

**COLEOPTERA COLLECTED FROM ROTTING FISHHOOK BARREL CACTI
(*FEROCACTUS WISLIZENI* (ENGELM.) BRITTON AND ROSE), WITH A REVIEW OF
NEARCTIC COLEOPTERA ASSOCIATED WITH SUCCULENT NECROSIS**

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ABSTRACT

Sixteen dead *Ferocactus wislizeni* (Engelm.) Britton & Rose (Cactaceae), known variously as fishhook barrel cactus, candy barrel cactus, or compass plant, were discovered in various states of decay near Portal, Arizona during July 2011. A survey of the Coleoptera in the rotting cacti resulted in the collection of 976 specimens representing 11 families and 35 species. Volume of cactus was significantly positively correlated with moisture content and moisture content was significantly positively correlated with species richness and abundance. Findings indicated that there may be three distinct successional stages—wet (saturated), moist, and dry—during cactus late decomposition. A review of literature listing species collected from decaying cacti and succulents is provided with updated nomenclature. Photographs and basic biological information are provided for 20 taxa of interest and relevant literature containing descriptions, keys, distributional data, and biological/life history data is reviewed.

Key Words: ecology, Cactaceae, Histeridae, Staphylinidae, Chihuahuan Desert, Sonoran Desert

Cactaceae (cacti) are a family of New World plants possessing thick stems modified for moisture storage and photosynthesis. Functional leaves are absent or small and deciduous in most species, and the exterior is protected by spines. Most species occur in arid environments and are major floristic elements in New World arid landscapes; many species have become established in other areas of the world. Many larger cactus species are represented by long-lived, slow-growing individuals, some of which may survive for a century or more (Anderson 2001). Insects associated with cacti in the United States were treated as a group by Hunter *et al.* (1912), and an international update

was provided by Mann (1969). However, both publications were predominantly concerned with insects that attack living cacti and only briefly mention “scavengers” or species associated with necrotic tissue or dead plants.

Necrotic and decomposing cacti and other succulents are a distinct and unique ephemeral microhabitat within desert ecosystems. The overall succession and dynamics of the obligate and opportunistic organisms that inhabit succulent rot in deserts are poorly understood. Baseline faunal surveys have not been conducted in a systematic fashion, making rigorous research concerning secondary or tertiary questions currently impossible

to conduct. Without a basic survey associating succulent rot fungi and faunae with plant species, an understanding of succession, community dynamics, and adaptation within the microhabitat is not achievable.

One system involving necroses in cacti has been the subject of abundant research—the evolution and ecology of tri-trophic interactions among cacti, yeasts, and cactophilic *Drosophila* Fallén (Diptera: Drosophilidae) in the Sonoran Desert (Heed 1978, 1982, 1989; Etges *et al.* 1999). Additionally, members of the hoverfly genus *Copestylum* Macquart (Diptera: Syrphidae) have received much attention for their role in the decomposition of columnar cacti (Martínez-Falcón *et al.* 2012, and references therein).

However, general studies or surveys of insects involved in necrotic cacti are rare. Only four studies involving Coleoptera were found during our literature search. During a standardized survey of necrotic arms and stems of three species of columnar cacti in the Sonoran Desert, Castrezana and Markow (2001) recorded 34 arthropod species, including eight Coleoptera. In a series of letters epitomizing the joy of entomological discovery, Hubbard (1899) gave several accounts of serendipitous collections of insects associated with rotting or dead saguaro cacti (*Carnegiea gigantea* (Engelm.) Britton & Rose). In total, he collected at least 65 species (47 Coleoptera) (Schwarz 1899a) including several species new to science (Schwarz 1899b). Hubbard (1901) also provided an account of insects associated with dead and dying members of the non-cactus succulent *Dasylyrion wheeleri* S. Wats. (Asparagaceae) (sotol), adding to the list of insect desert succulent decomposers.

Dury (1916) described decaying barrel cactus (*Ferocactus wislizeni* (Engelm.) Britton & Rose) he discovered in Arizona: “Approaching one of these Barrel Cactus or “Bisnagas,” in a half-decayed condition, one can not see any insect life from the outside, but cut or break it open and the interior will be swarming with insects, mostly beetles, of many species.” Dury collected seven beetle taxa that could be identified.

The Coleoptera from historic surveys are tabulated in Appendix A with updated nomenclature and compared to the current study.

During July 2011, Louisiana State Arthropod Museum researchers discovered many dead, rotting *F. wislizeni* near Portal, Arizona. With the exception of Dury (1916), no literature could be found treating the necrofauna of *F. wislizeni*. *Ferocactus wislizeni* is found in the Sonoran and Chihuahuan Deserts of the United States and northern Mexico. Individuals are typically 0.6–1.6 m tall, 45–83 cm in diameter, and have 20–30 ribs

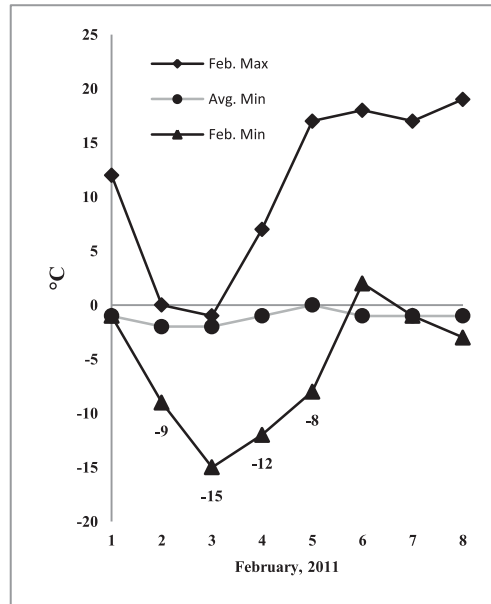


Fig. 1. Daily temperatures, 1–8 February 2011, Safford, Arizona.

(Turner *et al.* 1995). The estimated average growth rate is approximately 1.4 cm in height per year (Turner *et al.* 1995). The northern range of the species is limited by cold (Nobel 1980, 1982; Turner *et al.* 1995). Freeze-killed *F. wislizeni* were reported after catastrophic freezes near Tucson during 1962 and in Saguaro National Monument during 1971 (Steenbergh and Lowe 1977). The Portal area experienced four days of extreme cold during 2–5 February 2011 (Fig. 1), including two record lows (on 2 and 3 February, 4 February tied for a record low set in 1955) (Weather Underground 2013). The unusually high mortality of *F. wislizeni* was probably due to this event, in which case the Portal population would have died at approximately the same time and undergone nearly six months of decay before the time of our discovery.

Here we report on the community of Coleoptera collected from rotting *F. wislizeni*, comment on faunal succession within the decomposing cacti, and provide natural history information for select taxa.

MATERIAL AND METHODS

Study Area. “Arizona—That anomalous country, with a fauna and flora so peculiar, and different from other sections of North America; with faunal areas so very unlike each other, even

though separated by short vertical distances; where the torrid dry desert of the lowlands is replaced at higher altitudes by a climate most delightful, and with peculiar and beautiful vegetation.” (Dury 1916).

The study area was spread over several hectares centered at N31.999°, W109.173° in Cochise Co., Arizona, on Foothills Road approximately 10 km north of Portal (Fig. 2). The biotic community is designated Chihuahuan Desert Scrub (153.2, see Brown *et al.* 1979 for a description of southwestern biotic community classifications) and is immediately (~2 km) bordered to the west by higher elevation Madrean Evergreen Woodland (123.3) and to the east and south (~10 km) by Semidesert Grassland (143.1) (Brown 1994). Chihuahuan Desert Scrub is a “high” desert, approximately 1,400 m in elevation at the study location, dominated by the Chihuahuan ecotype (diploid) creosotebush (*Larrea tridentata* (DC.) Coville) (Zygophyllaceae), tarbush (*Flourensia cernua* DC.) (Asteraceae), and whitehorn acacia (*Acacia neovernicosa* Isely) (Fabaceae) (Brown 1994). The study site also contained numerous pricklypear (*Opuntia* Mill.) (Cactaceae), and ocotillo (*Fouquieria splendens* Engelm.) (Fouquieriaceae).

The study area is located in the northwestern extreme of Chihuahuan Desert Scrub biotic community and receives an average of 200–300 mm of rainfall yearly (Brown 1994). The majority of precipitation occurs during the summer monsoon season of July–August, but significant winter precipitation also occurs. Temperatures range from summer daytime highs over 40°C to winter nighttime lows below freezing (Brown 1994).

In an effort to provide a quantitative description of cacti mortality, a full census of all living and dead *F. wislizeni* within a 3-ha (100 m × 300 m) subsection of the study area was conducted on 24 July 2011. Height and circumference measurements to the nearest centimeter were taken for each cactus. A total of 28 cacti were found. Living cacti ($n = 23$) averaged 27 cm tall and 31 cm diameter, while dead cacti ($n = 5$) averaged 21 cm tall and 29 cm diameter. Desiccation may have resulted in some shrinkage in dead cacti.

