Status, Distribution, Habitat, and Stressors of the Sonoran Talussnail

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Prepared for:

Arizona Game and Fish Department
5000 West Carefree Highway
Phoenix, Arizona 85086

Prepared by:

Aaron D. Flesch[1,2] and Hans-Werner Herrmann[1]
University of Arizona
School of Natural Resources and the Environment[1] and
The Desert Laboratory on Tumamoc Hill[2]
1675 West Anklam Road
Tucson, Arizona 85745
flesch@email.arizona.edu
hwh@arizona.edu


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EXECUTIVE SUMMARY

The Sonoran talussnail (*Soronella magdalenensis*) is known from eight mountain ranges in Pima and Santa Cruz counties in southern Arizona, and also occurs in adjacent Sonora, Mexico. Despite recent conservation concern and various threats to this species, little is known about current distribution and abundance or the ecology and habitat of populations. We assessed the distribution and relative abundance of talussnails across the potential range of the Sonoran talussnail in Arizona, modeled factors that explain occurrence and relative abundance, and estimated persistence of talussnail populations that had been documented historically. We surveyed talussnails in the field by sampling a broad set of randomly-selected plots stratified among four landforms (talus, mountain slope, upper bajada, drainage) and various historical sites, and quantified a range of environmental attributes and land-use intensity at all survey sites. Complications in species identification precluded unequivocal determinations that all observed talussnails were in fact Sonoran talussnails, but morphological measurements and tissue samples we gathered can help foster future efforts to identify individuals to the species level.

We surveyed 130 plots between mid-September 2018 and late February 2021 in 22 mountain ranges and adjacent landscapes and between 627 and 2,350 meters (m) elevation. Most surveyed plots were selected randomly (81%) with others mainly at old historical sites first documented before the 1970's (*n* = 15) versus more recently (*n* = 10). Although we targeted wet periods for surveys, only 37% of plots were surveyed within 2 days of local rainfall and time since the last rain event at the time of surveys averaged 12 ± 1 days (± SE; range 0-60 days). We found evidence of *Sonorella* presence within 37.7% of surveyed plots (which included 24.5% occupancy at random plots), and detected an estimated 526 live or dead individuals across the full range of sampled elevations in or around 17 mountain ranges. Relative abundance scaled by linear survey effort averaged 1.18 ± 0.31 individuals per 100 m (range = 0-31.1) across 131.9 km of linear survey effort and 128 person hours. Auspiciously, we documented evidence of recent occupancy of talussnails at 93% of old and 90% of new historical sites, suggesting high levels of population persistence. Plots at old historical localities were in the Santa Rita, Baboquivari, Cerro Colorado, Tumacacori, and Tucson mountains, on Tumamoc Hill, and on Black Mountain, and included most known historical localities from the early and mid-1900s within the range of the Sonoran talussnail. Some old historical localities in the Santa Rita, San Cayetano, Roskruge, and Comobabi mountains were not surveyed, some of which were on private or reservation lands.

Probability of occurrence at random sites varied widely among landforms ($P = 0.012$) and ranged from 0.58 ± 0.16 on talus, 0.27 ± 0.10 on mountain slopes, to much lower on bajadas and drainages (0.04-0.10 ± 0.04-0.06), with similar patterns for relative abundances that also increased across the same landscape gradient. There was limited evidence (P = 0.12-0.17) that occurrence probabilities and relative abundances varied among seven vegetation types we considered, but no evidence ($P \geq 0.41$) of variation among slope aspects or rock types. Across all plots, probability of talussnail occurrence increased with increasing volume of oak vegetation and decreased with increasing volume of succulents and basal cover of woody debris, after controlling for the effects of landform and site classification (e.g. random vs. historical). Across all 49 plots occupied by *Sonorella*, relative abundances increased with elevation and basal cover of rocks, and decreased with increasing volume of conifers and succulents. Relative abundances also decreased with increasing land-use intensity, which was linked mainly to off-road vehicle and foot traffic, invasive plants, and livestock grazing. Within 39 plots where we obtained measurements, relative abundances also increased strikingly with increasing mean size of rocks.

We submitted 23 specimens from seven mountain ranges to an expert for morphological measurements, and obtained data on external traits for all specimens and internal traits from 18 specimens with developed genitalia. Shell height ranged from 8.8 to 18 mm (mean ± SE = 12.6 ± 0.4 mm), shell width ranged from 14.0 to 28.5 mm (21.3 ± 0.7), and number of whorls ranged from 3.9 to 4.9 (4.4 ± 0.1). Penis length ranged from 3.4 to 22.2 mm (mean ± SE = 8.3 ± 1.3), verge length ranged from 2.3 to 12.4 mm (5.3 ± 0.8), and vagina length ranged from 3.3 to 12.9 mm (6.9 ± 0.6 mm); 50% of specimens had longer penis than vagina lengths, 39% had longer vagina length, and 11% had relatively equal genital lengths. Observed trait values were within known ranges for *Sonorella magdalenensis* for a specimen from Cat Mountain, Tucson Mountains, whereas specimens from Madera Canyon in the Santa Rita Mountains and one specimen from the Atascosa Mountains were more consistent with *Sonorella walkeri* based on diagnostic characters from Miller (1967). However, sample sizes were small and there was uncertainty as to whether fully mature specimens were examined, which are required for reliable identification. Therefore, morphological traits did not provide unequivocal identifications to species level.

Our findings provide some of the first recent and some novel inferences on talussnail distribution, abundance, habitat, threats, and population persistence across broad spatial gradients that spanned the entire known geographic and elevation ranges of the Sonoran talussnail. Auspiciously, we found that talussnails were broadly distributed across much of the study region and had relatively high occurrence probabilities in randomly-selected plots on talus and mountain slopes. Although more work remains, our findings suggest talussnails are generalists that use a broad range of vegetation and substrate types across a diversity of landforms, slopes, and aspects. Key habitat factors that explained distribution and abundance were linked to: 1) rock cover, rock size, and presence of talus and other rock-dominated landforms that can provide needed protection from high temperatures and desiccation, 2) factors such as ground cover of woody debris that influence access to sheltered microhabitats between and under rocks, and 3) cover of arid-adapted plants such as succulents and elevation that are linked to local and regional moisture availability. Importantly, we also found evidence that talussnail populations are sensitive to increasing land-use intensity, which poses a range of potential challenges and opportunities for conservation and management. Regardless, high levels of persistence of populations that were documented historically suggest broad-scale patterns of distribution are stable despite threats. Future efforts should assess local demographic attributes and how they are influenced by climate, microhabitat resources and conditions, and land use, and the phylogenetic and taxonomic status of populations.

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<u>Author Contributions</u>: HWH managed snail collections and processed live snail specimens, recruited an expert to measure specimens, and maintained permits. HWH participated in 61% of plot surveys, researched historical localities, and prepared GIS data and maps (Figs. 5-6). He drafted the introduction and reference list, and wrote sections on species identification, morphology, and genetics. ADF designed sampling and field methods, managed project implementation, and participated in 20% of plot surveys. ADF performed all data analyses, interpreted results, wrote the report, and addressed comments from peer reviewers.

<u>On the Cover</u>: Basaltic talus on the north slopes of Black Mountain on the San Xavier District southwest of Tucson where Henry Pilsbry documented *Sonorella* in 1910, and where we surveyed and found evidence of talussnails with help of the Tohono O'odham Nation (left; credit A. D. Flesch). Live *Sonorella* observed on 1/29/2021 at 1,820 m on the southeast slopes of Baboquivari Peak, Baboquivari Mountains (right; credit H.-W. Herrmann).

INTRODUCTION

Talussnails (*Sonorella*) are a diverse genus of land snails that include approximately 80 species (Miller 1967, Hall and Guralnick 2010). Typically, talussnails occur in steep rocky areas that have sufficient space between rocks to provide habitat. In these areas, access to sheltered places between and under rocks provides microhabitat and protection from high temperatures and desiccation (Bequaert and Miller 1973, Hoffman 1990, 1995). Talussnails are active during and shortly after rains and when sufficient humidity fosters activity that does not result in excessive environmental exposure or damaging water loss. Live individuals are infrequently encountered on the surface because activity periods are limited to these periods and are uncommon in arid environments. Although it is uncommon to find living snails in the wild, empty shells and shell fragments are commonly found in areas that support populations and provide evidence of talussnail presence. Nonetheless, because shells can persist in the environment for at least ~15 years following the death of an individual and may last decades before degrading, presence of shells does not necessarily provide evidence of recent occupation (Sorensen 2018, Jeff Sorensen, AZGFD, *pers. comm.*).

The genus *Sonorella* was first described by Henry Pilsbry in 1901 based on snails formerly placed in the genus *Helix*. In decades that followed, Pilsbry and his colleague James Ferriss led extensive field expeditions that resulted in the description of numerous species and subspecies, many of which were restricted to individual and often isolated mountain ranges (e.g., Pilsbry and Ferriss 1915, 1923). Differentiating and identifying talussnails to the species level has been based largely on shell and genital morphology. Identifications based on shell morphology alone are challenging or not possible and so genital morphology of mature snails has provided the most operational diagnostic characters (Miller 1967). In his revision of the genus, Miller (1967) noted that either shell or genital characters or a combination of both, together with locality information can be used to differentiate taxa. The use of locality information to identify taxa, however, highlights the limited utility of independent diagnostic characters. Miller (1967) recognized 64 species and 20 subspecies as valid but several additional species have been described since his seminal revision of the genus. The center of distribution and diversity of *Sonorella* is in southeastern Arizona, especially in the Madrean Archipelago or Sky Islands region and surrounding areas (Miller 1967, Bequaert and Miller 1973, U.S. Fish and Wildlife Service 2012).

In land snails, high intraspecific plasticity of shell traits has been repeatedly demonstrated (Köhler and Burghardt 2016, Simison and Lindberg 1999, Teshima et al. 2003, Nekola et al. 2015, 2018). Such variation can lead to the unwarranted inflation of species numbers without biological justification. Early on, malacologists realized that the “fact that dwarf specimens occur rather frequently with nearly all the species (of *Sonorella*) renders it difficult to distinguish the normally small species from small individuals of similar larger species. All the species being more or less variable in form and surface texture, the group is one which presents unusual difficulties to the student” (Dall 1897). Furthermore, it was also noted that “the shells of the various species of *Sonorella* bear close resemblance to each other” (Bartsch 1905). The integration of genetic data with traditional morphological traits can hence be vital in determining reliable species-level identifications (Horsakovo et al. 2019). In some cases, where genetics and morphology have been integrated, genital morphology and genetic divergence are more consistent and useful in delimiting species, while in other cases shell traits provide little utility (Sutcharit et al. 2020). Species delimitations based on morphology alone often include a high degree of homoplastic characters, which are traits shared by a set of species but not present in their common ancestor and can lead to misleading conclusions (Giokas 2000, Elejalde et al. 2008).

Here, we focus generally on the distribution and habitat of *Sonorella* within and immediately around the known range of the Sonoran talussnail (*Sonorella magdalenensis*). Given a lack of associated genetic work, we assumed individuals from the genus *Sonorella* that we observed in this region represented this species, but also evaluated this assumption based on morphological traits. This approach is not without issue given that in Arizona *S. magdalenensis* co-occurs with other *Sonorella* species. For example, following Miller (1967) *S. sabinoensis tucsonica* occurs in the Tucson Mountains with *S. papagorum* being found close by on Black Mountain. *Sonorella ambigua* and *S. baboquivariensis berryi* occur in the Roskruge Mountains. The Santa Rita Mountains harbor several species: *S. h. huachucana*, *S. santaritana*, *S. walkeri* including the now synonymized *S. rosemontensis* (Hoffman et al. 2012), and *S. clappi* and *S. tryoniana* along Sonoita Creek near the Santa Rita Mountains. Whereas no other species are mentioned from Tumacacori Peak, *S. walkeri* occurs in the adjacent Atascosa Mountains.

The Sonoran talussnail was originally described as *Helix magdalenensis* by Stearns in 1890 based on nine specimens collected by Vernon Bailey near the town of Magdalena de Kino, Sonora, Mexico (Stearns 1890). In 1893, live specimens from the Death Valley area of California were collected and classified as the same species, but presently these populations are not included in the genus *Sonorella*. Subsequently, Pilsbry (1939) synonymized *S. hinkleyi*, *S. tumacacori,* and *S. cayetanensis*, which he and Ferriss described in 1919, with *S. arida* now considered a synonym of *S. magdalenensis*. Later, Miller (1967) synonymized *S. tumamocensis*, *S. linearis*, and *S. sitiensarida* with *S. magdalenensis*. The distribution of the Sonoran talussnail was originally described as being from the Tucson Mountains south through the Santa Cruz Valley into Sonora south to the Sierra Pajaritos near Ures, Sonora (Miller 1967). Bequaert and Miller (1973) provided a more detailed description of the range noting occurrences in seven mountain ranges in Pima and Santa Cruz counties, Arizona: the Tumacacori and San Cayetano mountains in Santa Cruz County, and the Cerro Colorado, Roskruge, Tucson, and Santa Rita mountains, and on Tumamoc Hill in Pima County. Miller (1967) and Naranjo-Garcia (1988) also provided distribution maps (Figure 1). Although widely overlooked, Pilsbry and Ferriss (1923) also noted the now synonymized *S. tumamocensis* in the Silver Bell Mountains.

The current distribution of species within the genus *Sonorella* has been explained by Pleistocene glacial advances during pluvial periods and glacial retreats during drier and warmer periods, which created conditions suitable for dispersal and vicariance (Miller 1967, McCord 1995). In this context, current distributions are viewed as relicts restricted to disjunct and often isolated refugia. These distributions may narrow further in the future as a result of increasing temperature and decreasing rainfall linked to climate change.

Little is known about the ecology and habitat use of the Sonoran talussnail. Like many other species in the genus *Sonorella,* it is reasonable to assume *S. magdalenensis* prefers steep rocky areas with deep interstitial spaces among rocks, which provide protection from heat and desiccation. Most historical localities match this general description (Pilsbry and Ferriss 1915, 1923, Bequaert and Miller 1973, Hoffman 1990, 1995). Currently, however, there are virtually no inferences on how distribution or abundance is influenced by vegetation and other physical environmental features, although the broad elevation range of past observations (e.g., 839-1,830 m; Bequaert and Miller 1973) suggests use of a wide range of environments. Not surprisingly, talussnail activity is highly dependent on weather conditions with snails being active on the surface only during or shortly after rains. Long periods of drought can greatly restrict activity and estivation can last up to three years (Hoffman 1990). These large fluctuations in activity may drive variation in growth, reproduction, and survival. Talussnails are thought to live for up to 9 years but there is little information from across the range (Hoffman 1995).

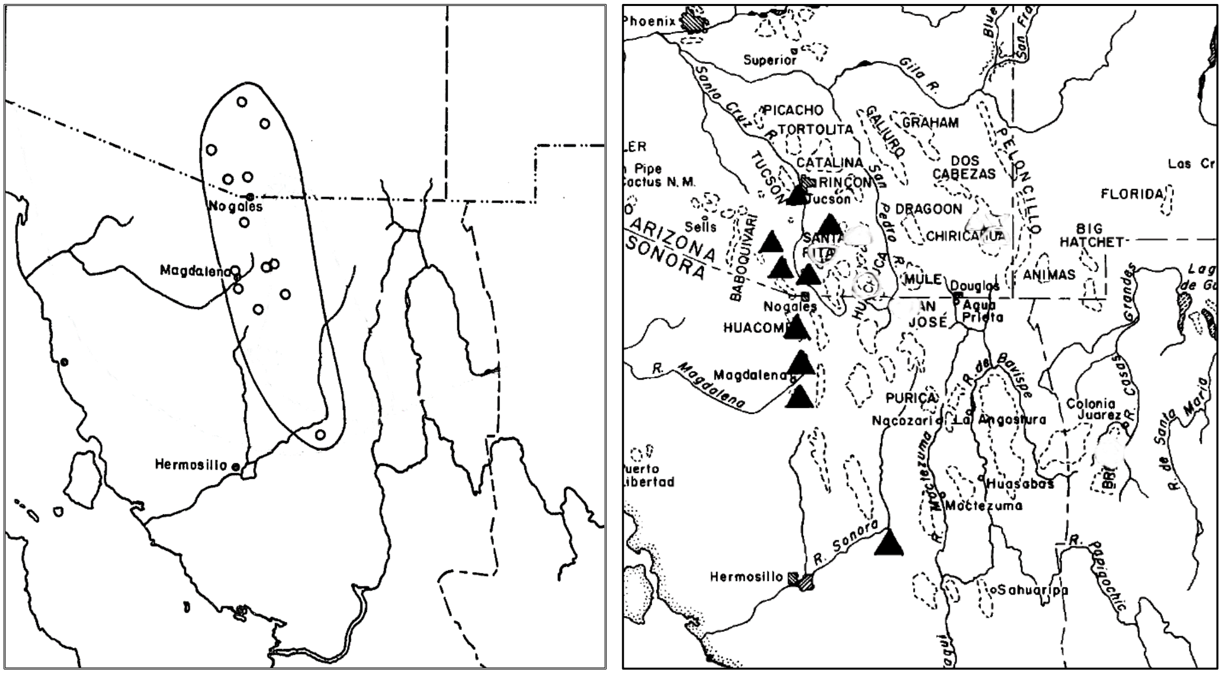

Figure 1. Distribution of *Sonorella magdalenensis* adapted from Miller (1967; left) and from Naranjo-Garcia (1988; right).

