reduced to tubercle in small individuals); pronotum (seen in profile) enlarged and expanded toward head. Female (Fig. 60–61) – Head with transverse, curved carina in front of and between eyes; pronotum flattened, rounded on sides. This species was re-described by Janssens (1953).

Big Bend collection sites (altitudinal range:1055–1550 m [2490 m in Sierra El Carmen]). Brewster Co.: **[1]** ~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul); **[2]** *Elephant Mountain Wildlife Management Area, 30°03′04″N 103°32′56″W, 1345 m (Apr).

Jeff Davis Co.: **[1]** Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m (Sep).

Presidio Co.: **[1]** ~96 km SSE Marfa (Old Alazan Ranch, headquarters), 29°33′01″N 103°53′25″W, 1275 m (Mar); **[2]** 37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); **[3]** ~6 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m (Aug–Sep); **[4]** 60 km SSE Marfa (along FM 169), Casa Piedra, 29°44′07″N 104°03′03″W, 1055 m (Sep).

MEXICO: Coahuila, Sierra El Carmen, Maderas del Carmen, 29°00′06″ N 102°35′48″ W, 2490 m [Jul].

Collection method(s). a) baited pitfall trap (human feces); b) direct capture (cow dung; horse dung).

Surface activity. Diurnal.

Habitat. Generally distributed throughout the region in all habitats, although more common in open pasturelands in association with livestock.

Comments. This species spends its life in a dung pad and, because it is often dirtied by adhered fragments of dried dung and has the habit of feigning death (thanatosis) when disturbed, it is splendidly camouflaged. It is common in the Big Bend, but I have never observed population levels to even closely approximate those of *D. gazella*. The efficacy of the activities by *E. intermedius* in the control of nematodes is discussed by Martínez et al. (2018).

