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Taxonomy and Ecology of the Cactophilic Beetle *Carcinops* in the Sonoran Desert

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by

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ABSTRACT OF THE THESIS

Taxonomy and Ecology of the Cactophilic Beetle *Carcinops* in the Sonoran Desert

by

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Cacti (family *Cactaceae*) are an important part of desert ecosystems. These plants are known for their many defensive adaptations, but occasionally, when a cactus becomes damaged or stressed, it becomes prone to invasion by microorganisms, which induce rot within the cactus. Rotting cacti host a diverse assemblage of desert arthropods, particularly beetles (Coleoptera) and flies (Diptera). Detailed research on cactus arthropods has been mostly limited to flies, while cactus beetles remain relatively understudied. This thesis serves as an

investigation of the taxonomy, phylogenetics, and host-cactus preferences of the cactophilic species of the beetle genus *Carcinops*. For this study, five hundred and fifty *Carcinops* specimens were collected from rotting cacti in the Sonoran Desert. Key morphological differences between species were evaluated and summarized. Detailed photographs were taken of all known cactophilic *Carcinops* species and were used to construct an interactive identification key. COI sequenced were used to create a gene tree. Based on species distributions among different species of cacti, some species of *Carcinops* appear to exhibit host-plant specificity, although not to the degree seen in some species of cactus *Drosophila.* Populations of *C. rugula* and *C. stenocereus* showed evidence of genetic isolation from mainland Mexican populations, possibly due the Gulf of California acting as a geographic barrier. One new species of *Carcinops* was discovered during the course of this research, and is described herein.

INTRODUCTION

The Rotting Cactus Niche

Cacti (family *Cactaceae*) are an important part of desert ecosystems. These plants are known for their many adaptations that prevent water and tissue loss. However, when a cactus becomes damaged or stressed, its defenses are lowered, and it becomes prone to invasion by microorganisms. These microorganisms, typically yeast or bacteria, can induce rot, or "necrosis," within cactus tissues. Depending on cactus size and thickness, a cactus rot can last from as few as three months to as long as a year (Breitmeyer and Markow, 1998). Rotten cactus tissues, as well as the yeast and bacteria within them, are often eaten and colonized by large numbers of arthropods until the tissues dry out from exposure to the desert air.

Cactus Arthropods

The ecology of rotting cacti and the arthropod communities they support is relatively understudied. Thorough community-level surveys of cactus arthropods are time-consuming, and as a result few have been conducted. While more research is needed to fully understand the intricacies of the rotting cactus niche, standing literature on this subject agrees that rotting cacti host a diverse assemblage of arthropods (Hubbard, 1889; Castrezana and Markow, 2001; Ferro et al., 2013). A single cactus rot can contain up to 30 different arthropod species, with the most diverse arthropod orders being Coleoptera (beetles) and Diptera (flies) (Hubbard, 1899; Castrezana and Markow, 2001).

Rotting cacti support numerous beetle taxa. So far, 88 species of beetles from 18 different families have been documented in rotting cacti (Ferro et al., 2013). The most diverse family of beetles occurring in cacti is Staphylinidae, with 33 documented species (Ferro et al., 2013). The staphylinids are also often the most abundant beetle group, particularly the Aleocharinae, (Hubbard, 1899; Ferro et al., 2013). Histeridae is another commonly occurring beetle family, the most abundant being species in the genus *Carcinops* (Hubbard, 1899; Ferro et al., 2013). Ferro et al. (2013) found more Carcinops individuals than any other beetle taxon in their survey of 16 rotten fishhook barrel cacti (*Ferocactus wislinzeni*)(Ferro et al., 2013). The majority of staphylinids and histerids in cactus rot communities are predators of dipteran eggs, larvae and pupae, and are believed to invade cactus rots in pursuit of their cactophilic prey (Ferro et al., 2013). A third family of beetles, Hydrophilidae, is often present in the wetter sections of cactus rots (Hubbard, 1899). While other beetles are known to occur in rotting cacti, Staphylinidae, Histeridae, and Hydrophilidae are the three most commonly reported.

Flies are another order commonly found in rotting cacti, and are the most-studied cactophilic arthropod group. Fly larvae occur in large numbers within rotting cacti, while adult dipterans can be found on and around the cactus exterior. Common families of adult dipterans include Cecidomyiidae, Muscidae, and Drosophilidae (Castrezana and Markow, 2001). Syrphidae and Scatopsidae larvae are found in high abundance within rots, but are collected less frequently as adults (Hubbard, 1899, Castrezana and Markow, 2001). Cactus rots are an important step

in the life cycle of desert flies. Adult flies lay their egg in rotting cactus tissue, where the larvae hatch and feed until they pupate and emerge from the cactus as adults (Castrezana and Markow, 2001). Adults and larvae consume the yeast, bacteria, and cactus tissue present in the rot and are consumed as prey by other desert arthropods (Castrezana and Markow, 2001). Cactus rot tissues contain many alkaloids and other allelochemicals, and some cactus *Drosophila* have been found to possess metabolic enzymes that detoxify these chemicals (Kircher, 1982). Different cactus species contain different quantities of allelochemicals, leading to host-plant specialization in some *Drosophila* species (Heed and Kircher, 1965; Heed, 1978). Compared to the amount of standing literature on cactophilic flies, little is known about the biology of cactus beetles or other cactus arthropods.

Current Research

My laboratory group is currently researching the taxonomy, ecology, and diversity of North American cactus arthropods. As of June 2015, we have systematically collected arthropod communities from 14 different cacti from Baja California Sur and Southern California, yielding over 5000 individual arthropods. Because most research on cactus arthropods has been restricted to flies, I wanted to focus my research on the taxonomy and ecology of cactus beetles. I chose to study *Carcinops* because the genus was highly abundant in our collection and was widespread across all the cactus species and localities that we sampled. Using the *Carcinops* collected by my lab, I aim to address the following questions: (1) How many species of *Carcinops* are in our samples? (2) How are these species related to

one another? (3) Do *Carcinops* exhibit host-cactus specificity similar to the kind observed in cactus *Drosophila*? (4) Is there genetic isolation between mainland (Mexico) and peninsular (Baja) *Carcinops* populations?

Histeridae

Carcinops are members of the beetle family Histeridae (Gyllenhaal, 1808); members of this family are commonly referred to as "clown beetles" or "hister beetles." Histerids are small, ranging from 0.5-12 millimeters in length, and are typically black, though a few species are red-tinged, metallic blue or green, or have red markings (Kovarik and Caterino, 2000). Most are round or oval-shaped, but a few (such as *Hololepta* species) are cylindrical and dorsoventrally flattened (Kovarik and Caterino, 2000). The family occurs worldwide and contains 4252 species in 391 genera (Mazur, 2011). Notable contributors to the identification of North American taxa are LeConte (1845), Horn (1873), and Casey (1893, 1916). At present there are 435 species belonging to 57 genera that are known to occur within the US (Kovarik and Caterino, 2000).

Histerids are a predacious family of beetles that consume soft-bodied, typically dipteran, insect larvae and eggs (Kovarik and Caterino, 2000). As a result, histerid habitats tend to occur where large quantities of fly larvae can be found, particularly in decaying organic matter. Some examples of common histerid habitats are animal carcasses, rotting plant tissues, dung, and leaf litter. A few taxa are known to inhabit ant or termite nests, where they consume larvae. Most species inhabiting this niche are unwelcome guests, but a few coexist with the colony

(Kovarik and Caterino, 2000). Some histerids are associated with carrion and have been found to be good indicators of time since death in both pigs and humans and have the potential to be used in forensic analysis (Wolff et al., 2001; Arnaldos et al., 2005; Aballay et al., 2013).

Carcinops

The genus *Carcinops* is in the tribe Paromalini (Reitter, 1908). Originally described within the genus *Paromalus* (Erichson, 1834), the group was later removed from *Paromalus* and reclassified as *Carcinops* (Marseul, 1855) on the basis of its elytral striae. There are currently 52 described *Carcinops* species, the majority of which are Neotropical, though species also occur in Nearctic, African and Asian regions. *Carcinops* contains two subgenera; *Carcinops sensu stricto* and *Carcinopsida*. There is currently only one described member of *Carcinopsida*; the cactophilic *C. opuntiae*. An additional member of the subgenus, *C. wenzeli* (n. sp. Reese & Swanson, in prep.) inhabits rots of *Yucca spp*. The synapomorphy that defines *Carcinopsida* is the presence of clustered micropunctation on the pronotal surface, whereas *Carcinops s. str.* posses simple, un-clumped ground punctation (Swanson, 2008). There is currently no common name for *Carcinops*, but notes by Sergio Castrezana refer to the genus as "turtle-neck beetles," likely based on the ability of species in this genus to withdraw much of their head into their thoracic cavity.

