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Genetic Research Reveals Pleistocene Origin and Low Genetic Diversity of the Mojave Fringe-toed Lizard (*Uma scoparia*)

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When I first visited the Mojave National Preserve (MNP) in May 2006 with my herpetology class to learn about the biology of desert reptiles, I was impressed by the population of Mojave Fringe-toed Lizards (*Uma scoparia*) that inhabit the Kelso Dunes. Unlike most reptiles in the Mojave Desert that occur in a variety of habitats, fringe-toed lizards are restricted entirely to windblown sand, including large dunes like those at Kelso, but also smaller hummocks and sandy

In this Issue:

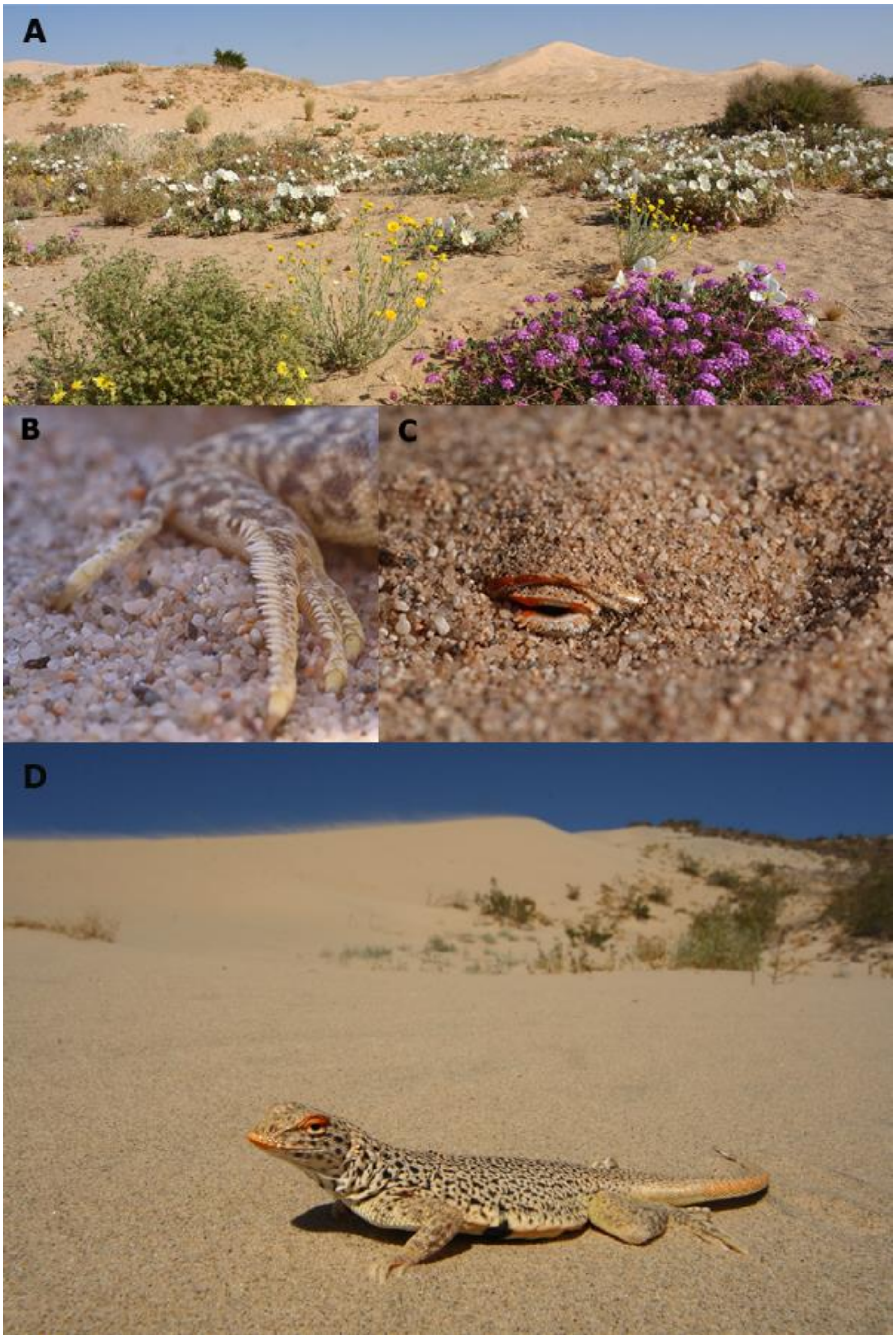

Figure 1. A) Fringe-toed lizard habitat at Kelso Dunes in the Mojave National Preserve. B) Toe fringes increase surface area and traction in loose sand. C) Fringe-toed lizards often conceal themselves below the sand, with only their eyes protruding above the surface. D) A camouflaged pattern helps them escape predators while active above the sand. Photos: Cameron Rognan.

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flats (e.g., Devil's Playground). They have evolved a number of adaptations to survive in this exposed habitat (Figure 1), including their namesake toe fringes – elongated scales which increase the foot's surface area to facilitate efficient locomotion in loose sand (*1*). They also possess shovel-shaped snouts, overlapping eyelids and earflaps, a counter-sunk lower jaw, and granular scales to assist in rapid burial (*2*). Fringe-toed lizards spend the night buried under the sand or in a burrow, emerging in the morning to bask, forage, and socialize. When confronted by predators, they either remain motionless, relying on their camouflaged pattern to avoid detection, or rapidly run several meters to a shrub or dune where they disappear under the sand, their concealed position given away only by their tracks.

Uma scoparia, the northernmost of several fringe-toed lizard species, currently ranges across much of the southwestern Mojave Desert, from southern Death Valley in the north, to Parker, Arizona, in the east, Joshua Tree National Park in the southwest, and the vicinity of Barstow in the west. Although *U. scoparia* are abundant in appropriate habitat, their geographic distribution is fragmented by rocky hills, dry playas, bajadas, and desert pavement. The distribution of *U. scoparia* is puzzling – if these lizards are never observed away from windblown sand, how did they cross the intervening barriers? Where did these lizards come from, and how long have they been here?

These unsolved questions inspired me to study *U. scoparia* for my master's degree in Biology at Humboldt State University in 2007. In 2008, with help from my advisors, Dr. Bryan Jennings and Dr. Sharyn Marks, I received grant funding and permits from several government agencies and non-profit organizations to pursue genetic research on *U. scoparia* (see Acknowledgements). Our primary goal was to estimate when *U. scoparia* speciated – that is, when it diverged from its closest relatives, the *U. notata* species complex in the Colorado Desert of southernmost California, Arizona, and northwestern Mexico (*3*). We also wanted to test whether the various populations of *U. scoparia* are genetically distinguishable using nuclear DNA (nDNA) sequences, which might be expected considering they are isolated across the Mojave Desert with few apparent opportunities to migrate and interbreed. The northernmost populations at Ibex Dunes, Dumont Dunes, and Coyote Holes, located just to the north of the MNP near the Amargosa River, were previously found to have minor differences in mitochondrial DNA (mtDNA) compared to southern populations in the Mojave River and Colorado River watersheds (*4*). We wanted to test whether the same pattern could be detected in the nDNA.