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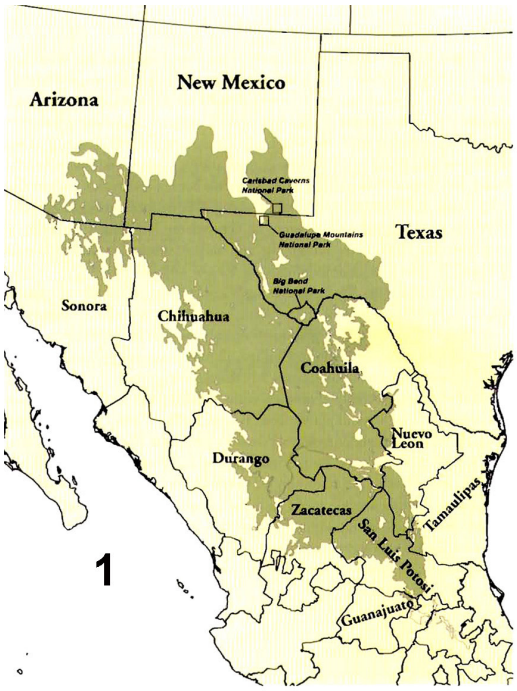
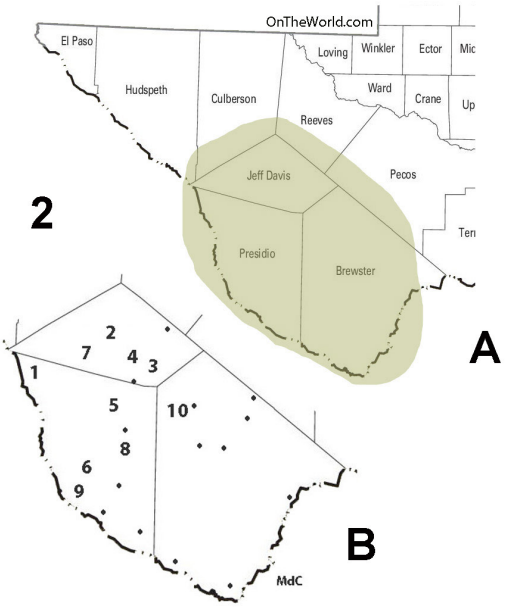
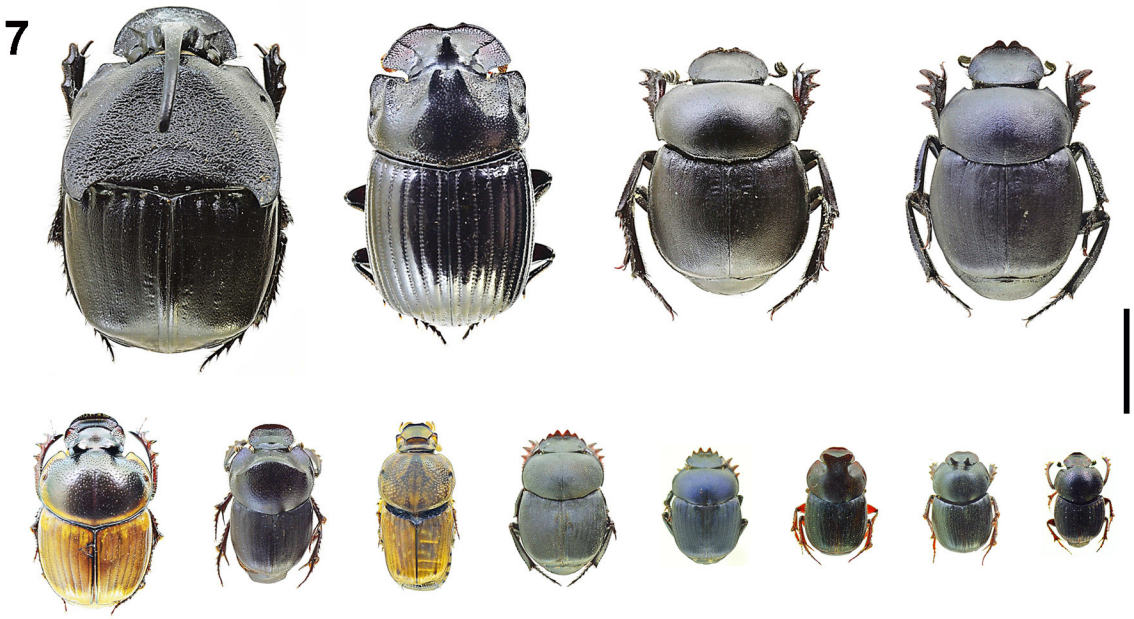
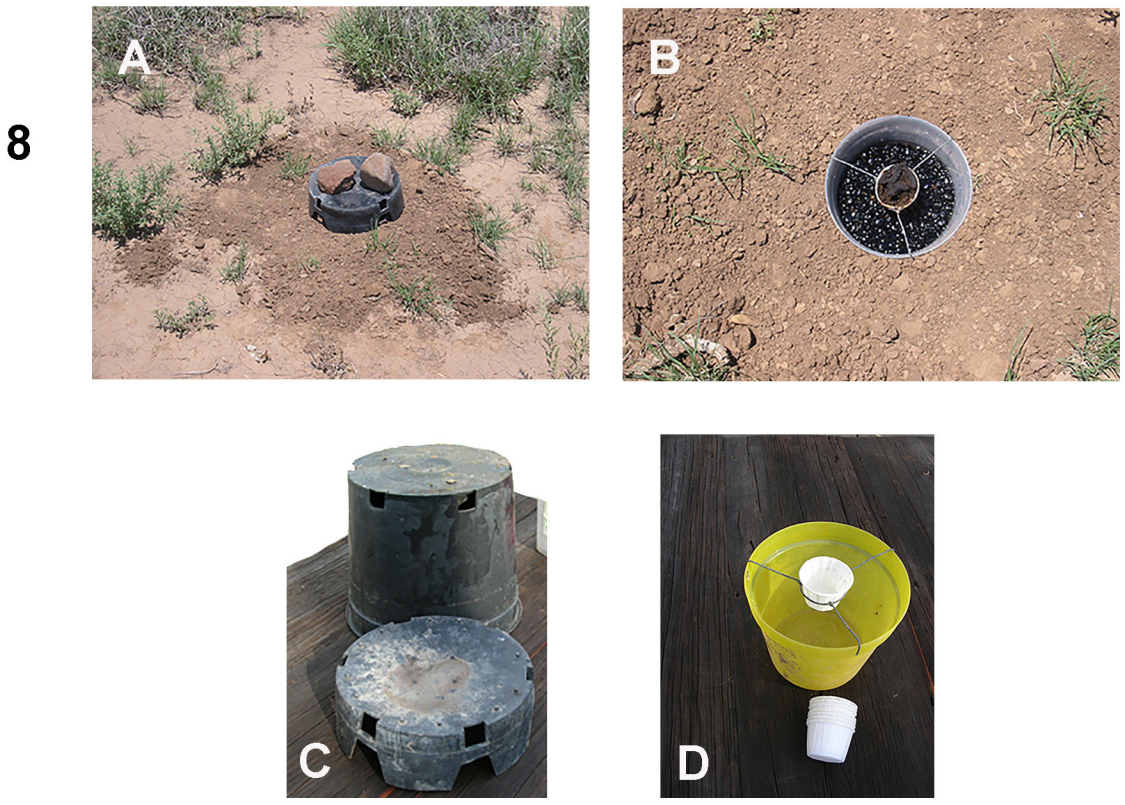