Like most histerids, *Carcinops* is a predator of fly larvae and eggs. Most research on this genus is focused on *Carcinops pumilio* (Erichson, 1834), a cosmopolitan species that is used in poultry farms as a pest control agent against

manure-breeding house flies (*Musca domestica*, Linnaeus). Studies on *C. pumilio* have revealed that it is relatively long-lived, with adults living up to 140 days in captivity (Achiano and Giliomee, 2005). The average generation time is around 50 days, and populations of *C. pumilio* are adult-biased due to low rates of fecundity (Achiano and Giliomee, 2005). Egg cannibalism has been observed in adults of *C. pumilio,* which, if commonly practiced, could also result in adult-biased populations (Kaufman et al., 2001). The juvenile stage of *C. pumilio* consists of two larval instars and takes about 20 days to develop from egg to adult (Achiano and Giliomee, 2005).

Cactophilic Carcinops – Taxonomy and Phylogenetics

Eight species of *Carcinops* are currently known to inhabit the rotting cactus niche. Four of these species have been formally described. These are *Carcinops gilensis* (LeConte, 1851), *C. consors* (LeConte, 1851), *C. corticalis* (LeConte, 1851), and *C. opuntiae* (LeConte, 1851). Four additional species of cactophilic *Carcinops* were discovered in 2008 by Alex Swanson but formal descriptions were never published. Swanson has since left the field of biology but has agreed to co-publish these species with me in the near future. The planned names for these species are *C. stenocereus* (n. sp. Reese & Swanson, in prep.), *C. rugula* (n. sp. Reese & Swanson, in prep.), *C. torquata* (n. sp. Reese & Swanson, in prep.) and *C. yaquiana* (n. sp. Reese & Swanson, in prep.). There are two additional species, *C. papagoana* (Casey, 1916) and *C. wenzeli* (n. sp. Reese & Swanson, in prep.), that occur in rots of non-cactus succulents such as *Agave* and *Yucca*, which is similar to the rotting cactus niche (Swanson, 2008). Gene trees constructed from COI and CAD sequences of all eight

known species of cactophilic *Carcinops* support their morphology-based delineations (Swanson, 2008). Genetic data show that *C. papagoana* experienced a rapid host shift to species of *Agave* after diverging from a strictly cactophilic ancestor (Swanson, 2008). *Carcinops s. str.* and *Carcinopsida* resolve as monophyletic groups, supporting their designation as subgenera (Swanson, 2008). Genetic data indicate that *C. opuntiae* may represent several different species but morphological differences have been hard to isolate (Swanson, 2008). A recent phylogeographic analysis of *C. gilensis* collected from mainland Mexico and the Baja peninsula suggests a lack of population structure based on COI sequences, supporting the hypothesis that cactophilic beetles like *Carcinops* readily disperse in order to quickly locate and inhabit cactus rots (Pfeiler et al., 2013). The lack of population structure between mainland and peninsular *C. gilensis* led the authors to propose that the species use the Midriff Islands as "stepping stones" to cross the Gulf of California. The study also revealed a recent divergence of mainland *C. rugula* with a peninsular sister species. The authors did not mention the demographic implications of this divergence, only stating that the two lineages had enough genetic distance between their COI sequences to be declared separate species. The species shares senita (*Lophocereus schottii*) as a host species, and while other factors cannot be ruled out, the genetic distinction between the two localities seems to suggest that geography plays a role in the divergence. More phylogeographic research is needed to determine if the Gulf of California acts as a reproductive barrier to some species of *Carcinops*.

Cactophilic Carcinops - Ecology

Cactophilic *Carcinops* are predators of dipteran eggs, larvae and pupae, and are believed to invade cactus rots in order to pursue their prey (Ferro et al., 2013). It is not known whether *Carcinops* themselves reproduce within cactus rots. If the genus does complete its life cycle within cactus rots, its development time is likely short, given the ephemeral nature of cactus rots and the relatively short development time observed in the non-cactophilic *C. pumilio*. The different species of cactophilic *Carcinpos* exhibit a range of host specificity. *Carcinops consors* and *C. corticalis* are the most generalist cactophilic species, occurring not only in a range of different cactus species, but also in rotten agave, rotten fruit, and under tree bark (Swanson, 2008). *Carcinops opuntiae* occurs in both cactus and *Yucca* rots (Swanson, 2008). All other cactophilic *Carcinops* species are strictly cactophilic. *Carcinops gilensis* shows some degree of specialization, and is most frequently found in saguaro (*Carnegiea gigantea*) and cardón (*Pachycereus pringlei*), though it may also be associated with barrel cacti (*Ferocactus sp.*) in California (Hubbard, 1899; Swanson, 2008). *Carcinops torquata* and *C. yaquiana* are rarely collected in Sonoran surveys, and likely have more southern distributions (Swanson, 2008). *Carcinops stenocereus* is the most host specific species, and has only been found on organ pipe (*Stenocereus thurberi*) rots (Swanson, 2008).

My thesis serves as an investigation of the taxonomy, phylogenetics, and host-cactus preference of *Carcinops* collected from rotting cacti in the Sonoran Desert.

MATERIALS AND METHODS

Collection

The specimens examined for this project were collected by myself and other members of the Markow lab as part of the Cactus Arthropod Project. The Cactus Arthropod Project (CAP) is a collection of arthropods found in rotting cacti in the Sonoran Desert. Cacti were collected in two localities; Baja California Sur and Anza-Borrego Desert State Park, CA (Table 1). Four different species of cacti were collected; cardón (*Pachycereus pringlei*), organ pipe (*Stenocereus thurberi*), senita (*Lophocereus schottii*), and California barrel (*Ferocactus cylindraceus*). We collected cactus rots on four separate trips between Dec 2012 and April 2014. The rots were identified in the field by the following indicators: tissue dark green to brown, exuding a dark liquid, soft when prodded, foul or sour odor sometimes present. Adult insects were captured by net if they were found within the cactus rot's vicinity. The necrotic tissue sections of the cactus were measured, excised, and brought back to a lab for dissection. The tissues were disassembled into smaller pieces using a saw. These pieces were then further dissected using forceps, and any arthropods found within them were removed and placed in 95% ethanol. Cactus tissues were stored in large buckets with cheesecloth covers to prevent arthropods from escaping. Cactus rots collected from Anza-Borrego Desert State Park were kept for up to a week after all adult arthropods were removed but with all larvae left in place. My lab partner and I thoroughly reexamined the tissues one week later, and if additional adult specimens of the same morphospecies were found during the

second round of examination, this observation was taken as evidence that these taxa use cactus rots to complete their life cycle. Due to time constraints, rots collected from Baja California Sur were not subjected to this treatment. All arthropod specimens were sent to the Markow Lab at UCSD, where they were sorted and morphologically identified by myself and my lab partner for the Cactus Arthropod Project.

Although we went to great efforts to prevent arthropods from escaping from the cactus containers, a few inevitably escaped during the transfer of cactus tissues between containers. These specimens were collected and preserved but were not included in our collection. However, *Carcinops* that escaped from cacti collected on our most recent Anza-Borrego collection were used for "trial-and-error" PCRs, yielding several successful sequences. Two cacti, "A2" and "A3" (Table 1) were collected during that trip, and were stored in the same room. Because there is no way to discern which cactus these escaped specimens originated from, they are not included in the formal analysis of this paper. However, because the two cacti are of the same species and are from the same location, there was enough information available to include sequences from these individuals in this paper's gene tree.

Only the *Carcinops* collected from the Cactus Arthropod Project were used for this paper. However, I had access to several other collections of *Carcinops* for ID verification purposes. Alex Swanson's personal collection contained several paratypes of the five unpublished species (Swanson, 2008). Specimens collected by Sergio Castrezana and Therese Markow (Castrezana and Markow, 2001), and

additional specimens collected by Teri in Sonora, Mexico were examined, but could not be analyzed to the same degree as the CAP samples because they only represented partial samples. The *Carcinops* collected by Ferro et al. for their 2013 paper were also examined. However, it became clear that the species had been misidentified (likely due to a lack of available identification literature) and so these samples were not included in the formal analysis of this paper either, as it would likely cause confusion.