Collection Protocol. Collections took place during 21–28 July 2011. Height and circumference measurements to the nearest centimeter were taken at tissue level for each cactus from which collections were made. All dead cacti were discovered



Fig. 2. View of the study area from extreme western edge looking east. The area extends to the pond in the background and is bisected by Foothills Road.

in an erect position. Death was assessed by 1) visual inspection: green photosynthetic tissue not apparent; cuticle dark brown to gray in color; and 2) by probing: surface soft, weeping fluid when punctured; or dry, hard, and desiccated. No cactus with living tissue was disturbed. Each dead cactus was then pushed on its side and a shovel was used to make a median sagittal incision from base to crown. The two halves were pulled apart to expose the inner mass. Photographs were taken pre- and post-dissection. The inner, rotting mass of the cactus presented a complex environment with numerous harborage, but care was taken to collect representative specimens of all arthropods, adult and immature. Coleoptera were prioritized and all specimens were collected until new specimen discovery fell below a standardized level of diminishing returns.

Adult Coleoptera were pinned or point-mounted as needed, and labeled. Identification to the lowest level feasible (typically species) was performed with the appropriate taxonomic literature (see Species Accounts below), and/or comparison with authoritatively identified reference specimens. All immature Coleoptera and other macroinvertebrates were labeled and preserved in 90% ethanol. Specimens are deposited in the Louisiana State Arthropod Museum, LSU AgCenter, Baton Rouge, Louisiana. Data integrity protocols and taxonomic practices follow recommendations in Bortolus (2008), Gotelli (2004), and Grove (2003).

Dead cacti were evaluated for moisture content using an informal, qualitative scale. Cacti were considered "Dry" if the internal portion of the cactus was dry and flaky throughout. "Moist" referred to cacti whose wettest portions consisted of damp, moist pulp that retained voids such as tunnels. Cacti designated as "Wet" had a pulp slurry at the base and had fully saturated pulp in at least the lower third (Fig. 3).

Data Analysis. Several readily available statistical software packages were used to test for community differences based on cactus moisture (Dry, Moist, Wet) and size (volume). EstimateS (Colwell 2006) was used to produce alpha diversity metrics (Simpson, Shannon, Chao1) and a species accumulation curve. Linear regression and Pearson's correlation analysis (2-tailed) was run through R (R Development Core Team 2010) to correlate species richness and abundance of beetles with moisture and size of cactus host. Principal coordinates analysis (PCoA) ordination in QIIME (Caporaso *et al.* 2010) was used to visually compare the differences between communities. QIIME was also used to implement *adonis* to test for overall and pairwise community differences (with 1,000 replications). *P*-values were adjusted with Bonferroni correction for all multiple comparisons. All tests were performed using weighted

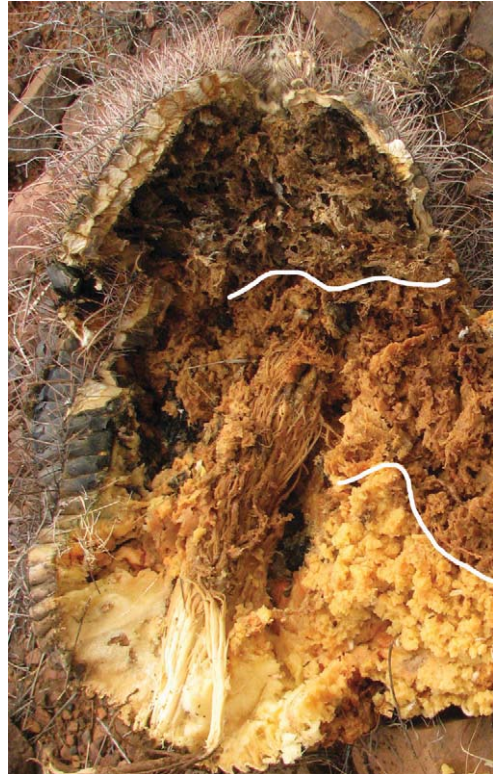


Fig. 3. Barrel cactus #10. White lines designate border between subsections: bottom, completely saturated; middle, moist; top, relatively dry.

abundance data, $\alpha = 0.05$. Only adult beetle specimens were considered in the analyses.

RESULTS

All dead *F. wislizeni* ($n = 22$) found in the study area were searched for insects. Six were completely desiccated and yielded no specimens. These desiccated individuals averaged 28 cm high and 33 cm diameter and are excluded from further analysis and discussion. Sixteen dead Dry (3), Moist (7), or Wet (6) cacti yielded beetles and averaged 58 cm tall and 43 cm diameter (Table 1).

A total of 976 adult beetles representing 11 families, 28 genera, and 35 species were collected (Table 2). Staphylinidae were represented by the most species (11), followed by Histeridae (7) and Tenebrionidae (7). However, the family Histeridae was numerically the most dominant family (533 specimens), followed by Staphylinidae (223) and Hydrophilidae (180) which was represented by only two species. Only 10 specimens of the seven Tenebrionidae species were collected.

Table 1. Description of dead cacti from which Coleoptera were collected. Notes describe the internal moisture gradient from base to crown.

Cactus ID	Height (cm)	Diameter (cm)	# spp.	# specimens	Notes	Moisture rank
BC01	76	56	15	153	saturated to wet	1 Wet
BC02	48	26	3	5	wet to slightly moist	2 Moist
BC03	18	21	7	12	slightly moist throughout	2 Moist
BC04	61	35	3	7	dehiscent throughout	3 Dry
BC05	91	39	12	69	wet to slightly moist	2 Moist
BC06	46	44	7	37	saturated to wet	1 Wet
BC07	51	34	7	14	wet to slightly moist	2 Moist
BC08	30	31	7	12	slightly moist throughout	2 Moist
BC09	30	29	4	6	slightly moist to dehiscent	3 Dry
BC10	81	49	11	123	saturated to slightly moist	1 Wet
BC11	81	53	17	314	saturated to slightly moist	1 Wet
BC12	30	34	2	3	dehiscent throughout	3 Dry
BC13	61	47	7	63	slightly moist to dehiscent	2 Moist
BC14	56	68	2	3	slightly moist to dehiscent	2 Moist
BC15	74	47	6	29	saturated to wet	1 Wet
BC16	97	68	12	126	saturated to slightly moist	1 Wet
Average	58	43	7.6	61		

Eleven species were collected from five or more cacti, while 15 species were collected from only a single cactus. Six species were represented by more than 50 specimens, and 10 species (29%) were singletons.

Wet cacti yielded a total of 782 (80%) specimens representing nine families, 22 genera, and 28 species; Moist cacti yielded 178 (18%) specimens representing seven families, 16 genera, and 21 species; and Dry cacti yielded only 16 (2%) specimens representing five families, seven genera, and seven species.

An estimate of a total community of 43 species (95% confidence interval = 37–69 species) was generated by the Chao1 richness estimator (Fig. 4), for an average of 81% of inventory completeness (51–97% complete). Although the actual species collected were reaching saturation, the estimator reached saturation by sample #13. Saturation of the estimator and the overlapping of 95% confidence intervals (not shown) between observed and estimated richness curves indicate that the collected samples are robust for beta diversity comparison between communities (Colwell *et al.* 2012). The Shannon Index was 2.14 and Simpson's diversity was 5.01.

Correlation analyses showed that cactus volume and moisture level were significantly correlated ($r^2 = 0.4601$, $r = 0.6783$, $P = 0.004$). Higher beetle abundance was significantly correlated with cactus volume ($r^2 = 0.3695$, $r = 0.6452$, $P = 0.007$) and cactus moisture ($r^2 = 0.4163$, $r = 0.6079$, $P = 0.013$). Higher beetle species richness was also positively correlated with volume ($r^2 = 0.5772$, $r = 0.7597$, $P = 0.019$) and moisture ($r^2 = 0.3928$,

$r = 0.6268$, $P = 0.009$). In general, the larger, wetter cacti had a higher abundance and richness of beetles.

Principal coordinates analysis (Fig. 5) showed a distinct grouping of Dry and minimal overlap between Moist and Wet. The first and second axis of the ordination explain 26.9% and 19.4% of the variation, respectively.

Adonis analysis provided a comparison between the beetle communities found in different cactus moisture levels. Overall, the communities found in each of the Dry, Moist, and Wet cacti were distinct from each other ($r^2 = 0.4154$, $P = 0.001$). Similarly, pairwise comparisons showed significant differences between Dry vs. Moist ($P = 0.039$), Dry vs. Wet ($P = 0.018$), and Moist vs. Wet ($P = 0.021$). Size of cacti also had a significant effect on the community ($r^2 = 0.2332$, $P = 0.026$).

DISCUSSION

The discovery of a large number of dead mature cacti was a singular experience. True to Dury's (1916) description, no indication of insect life was seen until the cactus was toppled and dissected. The 35 beetle species collected represented about 80% of the total expected richness (43 species based on the Chao1 estimator), indicating that this study offers a robust view of the beetles associated with this species of cacti necrosis in the area. Many of the beetle species collected are poorly represented in the literature and detailed habitat and natural history information is lacking (see Species Accounts below). Additionally, this study represents one of only a few censuses of

Table 2. Species of Coleoptera collected from dead *Ferocactus wislizeni* during this study.