In 2010 the Center for Biological Diversity filed a petition to list the Sonoran talussnail, together with the now synonymized Rosemont talussnail (*Sonorella rosemontensis*), as a threatened or endangered species under the Endangered Species Act. Subsequently, the U.S. Fish and Wildlife Service (USFWS) published a 90-day finding in 2012 concluding *Sonorella magdalenensis* is, based on the available data, a valid species and requested information to guide an upcoming species status assessment (USFWS 2012). Currently, however, there are little data on the abundance, status, and trends of populations, or information on threats to help guide assessments. Proposed and ongoing mining is considered a potential threat to the Sonoran talussnail, either through direct habitat loss and fragmentation or by degrading habitat by impacting water quantity and quality, or potentially other impacts. Invasive plants such as exotic buffelgrass (*Pennisetum ciliare*) are also considered threats to talussnail populations because they can increase the frequency of fires. Herbicides used to control buffelgrass may also be an additional threat to populations (Center for Biological Diversity 2010, USFWS 2012).

We assessed the distribution, relative abundance, persistence, threats, and habitat use of the Sonoran talussnail by surveying snails in the field and describing the environment at both previously documented historical localities and at randomly-selected locations across a range of landforms. We also gathered data on potential threats to talussnails at survey sites and collected live specimens to foster morphological measurements and tissue samples for follow-up genetic analyses (Herrmann 2021, and in prep.). A challenge and limitation of this study is the complexity of identifying talussnails to the species level given unresolved phylogeny of the genus and phylogenetic relationships of the Sonoran talussnail in particular. Because the extents of species' ranges are uncertain and shell and genital morphology provide somewhat poor diagnostic characters, we assumed individuals observed within and immediately around the known range of the Sonoran talussnail represented *Sonorella magdalenensis*. Although genital morphology may provide useable data to separate species, it requires mature individuals with fully developed genitalia, specialist knowledge, and dissecting skills that cannot be used in the field or with shells that represented the majority of our talussnail observations. Therefore, this work embodies a study of talussnails (*Sonorella*) within and adjacent to the known range of the Sonoran talussnail, rather than an exclusive study of only the Sonoran talussnail (*Sonorella magdalenensis*) per se. Ultimately, a new and comprehensive effort to uncover the phylogeny of *Sonorella* based on genomics and morphology will be necessary to validate species and possibly provide more useful diagnostic characters for field identification.

OBJECTIVES

Objectives of this study are to:

1. Gather data on the presence, relative abundance, stressors, and habitat of the Sonoran talussnail at historical localities and new areas that had not been surveyed in the past across its potential range in Arizona.
2. Assess associations between Sonoran talussnail occurrence and relative abundance and various environmental factors focused on habitat attributes, anthropogenic stressors, and climate.
3. Assess the potential distribution of the Sonoran talussnail at broad scales based on observed patterns of occurrence.
4. Collect voucher specimens for species identification and future genetics studies of the taxonomy, differentiation, and connectivity among populations.
5. Gather vouchers and data on presence of other land snails in this and other genera encountered during surveys.

METHODS

Study Design: We selected survey sites across the potential range of the Sonoran talussnail by considering mountain ranges and adjacent valleys within and immediately around the known U.S. range as our sampling frame. This included a region bounded by the Roskruge and other nearby mountains to the north, Baboquivari Mountains to the west, Santa Rita, San Cayetano, and adjacent mountains to the east, and the U.S.-Mexico border to the south. Within this region, we selected two types of sites for surveys, historical sites and random sites. Historical sites included two groups of sites: 1) those described by Pilsbry and Ferriss (1915) and Bequaert and Miller (1973) that were documented between approximately 1910 and 1967 and located on public lands we could access (hereafter "old sites"), and 2) more contemporary observations of talussnail that were mostly documented on the Pima County Conservation Land System by our partners and collaborators with the Pima County Office of Sustainability and Conservation between 2016 and 2020 (hereafter "new sites"). To locate old sites, we used descriptions and maps from the literature, which were often fairly detailed. We acknowledge, however, that not all survey locations were in the exact locations of past efforts, but all sampled the same general populations. Second, we randomly selected sites within the study area using a two-stage, stratified-random sampling design. This involved selecting a set of 500 random points across the study area and surveying plots in the nearest accessible potential habitat in as many as four landforms (1-talus, 2-mountain slope, 3-upper bajada, and 4-drainage) present within approximately 5 km of each random point. Landforms included talus composed of loose or more stable rock piles or scree, and rocky or forested slopes in mountains, which we focused on given known associations with talussnails. They also included rocky upper bajadas at or near the toe-slopes of mountains and drainages that included rocky canyon and drainage bottoms. Among all 500 random points, we only considered areas on public lands that we could obtain legal access to for field surveys and attempted to allocate effort broadly so as to cover the study region with similar sampling effort. This design ensured a broad scope of inference both spatially and to specific landforms, which likely provide habitat for the species of varying quality and support a full range of natural variation in densities. When surveying historical sites limited to single landforms, we surveyed other adjacent landforms in the surrounding landscape if they were linked to random points to obtain broader coverage and for efficiency. We focused surveys after rain events and during prolonged rainy weather in winter and late summer when soils were relatively wet and humidity was higher. Given the rarity of these conditions during much of the project period, and our goal to augment survey coverage, we also surveyed during dryer periods primarily in fall and winter.

Survey Methods: To survey snails, we followed the Arizona Game and Fish Department (AZGFD) Land Snail Survey Protocol (AZGFD 2016), but added additional methods and measurements to better describe habitat. This method involves visual encounter surveys during fixed 30-minute search periods per plot. When implementing surveys, we arranged plots to best cover the available habitat in an area within each focal landform type so that surveys were constrained by time and not by area. To estimate spatial survey effort, we used track lengths from handheld global positioning systems (GPS; Garmin brand) to quantify the area covered by observers within each 30-minute search period. We typically worked in teams of 2 surveyors that each recorded data during the survey period, with all surveyors starting and stopping at the same time; some plots were surveyed by 1, 3, or rarely more observers. During surveys, we systematically searched for live and dead snails on the ground, on and under rocks, within interstitial spaces among rocks, and under branches, leaf litter, dead wood, and live and decaying plants, and focused on and near the ground. Empty shells from recently deceased talussnails have a glossy, pigmented keratinaceous outer coating, or periostracum that is intact on the shell. Shells from individual snails that have been dead for longer periods lose this pigmented outer coating including the stripe on the outer shell, and appear chalky white when worn (Ian Murray, Pima County, *pers. comm.*).

During surveys, we used headlamps to illuminate dark crevices among rocks, in debris, and in other potential hibernacula where snails may estivate or be found active. We also searched for “mucous trails” and epiphragm marks because they are useful indicators of snail presence (AZGFD 2016). During surveys, each surveyor counted the total number of mature and juvenile live snails and shells, and number of shell fragments. In general, mature Sonorella may be separated from juvenile specimens based on the number of whorls on the shell. Mature Sonoran talussnails have about 4.5 whorls (Pilsbry 1915), and though there is likely some degree of plasticity in body size within populations (Miller 1967), the number of whorls for mature specimens may remain relatively consistent across small-bodied and larger-bodied individuals (Ian Murray, Pima County, *pers. comm.*). At the end of a plot survey, we totaled numbers in these categories and recorded them on data sheets.

We recorded all information noted in the AZGFD Land Snail Survey Protocol datasheet and developed methods and an associated datasheet to accommodate additional habitat measurements (Appendix A). This information included measurements of the following resources and conditions within each plot based on rapid visual-based field estimation: 1) dominant major vegetation type in eight categories (1-rocky un-vegetated area, 2-desert shrubland, 3-arborescent mixed desertscrub or desert woodland, 4-grassland, 5-montane shrubland, 6-oak woodland, 7-oak-pine woodland, 8-riparian vegetation), 2) average vegetation canopy cover, 3) percent basal cover in five categories (1-bare ground, 2-rock, 3-live vegetation, 4-litter, 5-dead woody debris), and 4) percent vegetation volume in each of seven physiognomic categories (1-oak, 2-conifer, 3-broadleaf deciduous, 4-broadleaf evergreen, 5-microphyllous, 6-succulent, and 7-grass or forb). Similar to the AZGFD Land Snail Survey Protocol, we also described presence of various land uses and potential stressors and estimated intensity (0-none, 1-low intensity or coverage on small portion of plot or adjacent to plot, 2-moderate to high intensity or coverage on much of plot). Cover and volume were estimated visually to the nearest 10% for values between 20 and 80% and to the nearest 5% otherwise. Mean diameter of rocks on the surface was also estimated within some plots but missing values prevented use of this metric in models. We used GPS and clinometers to estimate elevation, slope, and aspect. To classify rock types, we used GIS data (Horton et al. 2017) to differentiate four basic rock types (1-alluvium or unconsolidated, 2-volcanic, 3-sedimentary, 4-granitic) and local field observations to separate basalt and limestone, which we could readily identify in the field and considered separately because we suspected they may be important substrates. Finally, we recorded air temperature and relative humidity at the start of each plot survey with use of handheld weather meters (Kestrel brand), and the time since the last rain event that occurred prior to surveys based on data from the closest or most comparable weather stations.

Laboratory and Collection Methods: During this work we emphasized the collection of voucher specimens for species identification efforts linked to this project and for future studies of species delimitation and population genetics (Herrmann 2021 and in prep.). All shells, and where found, live specimens from each population were collected, except on San Xavier lands where we did not collect samples. AZGFD recommends taking no more than half the live individuals encountered or a maximum of 15 individuals from a population, and we collected no more than five live snails at any one site and all shells where possible. Specimens were handled following Nick D. Waters' "Recommended Terrestrial Gastropod Handling Procedures" (AZGFD 2016). All tissues for future genetic analyses were stored in 95% EtOH and along with shell specimens will be submitted to the Santa Barbara Museum of Natural History in California. All voucher and tissue collection protocols followed standard malacological methods.

Identifying *Sonorella* snails to the species level is difficult and depends on inspection of microscopic features. To help ensure individual snails were correctly identified, we submitted a subset of specimen collections to an expert (Dr. Casey Richart) for measurement of genital morphology and various external traits. This work focused on measuring penis, verge, and vagina length internally with the use of microscopes, and shell height, width, and number of whorls externally with the use of micro-calipers and other measuring tools. Based on these measurements, we then assessed whether observed values of these traits for specimens we gathered were within or outside the known range of values for *Sonorella magdalenensis.* Photographs of internal and external traits were made for illustrative purposes, and to foster and aid future independent verification of trait values and species identifications (Appendix B and C). Shells and tissue samples we collected were submitted to the Invertebrate Zoology Department snail collections at Santa Barbara Museum of Natural History.

ANALYSES

We summarized patterns of occurrence and relative abundance across a range of spatial and habitat attributes including landform, mountain range, vegetation type, and across gradients in elevation, slope, aspect, and vegetation cover. To estimate relative abundance, we scaled number of all live and dead individuals observed within plots by total survey effort in meters estimated by lengths of GPS tracks of surveyors during each 30-minute search period, and computed number of individuals per 100 m. This approach is likely more reliable than scaling observations by search time given broad variation in area covered among plots, which depends on the spatial arrangement and density of habitat. Regardless, we also reported relative abundance scaled by time (no./30 mins/observer) over all surveys for comparison with other efforts. Relative abundance scaled by spatial effort was highly correlated with that scaled by search time ($r = 0.76$, $p < 0.0001$), especially on the log scale ($r = 0.90$, $p < 0.0001$). We considered all live and dead individuals combined when computing relative abundance and considered partial shells as individuals because they almost always included central whorls and hence represented different individuals.

We estimated persistence of populations by computing the proportion of both old and new historical sites we found occupied during the project period and with a model-based approach (see below). When estimating persistence, we considered shells as evidence of recent occupation despite the fact they can persist in the environment for nearly 2 decades and perhaps longer (Sorensen 2018, Sorensen, *pers. comm.*). Nonetheless, old historical sites were all documented before 1970, with most from the early 1910s that were indicative of populations in the more distant past. For each historical site, we also computed the number of past observations at the site and time since the first and last known observation for summary purposes.

To assess how occurrence and relative abundance of talussnails varied with environmental factors and potential stressors, we developed linear and generalized linear mixed models (GLMM and GLM). These models included either presence/absence or relative abundance as response variables, and different vegetation, physiographic, land-use intensity, and other factors as explanatory variables. Because presence of most land-use types was rare, we computed an overall index of land-use or stressor intensity by summing scores across all types for each plot. We considered observations from both historical and random plots when building models and used two subsets of the data depending on the response variable and question. When assessing factors that explained occurrence, we used all data from all plots. When assessing factors that explained relative abundances, however, we only used data from plots where at least one talussnail was observed and censored data from plots where no observations occurred, which eliminated zero-inflation in the distribution of the response and better met the assumptions of models. For each of the two responses, we also fit models that included only the design variable landform type and plot type (random vs. historical) and computed least square means and associated standard errors to estimate spatial variation in occurrence probability and relative abundance. These models also allowed us to estimate occurrence probabilities for historical vs. random plots across the four landform types, which was useful for evaluating population persistence at historical sites. Because data from surveys of plots located around the same random points were not independent, we fit random point or landscape identity (for historical sites) as a random effect. We assessed correlations among predictor variables before modeling and eliminated one variable from highly correlated pairs ($r > 0.60$). We used backwards elimination on a full model that included all predictors when assessing factors that explained occurrence, stepwise selection (StepAIC from *MASS* library) when assessing factors that explained relative abundance, and AIC_c to guide model selection. All models were fit with the *lme4* and *nlme* libraries in R with marginal effects computed by the *eemeans* and *ggpredict* libraries (Pinheiro et al. 2012, Bates et al. 2015, R Core Team 2021). We also explored using species distribution models combined with various large-scale data sets on elevation, topography, and climatic attributes to predict probability of occurrence across the range in southern Arizona. Such efforts were difficult due to lack of data availability on local presences and sizes of rocks that we could measure in the field, but were not well represented in available GIS data, which would have produced

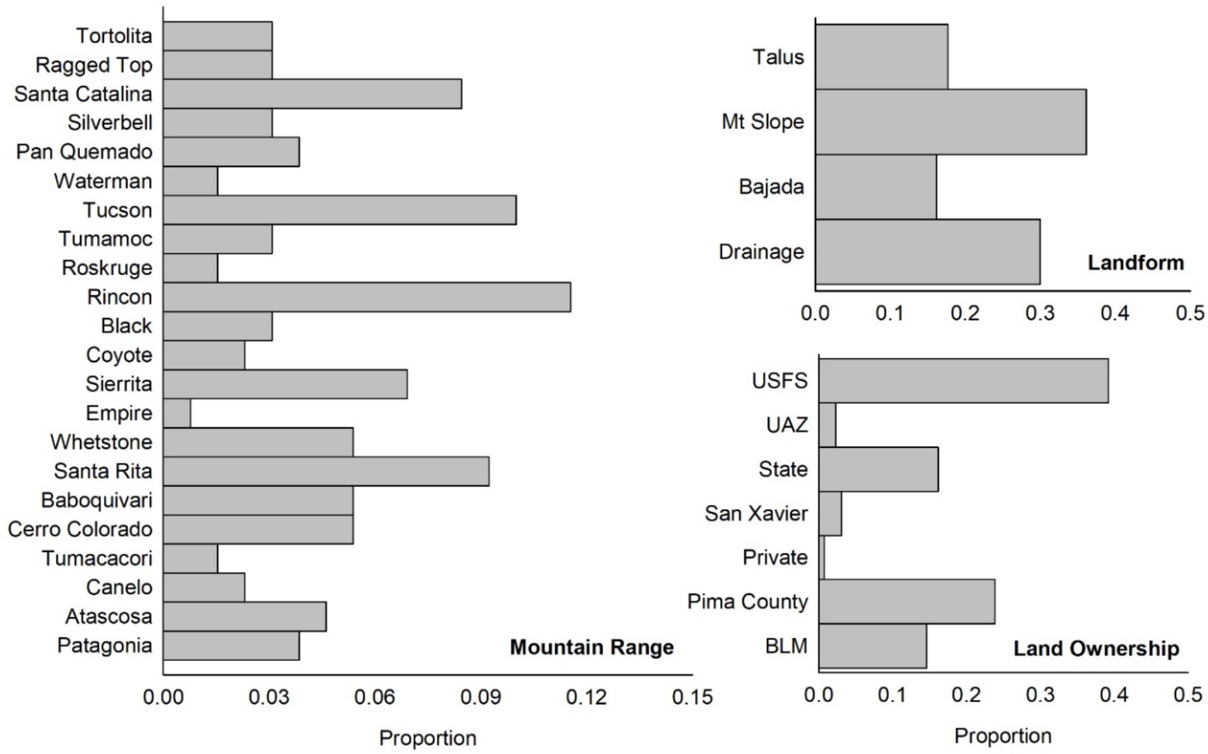

Figure 2. Survey effort in proportion of plots among various mountain ranges, landforms, and land ownership considered during talussnail surveys between Sept. 2018 and Feb. 2021 in southern Arizona. Mountain ranges are listed from north to south, and landforms are list in order of slope position.

questionable results. Hence inferences of potential distribution and abundance were based largely on results of GLMs and GLMMs.