In spring 2008, based at the Sweeney Granite Mountains Desert Research Center and Zzyzx Desert Studies Center, we collected DNA samples from 93 *U. scoparia* representing 20 localities spanning the Mojave Desert, including Kelso Dunes in the MNP, Ibex Dunes in Death Valley National Park, and Pinto Basin in Joshua Tree National Park (Figure 2). In 2009, we obtained 16 samples of their closest relative, the *U. notata* species complex, in the Colorado Desert of southern California and Arizona. Because *U. scoparia* and *U. notata* are protected in California as Species of Special Concern (SSC), we used minimally invasive methods to obtain DNA. Lizards were captured with a noose or by hand and a small portion (< 1 cm) of the tail tip was removed and preserved in 95% ethanol. Date, time, GPS coordinates, snout-vent length, sex, ventral surface temperature, and sand surface temperature were recorded. The lizards were photographed and released within five minutes of capture.

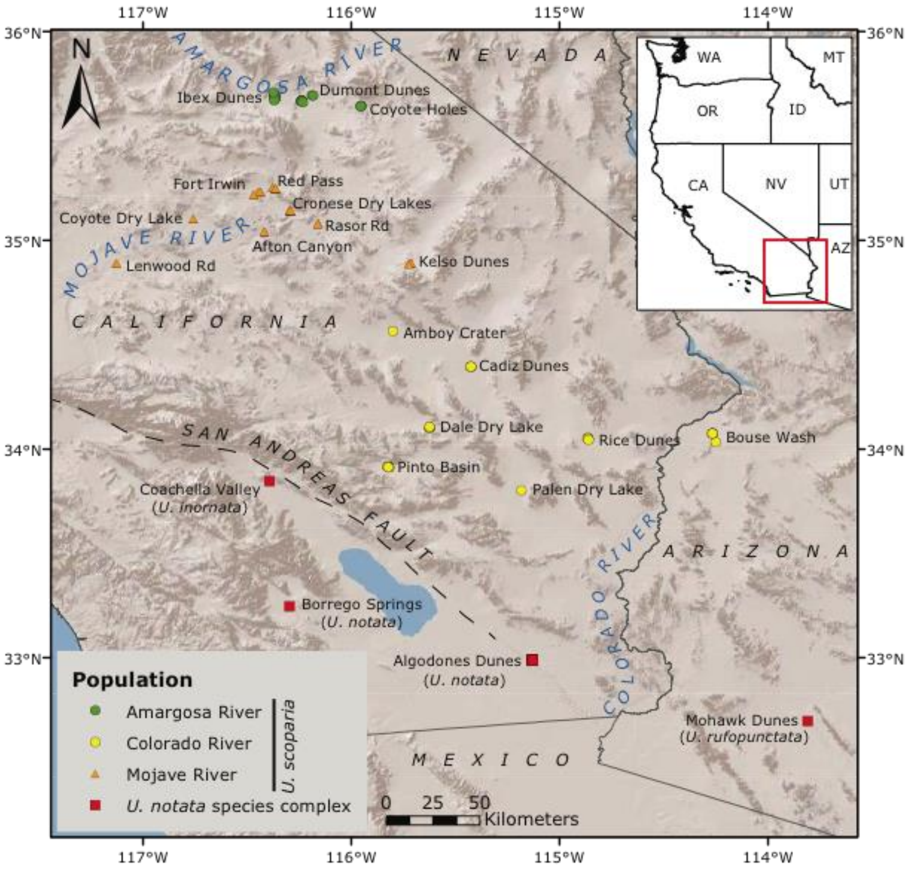

Figure 2. Map of fringe-toed lizard DNA samples used in our study.

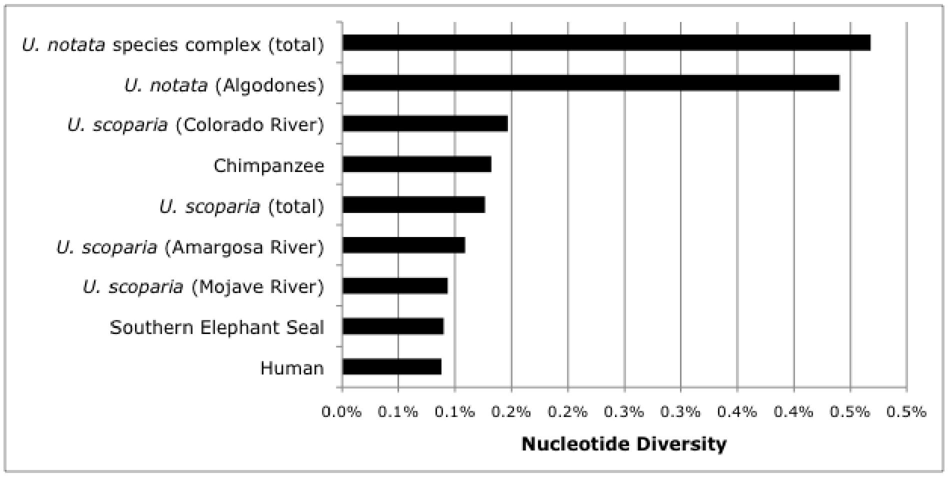

Figure 3. Comparisons of mean nucleotide diversity (a measure of genetic diversity) among fringe-toed lizards and selected mammal species with low genetic diversity. All estimates are based on nuclear DNA (nDNA).

Back in the laboratory, we extracted DNA from the tissues and sequenced 14 genes for a total of 7,046 base pairs, of which 157 (2.2%) were variable. We found that *U. scoparia* had quite low genetic diversity (Figure 3), comparable to the nuclear DNA of humans (*5*), chimpanzees (*6*), and elephant seals (*7*). Although genetic diversity was slightly higher in the southernmost populations, we were surprised that our data could not differentiate lizards in the Amargosa River watershed from those in the MNP and surrounding areas. However, we did detect 14 diagnostic single nucleotide polymorphisms (SNPs) that differentiate *U. scoparia* from the *U. notata* species complex. The low genetic diversity of *U. scoparia* was especially striking compared to the population of *U. notata* at the Algodones Dunes in extreme southeastern California. Our sample of only 13 lizards collected in a small area (< 2 km^2) of the Algodones Dunes contained more than three times the genetic diversity (Figure 3) than our sample of 93 *U. scoparia* collected across the Mojave Desert, and this difference was statistically significant (2-tailed t-test, P = 0.006).

We suspected that the low genetic diversity and lack of genetic differentiation among the various populations of *U. scoparia* might reflect a recent origin of this species, so we used a “molecular clock” to estimate the age of speciation of *U. scoparia*. DNA molecules mutate at a slow but roughly constant rate, so the longer since two species diverged, the more differences they accumulate in their DNA sequences (*8*). We calibrated our molecular clock with published mutation rates of other reptiles (*9*, *10*). We used a computer model to estimate the divergence time between *U. scoparia* and the *U. notata* complex while accounting for variation in individual gene divergence times (*11*).