Morphological Identification

Carcinops specimens were examined using a Leica S8AP0 microscope. Morphological identification was based on an unpublished key written by Alex Swanson. Morphological terminology follows Ôhara (1994). When choosing key traits, discreet character differences were favored over continuous ones, because discreet characters are presumably indicative of some form of reproductive isolation (Mayr, 1942).

Photographing Techniques

Specimens were temporarily glued to a pin with water-soluble glue to prepare them for photography. Micrographs were taken at 6-8 times magnification using a Canon Rebel T3 connected to a Leica S8AP0 microscope via a phototube. Two to four Fiber-Lite Series 180 illuminators and a diffusion tube were used to maximize surface detail visibility. Specimens were tilted slightly downward posteriorly when dorsally photographed to prevent the lens shadow from obscuring their elytral stria, an important morphological trait. The program EOS Utility v

2.12.2.0 (Canon) was used to remotely view and photograph the specimens from a computer screen. Photographs were taken in stacks of varying focus then merged into a single photo using Helicon Focus v 6.0.18. The resulting images often had artifacts due to lens dust and the image-stacking algorithm. These artifacts were removed using Adobe Photoshop CC 2014 v 15.2.2, which was also used to darken reflective glares and lighten the shadow cast by the microscope lens.

Many specimens had a fine layer of dust and other obstructive particles on their body surface. While these particles were too small to obstruct major morphological structures, they obscured surface punctation patterns. *Carcinops* are quite small, and because they had been preserved in 95% ethanol, the specimens were also very brittle. Because of this, a gentle cleaning method had to be improvised. A small "brush" was made by tightly rolling one end of a 1 cm^2 section of Kimwipe such that the opposite end flared out. This brush was then dampened with 95% ethanol and gently brushed on the mounted beetle in circular polishing motions. Beetles that were given this treatment photographed much better than their counterparts.

Interactive Key Construction

Images of key morphological traits (outlined in the morphological results section) for each *Carcinops* species, along with general dorsal and ventral photos, were used to create a visual interactive identification key using Lucid Builder v 3.5.20 (Lucid Central). The key will be made publicly available on Lucid Central's website following the publication of several *Carcinops* species descriptions.

Gene Sequencing

DNA was extracted from the thorax of each specimen with a Quiagen DNeasy Blood & Tissue Kit (QIAGEN Inc, Valencia, CA) using non-destructive methods. Tissues were lysed overnight at 56° C. AE buffer was reduced to 70 µl for the final elution step to increase DNA concentration. Specimen thoraxes were later re-glued to the corresponding abdomens and mounted to a point using water-soluble glue. Primers LCO1490 and HCO2198 (Folmer et al., 1994) were used to amplify the barcoding locus of the mitochondrial gene cytochrome oxidase I (COI) via polymerase chain reaction (PCR). The PCR protocol was as follows: start (94° C for 2:00), denaturing (94° C for 30 seconds), annealing (51° C for 30 seconds), and extension (65° C for 1:00) for a total of 35 cycles. Successful PCRs were cleaned with Thermo Scientific's Exonuclease I (Exo I) and Thermosensitive Alkaline Phosphate (FastAP) and sent to the genomic services companies Retrogen (San Diego, CA) and GENEWIZ (La Jolla, CA) for sequencing.

Analysis of DNA sequence data

Sequences were edited using Sequencher v 4.8 (Gene Codes) and were aligned using Se-Al v 2.0 (Rambaut, 2002). jModelTest v 0.1.1 (Posada, 2008) was used to find the best-fit model of molecular evolution for the genetic data. The sequences were then run in MrBayes v 3.2.2 (Huelsenbeck and Ronquist, 2001) under the appropriate model. Gene trees were constructed using COI sequence data from this study and two prior studies: (Swanson, 2008 and Pfeiler et al., 2013).

RESULTS

Cactus Arthropod Project – Preliminary Results

Over 5000 individual arthropods were collected from 14 cactus rots for the Cactus Arthropod Project. Based on external morphology, the samples are comprised of roughly 120 species belonging to 11 orders and 20 families (Richmond et al., in prep). Similar to previous studies of the necrotic niche, Coleoptera was the most species-rich arthropod group, the two most abundant families being Staphylinidae and Histeridae. *Carcinops* was the most common histerid found in the cactus rots. Few dipteran adults were captured via net collection. However, numerous Syrphidae, Scatopsidae, and Neriidae emerged from larvae contained in the cactus rots. Acari (mites) were found in high abundance in some rots, making the taxon the most abundant overall. However, due to difficulty of morphologically identifying mites, their species richness is currently unknown. Other common arthropod taxa found include Hemiptera, Hymenoptera, Dermaptera, Blattodea, Collembola, and Pseudoscorpiones. The Cactus Arthropod Project collections yielded 550 *Carcinops* individuals, all of which were examined for this paper.

Carcinops

Eight species of *Carcinops* were found (Table 2). Two species of *Carcinops* that are known to be cactophilic but that did not appear in the samples for this study are *C. yaquiana* (n. sp. Reese & Swanson, in prep.) and *C. torquata* (n. sp. Reese & Swanson, in prep.). However, specimens of *C. yaquiana* were present in Therese Markow's samples from organ pipe cacti from mainland Mexico, and, while not

included in the formal analyses of this paper, were accessible for morphological and genetic analyses. Similarly, Alex Swanson's personal collection contained a specimen of *C. torquata* that was used for morphological data. One species found in this study, *C. papagoana*, has not been found in cactus before, and was previously thought to only occur in rotten *Yucca spp*. (Table 2). One new species of *Carcinops* was present in the rot samples and was described under the name *Carcinops kumeyaayana*.

Re-examination of cactus tissue from Anza-Borrego samples revealed several recently-emerged adult *Carcinops*. Two individuals of *Hololepta sp.*, another cactus histerid, were also directly observed emerging from their pupal cases. These findings provide some of the first direct evidence that *Carcinops*, and perhaps cactus histerids in general, use rotting cacti to complete their development.

Carcinops consors was the most abundant species, followed by *C. gilensis* and *C. rugula* (Table 2). *Carcinops gilensis* had the widest distribution, appearing in 12 of the 14 rots collected and in all four cactus species (Table 2), albeit with low numbers in organ pipe (n=1, total=41) and senita (n=3, total=63) cacti. *Carcinops opuntiae* was also present in all four species of cactus, but had minimal presence in senita rots (n=1, total=63). All other *Carcinops* species were limited to three or fewer species of cacti. Two of the eight species found in this study, *C. papagoana* and *C. kumeyaayana,* were confined to California barrel cactus rots (Table 2).

Cardón rots were marked by high *C. consors* abundance. Organ pipe rots were mostly comprised of *C. stenocereus* and *C. opuntiae*. Senita rots had the lowest species richness (Figure 2) and were inhabited almost exclusively by *C. rugula*

(Table 2 and Figure 2). California barrel rots had the highest species richness overall, with nine different *Carcinops* species appearing in the rots (Figure 2), but over half of the species abundance was from *C. gilensis* alone.

Carcinops rugula occurred almost exclusively in senita and California barrel cactus rots (Figure 2). *Carcinops stenocereus* had an opposite distribution, appearing in cardón and organ pipe rots (Figure 2). *Carcinops consors* occurred in high numbers in cardón and California barrel rots but was absent in senita and had minimal presence in organ pipe (Figure 2).

Carcinops s. str. and *Carcinopsida* resolve as monophyletic groups, supporting their status as subgenera (Figure 3). All species designations, including that of the newly described *C. kumeyaayana*, were monophyletic (Figure 3). Cactophilic *Carcinops* do not form a monophyletic group within the genus (See *C. pumilio* in Figure 3). Sequence data for more species of non-cactophilic *Carcinops* are needed for a more detailed analysis of the evolution of cactophily within the genus. Gene sequences from *C. rugula* and *C. stenocereus* formed locality-based clades, indicating possible genetic isolation between mainland and peninsular populations.