RESULTS

Effort and Observations: We surveyed 130 plots during the project period between mid-September 2018 and late February 2021. Plots were located across much of the study region at a broad range of elevations (627-2,350 m; mean ± SE = 1,219 ± 32 m). We selected the vast majority of surveyed plots randomly (*n* = 105 of 130 or 81%) around 41 random points. All remaining plots we surveyed were at historical localities, which were mostly old sites that were first documented before the 1970's (*n* = 15) compared to those of more contemporary origin (*n* = 10). Effort was allocated across 22 mountain ranges and adjacent landscapes and was greatest in the Rincon, Tucson, Santa Rita, and Santa Catalina mountains, and also covered smaller ranges such as the Coyote, Tumacacori, and Waterman mountains, and Tumamoc Hill and Black Mountain (Figure. 2). With regard to landforms, effort was greatest on mountain slopes and in drainages, and lower in talus, which was rare in the study region, and on upper bajadas. With regard to land ownership, the vast majority of plots were on U.S. Forest Service lands, with moderate to high levels of effort on Pima County, State, and Bureau of Land Management lands, and much lower effort elsewhere (Figure 2). A broad range of vegetation types were covered from desert scrublands at low elevations to oak-pine woodlands in the mountains (Figure 3). Rock substrates we covered were mainly granitic in origin, but also included many plots on volcanic and sedimentary rock types, whereas alluvial or unconsolidated substrates were rare (Figure 3). Roughly half of plots in

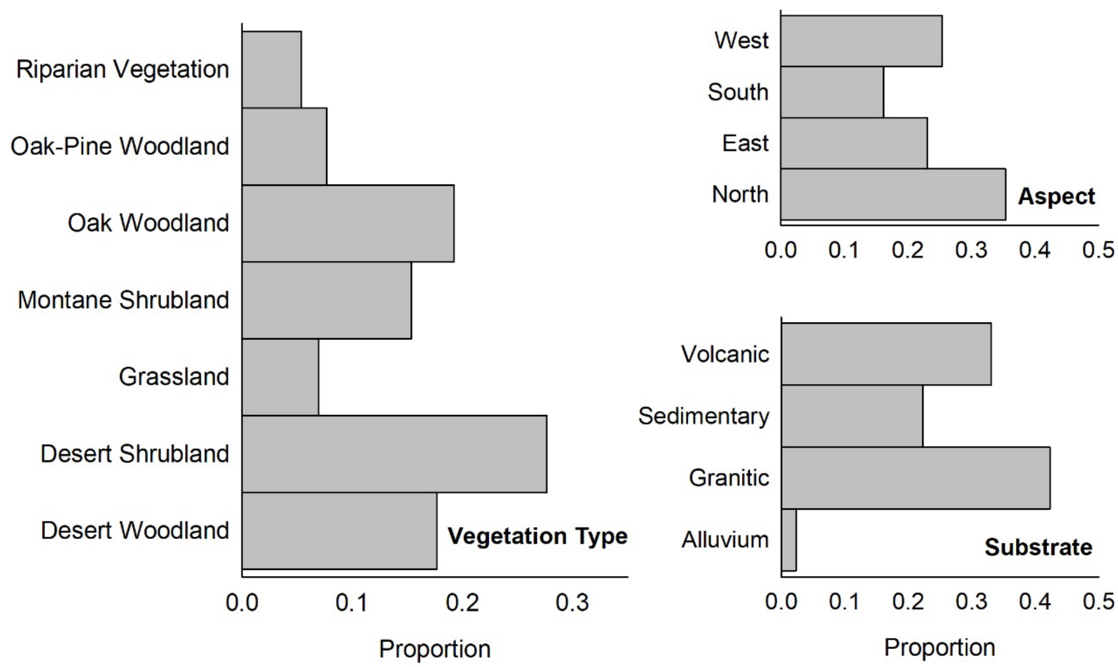

Figure 3. Survey effort in proportion of plots among various vegetation types, aspects, and rock substrates during surveys of talussnail between Sept. 2018 and Feb. 2021 in southern Arizona. Alluvium includes other unconsolidated substrate types.

sedimentary types were in limestone, whereas only 28% in volcanic types were in basalt. Effort was roughly equally divided between east and west-facing aspects, with more plots surveyed on north- than south-facing aspects (Figure 3). Linear survey effort across all plots totaled 131.9 km and averaged 1,015 ± 53 m per plot with 94.6% of plots surveyed by 2 or fewer observers. Survey time across plots totaled 128 person hours. We specifically targeted wet periods for surveys, with 37% of plots surveyed with 2 days of local rainfall. Days since the last rain event at the time of plot surveys averaged 12 ± 1 days (range 0-60 days) and relative humidity during surveys averaged 37.7 ± 1.6% (range = 9.3-97.8%).

Across all surveys, we observed evidence of *Sonorella* within 37.7% of all plots (*n* = 49 of 130) with live snails observed within 28.6% of occupied plots (*n* = 14 of 49) and 24.5% occupancy at random plots. In total, we documented 26 live *Sonorella* snails (18 adults, 8 juveniles), 266 shells of deceased individuals (219 adults, 47 juveniles), and 234 partial shells, for a total of 526 observations across all categories. Relative abundance scaled by linear survey effort averaged 1.18 ± 0.31 individuals per 100 m (range = 0-31.1) across all plots, and 3.14 ± 0.76 individuals per 100 m within occupied plots. Relative abundance scaled by time averaged 2.58 ± 0.63 individuals per 30 min per observer (range = 0-43) across all plots, and 6.86 ± 1.48 individuals per 30 min per observer within occupied plots.

Historical vs. Contemporary Occurrence Patterns: We resurveyed 15 plots at old historical sites located in the Santa Rita (5), Baboquivari (3), Cerro Colorado (2), Tumacacori (2), and Tucson (1) mountains, and on Tumamoc Hill (1) and Black Mountain (1). This included most accessible historical sites noted in Pilsbry and Ferriss (1915) and Bequaert and Miller (1973) with the exception of some in the Santa Rita, San Cayetano, Roskruge, and Comobabi mountains, some of which were on private lands or the Tohono O'odham Nation. Sites in the Comobabi Mountains may not represent true Sonoran talussnails localities.

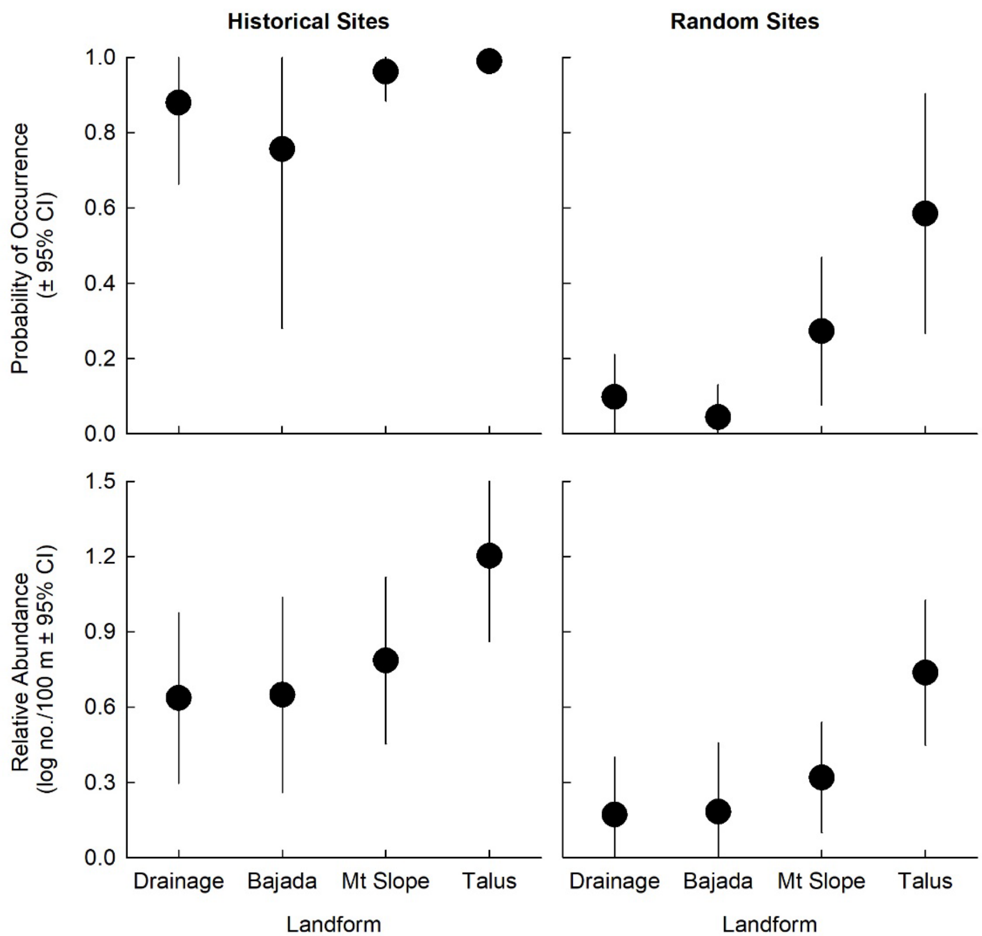

Figure 4. Probability of occurrence (top) and relative abundance of talussnails across four landforms we sampled at both historical (left) and randomly-selected (right) sites in southern Arizona, Sept. 2018 to Feb. 2021. Estimates and asymmetric 95% confidence intervals are predicted marginal effects from generalized linear mixed models of presence/unobserved data and linear mixed models of relative abundance data with both landform and site classification (random or historic) fit as fixed effects and random point or landscape identity fit as random effects. Data from all 130 plots are considered in each model.

Most old sites were first documented in 1910 with two first found in 1960 and 1967, and located mainly on mountain slopes (8) or in talus (5), with just one each on bajadas or drainages. Notably, we observed evidence of *Sonorella* within 14 of 15 plots (93.3%) at old sites, with live snails observed within 3 of 14 occupied plots. The only old site not found to be occupied was in a drainage located in the Santa Rita Mountains along Box Canyon (below the dam).

The 10 new historical sites we resurveyed were located in the Tucson (3), Santa Rita (2), Coyote (1), Sierrita (1), Roskruge (1), Santa Catalina (1), and Rincon (1) mountains. Most were first documented by Pima County in 2016 and 2017 with two first found by Hoffman et al. (2012) in 2011 and by Jeff Sorensen in 2017. All sites were on mountain slopes (3), talus (3) or along drainages (4). Similar to patterns at old sites, we observed evidence of *Sonorella* within plots at 9 of 10 (90%) new sites, with live snails observed within 5 of 9 occupied plots. The only new site not found to be occupied was in a drainage also in the Santa Rita Mountains (Box Canyon E. of Proctor Road; Hoffman et al. 2012).

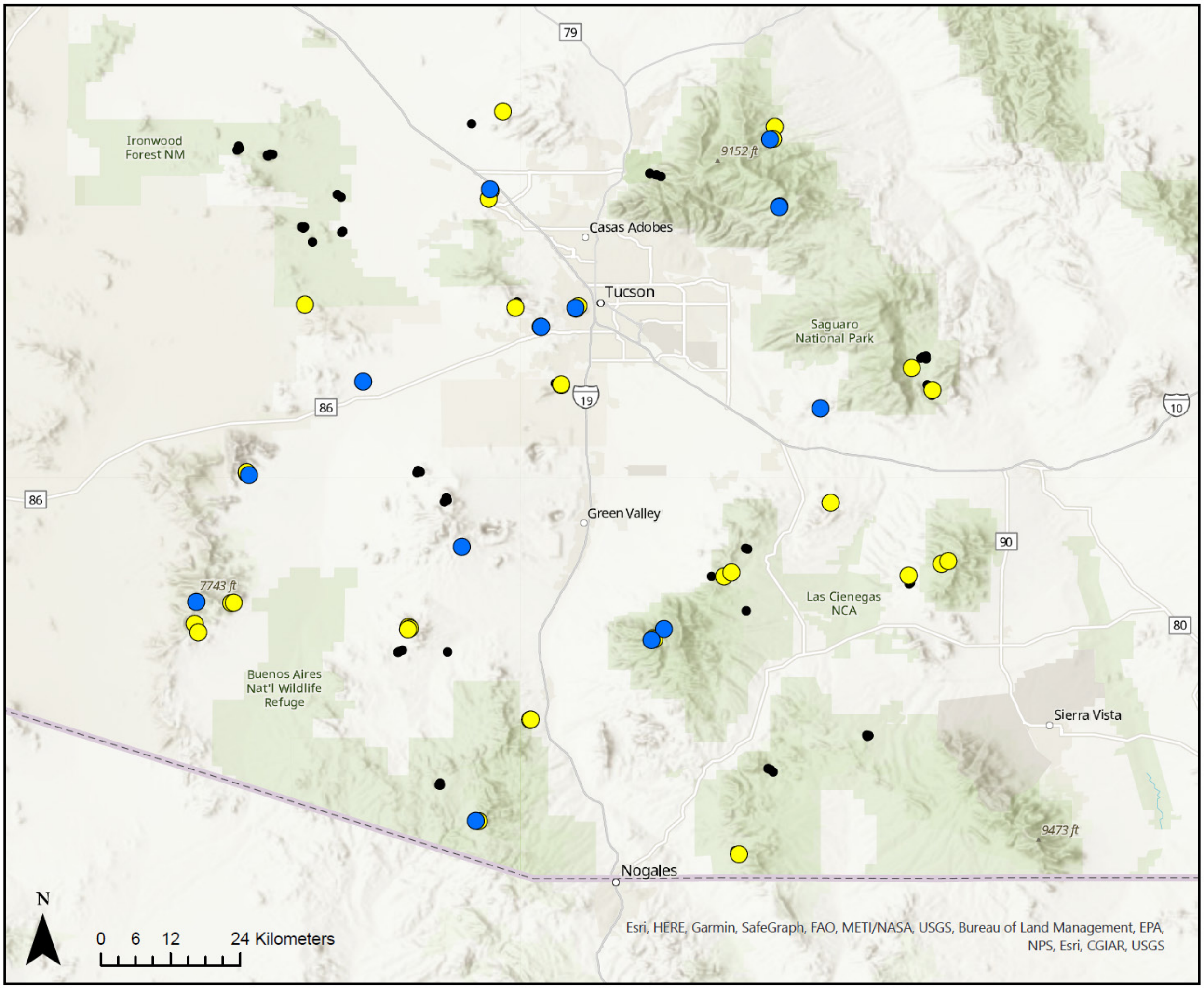

Figure 5. Distribution of survey plots and talussnail observations in southern Arizona across 130 plots surveyed between Sept. 2018 and Feb. 2021. Survey sites where no talussnails were observed are depicted by small black circles, blue circles depict locations where live talussnails were observed, and yellow circles depict locations where only talussnail shells were observed. With one exception, all sites where live individuals were observed also harbored shells.