Our results indicate that *U. scoparia* originated in the late Pleistocene epoch, commonly known as the “ice ages”, about 875,000 years ago (the 95% confidence interval is 540,000 – 1.3 million years ago). Although this seems like a long time ago, it is very recent on a geological time scale – for comparison, humans and chimpanzees share a common ancestor about 6 million years ago, and some of the rock outcrops in the Mojave Desert are hundreds of millions of years old.

In summary, our genetic analyses suggested that *U. scoparia* is a relative newcomer to the Mojave Desert, descended from ancestors in the Colorado Desert. Yet the mystery remains: if these lizards are entirely restricted to sand dunes, but the dunes are spatially isolated from each other, how did the lizards reach their current distribution?

To answer this question, I reviewed the geological literature of sand dunes in the Mojave and Colorado Deserts during the Pleistocene, when *U. scoparia* evolved. The climate during this epoch was cyclical, characterized by a series of cooler, wetter glacial maxima (the ice ages), interrupted by warmer and drier interglacial periods. Although this region escaped the direct impact of the northern glacial sheets during the last glacial maximum (LGM) 18,000 years ago, numerous streams and lakes graced the Mojave Desert, including the Mojave and Amargosa Rivers (*12*). Pollen extracted from fossilized packrat middens show that during the LGM, the lowlands supported a semiarid pinyon/juniper woodland that is currently confined to the Great Basin Desert and the highest elevations within the Mojave Desert (*13*). During arid interglacial periods, including the current Holocene epoch, most rivers and lakes dried up, exposing sediments to the wind and promoting a pulse of dune accumulation (*14*). For example, at the end of the Pleistocene the Mojave River terminated at Lake Manix east of Barstow, until 13,000 years ago when the natural dam containing the lake burst, rapidly eroding Afton Canyon and allowing the Mojave River to spill into Lake Mojave, now represented by Silver and Soda Lakes at the northwest corner of the MNP (*15*). When Lake Mojave evaporated, its exposed sand migrated southeast with the prevailing winds through the Devil’s Playground until the Granite and Providence Mountains blocked further movement, forming the massive Kelso Dunes. Similar scenarios have played out across the Mojave and Colorado Deserts (*16*).

Herein lies the answer to the apparent paradox: rather than fringe-toed lizards migrating across rocky terrain from dune to dune, which they have never been observed to do, the dunes are migrating over the years, carrying the lizards with them. Although it may take hundreds of years for the wind to blow a dune and its lizards across a valley or mountain pass (*17*), this is nothing on a geological time scale.

Our genetic results have important conservation implications for Mojave Fringe-toed Lizards, which are listed as a SSC due to their limited geographic distribution and anthropogenic threats that destroy or degrade dunes, including development, off-road vehicles, and exotic vegetation. The low genetic diversity within this species, the lack of genetic differentiation between isolated populations, and the late Pleistocene speciation date imply that *U. scoparia* recently dispersed among the various dunes of the Mojave Desert. Although future research using next-generation sequencing technology may reveal more subtle differentiation among populations, it appears that *U. scoparia* consists of a single evolutionary significant unit that has recently spread across the Mojave Desert (*18*). Thus, continued collaboration among the various federal agencies that control most *U. scoparia* populations, particularly the Department of the Interior (National Park Service, Bureau of Land Management) and Department of Defense (U.S. Army and Marine Corps), is needed to effectively manage this sensitive species for future generations.

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Past and present highlights of nematode research in the Mojave Desert

Paul De Ley[1]

Soil nematodes can be surprisingly abundant and diverse in desert soils. Anhydrobiosis allows them to persist for months in desiccated but viable condition, and to resume feeding, growth, and reproduction during the brief periods of elevated soil moisture after rain. Desert nematode diversity and systematics research started early last century and were focused on the American West, but focused mostly on the Great Basin while largely excluding the Mojave Desert. From the 1970s onwards, soil ecologists at UC Riverside conducted seminal studies on Mojave nematodes, focusing on trophic diversity and the process of anhydrobiosis. Targeted taxonomic surveys and descriptions from the Mojave Desert were initiated only fifteen years ago. To date, nine new species and one new genus were discovered from seven locations, and more discoveries are likely. This is especially true for habitats with peak diversity, such as sandy soils from vegetation bordering dune systems.

Moving from taxonomy to ecology, we recently initiated collaborative investigations of Mojave nematode associations with desert crusts, including feeding experiments to pinpoint the nature of nematode grazing on crust