Species	Cactus #			# Specimens
	Wet	Moist	Dry	
BUPRESTIDAE				
<i>Acmaeodera cazieri</i> Knull	11			1
CLERIDAE				
<i>Cymatodera</i> sp.		5		1
CURCULIONIDAE				
<i>Apotrepus densicollis</i> Casey	15		9	3
ELATERIDAE				
<i>Horistonotus</i> sp.		14		1
HISTERIDAE				
<i>Carcinops consors</i> (LeConte)	11, 15	2, 3, 5, 7, 8		8
<i>Carcinops opuntiae</i> (LeConte)		13		1
<i>Carcinops</i> n. sp. 1	1, 6, 10, 16	3, 5, 7, 8, 13		117
<i>Carcinops</i> n. sp. (rugula)	10, 11, 15, 16	1, 5		379
<i>Hololepta yucateca</i> (Marseul)	1, 6, 10, 11	2		10
<i>Iliotona cacti</i> (LeConte)	10, 11	2, 3, 7, 8		14
<i>Xerosaprinus martini</i> Fall	11		9	4
HYDROPHILIDAE				
<i>Agna capillata</i> (LeConte)	1, 6, 10, 11, 15, 16	5, 7, 8, 13, 14		141
<i>Dactylosternum cacti</i> (LeConte)	1, 10, 11, 15, 16	5, 13		39
MYCETOPHAGIDAE				
<i>Litargus balteatus</i> LeConte	16	13	4, 12	19
NITIDULIDAE				
<i>Carpophilus discoideus</i> LeConte	1			2
<i>Carpophilus lugubris</i> Murray	16			2
STAPHYLINIDAE				
<i>Aleochara (Maseochara) depressa</i> (Sharp)	1, 11, 16	5		7
<i>Aleochara (Maseochara) valida</i> LeConte	6, 10, 11, 16	3, 5, 7		52
<i>Belonuchus ephippiatus</i> (Say)	1, 6, 10, 11, 15, 16	3, 5, 7, 8, 13	4	72
<i>Carpelimus</i> sp.	11			3
<i>Deroderus</i> sp.	1, 6, 10, 11, 16	3, 7		18
<i>Diestota</i> sp. 1	1, 10, 11, 16	5, 8, 13		57
<i>Diestota</i> sp. 2	11	5		2
<i>Placusa vaga</i> Casey	1			3
<i>Platystethus spiculus</i> Erichson	6			2
<i>Tachinomorphus grandis</i> (Solsky)	11	5		2
<i>Tachinomorphus grossulus</i> (LeConte)	10, 11, 16			5
TENEBRIONIDAE				
<i>Araeoschizus</i> sp.			9	1
<i>Armalia</i> sp.		8		1
<i>Cynaesus angustus</i> (LeConte)	1			1
<i>Eleodes</i> spp.		3	4	3
<i>Hymenorus</i> sp.	1			1
<i>Opatrini</i> gen. sp.	1	9		2
<i>Triorophus</i> sp.			12	1
ZOPHERIDAE				
<i>Bitoma gracilis</i> Sharp	1			1
Total	28 spp.	21 spp.	7 spp.	976 specimens

Coleoptera found in rotting cacti and the only account of beetles collected from multiple rotting *F. wislizeni*.

The majority of species, 18, are predators in the families Histeridae and Staphylinidae that generally feed on dipteran eggs, larvae, and pupae (see Species Accounts below). Predacious Coleoptera are probably not associated with the initial invasion

of a dead cactus, but arrive after Diptera or other groups have become established. They probably abandon the cactus when suitable prey is no longer available and desiccation makes the microhabitat less hospitable. This is reflected in our data where histerid numbers increase from three (Dry) to 45 (Moist) to 495 (Wet) and staphylinids from one (Dry) to 46 (Moist) to 176 (Wet). In individual

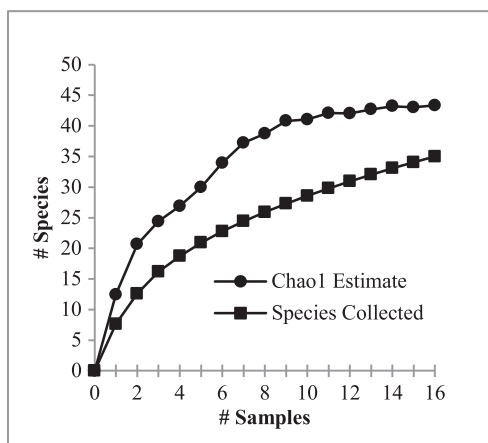


Fig. 4. Species richness and Chao1 richness estimator curves.

cacti, the Dry condition of the cactus is the final stage of succession and most of the dipteran larvae would have matured and left, along with their predators.

Seven species in the families Curculionidae, Hydrophilidae, Mycetophagidae, Nitidulidae, and Zopheridae are saprophagous (detritivores and/or fungivores). These species probably compete with other saprophages, especially Diptera, and may be in the first wave of invaders after a cactus dies (e.g., *Carpophilus* Stephens), or develop in the drier remains after others have left (e.g., *Apotrepus densicollis* Casey). Early invaders may have been

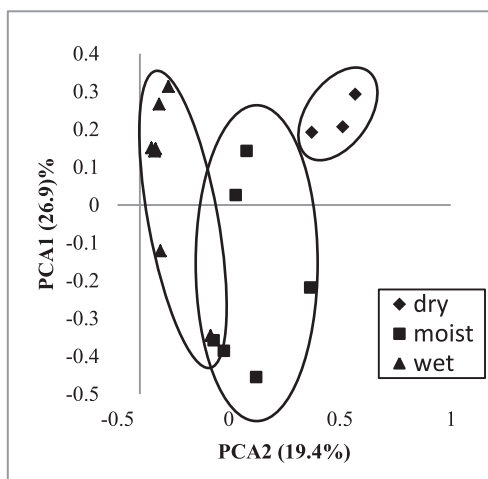


Fig. 5. Principal coordinates analysis based on moisture content. Dry is distinctly grouped, while Moist and Wet have minimal overlap.

poorly represented or absent in our collections due to the advanced stage of decay.

Other species, especially Tenebrionidae, may be generalist predators, scavengers, and detritivores, or may have been seeking harborage. *Cynaesus angustus* (LeConte) originated in the Sonoran Desert as a generalist detritivore in decomposing succulents but has recently spread across the USA and southern Canada as a minor pest in stored cereal products and agricultural waste (Dunkel *et al.* 1982). However, more specimens and more detailed life history observations of the other species will be needed before it can be determined if these species are typical or incidental in rotting cacti.

Comparison of necrophilic faunas between cacti and non-cactus succulents (Appendix A), even at the most basic level, such as differences in species richness, is currently impossible due to our overwhelming ignorance. Presumably, early invading detritivores would be more influenced by plant species than later invaders and may exhibit greater specialization. Conversely, secondary invaders, such as predators, may be generalists with regard to substrate and more influenced by prey species than by plant species.

A limited view of succession within rotting *F. wislizeni* is available from this study. The positive correlation between cactus size and moisture level implies that the cacti were killed at approximately the same time—smaller cacti dried faster than larger ones. At the time of discovery, the first stages of decomposition had passed, but middle stages transitioning to the last stage were present due to variation in size of cacti at time of death. Informal observations of the data as well as statistical evaluations (PCoA and *adonis*) show that the community composition in Dry, Moist, and Wet cacti were significantly distinct from each other. This indicates that there is a succession of Coleoptera in decomposing *F. wislizeni*.

However, accuracy and precision of the description of succession was probably confounded by the complexity of decomposition. Generally, a cactus tended to be drier at the top and wetter at the bottom. Cacti designated as Wet were saturated in at least the lower third, but the upper portions were often qualitatively indistinguishable from the lower portion of Moist cacti. Therefore, any given cactus represented a spectrum of decay conditions, and possibly multiple successional stages, but only the average of these stages within a cactus was available for statistical evaluation. An increase in the accuracy and precision of the collection data obtained, such as recording from which portion of the cactus each specimen was collected, would have aided in the statistical

evaluation of faunal succession and should be considered in future studies of cactus decay.

A distinct, measurable faunal succession takes place in decaying *F. wislizeni*, and moisture content can be used as a proxy to designate stages in later decay. However, succession, especially early, is probably influenced by other factors such as presence of secondary metabolites, nutrient content, fungi, appropriate prey species, and cause and season of death. While mass die-offs of mature cacti are relatively rare events, this case history indicates that mass die-offs may be located by surveying areas that experienced extreme cold and that rotting cacti are persistent for many months after death. Researchers should be vigilant for such events because they present great opportunities to study the complex nature of cactus decay.

SPECIES ACCOUNTS

The insects associated with dead and necrotic cacti in the deserts in southwestern USA are a relatively small and predictable group. Despite being well-known to researchers on an informal basis, they are poorly represented in the literature individually and as a cohort. The following summary is provided with the intent that it will serve as a starting point for the generation and accumulation of additional published natural history or ecological information on arthropods associated with cactus decay. Basic biological information is provided for select taxa and important resources with descriptions, keys, distributional data, and biological/life history data are referenced. In the following, "key to genus" refers to a reference that provides a key with which one can determine the identity of the particular genus being commented on.

CURCULIONIDAE

Cossoninae

Apotrepus densicollis Casey (Fig. 6)

Comments. Monotypic genus.

Range. Arizona (Casey 1892; Fall and Cockerell 1907; Hubbard 1899); Baja California, Mexico (Blackwelder 1957).

Habitat. Adults in dry "crusts" of dead saguaro (Hubbard 1899); incidental on *Opuntia* Mill. (Hunter *et al.* 1912); immatures from *Cereus* Mill. (Anderson 1952); adults and immatures from dried stalk of *Dasyllirion wheeleri* (Hubbard 1901).

Biology. Unknown beyond habitat.

Additional References. Anderson 1952 (immature description); Anderson 2002 (key to genus/species); Blackwelder 1957; Casey 1892; Horn 1894 (as *Apotrepes densicollis*); Kissinger 1964 (key to genus/species); Leng 1920.