Key Morphological Traits

Key traits used in the identification of Carcinops species (Table 3) were chosen based on the criteria outlined in the methods section. The different character states for each trait are outlined here for added clarity and simplicity.

Pronotal Marginal Stria: “Thin” striae are close to the pronotal margin, with a very thin gap between the two (Figure 4a); “Thick” striae are more distant from the

pronotal margin, with a thick gap between the two (Figure 4b); “Sinuate” striae are distant from the pronotal margin but are sinuate (or “pinched”) in the middle (Figure 4c).

Head Marginal Stria: “Short” marginal striae are incomplete and terminate at the anterior edge of the eye (Figure 5a); “Long” marginal striae are incomplete but are longer, converging inward along the head margin and reaching the mandibles before terminating (Figure 5b); “Complete” marginal striae form a continuous loop along the entire margin of the head (Figure 5c).

Elytral striae: Elytral striae 1-4 are always long, nearly reaching the elytral proximal base. Elytral stria 5 and the sutural stria (the two innermost striae) are the striae affected by this character state. Species with “long” elytral striae possess sutural and 5th striae that are as long as striae 1-4 and nearly reach the elytral base (Figure 6a). Species with “short” elytral striae possess sutural and fifth striae that are shorter than striae 1-4 and terminate at the basal third (Figure 6b). *Note*: “Short” type sutural and fifth may be continued as faint, striation-free punctures. These should not be confused with “long” type striae that fade basad. The two can be distinguished from each other by whether the striation ends abruptly (short) or gradually (long). “Short” type elytral striae give the appearance of a striation-free “window” in the basomedial third.

Internal subhumeral striae: Internal subhumeral striae are categorized on a presence-absence basis. If the striae are not apparent, they are designated as

"absent." If the striae are apparent, even if only faintly or as a row of punctures, they are designated as "present."

External subhumeral striae: External subhumeral striae are categorized on a presence-absence basis. If the striae are not apparent, they are designated as "absent." If the striae are apparent, even if only faintly or as a row of punctures, they are designated as "present." *Note*: While presence/absence is a sufficient measure for distinguishing most cactophilic *Carcinops* species, *C. stenocereus* and *C. torquata* require more detailed descriptions. *Carcinops stenocereus* possesses external subhumeral striae that are either faint or absent, whereas *C. torquata* has striae that are present as a row of punctures.

Ground punctation: Species of *Carcinops s. str.* possess "simple" ground punctation, which is evenly dispersed across the surface of the pronotum. Species of *Carcinopsida* (*C. opuntiae* and *C. wenzeli*) possess "clustered" punctation, with surface punctures that are clumped in groups of three or four.

Lateral disc of first visible abdominal sternite: All *Carcinops* species possess a stria that runs along the dorsal margin of the lateral disc. Punctation is present throughout the disc, and some elongate punctures may be present. *Carcinops* possessing this character state are designated as "unmodified" types. "Unmodified" types also have discs with smooth surface texture (Figure 7a). Some species of *Carcinops* are "bistriate" and possess an additional stria below the first one (Figs 7c, 7d). Members of *Carcinopsida* are "tristriate" and have a third stria present on their discs. The texture of the lateral disc also varies between species. *Carcinops rugula*

has a “microrugulose” texture apparent on the surface of its disc, especially when viewed under harsh lighting (Figure 7B). All other known cactophilic species of *Carcinops* do not possess microrugulation, and instead have smooth surface texture. *Notes:* 1. Elongate punctures on the lateral disc may appear to be secondary striae. Secondary striae can be distinguished from elongate punctures by the following two traits: parallel to first stria, at least half as long as first stria. 2. *Carcinops consors* and *C. yaquiana* both possess bistriate discs, but their secondary striae differ in shape. *Carcinops yaquiana* has a straight secondary stria (Figure 7C), whereas *C. consors* has a secondary stria that diverges ventrally in its posterior fourth (Figure 7D). The proximity of the stria to a spiracle can also give it a “forked” appearance on the posterior end in some specimens.

Species Description

***Carcinops kumyaayana* Reese, n. sp.**

(Figs. 8A-C)

Diagnosis

This species is recognized by the following combination of characters. HEAD: marginal stria incomplete, converging inward and terminating at mandible midpoint (Fig: 8A). PRONOTUM: marginal stria close to the pronotal margin, with a thin gap between the two (Figure 8A). ELYTRAL STRIAE: fifth and sutural stria long, nearly reaching elytral base (Figure 8B). SUBHUMERAL STRIAE: external and internal striae present, strongly impressed. LATERAL DISC OF FIRST VISIBLE

ABDOMINAL STERNITE: single stria present. GROUND PUNCTATION: punctation simple, un-clumped.

Description

L: 1.60mm; W: 1.12mm; E/Pn L: 1.67mm; E/Pn W: 1.08mm; Pn W/L: 0.93mm; E L/W: 0.89mm; Sterna: 0.50mm, 0.18mm, 0.54mm. Form oval, moderately depressed; color black to rufous, shining; frons slightly convex, coarsely, densely punctate; head marginal stria interrupted anteromedially, extending anterad just beyond antennal insertion to the clypeolabral structure.

Pronotal marginally convex, widest at base, converging anteriorly, sides gently curving; anterior angles acute, projecting; pronotal marginal stria complete to base, parallel and very close to anterior margin; pronotal disc coarsely densely puncate throughout; antescutellar puncture round and strongly impressed.

Prosternal lobe coarsely, densely punctate anteriorly; prosternal keel slightly convex posteriorly, carinal striae slightly inwardly arcuate, united posteriorly.

Elytra finely, densely punctate with coarse punctures densely distributed along apical margins and extending basad to about the apical half, external subhumeral stria strongly impressed, 0.3 mm long, centered on elytral midpoint; internal subhumeral stria strongly impressed along entire length of elytra except for a small section near apical third, where it is represented only by a puncture; first through fourth dorsal striae complete, strongly impressed, punctuated at regular intervals; fifth dorsal and sutural striae represented by dense rows of strong punctures apically, fading basad but nearly reaching elytral base where fifth dorsal

stria curves slightly inward.

Mesosternum coarsely, densely punctate with fine punctures interspersed, coarse punctures present throughout intercoxal disc except for along lateral midline; anterior margin slightly emarginate to receive posterior prosternal projection; marginal stria complete, deeply impressed, continuous with lateral metasternal stria; mesometasternal suture represented by a fine line; intercoxal disc of metasternum coarsely, densely punctate throughout; lateral metasternal stria straight, strongly impressed, nearly reaching outer margin of metacoxal cavity; posterior mesocoxal stria diverging from lateral metasternal, about as long as lateral metasternal stria; lateral disc coarsely, densely punctate.

Intercoxal disc of first visible abdominal sternite coarsely, moderately punctate throughout, bistriate on each side medial to metacoxal cavity; lateral disc coarsely, densely punctate throughout, bearing a single stria along outer margin.

Comparison with related species

Based on COI genetic data, this species is sister to *C. consors*, and can be distinguished from it by its long elytral stria and lack of a secondary stria on the lateral disc of its first visible abdominal sternite. Morphologically, *C. kumeyaayana* resembles *C. torquata*, as both have long head marginal striae, long elytral striae, and a single stria on the lateral disc of their first visible abdominal sterna. *Carcinops kumeyaayana* can be distinguished from *C. torquata* by its thin pronotal marginal stria.

Geographic distribution and natural history

Currently *C. kumeyaayana* is only known to inhabit rotting California barrel cacti in the Anza-Borrego desert. The species is sister to *C. consors*.

Derivation of specific epithet

C. kumeyaayana is named for the Kumeyaay natives, a group of people whose ancestral territory included what is now Anza-Borrego Desert State Park. The species name is pronounced “KOOM-yai-a-na.”

DISCUSSION

Summary of findings

In total, 8 different species of *Carcinops* were identified from the cactus samples, and one new species was discovered and described. Gene trees constructed from COI data show that *Carcinops* subgenera and species are monophyletic, lending support to their designation. Most species of *Carcinops* show signs of host cactus specificity, but not to the degree seen in cactophilic *Drosophila*. Gene trees for *C. rugula* and *C. stenocereus* indicate genetic isolation within Baja Peninsula populations.