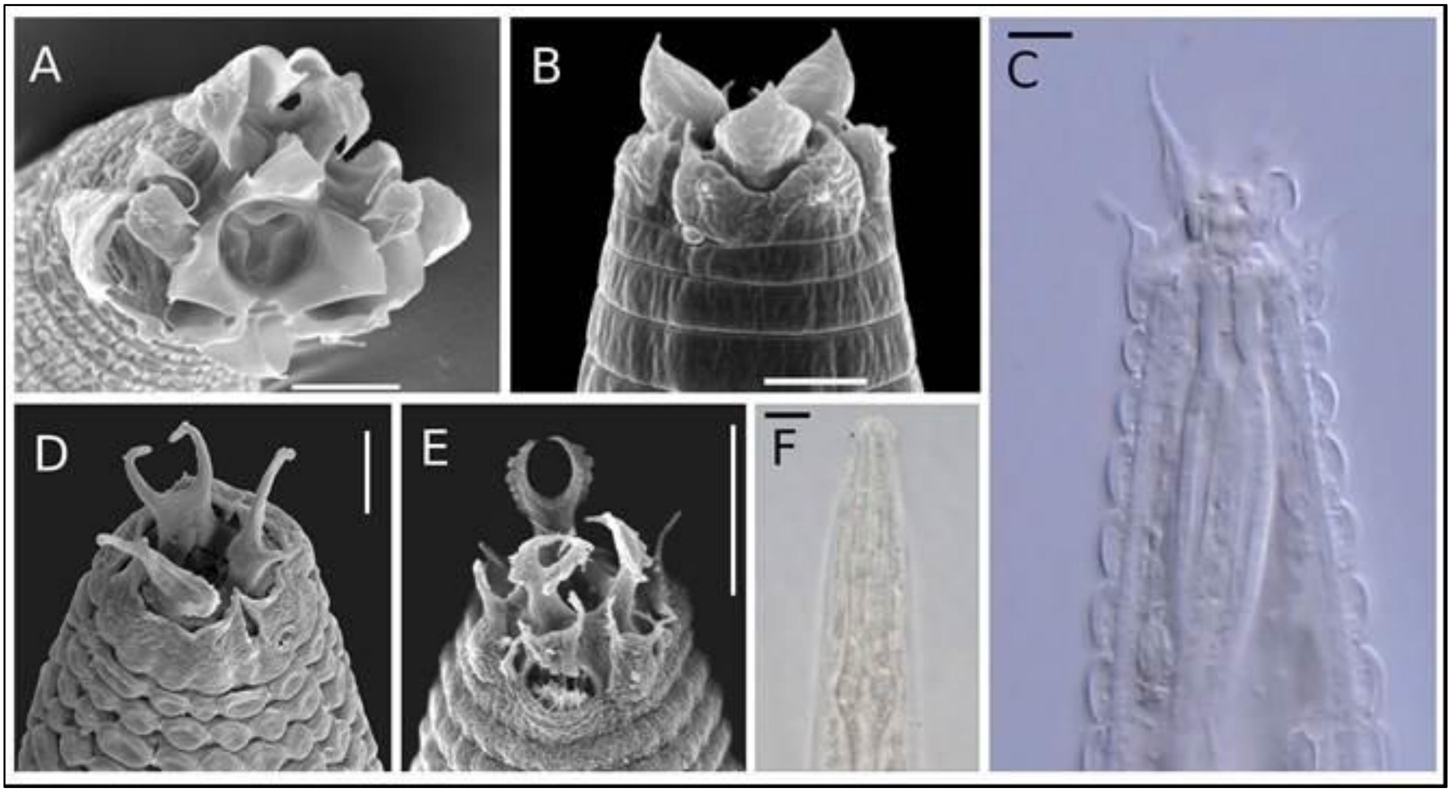

Figure 1. Examples of morphological complexity – or lack thereof – in the anterior processes of bacterivorous nematodes in the superfamily Cephaloboidea. All specimens shown originate from the Mojave Desert. A, B, D, E are scanning electron microscopy photographs showing surface anatomy at high magnification. C and F are light microscopy images showing transparent internal structures of preserved nematodes. A. *Acromoldavicus mojavicus* from Olancha; B. *Metacrobeles amblyurus* from Death Valley; C. *Paracrobeles mojavicus* from lava beds near Desert Oasis; D. *Stegelletina arenaria* from Kelso Dunes; E. *Chilodellus eremus* and F. *Medibulla* sp. from the same soil sample as D. Scale bar equals 2 um in D and 5 um in all others. A,B kindly provided by Dr. J.G. Baldwin and Dr. M. Mundo-Ocampo; D,E reproduced with permission from the Journal of Nematode Morphology and Systematics; C,F are original to this paper.

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organisms and to quantify its impacts. In parallel to surveys within California's deserts, we have also initiated research in the floristically and climatically similar Monte Desert of northwestern Argentina. This southern hemisphere desert harbors a number of species shared with the Mojave, as well as new discoveries in its own right. Even more interestingly, both the Mojave and Monte nematode faunas include some very poorly known taxa previously reported only from arid lands on other continents. Such biogeographical surprises raise new questions about the differential global dispersal abilities of the various groups and species of desert nematodes.

Nematodes or roundworms are a phylum of multicellular animals resembling fungi in their diversity: they occur in almost every environment imaginable on Earth, vary in size from microscopic to much larger, and probably include millions of species, even though only about 28,000 have been formally described (*1*). Also like fungi, the nematode phylum includes many species that are parasitic or pathogenic, as well as many others that are not. Most of these freeliving roundworm species are microscopic in size and feed on even smaller organisms like bacteria, fungal spores, other nematodes, etc. In fact, these microscopically small nematodes are often the most abundant type of animal found in soils, sediments, epiphytic plants, compost, plant litter, and so forth.

Science has studied nematodes for more than one and a half centuries, with the greatest efforts usually devoted to control or treatment of species affecting the health of crop plants, domesticated animals, or humans. A few free-living species (most notably *Caenorhabditis elegans*) have nevertheless become major research subjects as model organisms for genetics, embryology, and neuroscience. From an ecological point of view, free-living nematodes are an important part of subsurface food webs, not least because they are often the most abundant of all multicellular animals in soils and sediments. Bacterivores and fungivores interact with their respective food sources in complex ways, often with stimulating effects on nutrient cycling. Because the diversity and composition of nematodes reflects a cross-section of many biotic and abiotic properties, a range of methods for analysis of nematode communities are used in environmental assessment of soils and sediments.

Worms by definition have slender bodies and lack legs or wings. Despite the apparent limitations of such a simple body shape, the various phyla of invertebrate worms exhibit a great variety of body plans: roundworms are anatomically and genetically very different from flatworms, tapeworms and earthworms. Thus, the latter three kinds of worms have moving cilia on the outside of their bodies or inside various organs during at least part of their lives, but nematodes never do. Instead, the body is covered by a flexible non-cellular cuticle that is shed several times during their life cycle - similarities which roundworms share instead with animals like insects and tardigrades. Genetic analysis has actually revealed in the last two decades that these and other such phyla form their own evolutionary group (known as the Ecdysozoa), to the exclusion of most other types of worms.

As with many other organisms that are microscopic in size, research on nematode diversity started taking off in the late 19th century, with the development of the first high-powered light microscopy optics. The first scientist to study nematodes from desert soils was Gerald Thorne, a trailblazing nematologist and taxonomist who grew up in Utah, received his early research training there and collected soil samples prolifically from deserts and farmlands in Utah, Colorado, Idaho, and Nevada. He produced among others the earliest monographic articles and books on the subjects of the two groups of freeliving nematode species that are most diverse in arid soils, known as dorylaims and cephalobs in the vernacular of nematology systematics (*2, 3, 4*). Although we now know that the Mojave Desert shares with the northwestern high deserts many of the species first encountered and described by Thorne, only one of his more than one hundred species discoveries came from the Mojave Desert itself. As a result, nematodes in American deserts at lower latitudes remained largely unstudied until around the time of Thorne's passing in 1975.

In the early 1970s, Diana Wall and Reinhold Mankau started investigations at UC Riverside of Mojave nematode feeding types and anhydrobiosis, i.e. their ability to suspend all cellular processes during complete dessiccation and then to resume metabolic and reproductive activity weeks or months later upon rehydration. This work culminated in several seminal publications (*5, 6*) and continues to this day through ecological research in Death Valley by Amy Treonis and colleagues (*7*) at the University of Richmond. The investigations of Wall and Mankau did not extend to detailed systematics, however, and as a result no comprehensive nematode diversity data for the Mojave Desert were included in their studies.