Probability of occurrence at historical sites on mountain slopes and in talus were essentially one (0.96 and 0.99, respectively), but somewhat lower and more variable in other landforms that featured fewer historical sites (Figure 4). Not surprisingly, probability of occurrence was also much higher at historical than at random sites (Figure 4). Across all random sites, point estimates of probability of occurrence were 0.58 on talus and 0.27 on mountain slopes, but 95% confidence intervals overlapped. Probability of occurrence on talus, however, was significantly higher than that on bajadas or drainages (Figure 4).

<u>Current Patterns of Distribution and Relative Abundance</u>: We observed talussnails across much of the study area including in 77.3% of mountain ranges (n = 17 of 22) we surveyed (Figure 5). Exceptions were the Canelo Hills, and ranges to the north of the Roskruge Mountains (Pan Quemado, Silver Bell, Waterman, Ragged Top). Importantly, this included observations of live individuals in 10 ranges or 45.5% of mountain ranges or adjacent landscapes we considered. Elevation range of talussnail observations

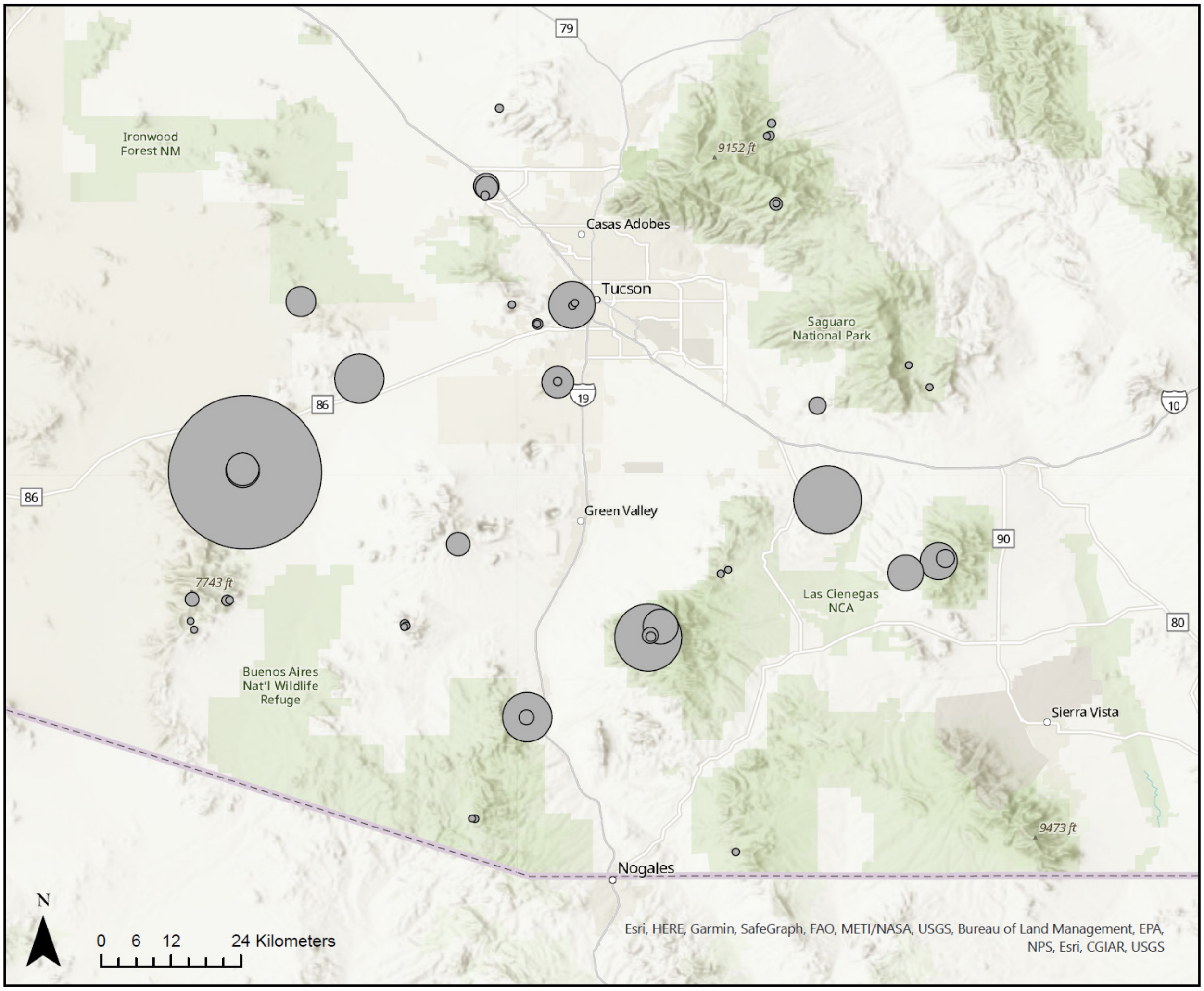

Figure 6. Relative abundance of talussnails across 49 plots where we observed at least one talussnail during surveys in southern Arizona between Sept. 2018 and Feb. 2021. Circles are scaled proportionally across the full range of relative abundances (range = 0.07-31.1) and expressed as number observed per 100 m of linear survey effort.

spanned the entire range of surveyed elevations from 627 m at the north end of the Tucson Mountains to 2,350 m on the summit of Apache Peak in the Whetstone Mountains, but this includes observations of *Sonorella* that may be species other than the Sonoran talussnail. Similar to patterns for probability of occurrence, relative abundance across all 130 plots peaked in talus and seemed to increase from lower (e.g., drainages and bajadas) to higher in landscapes (Figure 4). Similar to patterns for probability of occurrence, however, 95% confidence intervals of estimates overlapped across some landforms. Hence, relative abundance on talus was significantly higher than that along drainages but barely overlapped estimates on bajadas. At the plot level, relative abundances were highest in the Coyote, Santa Rita, and Empire Mountains, with moderate to high levels on Tumamoc Hill, and in the Tumacacori, Whetstone, and Roskruge mountains (Figure 6).

Table 1: Variation in probability of occurrence and relative abundance (log no./100 m) of talussnails across vegetation types, aspects, and rock types in southern Arizona, Sept. 2018 to Feb. 2021. Estimates, standard errors, and 95% confidence intervals are predicted marginal effects from generalized linear mixed models of presence/unobserved data and from linear mixed models of relative abundance data with both landform and site classification (random or historic) fit as covariates and random point or landscape identity fit as random effects. Data from all 130 plots are included.

Factor	Occurrence				Relative Abundance			
Group	Probability	SE	LCL	UCL	Estimate	SE	LCL	UCL
Vegetation Type								
Desert Woodland	0.659	0.070	0.522	0.796	0.926	0.158	0.609	1.243
Desert Shrubland	0.543	0.077	0.392	0.694	0.508	0.136	0.236	0.781
Grassland	0.504	0.123	0.263	0.744	0.350	0.224	-0.099	0.799
Montane Shrubland	0.570	0.069	0.433	0.706	0.459	0.167	0.124	0.795
Oak Woodland	0.719	0.065	0.591	0.847	0.580	0.160	0.258	0.901
Oak-Pine Woodland	0.637	0.108	0.425	0.848	0.751	0.274	0.201	1.301
Riparian Vegetation	0.299	0.182	-0.056	0.655	0.209	0.247	-0.287	0.706
Aspect								
North	0.588	0.069	0.452	0.723	0.652	0.117	0.418	0.887
East	0.487	0.100	0.291	0.682	0.528	0.139	0.249	0.806
South	0.576	0.086	0.408	0.745	0.542	0.150	0.243	0.842
West	0.603	0.069	0.467	0.739	0.561	0.129	0.303	0.819
Rock Type								
Alluvium	0.000	0.002	-0.004	0.004	0.226	0.366	-0.507	0.959
Volcanic (not Basalt)	0.603	0.080	0.446	0.760	0.404	0.152	0.100	0.708
Basalt	0.549	0.131	0.293	0.805	0.682	0.240	0.200	1.164
Granitic	0.551	0.070	0.415	0.688	0.623	0.130	0.362	0.883
Sedimentary (not Limestone)	0.527	0.115	0.301	0.753	0.540	0.182	0.175	0.905
Limestone	0.757	0.123	0.516	0.998	0.914	0.232	0.450	1.379

There was little variation in probability of occurrence or relative abundance of talussnails across different vegetation types, aspects, and rock types across the study area (Table 1). With regard to vegetation type, there was some evidence relative abundances varied among types ($P = 0.12$), with greater values in desert woodland and pine-oak woodland, but less evidence probability of occurrence varied among vegetation types ($P = 0.17$). In contrast, there was much less variation in both response variables among aspects and rock types ($P \geq 0.41$), after adjusting for the influence of landform and site classification (e.g., historical vs. random; Table 1).

Factors that Explained Occurrence and Relative Abundance: Few factors explained occurrence of talussnails across all 130 plots we surveyed, after considering important effects of the two design variables, landform and site classification (Appendix D). Probability of occurrence increased somewhat with increasing volume of oak vegetation ($P = 0.13$) and decreased somewhat with increasing volume of succulent vegetation ($P = 0.11$) and basal cover of woody debris ($P = 0.07$). Relative to the reduced model that included only the two design variables and a random effect for landscape identity, a model that also included these three explanatory factors reduced AIC_c by 11.63, providing strong support.

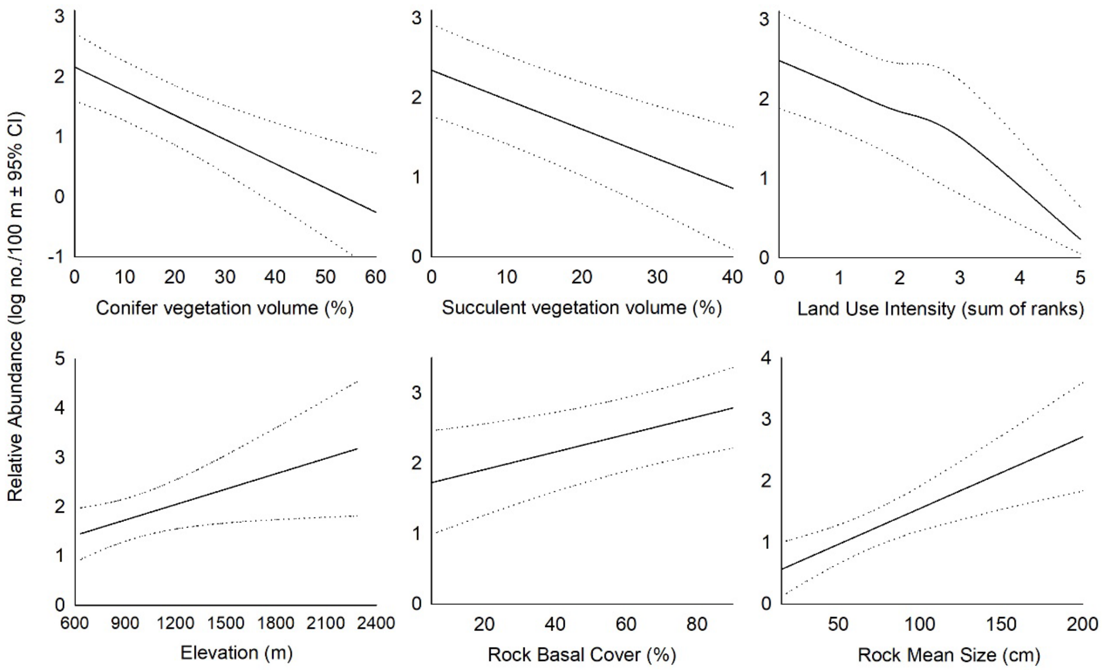

Figure 7. Factors that explained relative abundance (log no./100 m) of talussnails across 49 survey plots where we detected at least one talussnail in southern Arizona, Sept. 2018 to Feb. 2021. Estimates and 95% confidence intervals are predicted marginal effects from a linear mixed model where relative abundance was fit as the response variable, random point or landscape identity was fit as a random effect, and the first five factors and vegetation type (Figure 8) were fit as fixed effects (Appendix E). Mean rock size was not included in this multi-factor model due to 10 missing values, and estimates are based on a single-factor model. Land use intensity was estimated as the sum of all ranks (0, 1, 2) across all land use types.

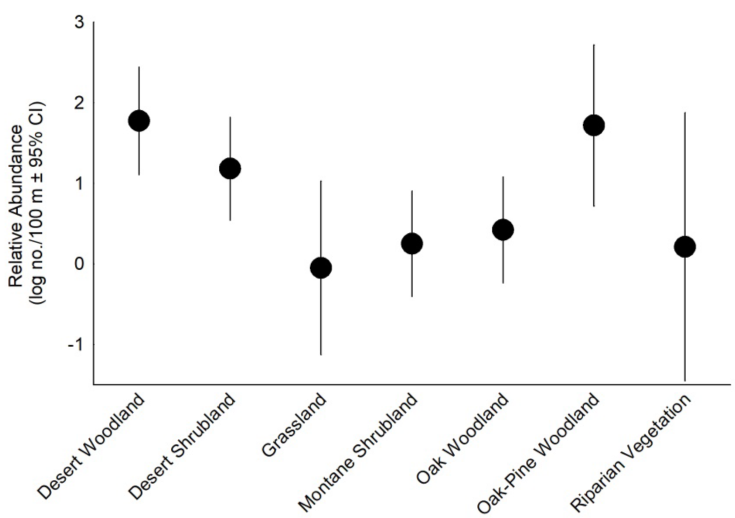

Figure 8. Variation in relative abundance (log no./100 m) of talussnails across seven vegetation types that dominated 49 survey plots where we detected at least one talussnail in southern Arizona, Sept. 2018 to Feb. 2021. Estimates and 95% confidence intervals are predicted marginal effects from a linear mixed model where relative abundance was fit as the response variable, random point or landscape identity was fit as a random effect, and vegetation community type and the first five factors shown in Figure 7 were fit as fixed effects.

In contrast, a fairly large number of factors with more significant effects explained relative abundance of talussnails within the 49 plots where we observed *Sonorella* during surveys (Appendix E). Relative abundance within occupied plots increased somewhat with increasing elevation ($P = 0.11$) and more so with increasing basal cover of rocks ($P = 0.044$), and decreased with increasing volume of conifer and succulent vegetation ($P \leq 0.0068$; Figure 7), and also varied somewhat among vegetation types ($P = 0.13$; Figure 8). Importantly, relative abundance within occupied plots also decreased with increasing land-use intensity ($P = 0.040$), with off-road vehicle and trail traffic ($n = 17$ occurrences), invasive plants ($n = 16$), livestock grazing ($n = 10$), wildfire ($n = 3$), and mining ($n = 1$) being the types of land use we observed. Although not included in the final multi-factor model due to 10 missing values, relative abundance of talussnails also increased markedly with increasing mean size of rocks within plots ($P = 0.0035$; Figure 7). After accounting for factors in the final model, relative abundance did not vary with slope ($P = 0.71$)

Morphology and Species Identification: We submitted 23 specimens from seven mountain ranges for morphological measurements, and obtained data on external traits for all specimens and data on internal traits from 18 specimens (Table 2, Appendix F). Internal morphology of specimens could not be measured for five immature individuals due to undeveloped genitalia. All specimens with flared apertures ($n = 9$) had developed genitalia. A surprising number of specimens ($n = 9$) had shell morphologies consistent with immature individuals (e.g., aperture not or slightly flared), yet had developed genitalia. Other individuals with unflared apertures ($n = 5$) had undeveloped genitalia as expected. Microscopy images of umbilical whorl texture and genitalia and provided in Appendix B and C.

With regard to external traits, shell height ranged from 8.8 to 18 mm and averaged 12.6 ± 0.4 mm (± SE), shell width ranged from 14.0 to 28.5 mm and averaged 21.3 ± 0.7 mm, and number of whorls ranged from 3.9 to 4.9 and averaged 4.4 ± 0.1. With regard to internal traits, penis length ranged from 3.4 to 22.2 mm and averaged 8.3 ± 1.3 mm (± SE), verge length ranged from 2.3 to 12.4 mm and averaged 5.3 ± 0.8 mm, and vagina length ranged from 3.3 to 12.9 mm and averaged 6.9 ± 0.6 mm. With regard to relative lengths of penis vs. vagina, 50% of specimens had longer penis lengths longer than vagina, 39% of specimens had longer vagina length, and 11% had relative equal lengths. Observed traits in shell width and the penis-vagina-ratio were in the range of *Sonorella magdalenensis* for one specimen from Cat Mountain, Tucson Mountains (Son15 in Herrmann 2021 and one of the historic sites in this study) following Miller (1967).