Host cactus specificity

Prior to this study, *C. consors* and *C. corticalis* were regarded as the most generalist species of cactophilic *Carcinops*. Both are known to inhabit cactus rots, rotting fruit, and tree bark. One would think that such a versatile species would be able to inhabit a wide variety of cactus species. Interestingly, the *C. consors* collected in this study showed a strong preference towards cardón and California barrel rots and had minimal appearance in organ pipe and senita rots. Only two *C. corticalis* specimens were obtained during collection efforts, and were found on rotting cardón and California barrel cactus (Table 2 and Figure 1). This is not entirely unexpected, as *C. corticalis* is rarely collected in rotting cactus (Swanson, 2008). More data is needed in order to draw conclusions about the host cactus preferences of *C. corticalis*.

Several species of *Carcinops* were found in more host cactus species than previously thought. Data for *C. gilensis* confirm that the species has a strong preference for Californian *Ferocactus.* The species was also found in high abundance in rots of cardón, which is concordant with previous studies (Hubbard, 1899; Swanson, 2008). Interestingly, the species also appeared in senita and organ pipe rots, but only in very small numbers. *Carcinops stenocereus,* which was thought to specialize on organ pipe cacti, was found in moderate abundance in cardón, making it less host-plant specific than previously thought.

Carcinops papagoana was found for the first time in rotting cactus, which is particularly interesting given its evolutionary history. This species shares a recent common ancestor with *C. rugula*, and was thought to have completely diverged from its cactophilic roots, instead specializing on rots of Agavaceae (Swanson, 2008). *Carcinops papagoana* is not the only *Carcinops* species to associate with both Cactaceae and Agavaceae. *Carcinops opuntiae* is known to inhabit rots of both plants as well (Swanson, 2008). Phylogenetically, Agavaceae and Cactaceae are very different, and the two host different communities of yeast (Lachance, 1993), which can affect rot conditions (Fogleman and Danielson, 2001). Despite these differences, *C. papagoana* and *C. opuntiae* readily inhabit rots of both plant families. This raises the question: what factors determine host cactus suitability for *Carcinops*? Because species like *C. papagoana* and *C. opuntiae* are able to inhabit rots with different yeast communities, it would seem that yeast communities don't have as strong of an effect on *Carcinops* host selection as other factors. This is not completely surprising, as

Carcinops species do not directly consume cactus yeast. Based on its natural history, *Carcinops* habitat selection is likely most heavily influenced by the presence of water, dipteran prey, and suitable breeding grounds.

Carcinops might not necessarily be reproducing in every cactus species that they are found in. Given the relatively long lifespan observed in *C. pumilio* (up to 140 days)(Achiano and Giliomee, 2005), and the large distances between rots of the same cactus species, it is possible that adults may use a wider selection of cactus species as "rest stops" before arriving at their host species of preference. This scenario would give *Carcinops* two levels of host selection; a general selection for cactus species that they use for food and water, and a more specific selection for cactus species that they lay their eggs in. This would explain why small numbers of more specific species like *C. gilensis* and *C. papagoana* were found on cacti outside of their presumed host preference.

Phylogenetics

Sequences from peninsular *C. rugula* and *C. stenocereus* formed distinct clades relative to sequences from mainland specimens of the same species. *Carcinops rugula* collected from Baja California Sur were in the same clade as the putative "sister species" of *C. rugula* mentioned in Pfeiler et al., 2013. These specimens were examined for morphological differences from *C. rugula* from mainland Mexico but no discrete differences were observed. Based on the lack of morphological differences and low genetic distance between the two taxa, there is not enough evidence to designate this peninsular clade as a separate species.

Interestingly, specimens of both mainland and peninsular haplotypes were present within cactus rots from southern California, which may indicate that southern Californian *C. rugula* experience gene flow from both peninsular and mainland populations. It was previously theorized that *Carcinops* crossed the Gulf of California by using the Midriff Islands. While this theory still holds weight, it is also possible that *Carcinops* species expanded their ranges by navigating northward around the gulf. Based on the genetic data currently available, peninsular populations of *C. rugula* and *C. stenocereus* appear to be isolated from their mainland populations due to geographic separation, while Californian populations of *C. rugula* experience less isolation due a lack of geographic barriers. Interestingly, peninsular *C. gilensis* did not show signs of genetic isolation. One possible explanation for this is the wider range of host cacti utilized by *C. gilensis*, which may give it greater dispersal ability.

Future research

The Cactus Arthropod Project is ongoing and a paper on the composition of cactus arthropod communities is in preparation. My lab partner Dionné Mejia plans to focus her graduate research on the many taxa of Staphylinidae that appear in cactus rots, which will greatly aid in our understanding of cactus beetle diversity. Compared to what we know about cactophilic flies, there is still much more to learn about the evolutionary adaptations and life histories of cactus beetles. A live-rearing experiment like the one conducted by Achiano and Giliomee (2006) could potentially be used to study the reproduction of cactophilic species of *Carcinops*. As a whole, *Carcinops* has not been formally revised as a genus, and morphological and

genetic data for its non-cactophilic species are lacking. There are likely many other cactophilic species outside of the Sonoran Desert that await discovery.

TABLES AND FIGURES

Table 1. Species and location data for cactus rots collected for the Cactus Arthropod Project.

Cactus Rot #	Species Name	Common Name	Collection Period	Locality	GPS Coordinates
B2	*Pachycereus pringlei*	Cardón	Dec, 2012	Baja California Sur	23.8257, -110.2720
B3	*S. thurberi*	Organ Pipe	Dec, 2012	Baja California Sur	23.8257, -110.272
B7	*P. pringlei*	Cardón	Dec, 2012	Baja California Sur	23.8379, -110.1908
B9	*S. thurberi*	Organ Pipe	Dec, 2012	Baja California Sur	23.4735, -109.5657
B10	*P. pringlei*	Cardón	Dec, 2012	Baja California Sur	24.4347, -110.6830
B12	*P. pringlei*	Cardón	Jun, 2012	Baja California Sur	23.83567, -110.28077
B13	*P. pringlei*	Cardón	Jun, 2012	Baja California Sur	23.8259, -110.28036
B18	*Lophocereus schottii*	Senita	Jun, 2012	Baja California Sur	24.29981, -110.31649
B19	*P. pringlei*	Cardón	Jun, 2012	Baja California Sur	24.31059, -110.31549
B23	*L. schottii*	Senita	Jun, 2012	Baja California Sur	24.29934, -110.31834
B24	*S. thurberi*	Organ Pipe	Jun, 2012	Baja California Sur	23.83675, -110.26765
A1	*Ferocactus cylindraceus*	California Barrel	Mar, 2013	Anza-Borrego Desert State Park	NA – Same sq km as A2
A2	*F. cylindraceus*	California Barrel	Mar, 2013	Anza-Borrego Desert State Park	33.1466696, -116.276726
A3	*F. cylindraceus*	California Barrel	Apr, 2014	Anza-Borrego Desert State Park	33.099932, -116.465996

Note: Rot "B3" did not contain any *Carcinops* specimens.

Table 2. Number of *Carcinops* individuals by species found per each cactus rot.

	Cardón						Organ Pipe			Senita		Barrel		
Cactus Rot #	**B2**	**B7**	**B10**	**B12**	**B13**	**B19**	**B3**	**B9**	**B24**	**B18**	**B23**	**A1**	**A2**	**A3**
C. gilensis		4	1	3	10	4		1		1	2	14	15	119
C. consors		17	57	30	7	3	1					21	7	18
C. corticalis	1													1
C. papagoana												2		
C. stenocereus		6		22			8	5	14				2	1
C. rugula					1			1		49	10	31	23	8
C. opuntiae		2			1	2	7	4		1		6	2	1
C. kumeyaayana													1	3

Cactus rot numbers are preceded by a locality code. “B” = Baja California Sur. “A” = Anza-Borrego Desert State Park.

Table 3. Character matrix summarizing the morphological differences between cactophilic *Carcinops* species.