In the last years of the 20th century, James Baldwin and Steve Nadler (from the respective Departments of Nematology at UC Riverside and UC Davis) started a targeted taxonomic project with funding from the National Science Foundation's program for Partnerships to Enhance Expertise in Taxonomy (PEET). The goal of this project was to investigate the systematics and evolutionary relationships of one particular group of nematodes: the cephalobs, formally known in taxonomy as the family Cephalobidae. These are widespread bacterivores that can have unusually complex structures projecting anteriorly around the mouth opening, and reaching especially high abundance and diversity in desert soils. They were also one of the groups on which Thorne focused his efforts nearly a century earlier. Through a fortuitous travel award by the Belgian Fund for Scientific Research I was able to join the project as visiting postdoc and to participate in sample collections from 1997 onwards. From the first sample series we encountered a variety of new or very poorly studied species, setting a trend of surprising discoveries in the Mojave Desert that continues to this day. To illustrate, here are just three examples of particularly striking cephalob species described in the course of the cephalob PEET project:

Acromoldavicus mojavicus was originally discovered around a single Joshua tree along Highway 395 near Olancha during the El Niño winter of 1997-98. It is characterized by petal-shaped anterior structures arranged into a striking pattern that looks to all effects very much like an iris flower (*8*). During subsequent years, it was found sporadically in several other locations spanning the Mojave Desert, near Granite Mountains and Kelso Dunes, as well as at Clark Mountains, but it also occurs much further north on the Colorado Plateau in Utah (*9*). The only other known species in the genus, *Acromoldavicus skrjabini*, has been reported from Spain, Moldova, Ukraine, Iran, and Israel – perhaps indicative of a vicariant path of evolutionary divergence between both species in which shared ancestry could, for example, date back to the opening up of the northern Atlantic Ocean some 65 million years ago.

Metacrobeles amblyurus was discovered in sand underneath iodineweed and inkweed growing on the eastern fringes of Mesquite Flats' dunes in Death Valley (*10*). It is the third species discovered in the genus, both others being known only from West Africa – suggesting again that the neotropical species could have diverged from its paleotropical siblings at least 60 million years ago. The original site where *M. amblyurus* was found remains to this day the only known location of the species. Sample processing procedures for taxonomic descriptions of nematodes usually do not allow observations to be made on behavior of the living animals, but, in this case, we were able to catch some interesting glimpses of its adaptations to life in the extreme environment of Death Valley's dunes. First of all, it is common to find many juveniles of a particularly interesting species in a soil extract, but few or no adults. This is a problem for nematode systematics, because species descriptions and diagnoses are almost exclusively based on adults. In the case of *M. amblyurus*, samples collected in several years during the late fall would produce juveniles only if extracted immediately. However, we did find adults after storing those same samples for one or two months in a refrigerated room at 7°C, suggesting strong seasonality in the life cycle with maturity and reproduction only occurring during the coldest months of the year. Some nematodes were transferred alive to agar plates and maintained for two or three generations, revealing some interesting complications for culture maintenance: although soil nematodes require water to be active, this particular species appeared to be averse to any but the absolutely thinnest water film on the agar – more often than not it would crawl up the dry sides and cover of the petri dish rather than staying on the hydrated agar surface. Furthermore, the female reproductive system opens to the exterior through a canal that is so long and narrow in this genus as to disallow egg laying. Instead, gravid females retain all eggs and the latter hatch internally, with the larvae feeding on bacteria ingested by, and decomposing tissues of, the dying parent animal. Such a process of matricidal internal hatching or “endotokia matricida” is known to occur facultatively in other bacterivorous nematodes, usually under very crowded or starved conditions, but *M. amblyurus* is the first recorded case of a species that never lays eggs and always follows the path of maternal self-sacrifice.

Paracrobeles mojavicus on the other hand is a new discovery that appears to be truly widespread in sandy environments throughout the Mojave Desert, such as the fragmenting lava beds east of Desert Oasis as well as Kelso Dunes (*11*). It also occurs in Joshua Tree National Park as well as in Anza Borrego State Park. The genus *Paracrobeles* is unusual because it has (among other differences) very long and tapering anterior projections, as well as the largest subdivisions of the body wall reported for cephalobs (Figure 1C). Only two other species were previously described, respectively from South Africa and Namibia versus Spain and Italy. Thus, it appears once again that the opening up of the Atlantic Ocean played a key role in the evolution of species diversity among desert cephalobs.

To date, the number of new cephalobs described from the Mojave Desert during the past fifteen years stands at nine species (*12, 13*), and one among these also represents a new genus named *Chilodellus* (Boström & Holovachov, 2012). Moreover, systematists not only aim to discover new species; it is often equally important to study named species that have not been reported on for many decades, so as to clarify aspects of their anatomy that were not studied before, or which could not be observed clearly with earlier state-of-the-art microscopes. In cephalobs for example, it has become essential to study the anterior processes with scanning electron microscope, because their minute size and transparency to light causes their shape and arrangement to be all but invisible with light microscopy, even at the highest magnifications and resolution possible.

Placodira lobata, the single species described by Thorne from a location in the Mojave Desert, was recently the subject of such an updated description, including first electron microscopy observations (*14*). We now know it to be widespread in eastern Mojave soils high in gravel content, and it has also been found in Libya (*15*). Several more "old" species have turned up in recent collections to become subjects of similarly expanded and updated redescriptions (*16*).

Figure 2. Irma Tandingan De Ley, Nicole Pietrasiak and Melissa Yoder collecting the first soil samples near Clark Mountains (Mojave National Preserve) in 2010 for analysis of nematode diversity.

The discovery of great diversity and novelty within the family Cephalobidae naturally suggests that other nematode groups in Mojave habitats need systematic attention as well. We have therefore expanded our identification efforts to include all groups of soil nematodes in three particular areas: UC's Sweeney Granite Mountains Desert Research Center, the vegetated fringes of Kelso Dunes, and the lower alluvial fans west of Clark Mountains. The UC staff and facilities at Granite Mountains have provided us with an ideal base of operations for conducting field work throughout our 15 years of Mojave Desert nematode investigations, and it is also the site of discovery of three new cephalob species, making it the logical starting point for surveying the entire nematode diversity in its soils. To date, the total number of taxa identified from this UC reserve tallies 33 genera representing an estimated 47 different species.

Nematode surveys near Clark Mountains were made possible through a fortuitous collaboration with Dr. Robert Graham (Department of Environmental Sciences, UCR) and Dr. Nicole Pietrasiak (now at John Carroll University, Cleveland OH). Both scientists had just completed field work to investigate associations between landforms and soil features with the abundance and diversity of mosses, lichens and microscopic soil algae (*17*). These organisms form complex communities known as biological crusts or bio crusts, found on exposed soil surfaces between scattered shrubs in many deserts including the Mojave (*18*). Bio crusts are ecologically important because they increase water retention as well as resistance of the soil surface to erosion and because many crust organisms can fix carbon through photosynthesis. Annual contributions of biological crusts worldwide to global carbon cycles remains as yet unquantified, yet could well be significant considering that arid and semiarid lands constitute 40% of our planet's terrestrial surface area. Furthermore, a variety of Cyanobacteria found in crusts are capable of nitrogen fixation, thus adding scarce nutrients to soils that are particularly important to desert plants.

Our prior nematode collecting elsewhere in the Mojave suggested that the distribution of nematodes in desert soils cannot be explained very well by presence and identity of plant root systems alone. Dr. Pietrasiak's site and data therefore presented an opportunity to begin investigating whether soil nematodes might associate with different types of bio crusts on the soil surface. Our survey at this location yielded 38 nematode genera representing an estimated 62 different species, levels of diversity considerably higher than we had expected to find in such a seemingly austere environment. Five genera appear to occur particularly in association with one type of bio crust, but others do not seem to correlate clearly with crust distribution, and we are therefore conducting further soil analyses to find out which combinations of biotic and abiotic factors best explain nematode distribution in these soils.