HISTERIDAE

Dendrophilinae

Carcinops Marseul

This genus is in need of revision. Mazur (2011) listed 50 valid species in the genus, 16 from the United States and/or Mexico. At least seven undescribed species are known from the deserts in southwestern USA (see below). Hunter *et al.* (1912) listed *Carcinops* sp. as a scavenger in cactus. Pfeiler and Markow (2011) offered a preliminary analysis of the phylogeography of *Carcinops* in the Sonoran Desert. Information on life history and rearing of *Carcinops pumilio* Erichson, a predator of fly eggs and larvae, can be found in Achiano and Gilioe (2005, 2006) and Kaufman *et al.* (2001) (and references therein). Key to genus: Hinton 1945a (species associated with stored products); Hatch 1962; Wenzel 1962 (United States); Kovarik and Caterino 2001 (North America north of Mexico); Mazur 2001 (Mexico); Bousquet and Laplante 2006 (Canada).

A review of cactophilic *Carcinops* of the Sonoran Desert was conducted and six additional species were identified but not formally described (Swanson 2008). One of the species we collected matches Swanson's (2008) manuscript species "rugula" and is referred to as *Carcinops* n. sp. (rugula) in this paper. An additional undescribed species, *Carcinops* n. sp. 1, distinct from all previous formally and informally described species, was also collected during our research.

Carcinops consors (LeConte) (Fig. 7)

Comments. See *Carcinops* above.

Range. Arizona, California, Texas, Mexico, Guatemala, Costa Rica (Mazur 2011).

Habitat. Collected from the moist part of a rotten cavity in saguaro (Hubbard 1899), rotten masses of *Opuntia* (Lewis 1888), and decaying vegetable matter (Fall 1901). Swanson (2008) reported specimens from *Ferocactus* sp., *Pachycereus pringlei* (S. Watson) Britton & Rose, *Pilosocereus alensis* (F.A.C. Weber) Byles & G.D. Rowley, and *Stenocereus montanus* (Britton & Rose) Buxb. (all Cactaceae).

Biology. adults and immatures feed on eggs and larvae of Diptera.

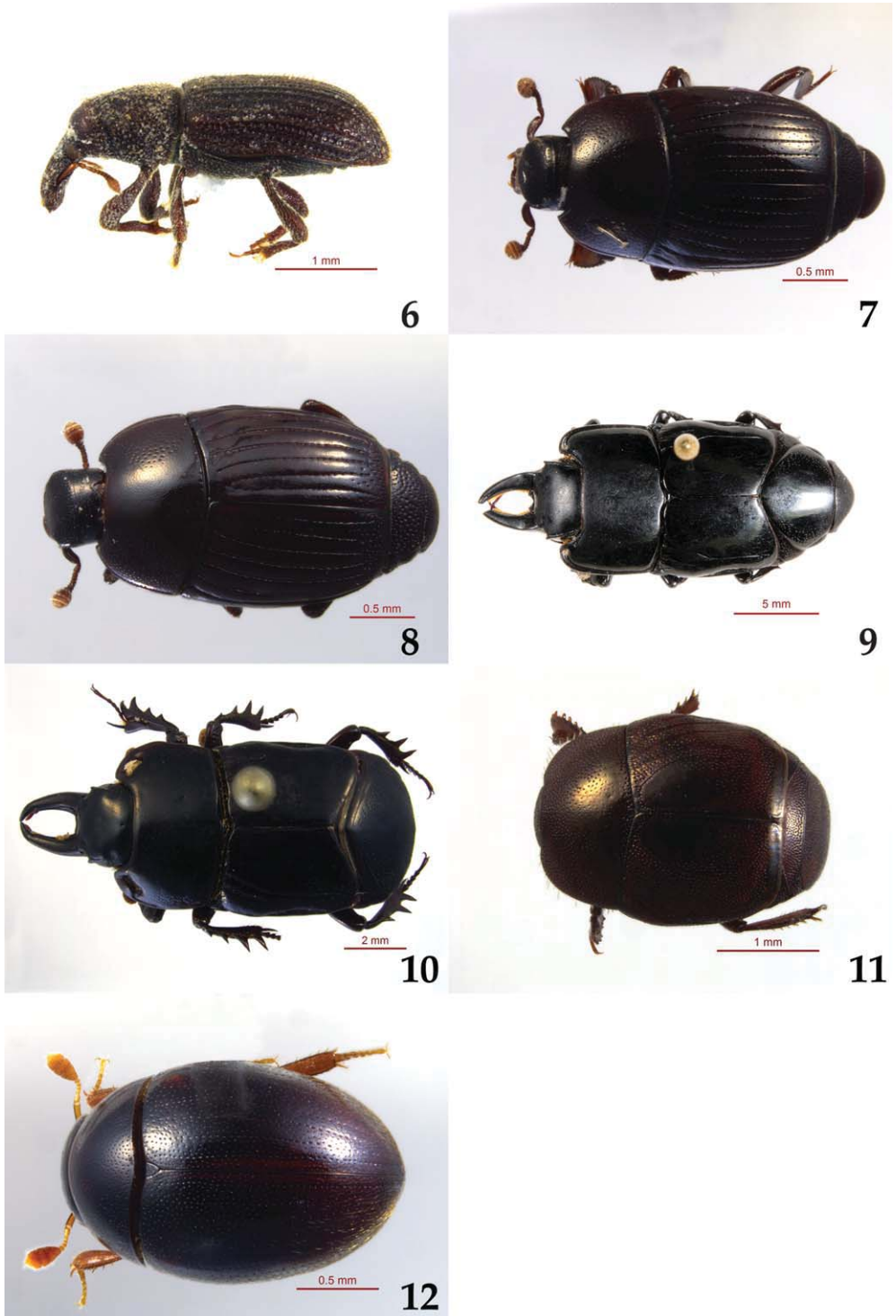
Additional References. Blackwelder 1939b, 1957; Fall and Cockerell 1907; Horn 1873, 1894 (as *Paromalus consors*); Leng 1920; Lewis 1905; Moore 1937; Woodworth 1913.

Carcinops opuntiae (LeConte) (Fig. 8)

Comments. See *Carcinops* above.

Range. Arizona, California, Texas (Mazur 2011).

Habitat. Collected from rotting *Opuntia* (Fall 1901; Horn 1873; LeConte 1858a, as *Paromalus*



Figs. 6–12. Habitus images of Coleoptera in decayed barrel cacti: **6)** *Apotrepus densicollis*; **7)** *Carcinops consors*; **8)** *Carcinops opuntiae*; **9)** *Hololepta yucateca*; **10)** *Iliotona cacti*; **11)** *Xerosaprinus martini*; **12)** *Agna capillata*.

opuntiae) and from the moist part of a rotten cavity in saguaro (Hubbard 1899). Swanson (2008) reported specimens from *Pachycereus pringlei*, *Pachycereus schottii* (Engelm.) D.R. Hunt (Cactaceae), and *Stenocereus montanus*.

Biology. Adults and immatures feed on eggs and larvae of Diptera.

Additional References. Blackwelder 1939b; Fall and Cockerell 1907; Horn 1873 (key to species, as *Paromalus opuntiae*); Leng 1920; Lewis 1905.

Carcinops n. sp. (rugula)

Comments. See above.

Range. Arizona and California, and Sonora, Mexico (Swanson 2008).

Habitat. *Opuntia*, *Ferocactus*, saguaro, *Pachycereus schottii*, and *Stenocereus alamosensis* (J. M. Coult.) A. C. Gibson & K. E. Horak (Cactaceae) (Swanson 2008).

Biology. Adults and immatures feed on eggs and larvae of Diptera.

Histerinae

Hololepta yucateca (Marseul) (Fig. 9)

Comments. *Hololepta* Paykull contains 10 species in North America north of Mexico.

Range. Arizona, southern California, New Mexico, Texas, Mexico (Carnochan 1917; Leng 1920; Lewis 1888).

Habitat. Decaying fruit of *Cucurbita* L. (Cucurbitaceae), *Ferocactus viridescens* (Torr. & A. Gray) Britton & Rose (as *Echinocactus viridescens*), leaves and stalks of *Opuntia* sp. (as *Opuntia occidentalis*), decaying flower stalk of *Hesperoyucca whipplei* (Torr.) Baker (as *Yucca whipplei*) (Agavaceae) (Fall 1901); necrotic *Pachycereus schottii* (Castrezana and Markow 2001, as *Lophocereus schottii*); decomposing saguaro (Griffith 1900); saguaro and *Opuntia engelmannii* Salm-Dyck ex Engelm. (Hubbard 1899); decaying trunks of *Yucca treculeana* Carrière (Schaeffer 1907); "stem of decaying maguey" (Wickham 1898).

Biology. Adults and immatures are predatory on fly larvae in rotting vegetation (Carnochan 1917; Kovarik and Caterino 2001; Mazur 2001). Carnochan (1917) described the immature, pupa, and development of *Hololepta aequalis* Say. Phylogenetic and phylogeographic studies of some Sonoran desert *Hololepta* have been performed (Pfeiler *et al.* 2010; Pfeiler and Markow 2011).