Species	Lateral Disc of the First Abdominal Sternite	Elytral Striae	Internal Subhumeral Striae	External Subhumeral Striae	Head Marginal Striae	Pronotal Marginal Striae	Ground Punctures
C. gilensis	Unmodified	Short	Absent	Absent	Long	Thick	Simple
C. consors	Bistriate	Short	Present	Present	Long	Thin	Simple
C. corticalis	Unmodified	Short	Present	Present	Complete	Thick	Simple
C. papagoana	Unmodified	Short	Absent	Absent	Long	Thin	Simple
C. stenocereus	Unmodified	Long	Absent	Absent or faint	Short	Sinuate	Simple
C. rugula	Single stria, microrugulose	Short*	Present	Present	Long	Sinuate	Simple
C. torquata	Unmodified	Long	Absent	Present**	Long	Sinuate	Simple
C. yaquiana	Bistriate	Short	Absent	Absent	Long	Thick	Simple
C opuntiae	Tristriate	Long	Present	Present	Complete	Thick	Clustered
C. kumeyaayana	Unmodified	Long	Present	Present	Long	Thin	Simple

Keywords used to describe character states correspond to those outlined in the morphological section of the results.
* The 5th elytral striae of *C. rugula* is long on some specimens
** The external subhumeral striae of *C. torquata* is present as a row of strong punctures

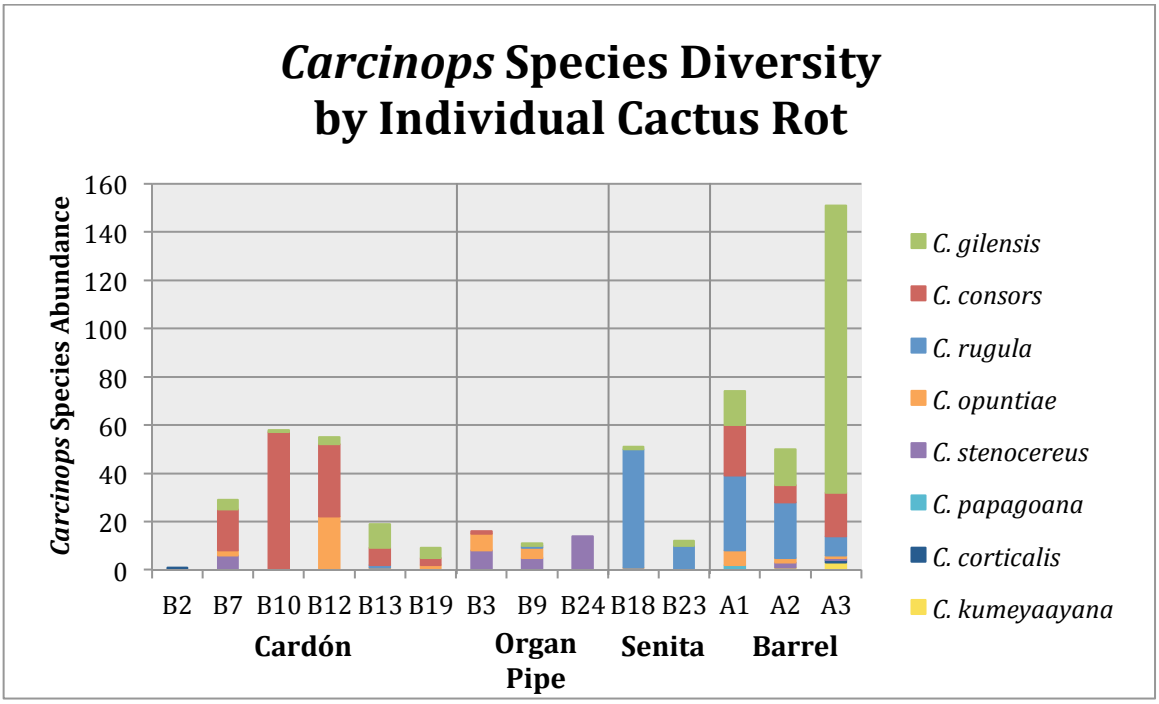

Figure 1. *Carcinops* species counts by individual cactus, arranged by cactus species. Cactus rot numbers are preceded by a locality code. "B" = Baja California Sur. "A" = Anzav Borrego Desert State Park.

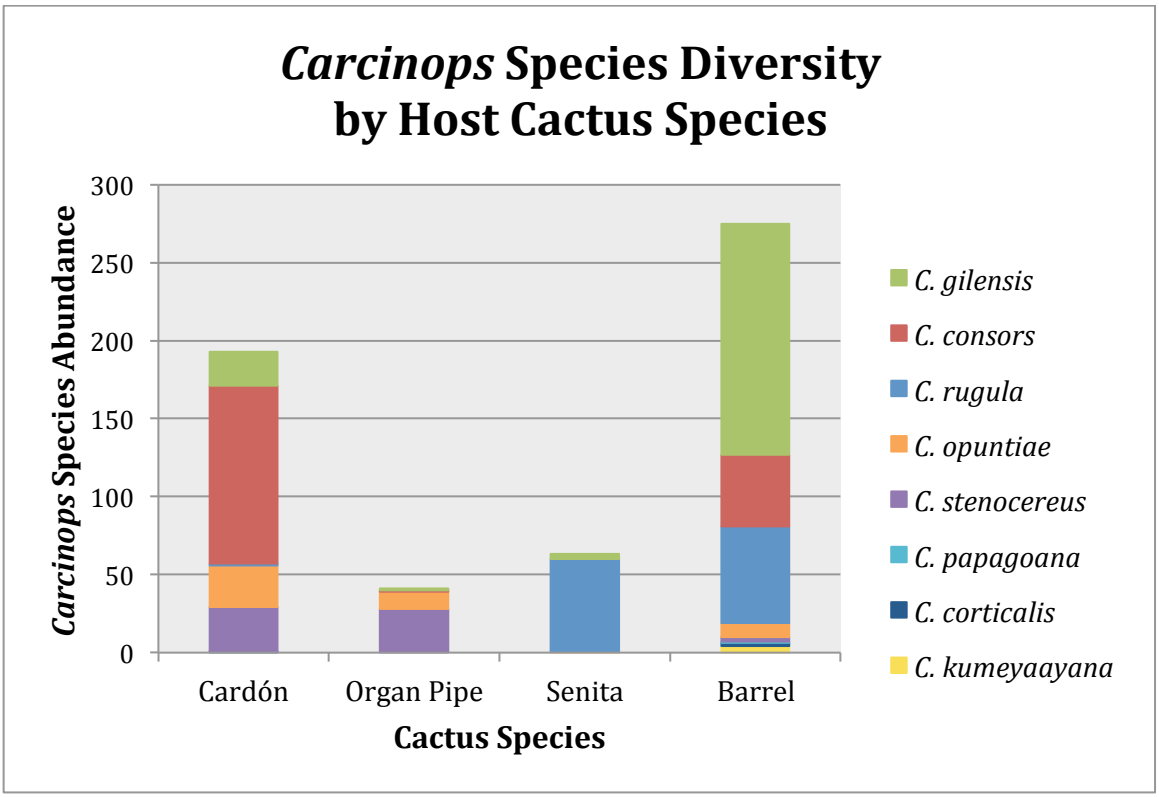

Figure 2. *Carcinops* species counts by species of host cactus. Same data as presented in Figure 1 but with cactus rots pooled together by cactus species. Sample sizes for cactus rots are: cardón (6), organ pipe (3), senita (2), California barrel (3).