Kelso Dunes initially attracted our attention because taxonomic diversity of cephalobs can be especially high in coarse sands with sparse vegetation and also because of the proximity of this dune system to the Sweeney Reserve at Granite Mountains. The first sample series we collected at the edges of the dunes did not disappoint: cephalobs were represented by no fewer than 16 genera and an estimated 28 species. We therefore revisited the dunes in 2010, this time to collect and identify material of all nematode groups, which produced an estimated total of 53 species in 40 genera, including 43 species also found at Granite Mountains. Aside from descriptions of the new species and genus already mentioned above, just a few specimens of the very poorly known genus *Medibulla* also turned up at both Kelso Dunes and Granite Mountains. This relative of cephalobs has greatly simplified external morphology and was until present only known from its original discovery in a wheat field in Libya and in forest soil from India.

As illustrated by multiple examples above, an intriguing biogeographical pattern emerges, in which North America shares species of desert nematodes or close relatives with arid lands in the mediterranean, middle east, and Africa. This raises various interesting questions, for example: why do certain nematode species occur in deserts of multiple continents and yet others do not? Although nematodes only travel tiny distances by their own active means, the capacity for anhydrobiosis allows them to disperse as airborne dust particles, and it is well known that desert dust can traverse continents or oceans following sandstorms. Presumably they can also hitchhike with dried mud on legs or beaks of migratory birds and mammals. They definitely travel along easily on or in plant roots and seeds as transported worldwide by our own species, beginning with human expansion around the globe as well as the spread of agriculture and culminating in modern globalized trade in plant crops and ornamentals. And yet, it is clearly not true that all desert nematode species occur in all deserts, despite their shared abilities for tolerating desiccation and for being transported over huge distances. We must therefore try to tease apart niche limits of particular species from the environmental factors that permit or constrain their distribution, as well as from historical factors such as tectonic processes.

One particularly obvious biogeographical question is: do these species (or related ones) also occur in South America and Australia? Given the history of tectonic plate movements on earth, any attempts at understanding of the dispersal and speciation histories of desert nematodes must also incorporate these two major pieces of the puzzle. With the exception of South Africa, free-living nematodes have hardly been studied at all in subequatorial deserts, and the major challenge in nematode biogeography remains a problem of extremely patchy sampling effort, usually complicated further by taxonomic focus on just a few groups rather than total nematode diversity.

We have therefore started laying the groundwork for international collaborations to begin filling in these gaps. Because of its similar climate and plant species, our expanded geographical focus began with preliminary surveys in the Monte desert of northwestern Argentina in 2007, 2009, and 2012 along a 900-mile loop of desert highways, in collaboration with Dr. Marcelo Doucet, Dr. Paola Lax, and Dr. Fernando Gomez of the Universidad Nacional de Córdoba. Although our efforts were hampered by lower nematode content of soil samples during the protracted drought in the region from 2008 onwards, results to date include a combination of nematode species shared with the Mojave Desert, but not arid lands in Eurasia or Africa, as well as species unique to subequatorial South America, and a number of nematode species occurring worldwide. More specimens are needed to confirm identities of two very rare species; one of these appears to be shared exclusively with Australia, while the other was previously reported from South Africa as a single occurrence only.

Our collaboration on bio crust/nematode associations from the Clark Mountain study site has led us to start sampling jointly with Dr. Pietrasiak for crust organisms and nematodes at Granite Mountains as well as near Kelso Dunes. One of the goals of this work is to obtain more information on interactions between crust types and particular nematode genera, including those that belong to a group known as the order Dorylaimida, aka dorylaims. Dorylaims are another group of nematodes that occur with particularly high diversity and abundance in some desert soils. Unlike cephalobs, they are equipped with a hollow tooth modified into a more or less needle-shaped stylet, which is used to pierce food items and ingest cytoplasm. In temperate soils they are usually considered to be indicative of stable conditions and very mature soil ecosystems, because they include many species that appear to have a slow life cycle (by nematode standards) and which are more sensitive to changes in soil chemistry than bacterivores such as cephalobs. Some dorylaims are capable of feeding on other nematodes and a few of these species have been cultured for predation studies to assess their possible relevance to biocontrol of plant parasitic nematodes. Certain species can also be very abundant in mosses, and a few have been cultured in the past on soil algae or fungal mycelium, suggesting that the group also includes desert species likely to graze actively on the algae or fungi that are major components of biological crusts.

Grazing on crust fungi and algae by microscopic organisms like nematodes also remains unquantified, and it is an open question whether it could channel significant amounts of fixed carbon back to the atmosphere (among others through herbivore respiration) or whether it might instead contribute more to carbon storage (for example through vertical migration of nematodes with temperature and moisture gradients in the soil column). To study the possible relevance of such processes to local as well as global nutrient cycles, we have begun experimenting with various species combinations of desert nematodes and soil algae, in order to design microcosms and develop easily replicated culture systems for crust-grazing species among dorylaims. Although we are still in very early stages with this work, our observations in vitro do confirm that at least one dorylaim from Granite Mountains and Kelso Dunes grazes actively on soil algae as well as fungal mycelium, and we have begun food preference and attraction experiments together with both Dr. Pietrasiak and Dr. Jeffrey Johansen, using the extensive collection of eukaryote algae and cyanobacteria maintained at John Carroll University, Cleveland OH.

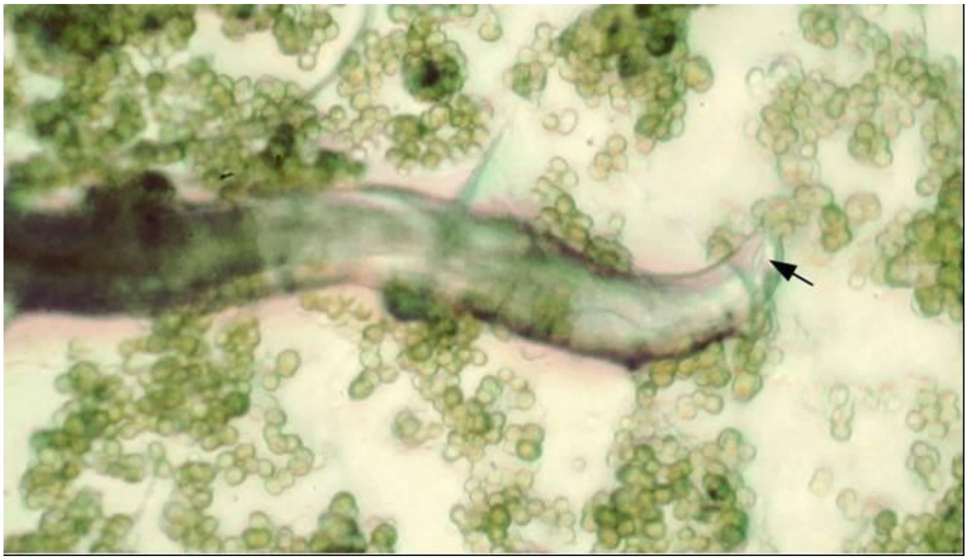

Figure 3. A live female nematode (*Tylencholaimus* sp.) from Kelso Dunes feeding on algal cells of a *Stichococcus* isolate from the culture collection maintained by Dr. Pietrasiak and Dr. Johansen at John Carroll University, Ohio. Arrow points at the 5 um long feeding stylet in the anterior end of this nematode.