Additional References. Blackwelder 1957; Bousquet and Laplante 2006 (key to genus, Canada); Carnochan 1917 (key to species); Crotch 1873; Fall and Cockerell 1907; Griffith 1900; Henshaw 1885; Horn 1894; Hunter *et al.* 1912; Kovarik and Caterino 2001 (key to genus, North America north of Mexico); Lewis 1888 (as *Lioderma yucateca*); Mazur 2001 (key to genus,

Mexico); Moore 1937; Schaeffer 1907 (key to species); Wenzel 1962; Woodworth 1913.

Iliotona cacti (LeConte) (Fig. 10)

Comments. *Iliotona* Carnochan contains one species in North America north of Mexico.

Range. Arizona, southern California, New Mexico, Texas, Mexico (Hunter *et al.* 1912, as *Hololepta cacti*; Leng 1920; Blackwelder 1957).

Habitat. In decaying cacti and beneath bark of decaying willow (Fall 1901, as *Hololepta cacti*; Moore 1937); in decomposing *Cereus* sp. (Horn 1873, as *Hololepta cacti*); in decomposing saguaro (Hubbard 1899, as *Hololepta cacti*).

Biology. Phylogenetic and phylogeographic studies of some Sonoran desert *Iliotona* have been performed (Pfeiler *et al.* 2010; Pfeiler and Markow 2011).

Additional References. Carnochan 1917 (key to species); Crotch 1873 (as *Hololepta cacti*); Fall and Cockerell 1907 (as *Hololepta cacti*); Henshaw 1885 (as *Hololepta cacti*); Horn 1873 (key to species, as *Hololepta cacti*); LeConte 1858a (as *Hololepta cacti*); Wenzel 1962; Woodworth 1913 (as *Hololepta cacti*).

Saprininae

Xerosaprinus martini (Fall) (Fig. 11)

Comments. *Xerosaprinus* Wenzel is divided into four subgenera (Wenzel 1962) and contains about 25 species (Bousquet and Laplante 2006) with 18 in North America north of Mexico (Kovarik and Caterino 2001). It is in need of revision.

Range. Arizona, California (Fall 1917, as *Saprinus martini*).

Habitat. Rotting *Ferocactus wislizeni* (this study).

Biology. Unknown. Other members of the genus have been reported from dung and carrion (Bousquet and Laplante 2006).

Additional References. Bousquet and Laplante 2006 (key to genus, Canada); Kovarik and Caterino 2001 (key to genus, North America north of Mexico); Leng 1920; Mazur 2001 (key to genus, Mexico); Wenzel 1962 (key to genus and subgenus, United States).

HYDROPHILIDAE

Sphaeridiinae

Agna capillata (LeConte) (Fig. 12)

Comments. *Agna* Smetana contains two species, only *A. capillata* is reported from the USA.

Range. Arizona, California, Texas (Smetana 1978).

Habitat. In decomposing saguaro (Hubbard 1899, as *Pelosoma capillosum*); scavenger in cactus (Hunter *et al.* 1912, as *Pelosoma capillosum*); in decaying agave (Smetana 1978).

Biology. Comes to light (Smetana 1978), otherwise unknown, immatures of *Agna* unknown.

Additional References. Fall and Cockerell 1907 (as *Pelosoma capillatum*); Griffith 1900 (as *Cercyon capillatum*); Hansen 1991 (key to genus), 1999; Henshaw 1885 (as *Cercyon capillatum*); Horn 1890 (as *Pelosoma capillatum*); LeConte 1855, 1858a (as *Cercyon capillatum*); Leech 1948 (describes but does not formally name a species "*Pelosoma* sp. near *capillatum*"), Ales Smetana (personal communication) did not review those specimens in his revision of the group (Smetana 1978), they may now be lost); Leng 1920 (as *Pelosoma capillatum*); Moore 1937 (as *Pelosoma capillatum*); Van Tassell 2001 (key to genus/species).

Dactylosternum cacti (LeConte) (Fig. 13)

Comments. *Dactylosternum* Wollaston has a worldwide distribution with 62 recognized species (Hansen 1999), three in North America north of Mexico (Smetana 1978).

Range. Arizona, southern California (Horn 1890; Smetana 1978).

Habitat. Decomposing *Cereus* sp. (Horn 1890; Fall 1901); moist part of dead saguaro (Hubbard 1899); putrid *Opuntia* (LeConte 1855, as *Cyclonotum cacti*); scavenger in cactus (Hunter *et al.* 1912); rotting *Pachycereus* sp., rotting cordon (Leech 1948).

Biology. Unknown. Costa *et al.* (1988) described the immature of *Dactylosternum subrotundum* (F.) and reported adults and larvae from well-rotted and wet fallen logs.

Additional References. Blackwelder 1931 (key to genus and species for Pacific Coast); Crotch 1873 (as *Cyclonotum cacti*); Fall and Cockerell 1907; Griffith 1900; Hansen 1991 (key to genus), 1999; Horn 1890 (key to species); LeConte 1858a (as *Cyclonotum cacti*); Leech 1948 (key to genus); Leng 1920; Moore 1937; Schwarz 1878 (key to species, as *Cyclonotum cacti*); Smetana 1978 (key to genus and species); Van Tassell 2001 (key to genus); Woodworth 1913.

MYCETOPHAGIDAE

Litargus balteatus LeConte (Fig. 14)

Comments. *Litargus* Erichson contains six species in the Nearctic region (Parsons 1975).

Range. Widespread throughout the USA and Canada (Young 2002); Mexico and Central America (Blackwelder 1957).

Habitat. Common in decomposing vegetable matter (Fall 1901); in a fungus (Fall and Cockerell 1907); adults collected from *Meripilus giganteus* Karst. and *Perenniporia fraxinea* (Bull.) Ryvarden (as *Perreniporia fraxinea*), *Litargus* spp. were commonly found in the summer months on dry

sporocarps of Agaricales in Arkansas (Leschen 1990); fungus growing on a dead holly log, Sherwood Forest, England (Tomlin and Joy 1908, as *Litargus coloratus*); feeding on *Ganoderma tsugae* Murrill (Ganodermataceae) (as *Polyporus tsugae*) (Weiss and West 1921).

Biology. *Litargus balteatus* is a cosmopolitan, synanthropic, stored product pest, commonly found in association with moldy produce or grains (Hinton 1945b; Bousquet 1990; Lawrence and Leschen 2010). Non-human-associated biology is poorly known, except for habitat associations above.

Additional References. Böving and Craighead 1930 (figure of immature, as *Alitargus balteatus*); Fall 1901; Griffith 1900; Henshaw 1885; Horn 1894; LeConte 1858a; Leng 1920; Moore 1937; Parsons 1975 (key to Nearctic species); Sharp 1905c; Woodworth 1913.

NITIDULIDAE

Carpophilinae

Carpophilus Stephens

The genus contains nearly 200 species worldwide (Williams *et al.* 1983) and is in need of revision. The Nearctic species were last treated by Parsons (1943, who stated "No one realizes more clearly than the writer how imperfect the key is."), with synonymies and additions by Connell (1984). Thirty-four species are recognized from the Nearctic region (Poole and Gentili 1996). Williams *et al.* (1983) provided a bibliography of literature on *Carpophilus*. Hinton (1945b) offered information on Nitidulidae associated with stored products (including some *Carpophilus*) with biological information and keys and figures to adults, larvae, and pupae. Jelínek *et al.* (2010) provided an overview of the distribution, ecology, morphology, and phylogeny of Nitidulidae, including reference to *Carpophilus*.

Carpophilus are found at flowers, at sap under bark, in decaying or dried fruit and in fungi (Parsons 1943). Adults and immatures are often found in the same area. Like most members of their family, *Carpophilus* feed on macro- and microscopic fungi that occur on decaying organic and vegetable matter (Jelínek *et al.* 2010).

Carpophilus discoideus LeConte (Fig. 15)

Comments. See *Carpophilus* above and Williams *et al.* (1983) for early papers that mention the species.

Range. Throughout the contiguous USA (Parsons 1943).

Habitat. Poorly known except in relation to human endeavors; decaying fruit in orchards (Fall 1901).

Biology. Poorly known.



Figs. 13–19. Habitus images of Coleoptera in decayed barrel cacti. **13)** *Dactylosternum cacti*; **14)** *Litargus balteatus*; **15)** *Carpophilus discoideus*; **16)** *Carpophilus lugubris*; **17)** *Aleochara (Maseochara) depressa*; **18)** *Aleochara (Maseochara) valida*; **19)** *Diestota* sp.

Additional References. Fall 1901; Fall and Cockerell 1907; Griffith 1900; Horn 1879; LeConte 1858a, b; Leng 1920; Moore 1937; Murray 1864 (key to species); Putnam 1876; Woodworth 1913.

Carpophilus lugubris Murray (Fig. 16)

Comments. See *Carpophilus* above.

Range. Temperate regions of Western Hemisphere, Brazil and Central America to Mexico and throughout the contiguous USA (Parsons 1943; Connell 1991).

Habitat. Poorly known except in relation to human endeavors (see Williams *et al.* 1983).

Biology. Associated with the spread of and emergent from trees killed by oak wilt (Dorsey and Leach 1956); associated with sweet corn (Williams *et al.* 1983); Harrison (1962) gave description of infestation of cornfields with life history data; attracted to exudate of *Verbesina encelioides* (Cav.) Benth. & Hook. f. ex A. Gray (Asteraceae) (Linsley and Cazier 1963).

Additional References. Blackwelder 1957; Connell 1956, 1977, 1991 (key to stored food pest species); Crotch 1873; Parsons 1943 (key to species); Murray 1864 (key to species); Sharp 1905b.