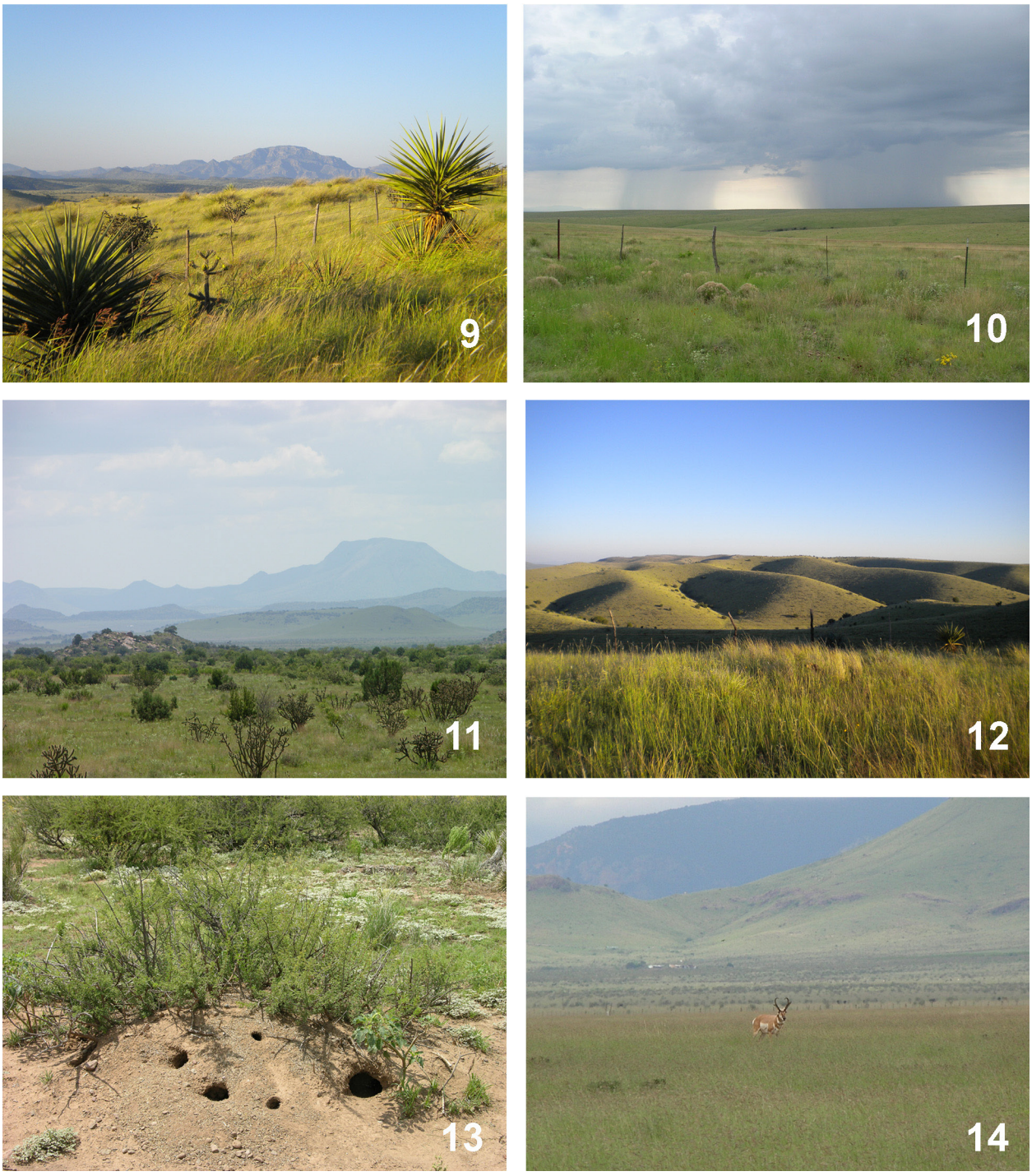
The Chihuahuan Desert Source: World Wildlife Fund

Figures 1–6. Big Bend maps and dung beetles. **1–3)** Location of study area and collection sites. **1)** Extension of the Chihuahuan Desert (dark green) in north-central Mexico and southwestern United States. **2)** [A] Trans-Pecos Texas showing counties and Big Bend region (shaded); [B] Tri-county Big Bend region (numbers indicate primary collection sites described in Materials and Methods; dots mark secondary sites). **3–6)** Beetles in natural settings. **3)** Aggregation of *Canthon imitator*, *C. praticola* and *C. mixtus* at cow dung. **4)** *Canthon imitator* rolling ball of cow dung. **5)** Stick nest of *Neotoma micropus* at base of mesquite brush, potential habitat for inquilinous *Onthophagus*. **6)** *Canthon blumei* feeding directly from javelina carcass.