DISCUSSSION

We assessed the distribution, relative abundance, potential threats, habitat use, and population persistence of talussnails within and immediately around the known range of the Sonoran talussnail in south-central Arizona. By sampling numerous old and new historical localities where the Sonoran talussnail was described in the past since 1910, and a much larger sample of new, randomly-selected plots across broad geographic, elevation, and landform gradients, we derived a range of inferences that help address major ecological knowledge gaps for *Sonorella* in southern Arizona. These knowledge gaps were and remain substantial given that in 2012, in response to a petition to list the Sonoran talussnail as a threatened or endangered species under the Endangered Species Act, the U.S. Fish and Wildlife Service (USFWS) concluded there was “no recent survey data for all of the known range, and… no information in our files to indicate that anyone has looked for this species throughout its range for almost 40 years” (USFWS 2012). With support from the Arizona Game and Fish Department, Heritage

Table 2: Measurements of individual 23 talussnail shells and 18 sets of genital traits and associated ratios. All data and calculations are by Casey Richart.

Locality	Specimen ID Herrmann 2020	ID from Appendix B-C	Shell Height (mm)	Shell Width (mm)	Shell Width/ Height	Umbilicus Width (mm)	Whorls	Penis (mm)	Verge (mm)	Vagina (mm)	Penis/ Verge	Penis/ Vagina
Atascosa Mountains	Son30	RP 99-1	12.0	20.0	0.6	2.5	4.8	-	-	-	-	-
Cerro Colorados, Lobo Peak	Son19	Pima 15	12.0	18.0	0.7	1.8	4.3	3.7	2.3	4.3	1.6	0.9
Cerro Colorados, Lobo Peak	Son18	Pima 10	9.0	14.0	0.6	1.5	3.9	-	-	-	-	-
Coyote Mountains, Hayhook Ranch	Son24	Pima 07	12.0	19.0	0.6	3.0	4.1	12.5	8.3	10.3	1.5	1.2
Coyote Mountains, Hayhook Ranch	Son28	Pima 17-1	14.0	25.0	0.6	2.5	4.4	17.4	10.3	6.4	1.7	2.7
Coyote Mountains, Hayhook Ranch	Son23	Pima 06	16.0	26.0	0.6	3.5	4.6	18.5	12.4	12.9	1.5	1.4
Coyote Mountains, Hayhook Ranch	Son22	Pima 01	14.0	27.0	0.5	3.0	4.5	22.2	12.3	10.2	1.8	2.2
Coyote Mountains, Hayhook Ranch	Son29	Pima 17-2	12.0	19.0	0.6	2.0	4.1	-	-	-	-	-
Coyote Mountains, Hayhook Ranch	Son25	Pima 05	12.0	20.0	0.6	2.0	4.3	-	-	-	-	-
Santa Catalina Mountains	Son16	RP 296-2	12.5	21.0	0.6	4.0	4.6	4.6	2.7	3.3	1.7	1.4
Santa Catalina Mountains	Son14	RP 296-2,1	12.0	21.0	0.6	4.0	4.5	5.3	3.5	5.5	1.5	1.0
Santa Catalina Mounts., Buehman Can.	Son17	Pima 13	12.0	21.0	0.6	4.0	4.6	8.2	4.2	4.6	2.0	1.8
Santa Catalina Mountains, Edgar Canyon	Son26	Pima 11	18.0	28.5	0.6	3.0	4.6	5.3	3.6	7.1	1.5	0.7
Santa Catalina Mountains, Edgar Canyon	Son27	Pima 12	12.5	22.0	0.6	3.0	4.6	8.5	4.6	8.4	1.8	1.0
Santa Catalina Mountains, Edgar Canyon	Son33	Pima 14	12.0	23.0	0.5	3.0	4.9	9.7	4.7	6.4	2.1	1.5
Santa Rita Mountains, Madera Canyon	Son10	Pima 03	14.0	24.0	0.6	3.0	4.7	3.4	2.4	5.7	1.4	0.6
Santa Rita Mountains, Madera Canyon	Son12	Pima 04	15.0	25.0	0.6	3.5	4.6	3.7	3.1	9.9	1.2	0.4
Santa Rita Mountains, Madera Canyon	Son11	RP 10-1	12.5	20.0	0.6	3.3	4.6	3.9	2.8	6.6	1.4	0.6
Santa Rita Mountains, Madera Canyon	Son09	Pima 02	13.0	23.0	0.6	2.5	4.2	4.2	2.8	7	1.5	0.6
Tortolita Mountains	Son21	Pima 16	11.0	18.0	0.6	2.0	3.9	-	-	-	-	-
Tucson Mountains, Cat Mountain	Son15	HS 164-2	8.8	15.0	0.6	2.0	4.1	6	3.4	6.9	1.8	0.9
Tucson Mountains, Los Morteros	Son32	Pima 09	12.0	22.0	0.5	2.5	4.6	6.2	6	4	1.0	1.6
Tucson Mountains, Los Morteros	Son13	Pima 08	11.0	19.0	0.6	2.0	4.4	6.7	6.7	5.4	1.0	1.2

Fund Grants Program and numerous partners, we helped addressed some of these questions but more work remains. Future efforts will be aided by resolving phylogenetic relationships of the genus *Sonorella* and of the Sonoran talussnail in particular to elucidate species boundaries and improve species identification.

Distribution: We found evidence of talussnail occurrence across much of our study area and in or around 77% of mountain ranges we surveyed. Mountain ranges where we failed to document talussnails included the Canelo Hills, which are east of the San Cayetano Mountains and outside the known range of *Sonorella magdalenensis* based on past descriptions (Miller 1967, Bequaert and Miller 1973). We also failed to document talussnails in the Pan Quemado, Silver Bell, Waterman, and Ragged Top mountains, which are north of the Roskruge Mountains, despite allocating significant survey effort in these northwestern ranges. Nonetheless, Pilsbry and Ferriss (1923) noted the now synonymized *S. tumamocensis* in the Silver Bell Mountains, and Ian Murray of Pima County has recently documented live talussnails in the Waterman Mountains and talussnail shells on Ragged Top (*pers. comm*.) indicating some of these areas are occupied by *Sonorella* and likely by the Sonoran talussnail. Importantly, probabilities of occurrence that we estimated with generalized linear mixed models were high on talus (e.g., 0.58) and to a lesser but significant level on mountain slopes (e.g., 0.27) in randomly-selected plots. We also documented talussnails across the full range of sampled elevations (e.g., 627-2,350 m), which was significantly broader than the elevation range of the Sonoran talussnail described in the literature (e.g., 839-1,830 m; Bequaert and Miller 1973), although we acknowledge that based on historical distribution patterns some areas we sampled may be occupied by talussnail species other than the Sonoran talussnail (Miller 1967, Bequaert and Miller 1973). These patterns together with our randomized sampling design and fact that mountain slopes occur across significant portions of the study area (even if talus is relatively rare), suggest our findings are broadly representative of non-sampled areas in the study region. Hence, our work provides strong evidence that talussnails are distributed broadly across the known range of the Sonoran talussnail.

Population Persistence: Understanding population trends and rates of population persistence are important for evaluating population status and guiding conservation and management efforts. With regard to the putative Sonoran talussnail, we provided the first estimates of population persistence by surveying a large proportion of both recent and older historical localities where talussnails had been observed in the past. Favorably, we documented recent occupancy of talussnails at 93% of old and 90% of new historical sites, indicating high levels of persistence. In a probabilistic sense based on generalized linear mixed models, we also estimated occurrence probabilities for historical localities on talus and mountain slopes that were statistically indistinguishable from one, also indicating very high rates of persistence. In fact, the only historical site where we failed to document evidence of occupancy by talussnails was along a drainage in September where recent water flows may have complicated efforts and reduced detection probability. Because old historical sites we surveyed covered seven of ten localities known from across the range of the Sonoran talussnail noted by Pilsbry and Ferriss (1915) and Bequaert and Miller (1973), such results are likely representative of broader patterns. Regardless, future efforts should attempt to gain access and survey historical localities in the San Cayetano, Roskruge, and Comobabi mountains that we did not visit (Pilsbry and Ferriss 1915, Bequaert and Miller 1973), and should also consider additional historical localities noted by others (e.g., Pilsbry and Ferriss 1923).

Habitat: Understanding habitat use and the relative importance of resources and conditions that comprise habitat for a given species is fundamental for guiding conservation and management. Although it was well known that most species of *Sonorella* use rocky areas with deep interstitial spaces among rocks for protection from heat and desiccation given past descriptions and the natural history of these species (e.g., Pilsbry and Ferriss 1915, 1923, Bequaert and Miller 1973, Hoffman 1990, 1995, Waters 2017), to our knowledge, this is the first ecological study to quantitatively model habitat use and selection across a broad range of environmental factors. Our results indicate that talussnails are generalists that occur across a broad range of vegetation and rock types, landforms, slopes, and aspects. Such findings are consistent with broad geographic and elevation distributions we documented during surveys across the range of the Sonoran talussnail and other species of talussnail that occur in these same or nearby mountain ranges. Regardless, a fundamental aspect of habitat was clearly the presence of medium- to large-sized rocks on the surface, as indicated by strong statistical associations between occurrence and relative abundance with mountain slopes and especially talus landforms. Although on average, basal cover of rock was 15% greater at occupied that at unoccupied sites and averaged 43% across occupied plots ($P < 0.0001$), rock cover and few other factors in general explained occurrence across the study region. These results further suggest that talussnails in our study area are generalists and that other unmeasured resource and conditions such as local microclimate drive distribution. Solar radiation may be one of these unmeasured factors given areas were talussnail shells were located had lower inputs of solar radiation than the surroundings in the Coyote and Tucson mountains (Ian Murray, Pima County, *pers. comm.*). With regard to relative abundance, we found that both basal rock cover and especially rock size had important effects likely because areas with more cover of larger rocks provide local refugia and safe sites that buffer individuals from high temperatures and desiccation. Additionally, basal cover of woody debris, which likely influences the accessibility of sheltered microhabitats provided by rocks, and cover of arid-adapted plants such as succulents and overall elevation, which are linked to local or regional moisture availability, were also important in explaining relative abundances. Future efforts to understand talussnail habitat should measure rock size and structure using more detailed methods, assess local microclimates and solar radiation, and estimate topographic complexity, ruggedness (e.g., Waters 2017) and habitat patch size from fine-resolution digital elevation models and other data sources. Despite challenges in estimating the spatial distribution of talus and rocky areas at large scales, these resources could provide tools to predict distribution and abundance in spatially-explicit ways across large areas.

<u>*Conservation and Management*</u>: An upcoming species status assessment by the U.S. Fish and Wildlife Service for the Sonoran talussnail will assess potential threats and stressors to populations and habitat (USFWS 2012). Proposed and ongoing mining is considered a potential threat because it can result in habitat loss and degradation. Based on observations from this work, such impacts seem most likely where mining activities significantly modify the natural arrangement, cover, and size of surface rocks in ways that promote desiccation. Invasive plants such as exotic buffelgrass (*Pennisetum ciliare*) are also considered threats to talussnail populations because they can increase the frequency of fires and reduce moisture availability (Center for Biological Diversity 2010, USFWS 2012). Although we observed buffelgrass, or other non-native plants, at 33% of occupied sites, sample sizes were too small to assess impacts of this potential stressor. Importantly, however, we found that relative abundances decreased significantly with increasing land-use intensity, which we quantified by summing intensity ranks across all land-use categories. At sites we studied, observed land uses were linked mainly to off-road vehicle and foot traffic, invasive plants, and livestock grazing, which in combination seemed to negatively impact relative abundance of local talussnail populations. Such findings assume that each one-level increase in overall ranked intensity scaled with true impacts on the ground, which is reasonable given how we ranked intensities, and also that land use is not associated with lower quality habitat in areas potentially with lower ruggedness and rockiness. Although additional studies are needed to better understand these patterns, managers should attempt to limit the impacts of land-use and land-cover change on habitat, especially where habitat patch sizes are small and populations are effectively isolated.

<u>Species identification and delimitation:</u> The operational taxonomic units (OTUs) "Tumamoc Hill and Cat Mountain (Tucson Mountains)" and "Santa Rita Mountains including Atascosa Mountains" fall within the described range of *Sonorella magdalenensis* and potentially represent the taxon. However, as these two groups are well separated from each other and are not monophyletic, only one of the two OTUs can potentially represent the Sonoran talussnail (Herrmann 2021). Following Miller (1967) only *S. magdalenensis* is present in the southern part of the Tucson Mountains while *Sonorella walkeri* inhabits the Santa Rita Mountains and the Atascosa Mountains and could be the taxon that represents the clade. Other delimited groups with specimens that were collected close to the distribution described for *S. magdalenensis* were well separated and are not conspecific with the Sonoran talussnail.

Morphological studies on the specimens used in the genetics study focused on shell and genital morphology (Casey Richart pers. comm. 2020). To identify species, we mainly followed the diagnostic characters in Miller (1967). From the genetically delimited two species that potentially could represent *Sonorella magdalenensis* the single specimen from Cat Mountain is consistent with *S. magdalenensis* in shell width and penis and vagina length as well as ratio. The specimens representing the other genetically delimited species that potentially could be *S. magdalenensis* from the "Santa Rita Mountains including Atascosa Mountains" have a larger shell with more consistent with *Sonorella walkeri*. Unfortunately, the studied diagnostic characters did not provide enough information to unequivocally identify described species. This is mainly due to largely overlapping morphological characters, the uncertainty of examining fully mature specimens (size and genitalia), and the overall small sample size.

Molecular characters are ideal to evaluate and test morphology-based systematics of poorly studied taxa. In *Sonorella*, so far only one study including a few species in the Pinaleno Mountains and some adjacent mountain ranges has used mitochondrial DNA and morphological data (Weaver et al. 2010). In this study, genetic results are consistent with the described species in the area. However, the authors used mitochondrial DNA which is extra-chromosomal and represents only a fraction of the genetic information and thus has limits in delimiting species (del Pedraza et al. 2019). Future delimitation studies should use mitochondrial DNA and genomic approaches to arrive at a robust species-level differentiation in *Sonorella*. While genital morphology seems to have some diagnostic utility in differentiating *Sonorella* species, genital characters are useless in the field. Considering rather poor availability of diagnostic characters, and the absence of robust phylogenies and species hypotheses, the current *Sonorella* taxonomy has to be seen as a working hypothesis only that is in urgent need of testing and confirmation. Species delimitation is a major quest in biology and is essential for adequate management of the organismal diversity (del Pedraza et al. 2019).

In a preliminary study on the phylogeny of *Sonorella* from southeastern Arizona Herrmann (2021) amplified two mitochondrial DNA fragments (COI, 16S rRNA), two nuclear DNA fragments (ITS1, ITS2) for 35 snail samples collected in southeastern Arizona and two outgroup samples from different genera. Additionally, they constructed ddRADseq libraries for a subset of 20 samples to recover genomic single nucleotide polymorphisms (SNPs). Most tissue samples used in the molecular study originated from our survey efforts here. The outcome established that 32 individuals were members of *Sonorella* while three individuals are not belonging to *Sonorella* and represent more distantly related snail species. Bayesian and maximum likelihood phylogenies to delimit species and test species hypotheses with a range of methods including barcoding (ABGD, ASAP), species trees (*Beast, bPTP, SD), coalescent models (Stacey, SNAPP, BPP), and genetic structure (DAPC) were used. An additional 119 COI sequence fragments from GenBank were also added to our COI dataset. Over all analyses for the samples, and with differing numbers of samples per dataset, the phylogenetic and species trees support eight well separated clades, with branch lengths indicating species level. This is supported by the various species delimitation tests. The six OTUs that are well delimited as putative species in the majority of tests are: Middle Bear (Santa Catalina Mountains), Coyote Mountains, Mount Bigelow (Santa Catalina Mountains), Empire Mountains, Sierrita Mountains, and Tumamoc Hill & Cat Mountain (Tucson Mountains). An additional three well supported OTUs, considering all analyses together, are: Santa Rita Mountains (including Atascosa Mountains), Edgar and Buehman Canyons (Catalina Mountains) and Los Morteros (Tucson Mountains). However, there are phylogenetic subgroups that may warrant the designation of two distinct species after additional samples are available.