STAPHYLINIDAE

Aleocharinae

Aleochara (Maseochara) depressa (Sharp) (Fig. 17)

Comments. The genus is relatively well known in North America (Klimaszewski 1984). Detailed life history observations for the genus were made by Wadsworth (1915), life history and host records were reviewed and updated by Maus *et al.* (1998).

Range. Arizona, southern California, western Texas, Mexico, Guatemala (Klimaszewski 1984).

Habitat. Collected from decaying saguaro (Hubbard 1899, as *Maseochara puberula*); collected from decaying cacti and dead sotol (Klimaszewski 1984).

Biology. Members of subgenus *Maseochara* Sharp are typically found in decaying cacti and occasionally carrion (Klimaszewski 1984), adults are predators of eggs and larvae of Diptera, typically Syrphidae, and larvae are ectoparasitic on fly pupae within the puparium; collected March to August (Klimaszewski 1984, and references therein). Larva illustrated as *Maseochara* sp. in Böving and Craighead (1930).

Additional References. Blackwelder 1957; Casey 1893 (as *Maseochara puberula*), 1906 (as *Maseochara basalis* Casey), 1911 (as *Maseochara musta* Casey); Fall 1901 (as *Maseochara puberula* Casey); Fall and Cockerell 1907 (as *Maseochara puberula* Casey); Hunter *et al.* 1912 (as *Maseochara puberula*); Klimaszewski 1984 (key to species); Moore 1937 (as *Maseochara puberula*); Navarrete-

Heredia *et al.* 2002 (key to genus, Mexico); Sharp 1887 (as *Maseochara depressa*); Woodworth 1913 (as *Maseochara basalis* Casey and *Maseochara puberula* Casey).

Aleochara (Maseochara) valida LeConte (Fig. 18)

Comments. See comments under *A. depressa* above.

Range. Arizona, southern California, and Mexico (Klimaszewski 1984).

Habitat. Reared from fly puparium from *Opuntia engelmannii* (Coquillett 1891); decaying cacti at altitudes up to 1,371 m (Klimaszewski 1984); under decomposing *Opuntia* stems (LeConte 1858a).

Biology. See *A. depressa* above and Coquillett (1891) for description of life history; adults collected February to September and December from decaying cacti; host species *Copestylum marginatum* (Say), some sawflies (Klimaszewski 1984).

Additional References. Blackwelder 1957 (as *Maseochara robusta*); Bland 1865; Casey 1884b (as *Tithanis valida* (LeConte)), 1885 (as *Maseochara californica* Casey), 1906 (as *Maseochara ponderosa* Casey and *Maseochara ruficauda* Casey); Fall 1901 (as *Maseochara valida*); Henshaw 1885 (as *Maseochara valida*); Horn 1894 (as *Maseochara valida*); Hunter *et al.* 1912 (as *Maseochara valida*); Klimaszewski 1984 (key to species, figure); LeConte 1858a; Moore 1937 (as *Maseochara valida*); Navarrete-Heredia *et al.* 2002 (key to genus, Mexico); Riley 1893; Woodworth 1913.

Diestota Mulsant and Rey (Fig. 19)

Comments. *Diestota* is in need of revision. About 50 species are known worldwide, with the highest diversity in the Neotropical region (Navarrete-Heredia *et al.* 2002) and Hawaii (Nishida 2002). Members of this genus are generally found in moist, decaying vegetable matter. Numerous specimens of *Diestota rufipennis* (Casey) in the Snow Entomological Museum (SEMC) were collected in Arizona during 2003 from rotting saguaro cactus (Zachary Falin, personal communication). Pace (1986) provided a key to subgenera. Scattered records and numerous generic and specific synonymies make this a difficult group to assess. The status of the named species known from America north of Mexico is summarized below.

Diestota ambiguum (Notman)

described as *Elachistarthron ambiguum*
Notman 1920: 715

= *Elachistarthron anomala* Notman 1920
(*sensu* Moore and Legner 1975)

Range. Florida (Notman 1920, Peck and Thomas 1998)

Diestota angustula (Casey)

described as *Amenusa angustula* Casey 1906: 349

= *Amenusa spissula* Casey 1911: 197

Range. California (Casey 1906, 1911)

Diestota funebris Sharp 1887: 252

Range. Guanajuato, Mexico; USA (Navarrete-Heredia *et al.* 2002)

Diestota flavipennis innotabilis (Notman)

Homalota flavipennis Erichson (1840: 118) was transferred to *Diestota* by Pace (1986: 421), then *Orthodiatelus innotabilis* Notman (1920: 716) was made a subspecies of *H. flavipennis* by Pace (1986: 422)

Range. Florida (Notman 1920, as *Orthodiatelus innotabilis*; Peck and Thomas 1998, as *Diestota innotabilis*), St. John Island, U.S. Virgin Islands (Erichson 1840, as *Homalota flavipennis*)

Diestota oblonga (Casey)

described as *Pectusa oblonga* Casey 1911: 198

Range. Mississippi (Casey 1911)

Diestota rufipennis (Casey)

described as *Apheloglossa rufipennis* Casey 1893: 349

Range. Arizona (Casey 1893)

Paederinae***Deroderus*** Sharp (Fig. 20)

Comments. The genus is in need of revision. Frania (1986b) provided a review of the complicated history of the genus and several species of *Deroderus*. The only species reported in North America north of Mexico, *Deroderus tabacinus* (Casey), was originally described in the genus *Lithocharis* Casey (1884a), moved to *Polymedon* Casey (1905), and then moved to *Lypomedon* Blackwelder (1952) before being placed in *Deroderus* (Frانيا 1986b). Five named species and about 10 undescribed species are known (Frانيا 1986b).

Range. Arizona, Mexico, Guatemala, Costa Rica, and Panama (Frانيا 1986b).

Habitat. Moist pulp of saguaro (Hubbard 1899, as *Lithocharis tabacina* Casey); tropical and subtropical evergreen forests, under loose bark, xeric uplands on rotting cacti (Frانيا 1986b; Newton *et al.* 2001).

Biology. Unknown; immature described by Frانيا (1986a).

Additional References. Blackwelder 1939a (as *Polymedon tabacinus* Casey), 1939b, 1952 (*Deroderus* and as *Lypomedon* Blackwelder), 1957; Casey 1884a (as *Lithocharis tabacina*), 1905 (as *Polymedon tabacinum*); Leng 1920 (as *Polymedon tabacinum* Casey); Navarrete-Heredia *et al.* 2002 (key to genus, Mexico); Newton *et al.* 2001 (key to genus); Sharp 1887.

Staphylininae***Belonuchus ephippiatus*** (Say) (Fig. 21)

Comments. A quandary exists concerning whether *B. ephippiatus* and *Belonuchus erythropterus* Solsky represent separate species (Smetana 1995). Both species are sympatric in southern Texas, and both are associated with rotting cacti. Nine species of *Belonuchus* Nordmann are known from America north of Mexico and were reviewed by Smetana (1995). The genus is pantropical with greatest diversity in the Neotropical region. It contains about 200 species (Newton *et al.* 2001) and is in need of revision (Smetana 1995).

Range. Southern California, Arizona, New Mexico, and Texas (Smetana 1995).

Habitat. Typically occurs in decaying large *Cereus* and *Opuntia*, occasionally in *Agave* (Smetana 1995).

Biology. Unknown; larvae and pupae of *Belonuchus formosus* Gravenhorst described by Mank (1923); members of this genus are predacious and are generally found in decaying organic material (Smetana 1995).

Additional References. Blackwelder 1957; Crotch 1873; Fall 1901 (under rotting squash and in decaying yucca); Fall and Cockerell 1907; Griffith 1900; Henshaw 1885; Horn 1894; Hubbard 1899 (collected from decaying *Carnegiea gigantea*); LeConte 1858a; Leng 1920; Moore 1937 (under dead *Opuntia* leaves); Navarrete-Heredia *et al.* 2002 (key to genus, Mexico); Wickham 1898 (in decaying yuccas).

Additional References for *B. erythropterus*. Blackwelder 1957; Leng 1920; Navarrete-Heredia *et al.* 2002 (key to genus, Mexico); Sharp 1887.

Tachyporinae***Tachinomorphus grandis*** (Solsky) (Fig. 22)

Comments. The genus contains 19 species scattered around the world, five in North and Central America. See Campbell (1973) for a recent revision and key to species.

Range. Arizona and southern California south to Costa Rica (Campbell 1973).

Habitat. Collected from decaying agave and rotting banana pseudostems (*Musa* sp.) (Campbell 1973).

Biology. Unknown other than habitat, collected December through August (Campbell 1973).