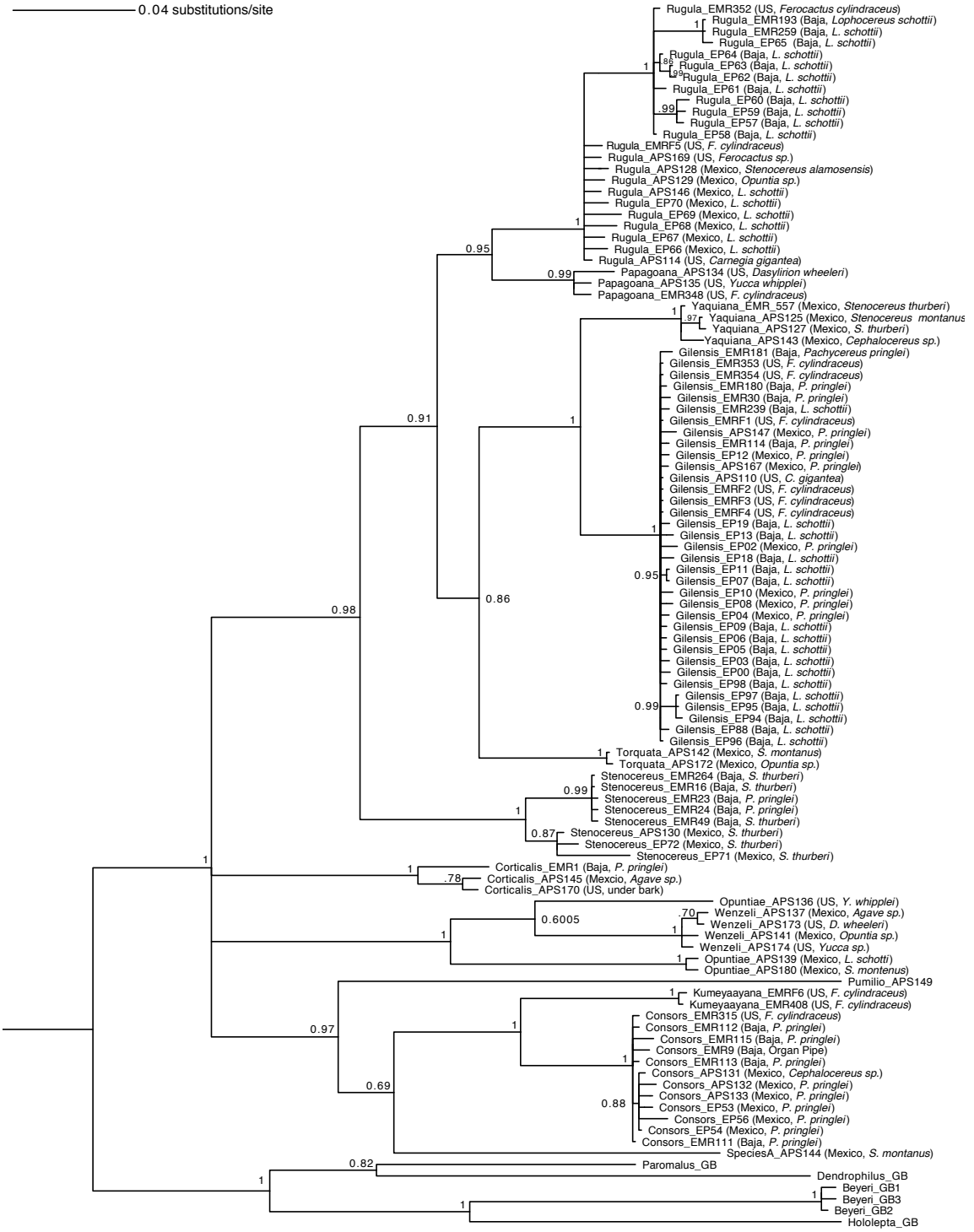

Figure 3. *Carcinops* gene tree constructed from COI data from three papers. Specimens are labeled by species name, their paper of origin, and a catalogue number. Specimen localities and host cactus species are listed in parentheses. "EMR" designates sequences from this study, "APS" designates sequences from Swanson (2008), and "EP" designates sequences from Pfeiler et al. (2013). "US" specimens are from the continental United States, specifically California or Arizona. "Baja" specimens are from the Baja Peninsula, and "Mexico" specimens are from mainland Mexico.

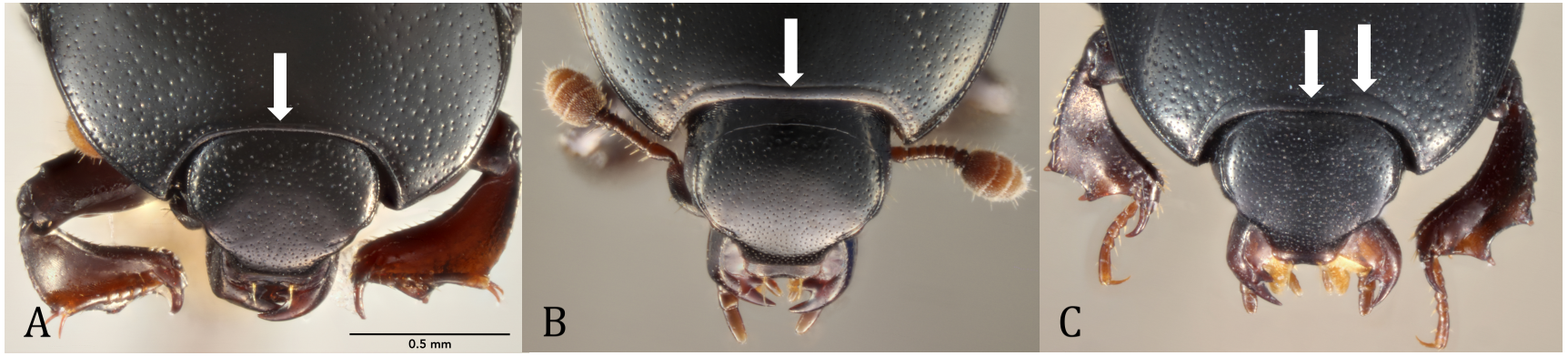

Figure 4. *Carcinops* pronotal marginal stria variation. A: Thorax marginal stria "thin" type. Stria is close to pronotal margin. (*C. consors*). B: Thorax marginal stria "thick" type. Stria is more distant from pronotal margin and is approximately parallel to margin behind the head. (*C. gilensis*). C: Thorax marginal stria "sinuate" type. Stria is distant from the pronotal margin but is "pinched" closer in the middle. (*C. stenocereus*).

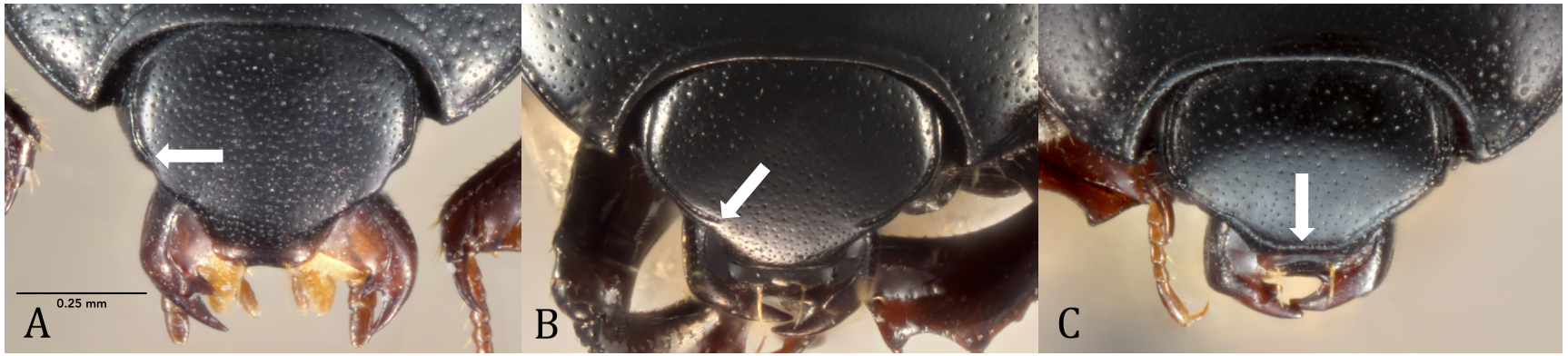

Figure 5. *Carcinops* head marginal stria variation. A: Head marginal stria "short" type. Stria reaching anterior edge of eye. (*C. stenocereus*). B: Head marginal stria "long" type. Stria converging inward along head margin, reaching past mandibles. (*C. yaquiana*). C: Head marginal stria "complete" type. Stria present along entire outer margin of head. (*C. corticalis*)