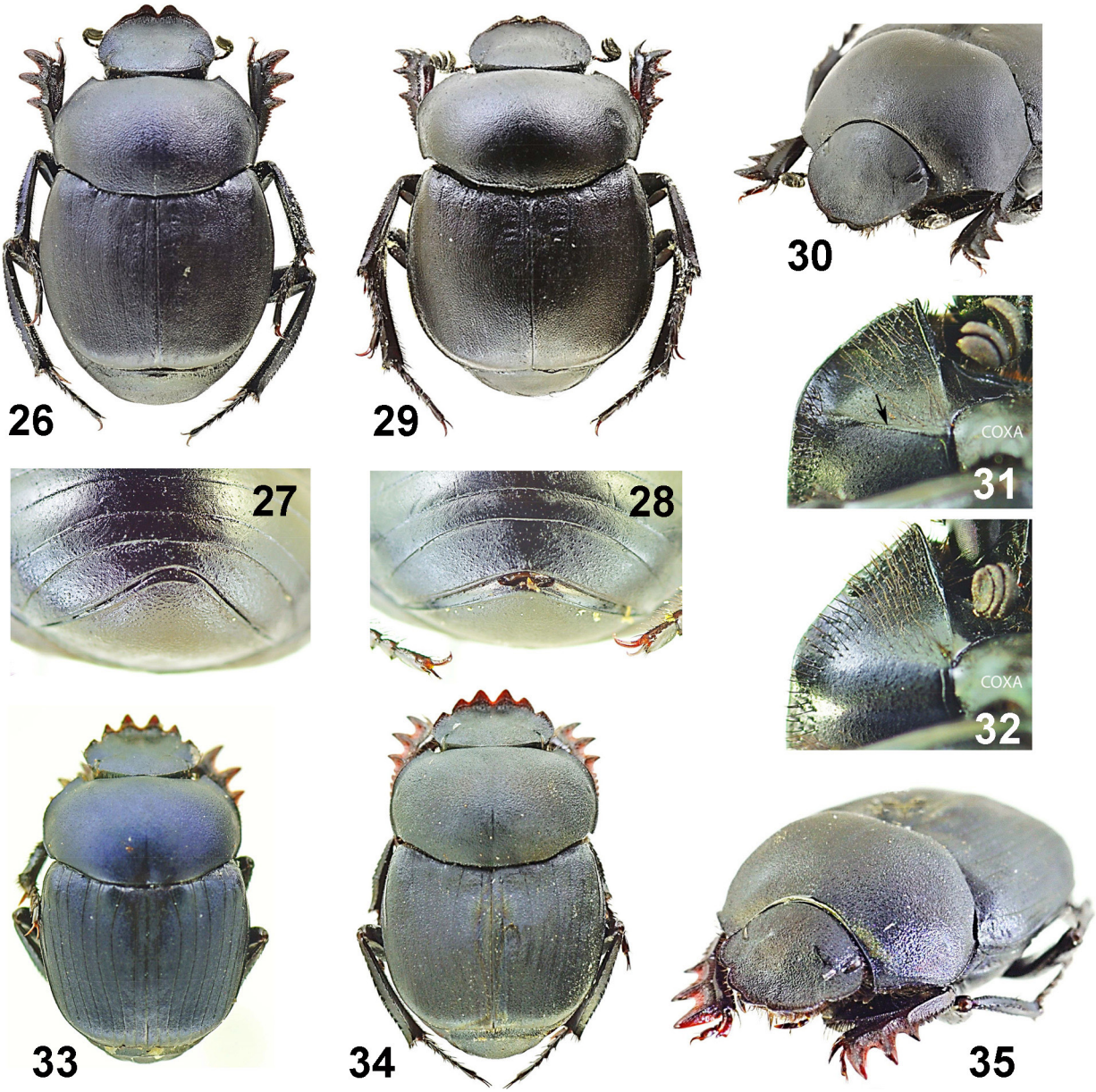
Figures 7–8. Big Bend dung beetles and pitfall trap design. **7)** Big Bend species arranged left to right in order of descending size (scale bar = 5mm): Above – *Phanaeus texensis*, *Copris arizonensis*, *Canthon blumei*, *C. imitator*; Below – *Digitonthophagus gazella*, *Onthophagus brevifrons*, *Euoniticellus intermedius*, *Canthon praticola*, *C. mixtus*, *O. browni*, *O. velutinus*, *O. knausi*. **8)** Pitfall trap design: [A] active trap with cover (anchored with rocks); [B] cover removed to expose suspended bait and catch; [C] plant nursery container from likes of which trap cover fashioned (foreground); [D] trap receptacle, wire bait hanger and bait cup.