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Appendix A: Survey and Habitat Datasheets used for surveys

UAZ *Sonorella* Survey Form **Date (m/d/yr):**____________________ Surveyors________________________

Mt./Site:______________________ **Pt & Plot No.**______ - ______ **Land Form:** Talus Mt Slope Up. Bajada Drainage

Location Description:____

Landowner: USFS BLM NPS DOD ASLD County Private Other _________________ **Historical Site Y N**

UTM (WGS84): Start E____________N____________WP No.____ **End:** E____________N____________WP No.___

Elev. (m) Min.___________ Max._____________ **Weather:**____

____ **Air Temp:**__________°C **Rel. Humidity:**__________%

Last Rain Event:__________________ **Quantity (in.)**_________ **Other Weather**______________________________

Survey Start Time:___________ **Survey End Time:**___________ **Total Search Time:**___________________minutes

GPS track Route Length:_____________ **No. of Observers**:__________ Landform patch size (m x m)______________

Route Desc.____

Time to 1st Snail:____________minutes **Photo Voucher Nos.**____

Mollusk Genus (Common Descriptor)	# Mature Live	# Juvenile Live	# Mature Shells	# Juvenile Shells	# Partial Shells	# Marked Live	# Marked Shells	# Voucher Specimens
Sonorella (talussnail)								
Eremarionta (desertsnail)								
Oreohelix (mountainsnail)								
Ashmunella (woodlandsnail)								
Other								
Other								
Other								

Notes (including mucus color for live specimens):

____

____

UAZ *Sonorella* Habitat Form

Mt./Site:______________________ **Pt & Plot Nos.**______ - ______ **Land Form:** Talus Mt Slope Up. Bajada Drainage

Dominant Veg. Comm: Rocky Un-vegetated Desert shrubland Arborescent Mixed Desert Scrub Desert Woodland

Desert Grassland Montane Shrubland Montane-Grassland Oak Woodland Oak-Pine Woodland Riparian Vegetation

Woody Veg. Canopy Cover %:_______ **Canopy Ht (mean m)** ________ **Basal Cover %** Bare Ground_______Rock_______

Live Veg________Litter_______Dead Woody Debris _________ **Rock Size (mean diam. cm):** _______________________

Veg Physiognomy % Volume: Oak _________ Conifer__________ Broadleaf Decid._________ Broadleaf Everg._______

Microphyllous_______ Succulent________ Grass/Forb_______Other___________**Aspect (°)**_______**Slope (%):**_______

Rock Type: Limestone Sandstone Siltstone Basalt Granite/Metamorphic Conglomerate None Unknown

Plot Photo Nos. ____**Site Notes**___________________________

____

Land Use and Stressors:	**Rank**	**Describe Stressor and Impact Level:**
Mining or rock and gravel extraction (removal or infill)	0 1 2	
Development (construction, roadways & utility corridors)	0 1 2	
Woodcutting (loss of tree canopy and moisture)	0 1 2	
Livestock (trampling or sedimentation)	0 1 2	
Off-trail OHV use or hiking trails (trampling or sedimentation)	0 1 2	
Wildfire (scaring, loss of tree canopy, or sedimentation)	0 1 2	
Invasive plants (bufflegrass, lovegrass, red brome, Russian thistle)	0 1 2	
Invasive mollusks (predatory or competitor snails and slugs)	0 1 2	
Chemical contamination (pesticides or fire retardant by-products)	0 1 2	
Other [describe]	0 1 2	

Sketch of Habitat Searched (optional)

Appendix B. Pictures of internal traits of talussnail genitalia.

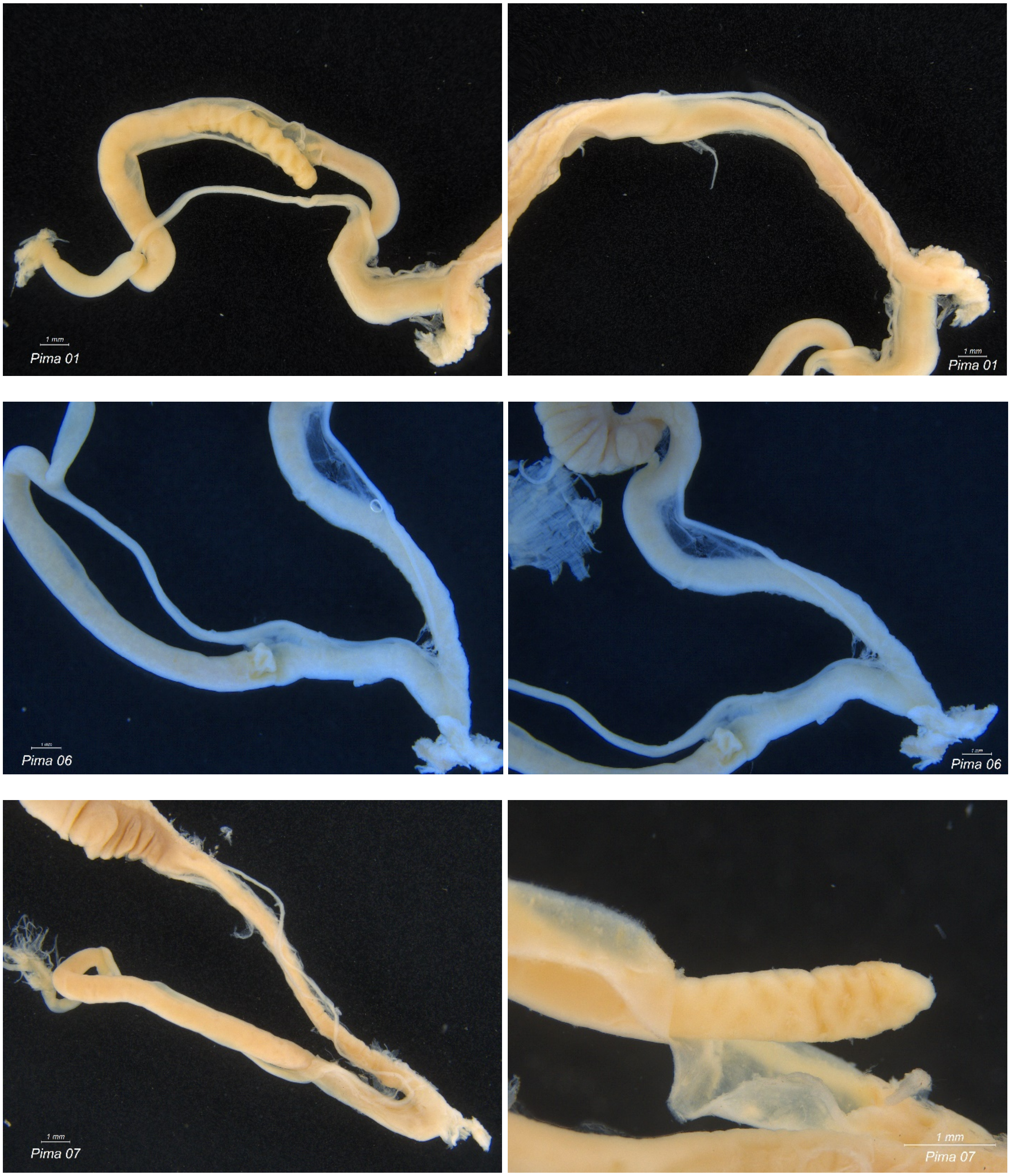

Figure B1. Son22 (Pima 01) penis (left) and vagina (right), Son23 (Pima 06) penis (left) and vagina (right), Son24 (Pima 07) genitalia (left) and verge (right). Photos by Casey Richart 2020.

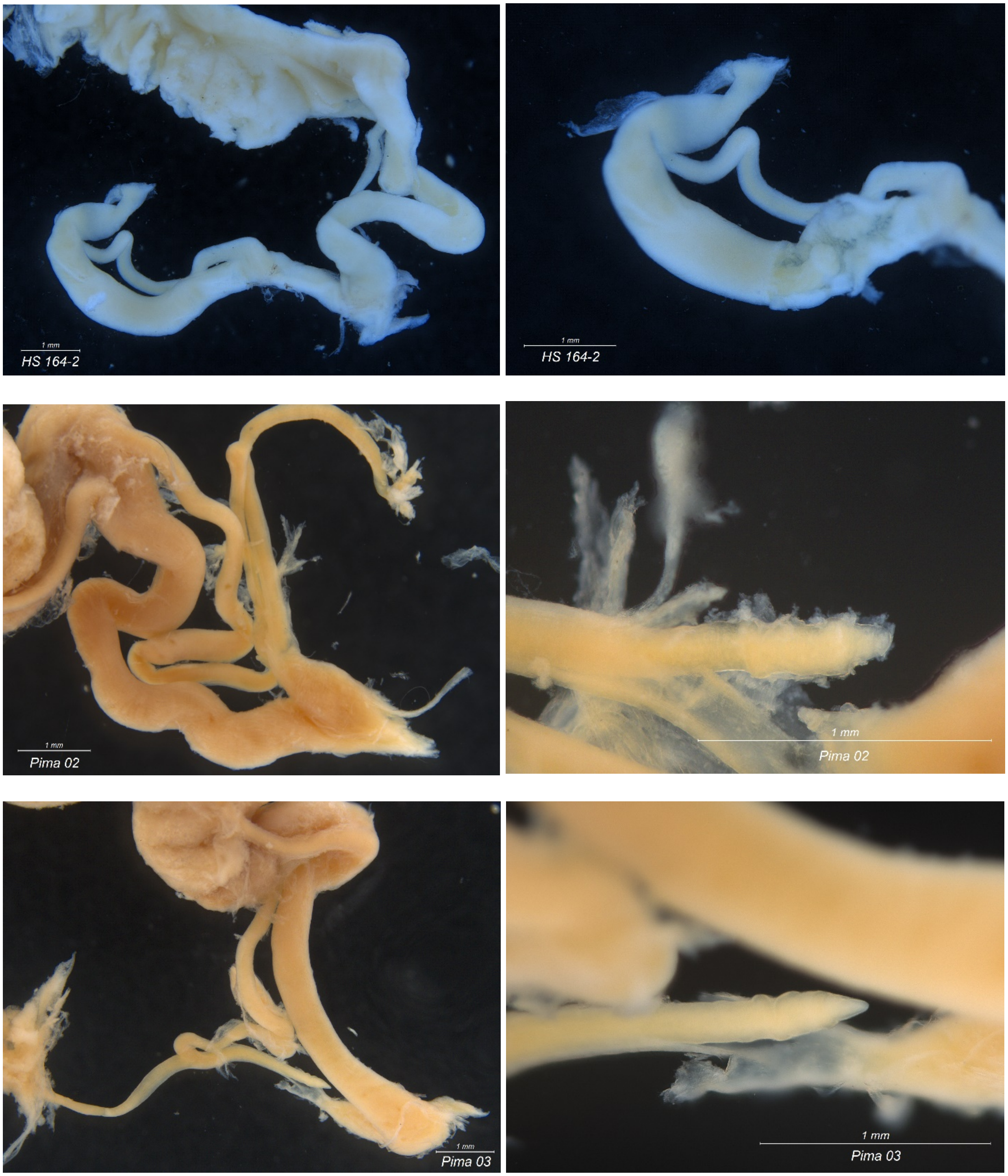

Figure B2. Son15 (HS 164-2) genitalia (left) and verge (right), Son09 (Pima 02) genitalia (left) and verge (right), Son10 (Pima 03) genitalia (left) and verge (right). Photos by Casey Richart 2020.

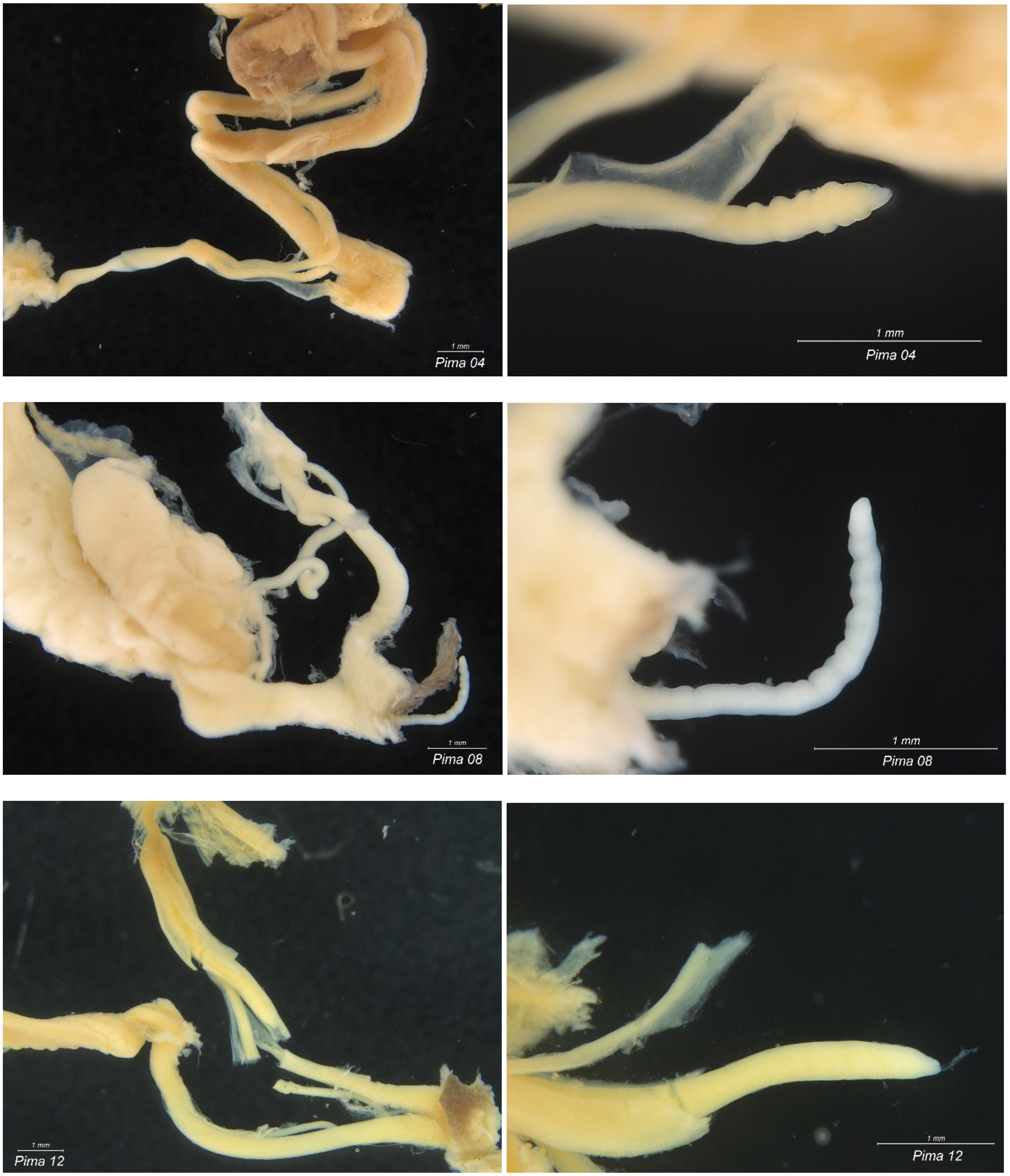

Figure B3. Son12 (Pima 04) genitalia (left) and verge (right), Son13 (Pima 08) genitalia (left) and verge (right), Son27 (Pima 12) genitalia (left) and verge (right). Photos by Casey Richart 2020.