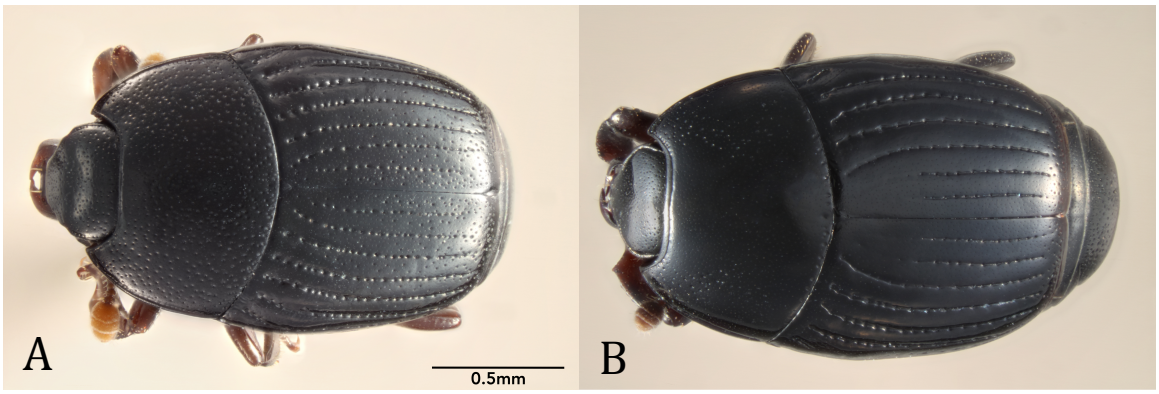

Figure 6. *Carcinops* elytral striae variation. A: Elytral striae "long" type. All elytral striae reaching or nearly reaching base of elytra. Sutural stria and stria 5 (the two inner-most striae) long, sometimes reduced to punctures in basal third. (*C. kumeyaayana*). B: Elytral striae "short" type. Elytral striae 1-4 reaching base of elytra, sutural stria and stria five only reaching basal third. (*C. yaquiana*)

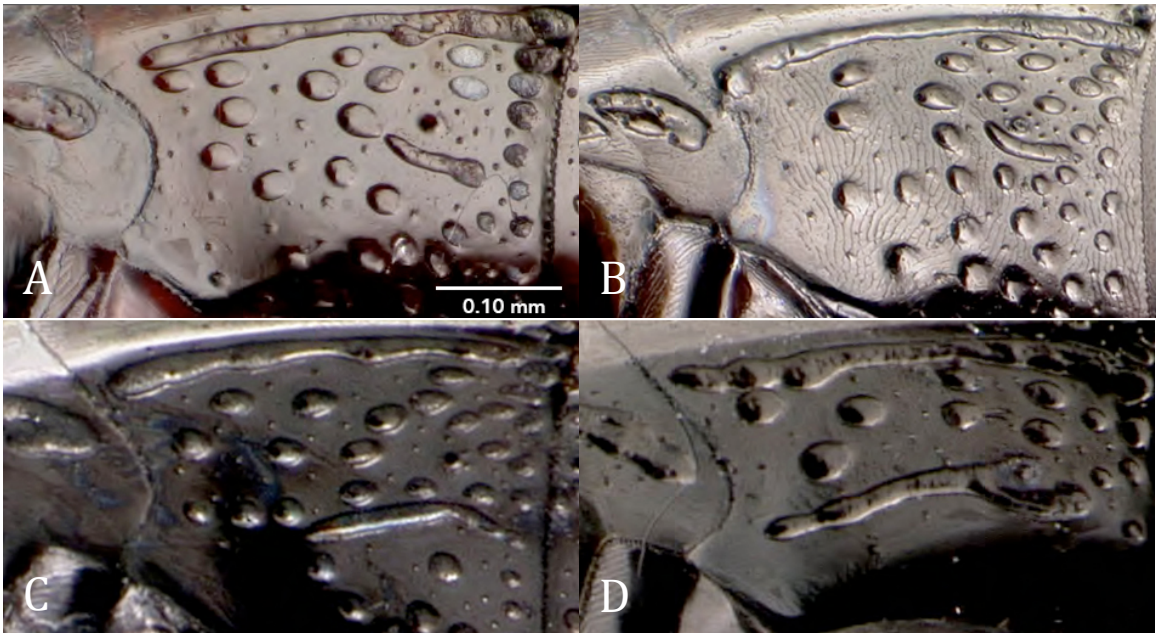

Figure 7. Variation in the lateral disc of the first visible abdominal sterna of *Carcinops*. A: Lateral disc "unmodified" type. Disc surface is smooth and only one stria is present. (*C. torquata*). B: Lateral disc "microrugulose" type. Disc surface has microrugulose texture and one stria is present. (*C. rugula*). C: Lateral disc "bistriate" type in *C. yaquiana*. Disc bearing an additional stria below the first one. Secondary stria straight or slightly notched at posterior end. (*C. yaquiana*). D: Lateral disc "bistriate" type in *C. consors*. Disc bearing an additional stria below the first one. Secondary stria diverging ventrally in posterior fourth. (*C. consors*). Photos by A. Swanson

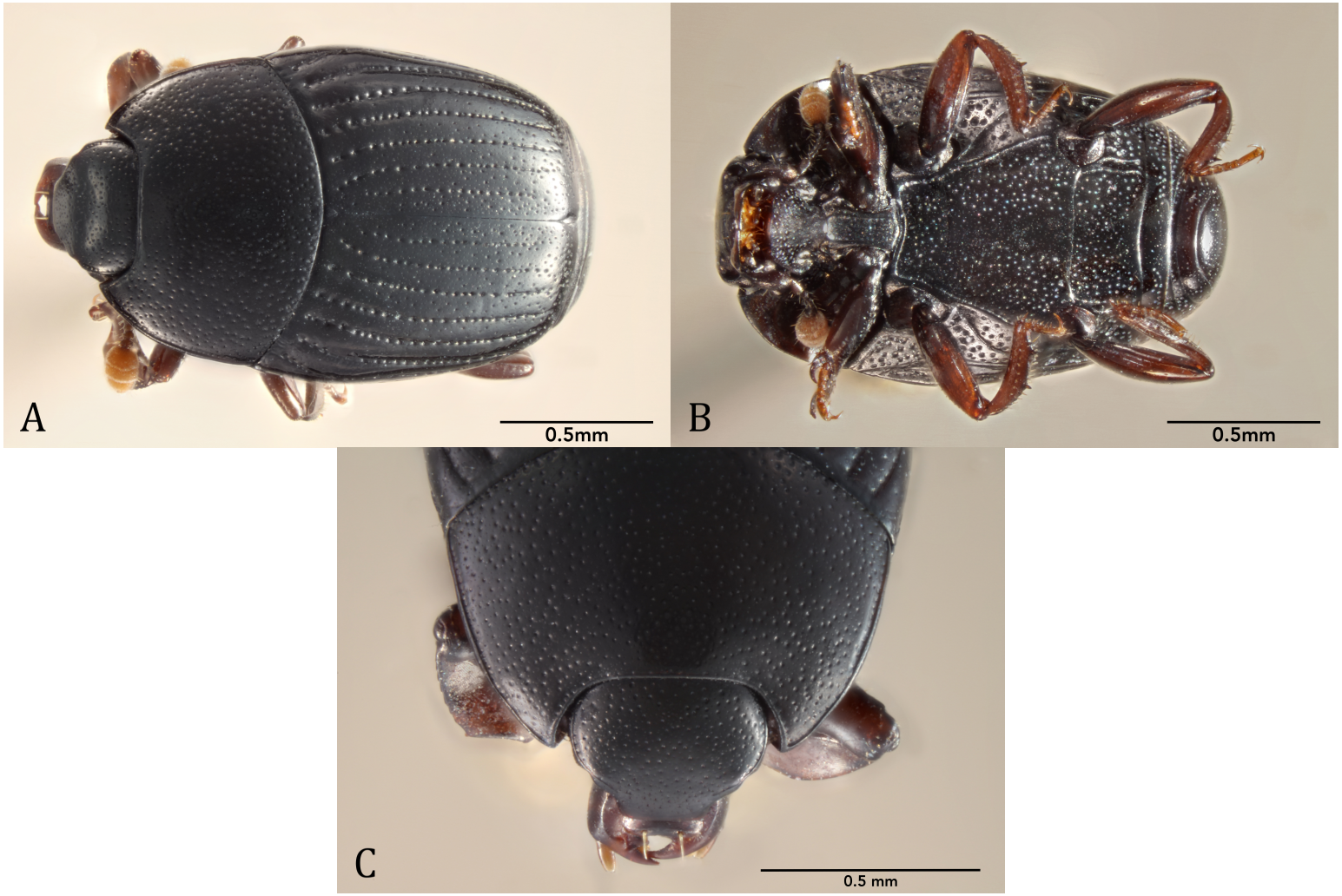

Figure 8. Photos of *Carcinops kumeyaayana* morphology. A: Dorsal view. B: Ventral view. C: View of head and pronotum.

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