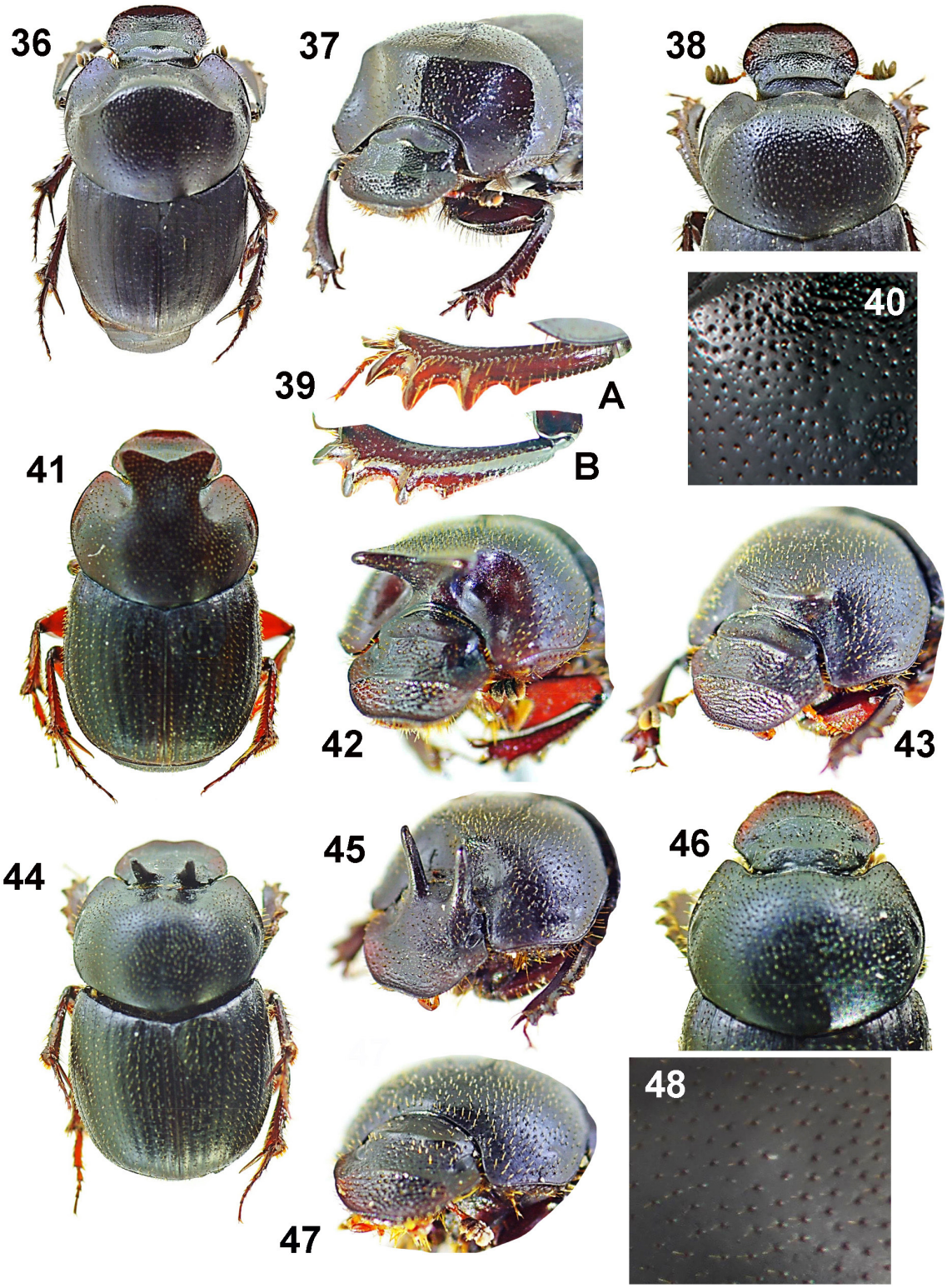
Figures 9–14. Big Bend grassland habitat. **9)** Marfa plateau (Chinati Mountains in background; Presidio Co.). **10)** Summer rain near Valentine (Jeff Davis Co.). **11)** Foothills south of Davis Mountains (Blue Mountain in background; Jeff Davis Co.). **12)** Rolling tableland south of Marfa (Presidio Co.). **13)** Abandoned banner tail kangaroo rat (*Dipodomys spectabilis* Merriam) den occupied by *Neotoma micropus*, Miller Ranch (Presidio/Jeff Davis Co.). **14)** Pastureland south of Fort Davis (Jeff Davis Co.) shared by cattle and pronghorn (*Antilocapra americana* [Ord]; large male in foreground).

Figures 15–18. Big Bend desert scrubland habitat. **15)** Rocky hillside, Pinto Canyon (Presidio Co.). **16)** Rio Grande valley, southeast corner of Presidio Co. (Mexico to the left; United States to the right). 17) Scrub hillside, south Brewster Co. **18)** Creek bed, Chinati Hot Springs (Presidio Co.).