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Three Wasps, Three Plants, One Ant: Life History of Desert *Orasema*

John Heraty [1]

We are surrounded by small parasitic wasps that at 1-4 mm in size are largely invisible to us. Some species are phytophagous (plant-feeders), inquilines (commensal with the products of other insects), or gall makers. However, the vast majority are parasitoids, attacking and killing the egg, larval, and pupal stages of other insects. There are currently 23 families in the superfamily Chalcidoidea, which contains more than 2,000 genera and 23,000 described species. The superfamily conservatively is estimated to contain more than 500,000 species. Within this group, the family Eucharitidae are exclusively parasitoids of the larval and pupal stages of ants. Eggs are deposited away from the host into plant tissue, and the first-instar larva (planidium) is responsible for gaining access to the ant brood. Successful parasitism is dependent on emergence of the adult wasps from the ant nest, choice of the plant host for oviposition, how the eggs are laid, and how the planidia associate with adult ants for transport to the waiting ant brood.

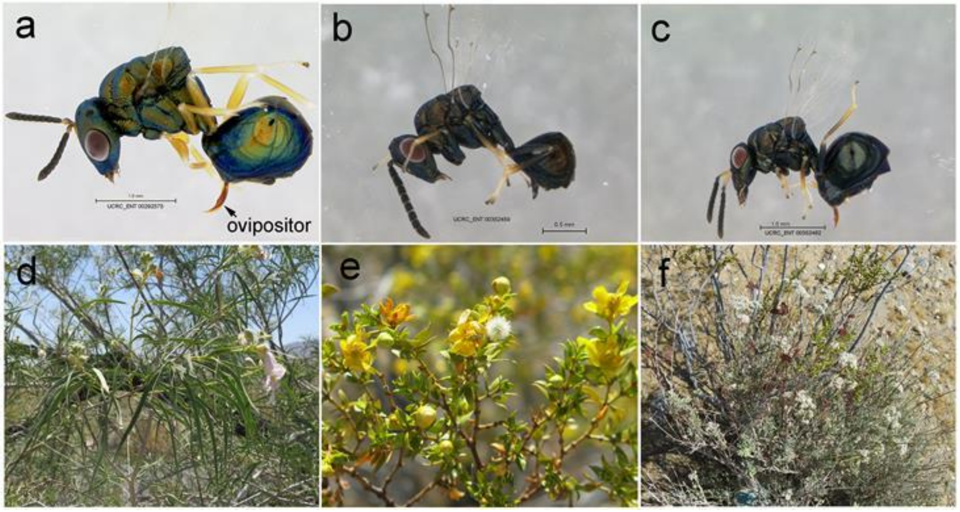

Figure 1. *Orasema* and their plant hosts. *Orasema simulatrix*, female (a) on *Chilopsis linearis* (d); *O. occidentalis*, male (b) on *Larrea tridentata* (e); *O. ?cockerelli*, female (c), on *Eriogonum* (f).

Species of the wasp genus *Orasema* (Eucharitidae: Oraseminae) are common throughout the desert regions of the southwestern United States from California to Texas. Using their enlarged ovipositors (Figure 1a), females deposit single eggs into punctures made into leaves (Figure 2a), flower stems, or involucral bracts of flowers. In the Mojave Desert, three common species (Figures 1a-c) are differentially associated with desert willow (*Chilopsis linearis*) (Figure 1d), creosote bush (*Larrea tridentata*) (Figure 1e), and buckwheat (*Eriogonum fasciculatum*) (Figure 1f). While the plant associations are diverse, only a single ant host, *Pheidole desertorum* (Myrmicinae), is known for two of the *Orasema* species, *O. simulatrix* and *O. occidentalis* (*1, 2*).

The subfamily Oraseminae (Eucharitidae) are parasitoids of the larvae of myrmicine ants (primarily in the genera *Pheidole*, *Solenopsis*, *Monomorium*, *Temnothorax* and *Wasmannia*), although there are some potentially mistaken records from *Formica* and *Eciton* (*3*). The ant genus *Pheidole* is the only host known from the Old World, for both *Orasema* and other orasemine genera (*Orasemorpha* and *Timioderus*), and is the predominant host for *Orasema* in the New World. Nothing is known of the biology of *Indosema* from India. Most of the undescribed diversity (~200 species) is in the New World species of *Orasema*.

Adults of *O. simulatrix* (Figure 1a) oviposit into leaves of desert willow (*Chilopsis linearis*) (Bignoniaceae). Eggs are deposited in close association with the extrafloral nectaries (EFN, Figure 2b) found on both leaves and flowers (*2*). Extrafloral nectaries produce secretions that are attractive to ants, and it has been postulated that in the plant family Bignoniaceae, they distract ants from the flowers, reducing competition with pollinating insects (*4, 5*). The well-sclerotized (hard and pigmented) first-instar larvae are less than 0.12 mm in size (cf. PL, Figure 2a-c) and appear to migrate into the fluid-filled nectaries (Figure 2c). *Pheidole desertorum* are common nocturnal visitors to the EFN on *Chilopsis*, and it is postulated that ants ingest the first instars while feeding on the nectaries, and then carry them within their infrabuccal pouch as solid food back to the larvae within the ant nest (adult ants do not ingest solid food). Once in the nest the planidia first attack and burrow into the ant larva (endoparasitoids), where they wait for the ant to pupate. They then become external (ectoparasitoids) and finish developing on the ant pupa.