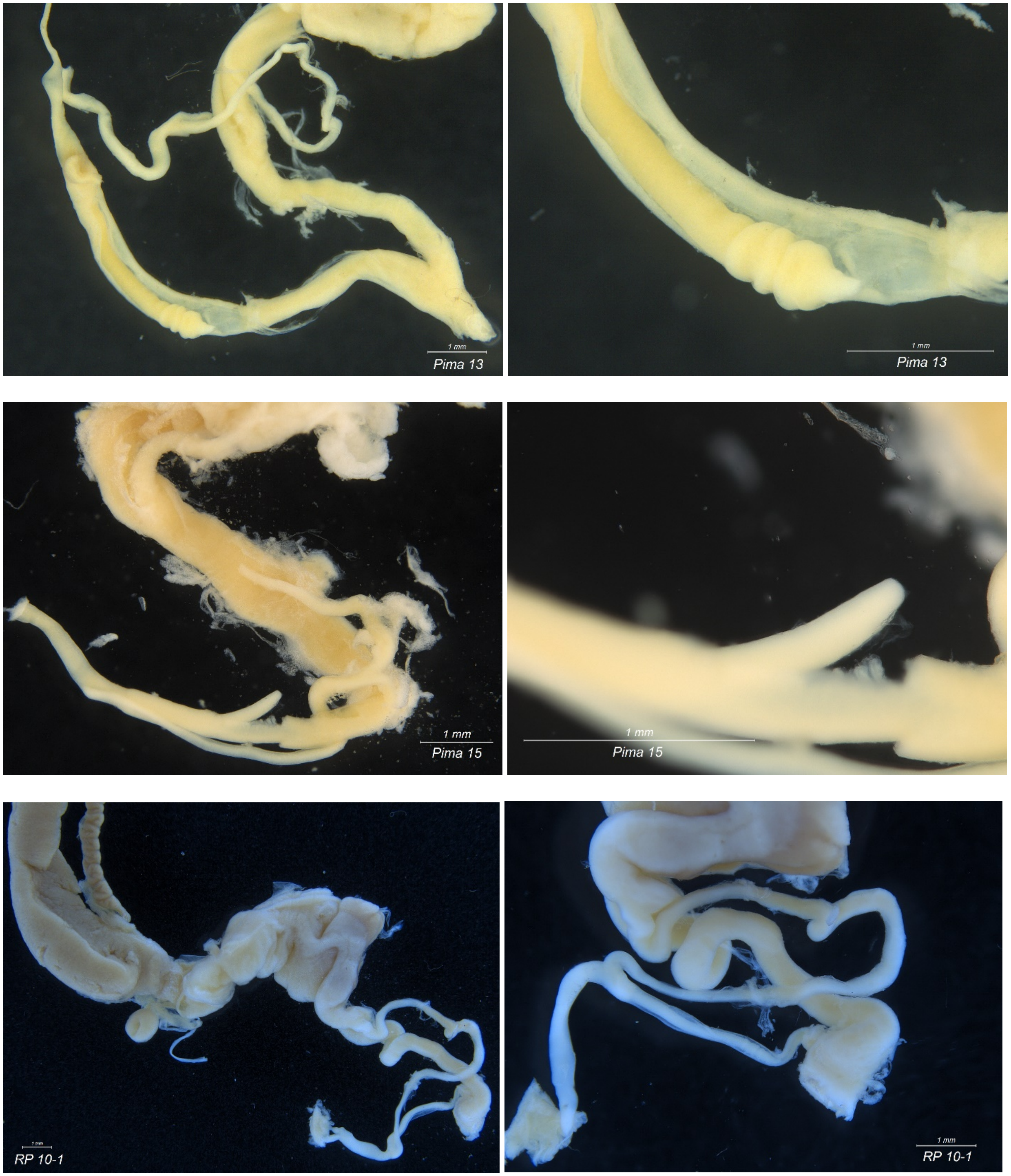

Figure B4. Son17 (Pima 13) genitalia (left) and verge (right), Son19 (Pima 15) genitalia (left) and verge (right), Son11 (RP 10-1) genitalia (left) and verge (right). Photos by Casey Richart 2020.

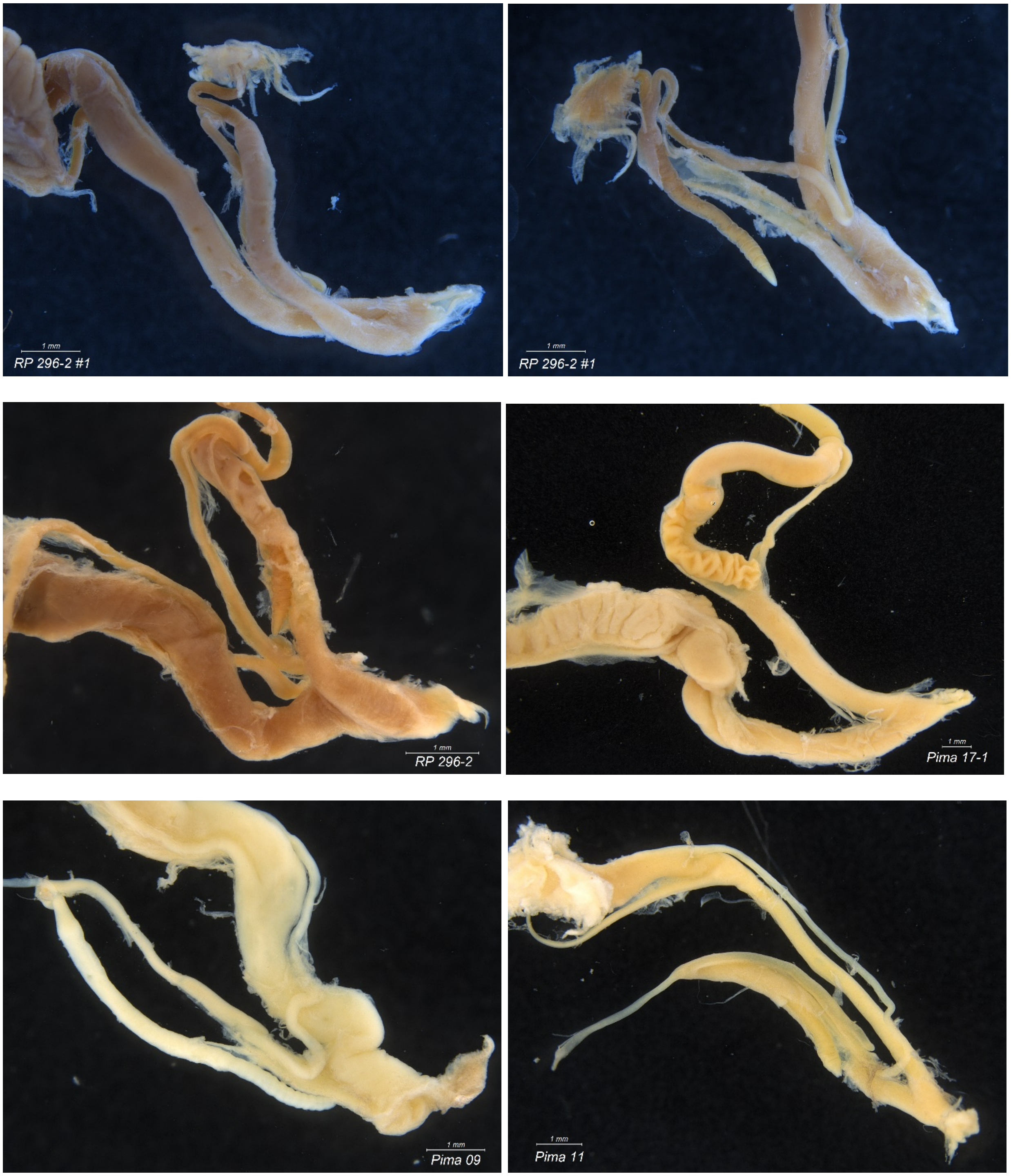

Figure B5. Son14 (RP296-2#1) genitalia (left) and verge (right), Son16 (RP296-2#1) genitalia, Son28 (Pima 17-1) genitalia, Son32 (Pima 09) genitalia, Son26 (Pima 11) genitalia. Photos by Casey Richart 2020.

Figure B6. Son33 (Pima 14) genitalia. Photo by Casey Richart 2020.

Appendix C. External shell trait pictures showing talussnail umbilical whorl texture.

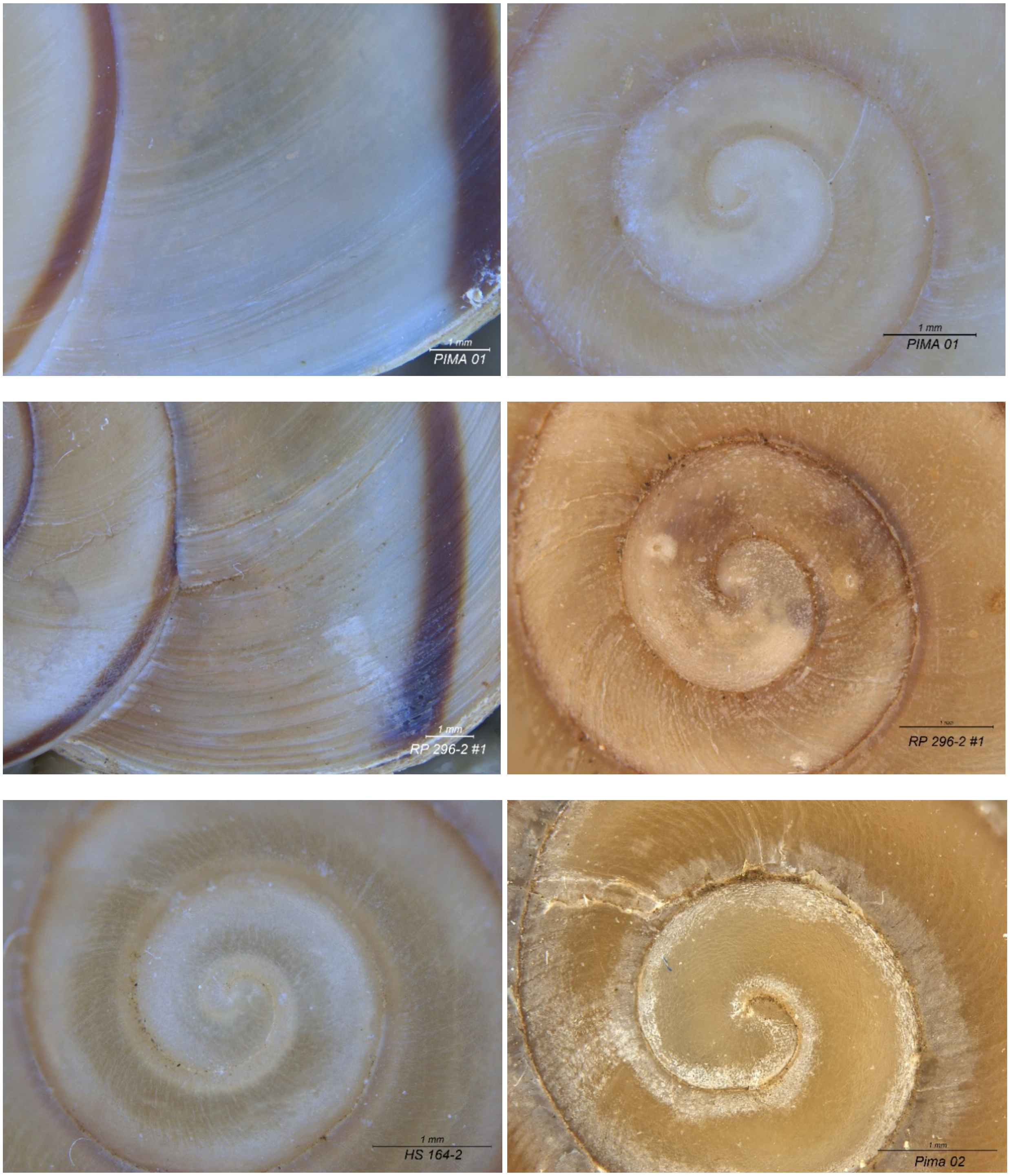

Figure C1. Son22 (Pima 01) body whorl (left) and embryonal whorl (right), Son14 (RP296-2#1) body whorl (left) and embryonal whorl (right), Son15 (HS 164-2) embryonal whorl, Son09 (Pima 02) embryonal whorl. Photos by Casey Richart 2020.

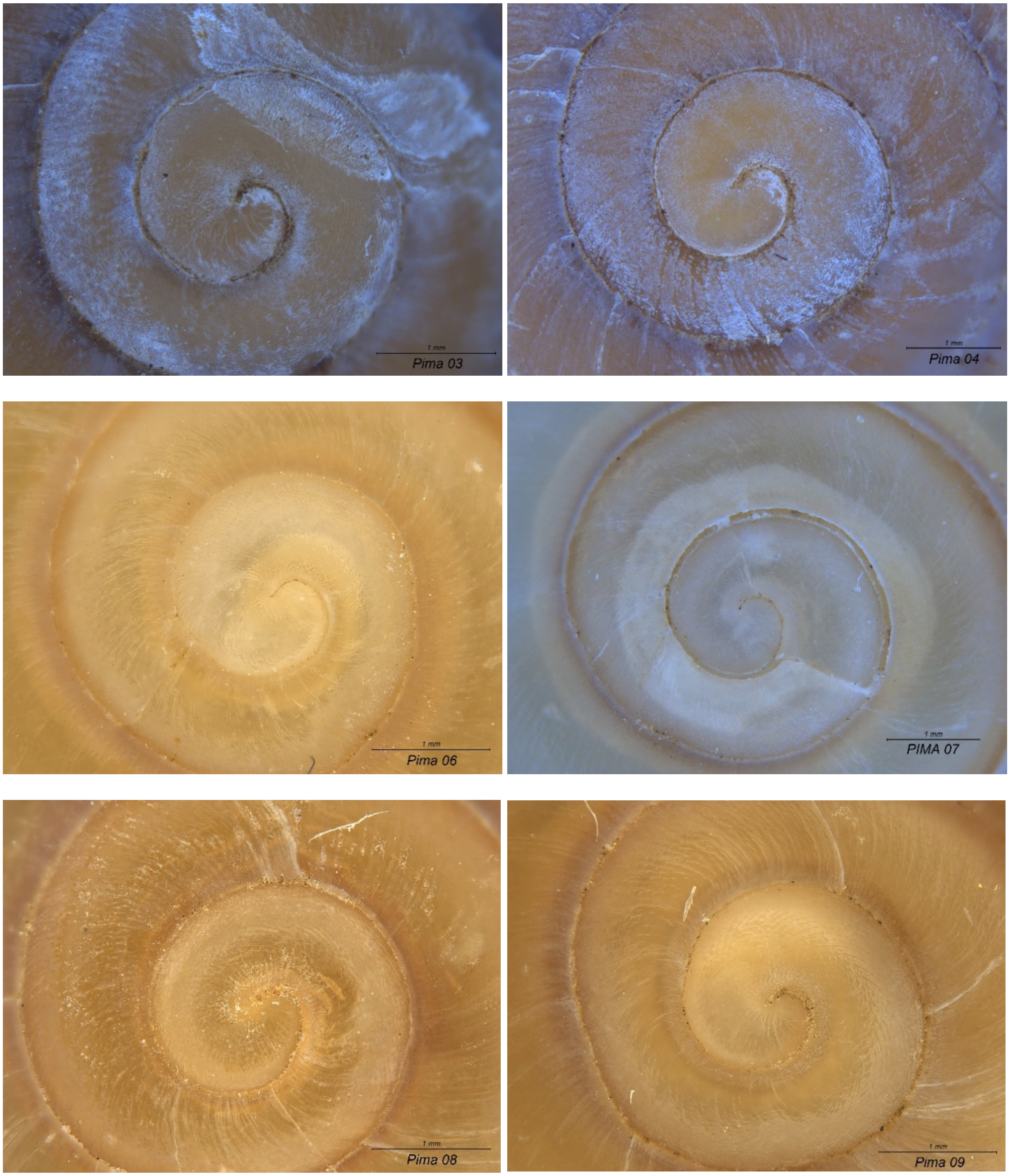

Figure C2. Embryonal whorls: Son10 (Pima 03), Son12 (Pima 04), Son23 (Pima 06), Son24 (Pima 07), Son13 (Pima 08), Son32 (Pima 09). Photos by Casey Richart 2020.