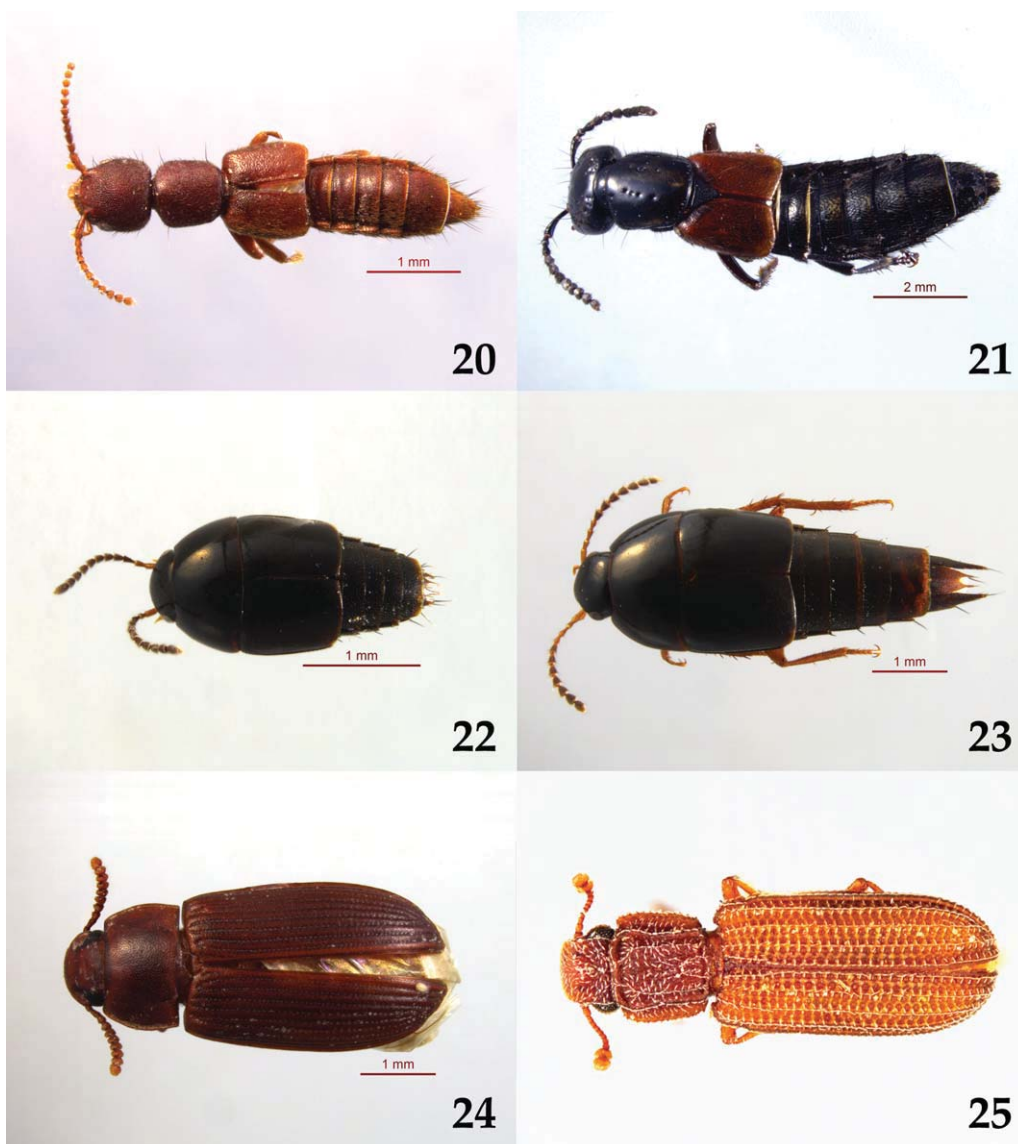
Additional References. Blackwelder 1957; Sharp 1887 (as *Tachinoderus grandis*).

Tachinomorphus grossulus (LeConte) (Fig. 23)

Comments. See previous account.

Range. Arizona and southern California, south to southern Baja California and Hidalgo, Mexico (Campbell 1973).

Habitat. Collected from rotting saguaro and *Agave* spp. (Campbell 1973); "Occurs



Figs. 20–25. Habitus images of Coleoptera in decayed barrel cacti. **20)** *Deroderus* sp.; **21)** *Belonuchus ephippiatus*; **22)** *Tachinomorphus grandis*; **23)** *Tachinomorphus grossulus*; **24)** *Cynaenus angustus*; **25)** *Bitoma gracilis*, photograph by Nathan Lord.

not rarely in the decaying stems of various Cactaceae in Arizona.” (Horn 1877); collected from the moist part of a rotten cavity in saguaro (Hubbard 1899, as *Physetoporus grossulus*); scavenger in cactus (Hunter *et al.* 1912, as *Physetoporus grossulus*).

Biology. Unknown other than habitat; collected December through August, the majority taken December through April (Campbell 1973).

Additional References. Blackwelder 1952 (as *Physetoporus grossulus*); Brodie and White 1883 (as *Physetoporus grossulus*, erroneously reported from Canada); Crotch 1873 (as *Coproporus grossulus* LeConte and *Physetophorus grossulus* (LeConte)); Griffith 1900; Henshaw 1885 (as *Physetoporus grossulus*); Horn 1877 (as *Physetoporus grossulus*); Leng 1920 (as *Physetophorus grossulus*); Moore 1937

(as *Physetophorus grossulus*); Sharp 1887 (as *Tachinoderus remotus* Sharp).

TENEBRIONIDAE

Diaperinae

Cynaesus angustus (LeConte) (Fig. 24)

Comments. *Cynaesus angustus* is a North American precinctive species that has recently expanded its range and become a minor pest of stored cereal products. Dunkel *et al.* (1982) provided a well-documented description of its recent expansion and synanthropic proclivities. The genus contains two species (Horn 1870).

Range. Originated in the Sonoran and Chihuahuan deserts of southwestern USA and Mexico; recently (1970s) distributed throughout the USA and southern Canada (Dunkel *et al.* 1982).

Habitat. Moist part of a rotten cavity in saguaro (Hubbard 1899); associated with decomposing flowering agave, one report from barrel cactus; may have been associated with corn as early as 800 C.E.; in recent times predominantly found in corn, also in wheat, soybeans, and other crops; see Dunkel *et al.* (1982) for a list of natural and synanthropic habitats.

Biology. Description of the larva and pupa as well as life history information in relation to development in corn and other grains were obtained by Krall and Decker (1946): development from egg to adult took 30–60 days; adults and larvae will feed directly on corn and other grains; first oviposition took place 5–7 days after eclosion; adults are active and strong fliers at night; no evidence of diapause; some adults may have lived as long as six months. Sinha (1971) reports *C. angustus* consumption of and reproduction within numerous fungal species. White and Sinha (1987) studied the energy budget of *C. angustus* reared on split corn kernels. Morrison and Dunkel (1983) described an infestation of cotton gin waste by *C. angustus* in Texas that drove people from their homes and sent two children to the hospital.

Additional References. Blackwelder 1957; Blaisdell 1943; Champion 1893 (as *Cynaesus opacus* Champion); Crotch 1873; Fall 1901; Horn 1894; Hunter *et al.* 1912 (incidentally associated with cactus); LeConte 1851 (as *Platydemus angustum* LeConte); Leng 1920; Woodworth 1913.

ZOPHERIDAE

Colydiinae

Bitoma gracilis Sharp (Fig. 25)

Comments. *Bitoma* Herbst is a large, world-wide genus in need of revision. Fourteen species occur in North America north of Mexico, see Stephan (1989) for a key to North American species.

Range. Arizona, California, New Mexico, Texas, Mexico, Guatemala (Leng 1920; Blackwelder 1957; Stephan 1989).

Habitat. Adults “not rare” in dry debris of dead saguaro (*Carnegiea gigantea*) (Hubbard 1899, as *Ditoma gracilis*); in *Dasyilirion wheeleri* (Hubbard 1901, as *Ditoma gracilis*); incidentally associated with cactus (Hunter *et al.* 1912, as *Ditoma gracilis*); occurs in lower deserts, taken from under bark of dead palo verde, leaf-axils of dying sotol, agave, and yucca, and nest piles of pack rats (Stephan 1989).

Biology. Poorly known; probably fungivorous; adults collected year round; taken at lights (Stephan 1989).

Additional References. Blackwelder 1957; Casey 1897 (as *Bitoma suffusa* Casey); Fall and Cockerell 1907 (as *Ditoma gracilis*); Leng 1920; Moore 1937 (as *Bitoma suffusa*); Sharp 1905a; Schaeffer 1907 (as *Bitoma prosopis* Schaeffer and *Bitoma vittata* Schaeffer); Stephan 1989 (key to species); Wickham 1898 (under bark, as *Ditoma suffusa*).

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APPENDIX A

North American Coleoptera reported from cacti and succulent necrosis. Only taxa from community-level surveys are included. Nomenclature used in prior surveys that differs from current nomenclature is copied verbatim from the original source and inserted in columns below those sources.