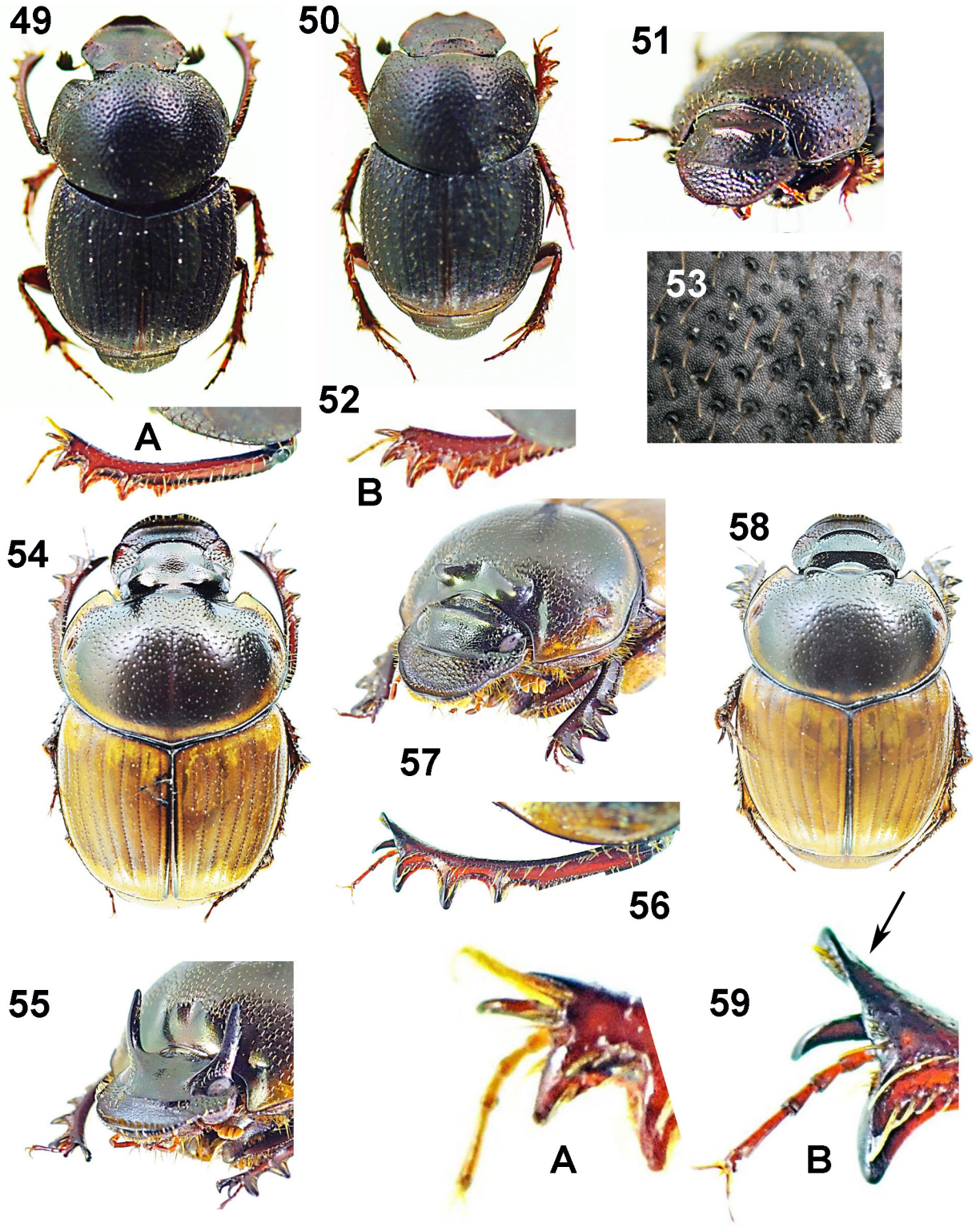
Figures 19–25. Big Bend montane habitat. **19)** Seasonal creek, Quarry section, Chihuahuan Desert Research Institute (wet season). **20)** same, dry season. **21)** Woodland/meadow enclave in summer, Quarry section, CDRI (Jeff Davis Co.). **22)** Davis Mountain woodland (Jeff Davis Co.). **23)** Same. **24)** Box Canyon, Miller ranch (Presidio Co.). **25)** Same, interior view.