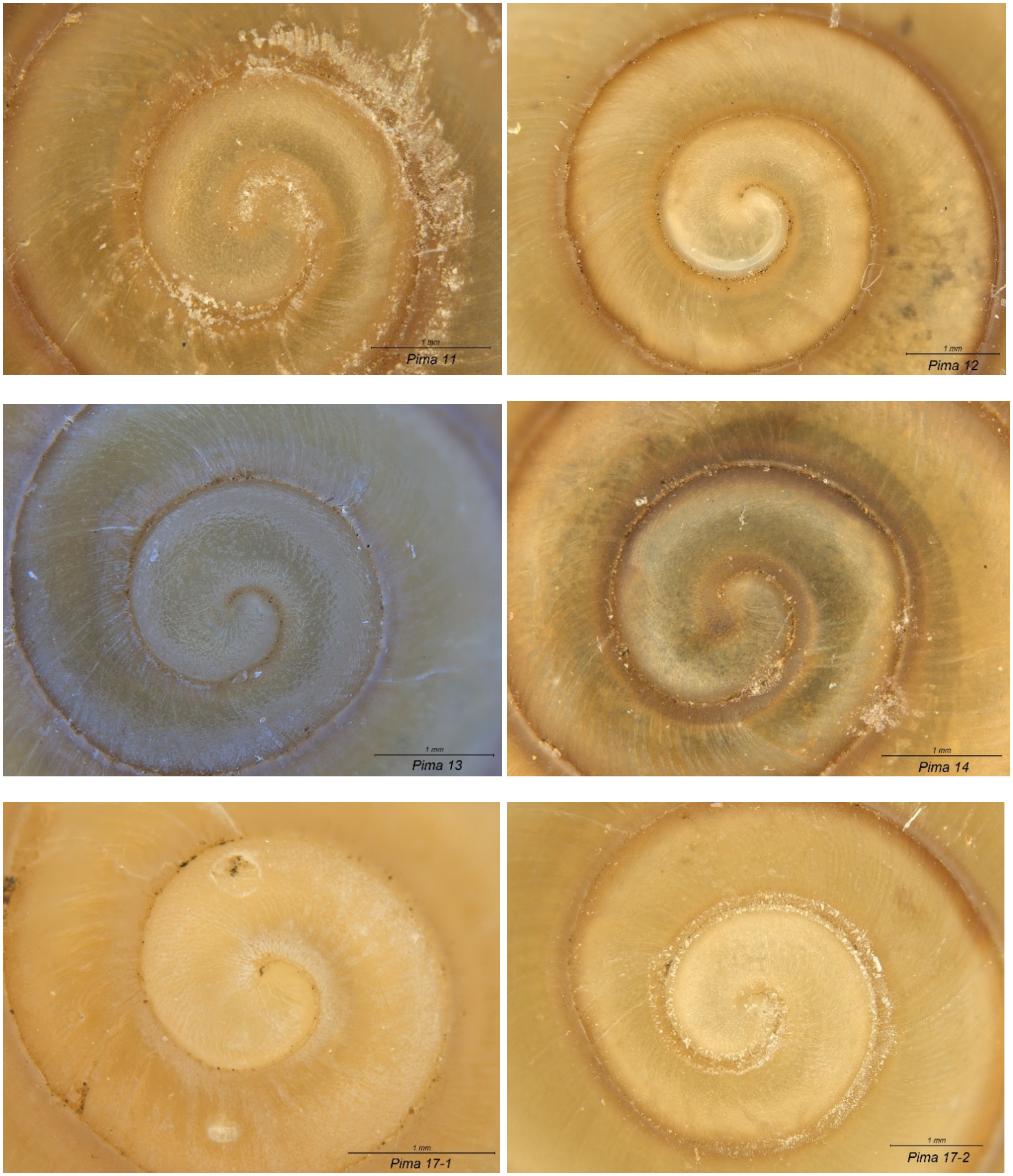

Figure C3. Embryonal whorls: Son26 (Pima 11), Son27 (Pima 12), Son17 (Pima 13), Son33 (Pima 14), Son28 (Pima 17-1), Son29 (Pima 17-2). Photos by Casey Richart 2020.

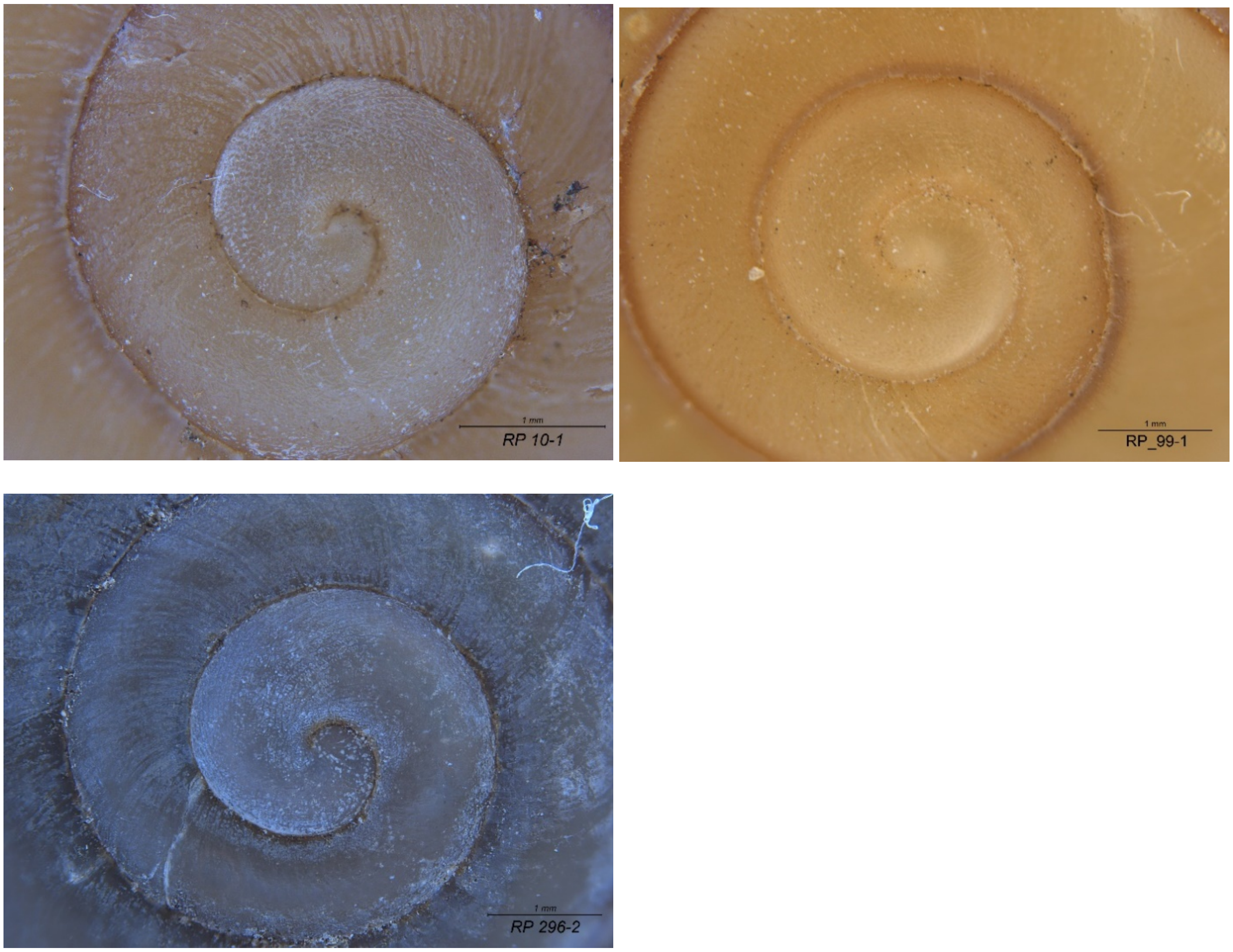

Figure C4. Embryonal whorls: Son11 (RP 10-1), Son30 (RP 99-1), Son16 (RP 296-2). Photos by Casey Richart 2020.

Appendix D: Models of talussnail occurrence based on a model that just included the two design variables (1) and a model developed using backwards elimination of all predictors and the two design variables (2).

```
1) Generalized linear mixed model fit by maximum likelihood (Adaptive
Gauss-Hermite Quadrature, nAGQ = 20) ['glmerMod']
 Family: binomial  ( logit )
Formula: Pres.Abs.All ~ Land.Form + Point.type + (1 | Group)
   Data: Data
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun =
2e+05))

     AIC      BIC   logLik deviance df.resid
   125.5    142.7    -56.7    113.5      124

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.5185 -0.4315 -0.2085  0.1880  3.1774

Random effects:
 Groups Name        Variance Std.Dev.
 Group  (Intercept) 1.652    1.285
Number of obs: 130, groups:  Group, 55

Fixed effects:
                    Estimate Std. Error z value Pr(>|z|)
(Intercept)           1.9880     1.0379   1.915 0.055434 .
Land.FormMt Slope     1.2421     0.6550   1.896 0.057928 .
Land.FormTalus        2.5663     0.9217   2.784 0.005363 **
Land.FormUp. Bajada  -0.8548     1.0725  -0.797 0.425432
Point.typeRandom     -4.2111     1.1864  -3.549 0.000386 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


Analysis of Variance Table
           npar  Sum Sq Mean Sq F value
Land.Form     3  9.1665  3.0555  3.0555
Point.type    1 16.0711 16.0711 16.0711



2) Generalized linear mixed model fit by maximum likelihood (Adaptive
Gauss-Hermite Quadrature, nAGQ = 20) ['glmerMod']
 Family: binomial  ( logit )
Formula: Pres.Abs.All ~ Land.Form + Point.type + Veg.Volume...Oak +
Veg.Volume...Succulent +      Basal.Cover...Woody.Debris + (1 | Group)
   Data: Data
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun =
2e+05))

     AIC      BIC   logLik deviance df.resid
```

```
   113.9    139.7    -47.9     95.9      121

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.01711 -0.20246 -0.04324  0.06404  1.90715

Random effects:
 Groups Name        Variance Std.Dev.
 Group  (Intercept) 8.257    2.874
Number of obs: 130, groups:  Group, 55

Fixed effects:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)                 4.69559    2.70714   1.735   0.0828 .
Land.FormMt Slope           2.56948    1.25347   2.050   0.0404 *
Land.FormTalus              4.80842    2.44961   1.963   0.0497 *
Land.FormUp. Bajada        -0.26193    1.53088  -0.171   0.8641
Point.typeRandom           -6.76550    3.44656  -1.963   0.0496 *
Veg.Volume...Oak            0.07680    0.05111   1.503   0.1329
Veg.Volume...Succulent     -0.10412    0.06604  -1.577   0.1149
Basal.Cover...Woody.Debris -0.34048    0.18770  -1.814   0.0697 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


Analysis of Variance Table
                           npar Sum Sq Mean Sq F value
Land.Form                     3 4.9024  1.6341  1.6341
Point.type                    1 6.3644  6.3644  6.3644
Veg.Volume...Oak              1 6.3015  6.3015  6.3015
Veg.Volume...Succulent        1 1.3147  1.3147  1.3147
Basal.Cover...Woody.Debris    1 6.4314  6.4314  6.4314
```

Appendix E: Model of talussnail abundance (log no./100 m) at occupied sites generated using the StepAIC function in R with mixed (option = both) variable selection of all predictors.

```
Linear mixed-effects model fit by maximum likelihood
 Data: Data1
       AIC      BIC    logLik
  109.5394 136.0249 -40.76969

Random effects:
 Formula: ~1 | Group
        (Intercept)  Residual
StdDev:   0.4080164 0.4196907

Fixed effects: log1p(RA.dist) ~ Veg.Comm. + Land.Use.Intensity +
Veg.Volume...Succulent +      Veg.Volume...Conifer + Elev.Mean +
Basal.Cover...Rock
                                 Value Std.Error DF   t-value p-value
(Intercept)                  0.7961197 0.7366395 29  1.080745  0.2887
Veg.Comm.Desert Shrubland   -0.5923267 0.3226766  8 -1.835667  0.1037
Veg.Comm.Grassland          -1.8234835 0.5825767 29 -3.130031  0.0040
Veg.Comm.Montane Shrubland  -1.5246328 0.4550367  8 -3.350571  0.0101
Veg.Comm.Oak-Pine Woodland  -0.0563685 0.5472400  8 -0.103005  0.9205
Veg.Comm.Oak Woodland       -1.3519425 0.4891323  8 -2.763961  0.0245
Veg.Comm.Riparian Vegetation -1.5620250 0.7911492 29 -1.974375  0.0579
Land.Use.Intensity          -0.3214114 0.1309006  8 -2.455385  0.0396
Veg.Volume...Succulent      -0.0371169 0.0101247  8 -3.665963  0.0063
Veg.Volume...Conifer        -0.0403066 0.0111299  8 -3.621462  0.0068
Elev.Mean                    0.0010427 0.0005711  8  1.825755  0.1053
Basal.Cover...Rock           0.0124820 0.0052246  8  2.389054  0.0439


Number of Observations: 49
Number of Groups: 32
> anova(Step.AIC)
                       numDF denDF  F-value p-value
(Intercept)                1    31 79.05375  <.0001
Veg.Comm.                  6     6  2.60219  0.1347
Land.Use.Intensity         1     6  6.67609  0.0416
Veg.Volume...Succulent     1     6 13.85158  0.0098
Veg.Volume...Conifer       1     6 13.63496  0.0102
Elev.Mean                  1     6  3.95700  0.0938
Basal.Cover...Rock         1     6  5.70758  0.0541
```

Appendix F. Descriptions and notes on talussnail shells and genitalia measured and provided by Casey Richart.

Locality	Specimen ID from Herrmann 2020	Incised Lines Body Whorl	Aperture Description	Shell Color Description	Notes
Atascosa Mountains	Son30	-	slightly flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	genitalia undeveloped
Cerro Colorados, Lobo Peak	Son19	no	flared	translucent bronze with reddish-brown shoulder	shell heavily damaged and specimen damaged; shell further cracked as the animal was being tugged out; see images for damage; penis, vagina, uterus, and epiphallus are present, but the spermatheca duct, spermatheca, hermaphroditic duct could not be located. The albumen gland was not connected to the uterus. Either the genitalia are not fully developed or parts of the genitalia were lost when it was
Cerro Colorados, Lobo Peak	Son18	-	flared	translucent bronze with reddish chocolate shoulder	unable to take animal out of shell with water bath; genitalia absent
Coyote Mountains, Hayhook Ranch	Son24	no	slightly flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	
Coyote Mountains, Hayhook Ranch	Son28	yes, weak top of body whorl	flared	bronzed pinkish tan apically, fading pale tan around umbilicus, with chocolate brown band	shell previously damaged and "recalcified"
Coyote Mountains, Hayhook Ranch	Son23	no	not flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	
Coyote Mountains, Hayhook Ranch	Son22	no	not flared	pale tan fading more pale around umbilicus and at border with chocolate brown shoulder band	
Coyote Mountains, Hayhook Ranch	Son29	-	flared	translucent bronze fading to pale tan around umbilicus with chocolate shoulder	genitalia not fully developed
Coyote Mountains, Hayhook Ranch	Son25	-	not flared	translucent bronze fading to pale tan around umbilicus with reddish chocolate shoulder	genitalia not fully developed
Santa Catalina Mountains	Son16	no	not flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	unable to take animal out of shell with water bath; last whorl strongly descends compared to previous
Santa Catalina Mountains	Son14	yes	flared	grayish tan fading to pale tan around umbilicus and at border with the chocolate shoulder	last whorl strongly descends compared to previous
Santa Catalina Mountains, Buehman Canyon	Son17	no	not flared	tan with chocolate shoulder	unable to take animal out of shell with water bath
Santa Catalina Mountains, Egar Canyon	Son26	no	flared	tan with chocolate shoulder	unable to take animal out of shell
Santa Catalina Mountains, Egar Canyon	Son27	no	not flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	unable to take animal out of shell; shell was broken to remove animal
Santa Catalina Mountains, Egar Canyon	Son33	yes, weak top of body whorl	slightly flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	unable to take animal out of shell
Santa Rita Mountains, Madera Canyon	Son10	yes	flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	unable to take animal out of shell with water bath
Santa Rita Mountains, Madera Canyon	Son12	yes, weak top of body whorl	not flared	tan with chocolate shoulder	
Santa Rita Mountains, Madera Canyon	Son11	yes, weak top of body whorl	slightly flared at umbilicus	translucent bronze fading to pale tan around umbilicus with chocolate shoulder	epiphalic caecum is absent
Santa Rita Mountains, Madera Canyon	Son09	no	flared	dark tan fading to tan at border with shoulder band and to pale tan around umbilicus, shoulder band chocolate	unable to take whole animal out of shell
Tortolita Mountains	Son21	-	flared	tan with chocolate shoulder	last whorl damaged; genitalia absent
Tucson Mountains, Cat Mountain	Son15	no	slightly flared	tan fading to pale tan around umbilicus and at border with the chocolate shoulder	
Tucson Mountains, Los Muertos	Son32	yes, weak top of body whorl	not flared	dark tan fading to tan at border with shoulder band and to pale tan around umbilicus, shoulder band reddish	
Tucson Mountains, Los Muertos	Son13	yes	not flared	translucent bronze fading to pale tan around umbilicus with reddish chocolate shoulder	aperture damaged