Species	<i>Carnegiea gigantea</i> (Hubbard 1899; Schwarz 1899a, b)	<i>Ferocactus</i> <i>wislizeni</i> (this study)	<i>Ferocactus</i> <i>wislizeni</i> (Dury 1916)	Columnar cacti (Castrezana and Markow 2001)	<i>Dasyllirion</i> <i>wheeleri</i> (Hubbard 1901)
BOTHRIDERIDAE					
1 <i>Bothrideres cactophagi</i> Schwarz	present				
BUPRESTIDAE					
2 <i>Acmaeodera cazieri</i> Knull		present			
CERAMBYCIDAE					
3 <i>Moneilema gigas</i> LeConte	as <i>Moneilema</i> <i>giganteum</i> LeConte				
CLERIDAE					
4 <i>Cymatodera</i> sp.		present			
CRYPTOPHAGIDAE					
5 <i>Ephistemus cactophilus</i> Schwarz	present				
CURCULIONIDAE					
6 <i>Apotrepus densicollis</i> Casey	present	present			present
7 <i>Cactopinus hubbardi</i> Schwarz	present				
8 <i>Cossonus hubbardi</i> Schwarz	present				
9 <i>Metamasius spinolae</i> (Gyllenhal)	as <i>Cactophagus</i> <i>validus</i> LeConte				
10 <i>Scyphophorus</i> <i>acupunctatus</i> Gyllenhal					present
11 <i>Yuccaborus frontalis</i> (LeConte)					present
DERMESTIDAE					
12 <i>Novelsis hornii</i> (Jayne)	as <i>Attagenus</i> <i>hornii</i> Jayne				
ELATERIDAE					
13 <i>Horistonotus</i> sp.		present			
ENDOMYCHIDAE					
14 <i>Holoparamesus</i> <i>pacificus</i> (LeConte)	present				present
HISTERIDAE					
15 <i>Acritus arizonae</i> Horn	present				
16 <i>Carcinops consors</i> (LeConte)	as <i>Paromalus</i> <i>consors</i> LeConte	present			
17 <i>Carcinops gilensis</i> LeConte	as <i>Paromalus</i> <i>gilensis</i> LeConte				as <i>P. gilensis</i> , <i>Paromalus</i> <i>tenellus</i> Erichson
18 <i>Carcinops</i> n. sp. (rugula)		present			
19 <i>Carcinops</i> n. sp. 1		present			

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APPENDIX A

Continued.

Species	<i>Carnegiea gigantea</i> (Hubbard 1899; Schwarz 1899a, b)	<i>Ferocactus</i> <i>wislizeni</i> (this study)	<i>Ferocactus</i> <i>wislizeni</i> (Dury 1916)	Columnar cacti (Castrejana and Markow 2001)	<i>Dasyliirion</i> <i>wheeleri</i> (Hubbard 1901)
20 <i>Carcinops opuntiae</i> (LeConte)	as <i>Paromalus</i> <i>opuntiae</i> LeConte	present			as <i>P. opuntiae</i>
21 <i>Epiurus planulus</i> Erichson					as <i>Epiurus</i> <i>planulatus</i> present
22 <i>Hololepta vicina</i> LeConte	present		present		
23 <i>Hololepta yucateca</i> (Marseul)	present	present	present	present	
24 <i>Iliotona cacti</i> (LeConte)	as <i>Hololepta</i> <i>cacti</i> LeConte	present	as <i>H. cacti</i>		
25 <i>Omalodes grossus</i> Marseul			present		
26 <i>Platysoma</i> sp.				present	
27 <i>Xerosaprinus</i> <i>martini</i> Fall		present			
HYDROPHILIDAE					
28 <i>Agna capillata</i> (LeConte)	as <i>Pelosoma</i> <i>capillosum</i> LeConte	present			
29 <i>Cryptopleurum</i> <i>impressum</i> Sharp	as <i>Cryptopleurum</i> <i>cerei</i> Schwarz, <i>Megasternum</i> <i>cerei</i> Schwarz				
30 <i>Dactylosternum cacti</i> (LeConte)	present	present			
LYCIDAE					
31 <i>Lucaina discoidalis</i> Horn	as <i>Lucaina</i> <i>discoidalis</i> Horn				
MYCETOPHAGIDAE					
32 <i>Litargus balteatus</i> LeConte		present			
NITIDULIDAE					
33 <i>Carpophilus discoideus</i> LeConte		present			
34 <i>Carpophilus lugubris</i> Murray		present			
NOSODENDRIDAE					
35 <i>Nosodendron</i> sp.				present	
PTILIDAE					
36 <i>Acrotrichis</i> sp.	as <i>Trichopteryx</i> sp.				
SCARABAEIDAE					
37 <i>Hemiphileurus illatus</i> (LeConte)					as <i>Phileurus</i> <i>illatus</i> LeConte
STAPHYLINIDAE					
38 <i>Aleochara (Maseochara)</i> <i>depressa</i> (Sharp)	as <i>Maseochara</i> <i>puberula</i> Casey	present			
39 <i>Aleochara (Maseochara)</i> <i>opacella</i> Sharp	as <i>Maseochara</i> <i>spacella</i> Sharp				
40 <i>Aleochara (Maseochara)</i> <i>semivelutina</i> Solsky	as <i>Maseochara</i> <i>semivelutina</i> Solsky				

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APPENDIX A

Continued.

Species	<i>Carnegiea gigantea</i> (Hubbard 1899; Schwarz 1899a, b)	<i>Ferocactus</i> <i>wislizeni</i> (this study)	<i>Ferocactus</i> <i>wislizeni</i> (Dury 1916)	Columnar cacti (Castrezana and Markow 2001)	<i>Dasyliirion</i> <i>wheeleri</i> (Hubbard 1901)
41 <i>Aleochara (Maseochara) valida</i> LeConte		present			
42 <i>Aleochara (Maseochara)</i> sp.			present		
43 <i>Apheloglossa rufipennis</i> Casey	present				
44 <i>Belonuchus ephippiatus</i> (Say)	present	present			
45 <i>Belonuchus</i> sp.			present		
46 <i>Belonuchus xanthomelas</i> Solsky (see Smetana 1995: 732)					present
47 <i>Carpelemus</i> sp.		present			
48 <i>Coproporus hepaticus</i> (Erichson)	as <i>Erchomus convexus</i> Erichson				
49 <i>Coproporus laevis</i> LeConte	as <i>Erchomus punctipennis</i> LeConte				
50 <i>Deroderus</i> sp.		present			
51 <i>Deroderus tabacinus</i> (Casey)	as <i>Lithocharis tabacina</i> Casey				
52 <i>Diestota</i> sp. 1		present			
53 <i>Diestota</i> sp. 2		present			
54 <i>Echiaster</i> sp.					as <i>Leptogenius</i> n. sp.
55 <i>Eleusis humilis</i> Erichson					as <i>Eleusis fasciata</i> LeConte
56 <i>Eumicrus lucanus</i> Horn	present				present
57 <i>Hamotus elongatus</i> (Brendel)	as <i>Tyrus elongatus</i> Brendal				
58 <i>Hapalaraea cacti</i> (Schwarz)	as <i>Omalium (Phyllodrepa) cacti</i> Schwarz				
59 many possible current genera and species	as <i>Falagria</i> sp.				
60 many possible current genera and species	as <i>Homalota</i> sp.				
61 <i>Neohypnus dimidiatus</i> (LeConte)	as <i>Xantholinus dimidiatus</i> LeConte				
62 <i>Oligota</i> sp.	present				
63 <i>Piestus extimus</i> Sharp					present
64 <i>Placusa vaga</i> Casey		present			
65 <i>Platydracus phoenicurus</i> (Nordmann)				present	
66 <i>Platystethus spiculus</i> Erichson		present			
67 <i>Tachinomorphus grandis</i> (Solsky)		present			
68 <i>Tachinomorphus grossulus</i> (LeConte)	as <i>Physetoporus grossulus</i> LeConte	present			
69 <i>Tachyporus</i> sp.				present	

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APPENDIX A

Continued.

Species	<i>Carnegieia gigantea</i> (Hubbard 1899; Schwarz 1899a, b)	<i>Ferocactus</i> <i>wislizeni</i> (this study)	<i>Ferocactus</i> <i>wislizeni</i> (Dury 1916)	Columnar cacti (Castrezana and Markow 2001)	<i>Dasyllirion</i> <i>wheeleri</i> (Hubbard 1901)
70 <i>Xanthopygus cacti</i> Horn	present		as <i>Xanthopyga</i> <i>cacti</i>		
71 <i>Zonaira puncticolle</i> (LeConte)	as <i>Trimium</i> <i>puncticolle</i> LeConte				as <i>T. puncticolle</i>
TENEBRIONIDAE					
72 <i>Araeoschizus</i> <i>decipiens</i> Horn					present
73 <i>Araeoschizus</i> sp.		present			
74 <i>Araeoschizus</i> <i>sulcicollis</i> Horn					present
75 <i>Armalia</i> sp.		present			
76 <i>Centrioptera</i> <i>variolosa</i> Horn				present	
77 <i>Cynaesus angustus</i> (LeConte)	present	present			
78 <i>Eleodes</i> spp.		present			present
79 <i>Hylocrinus longulus</i> (LeConte)					as <i>Emmenastus</i> <i>longulus</i>
80 <i>Hymenorus</i> sp.		present			
81 <i>Hypogena marginata</i> (LeConte)	as <i>Ulosonia</i> <i>marginata</i> LeConte				as <i>U. marginata</i>
82 <i>Opatrini</i> gen. sp.		present			
83 <i>Platydema</i> <i>inquilinus</i> Linell	as <i>Platydema</i> <i>inquilinum</i> Linell				
84 <i>Tribolium</i> <i>parallelus</i> (Casey)					as <i>Aphanotus</i> <i>parallelus</i> Casey
85 <i>Triorophus</i> sp.		present			
TROGOSSITIDAE					
86 <i>Airora cylindrica</i> (Serville)	as <i>Alindria teres</i> Melsheimer				
ZOPHERIDAE					
87 <i>Bitoma gracilis</i> Sharp	as <i>Ditoma</i> <i>gracilis</i> Sharp	present			as <i>D. gracilis</i>
88 <i>Bitoma sulcata</i> (LeConte)	as <i>Ditoma sulcata</i> LeConte				
Total Species	45	35	7	6	22

Coleoptera Collected from Rotting Fishhook Barrel Cacti (*Ferocactus wislizeni* (Engelm.) Britton and Rose), with a Review of Nearctic Coleoptera Associated with Succulent Necrosis

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