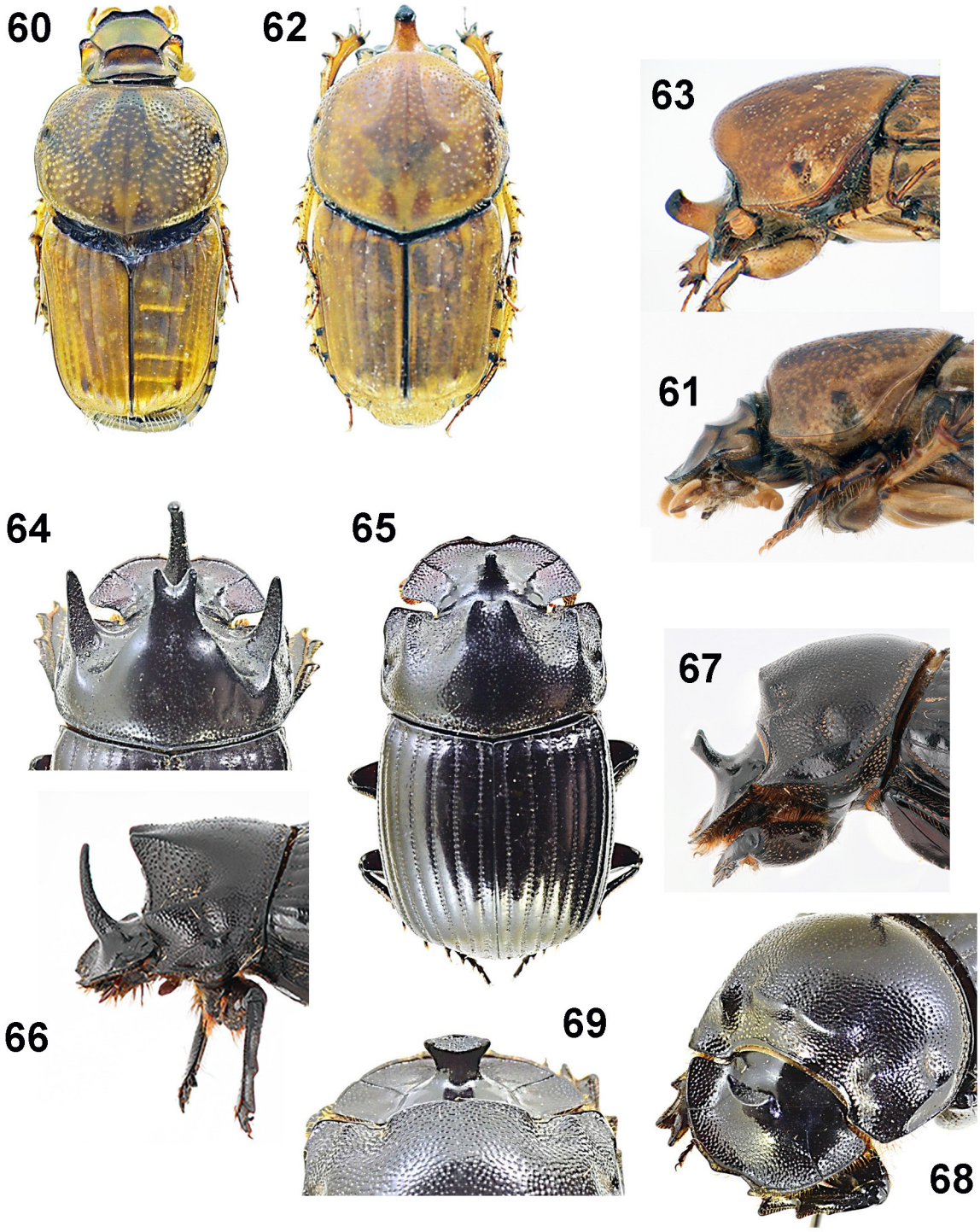
Figures 26–35. *Canthon*. **26)** *C. imitator*, dorsal view, male. **27)** Same, ventral view of abdomen. **28)** Same, ventral view of female abdomen. **29)** *C. blumei*, dorsal view, female. **30)** Same, oblique dorsal view of forebody. **31)** Same, ventral view of right propleuron (arrow marks transverse carina). **32)** *C. imitator*, ventral view of right propleuron. **33)** *C. mixtus*, dorsal view, male. **34)** *C. praticola*, dorsal view, female. **35)** Same, oblique view.



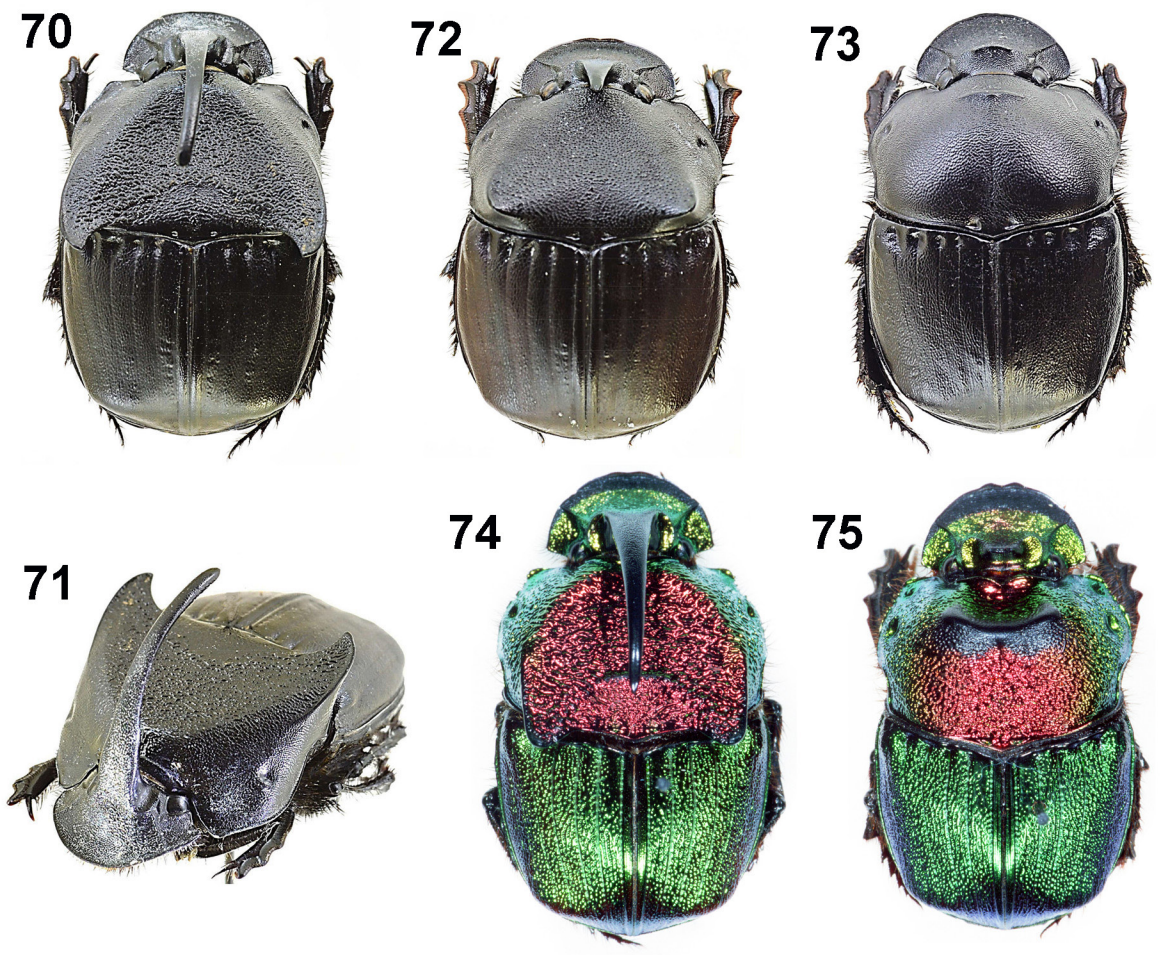
Figures 36–48. *Onthophagus*. **36**) *O. brevifrons*, dorsal view, male. **37)** Same, oblique frontal view. **38)** Same, dorsal view of forebody, female. **39)** Same, prolegs (A, female; B, male. **40)** Same, pronotal sculpturing**. 41)** *O. browni*, dorsal view, male. **42)** Same, oblique frontal view. **43)** Same, oblique frontal view, female. **44)** *O. velutinus*, dorsal view, male. **45)** Same, oblique frontal view. **46)** Same, dorsal view of female forebody. **47)** Same, oblique frontal view. **48)** Same, pronotal sculpturing.



Figures 49–59. *Onthophagus* and *Digitonthophagus*. **49)** *O. knausi*, dorsal view, male. **50)** Same, dorsal view, female. **51)** Same oblique frontal view, female. **52)** Same, prolegs (A, male; B) female). **53)** Same, pronotal sculpturing. **54)** *D. gazella*, dorsal view, male. **55)** Same, partial oblique frontal view of forebody. **56)** Same, proleg, male. **57)** Same, oblique frontal view of female forebody. **58)** Same, dorsal view, female. **59)** Same, apex of protibia and protarsus (A, female; B, male [arrow marks apical tibial "digit"]).



Figures 60–69. *Euoniticellus* and *Copris*. **60)** *E. intermedius*, dorsal view, female. **61)** Same, lateral view of forebody. **62)** Same, dorsal view, male. **63)** Same, lateral view of forebody. **64)** *C. arizonensis*, dorsal view of forebody, large male (southwestern Arizona). **65)** Same, dorsal view, small male (Big Bend). **66)** Same, lateral view of forebody. **67)** Same, lateral view of forebody, female. **68)** Same, oblique dorsal view. **69)** Same, dorsal view of head and prothoracic margin.



Figures 70–75. *Phanaeus*. **70)** *P. texensis*, dorsal view, large male. **71)** Same, oblique anterolateral view. **72)** Same, dorsal view, small male. **73)** Same, dorsal view, female. **74)** *P. difformis*, dorsal view, male. **75)** Same, female.