The parasitic wasp *Orasema occidentalis* (Figure 1b) uses a different strategy. Eggs are laid into bracts of unopened

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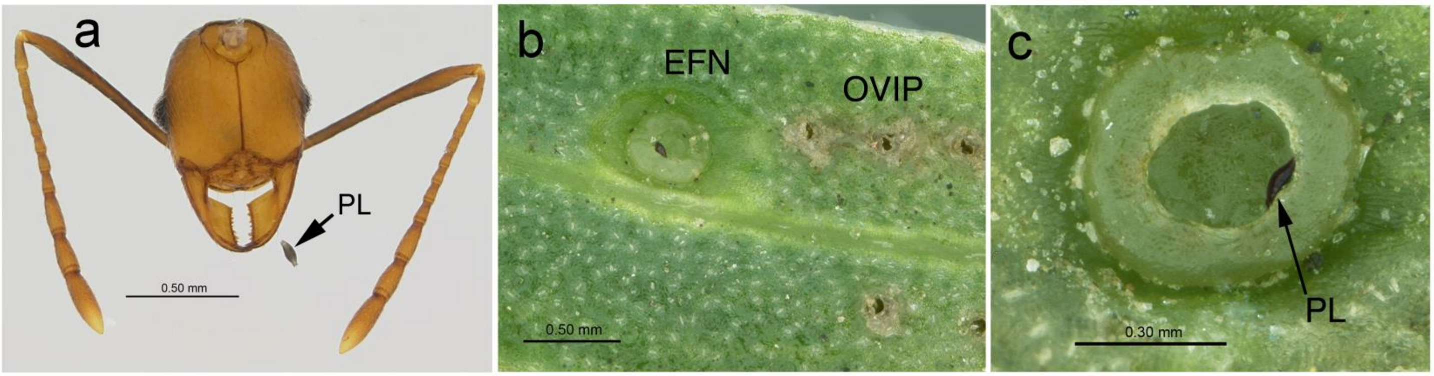

Figure 2. *Orasema simulatrix* and its host. Head of *Pheidole desertorum* next to planidium (PL) of *O. simulatrix* (a); oviposition punctures (OVIP) next to extrafloral nectary (EFN) (b); EFN with planidium (c).

flower buds of *Larrea*. When the planidia emerge in the opened flower bud, they attach to immature thrips (Thysanoptera: Thripidae) in the flowers, which can carry from 1 to 4 planidia on their abdomen. Thrips are likely prey items for *Pheidole* and thus act as an intermediate host of *Orasema* when fed to the ant larvae. So far, the oviposition habits and planidial behavior of the species associated with *Eriogonum* are unknown.

At least three species of *Orasema* wasps (Figure 1) are sympatric in the Mojave, with adults collected on the different plant species within a few meters of each other. *Pheidole desertorum* is one of the most common ants of the Mojave, dominating the landscape between dusk and dawn. It is unclear why *Orasema* partition themselves among different host plants and utilize different means of associating with foraging ant workers (nectaries versus intermediate hosts). To date, we have found only a single species within an excavated nest of *Pheidole*, although there are very few nest records to establish any pattern. We are just beginning to get a better idea of the species boundaries of *Orasema* using both morphological and molecular tools, and we hope over the next few years to establish the integrity of host plant choice and ant host specificity.

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Watching plants move: Tracking landscape effects on movement in the common desert shrub catclaw acacia [*Acacia (Senegalia) greggii* A Gray]

Keith D. Gaddis [1]

Due to the rise in environmental pressure and land development in the southwestern US, there is an increasing incentive to identify ecological data and tools to inform conservation. In the last 30 years, rainfall relative to evaporation rates have dropped throughout the region, and multiple climate models predict that this trend will continue into the foreseeable future (*1*). This change in climate is making deserts harder for plants and animals already living at the extremes of their drought tolerance. In addition, development of housing and industry within the Southwest is at an all-time high (*2*). This increase in human activity has led to a rise in air pollution (*3*), the introduction of invasive species (*4*), and the destruction or fragmentation of once pristine lands. All of these changes may jeopardize plant and animal life in this zone, and hamper their ability to move in response to environmental pressure. Movement can be important for the persistence of a species (*5*). Moving allows a species to escape an unfavorable environment, find mates, and share genetic information that might help adapt to new environments. If changing climate and habitat destruction inhibits the mobility of a species, there is a greater likelihood of local or global extinction.

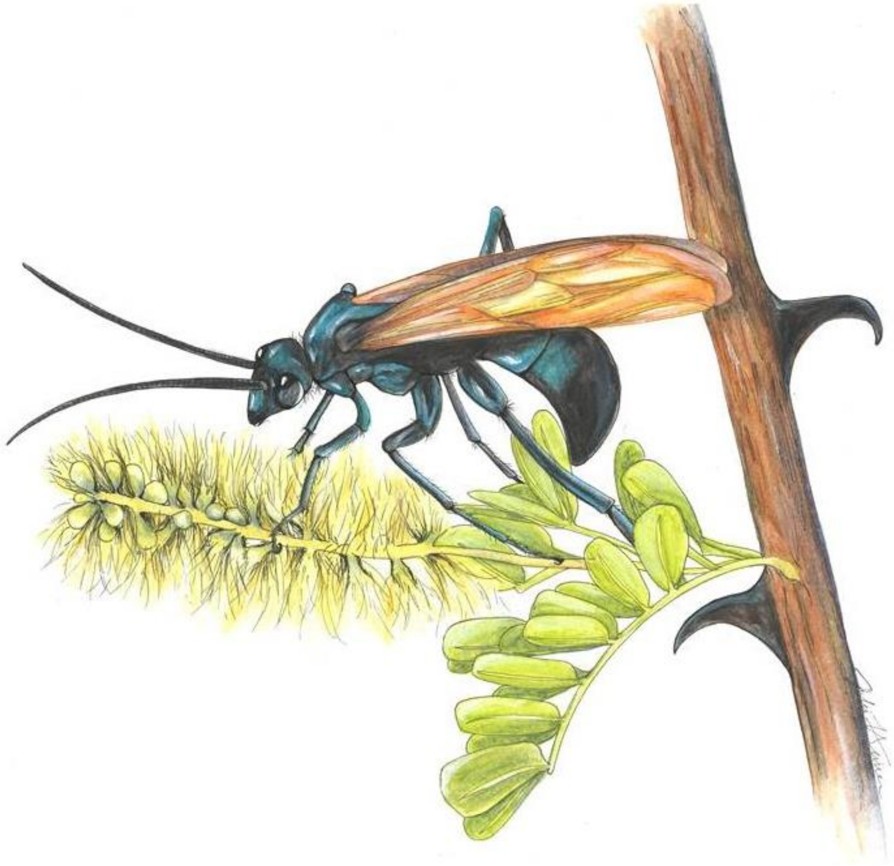

Figure 1. Catclaw acacia (*Acacia (Senegalia) greggii* A Gray) visited by Tarantula wasp (*Pepsis* sp.) (Illustration by Julie Himes, *juliehimes@gmail.com*).

I am studying the potential effects of landscape and climate change on the movement of a representative Mojave shrub, catclaw acacia (*Acacia (Senegalia) greggii* A Gray), and its pollinator community (Figures 1 & 2). Investigating these species will inform conservation efforts in this area and also suggest patterns in similar plants and pollinators. This is a multi-year study that has involved the use of ecological, genetic, and remote sensing tools. This article is an overview of my findings and the design for work and analysis still underway. The specific goals of this research are to: *1)* determine how seeds and pollen of catclaw move, and *2)* determine how the landscape affects that movement.

Because catclaw acacia is widely-distributed across the Mojave, it is an ideal system for understanding how landscape and climate change are affecting plant dispersal. Catclaw is a common Southwest species that extends across California and into northern Mexico. Throughout its range, catclaw is generally restricted within or around dry-washes (also known as arroyos), which are empty stream channels that fill with water during infrequent rainfall events. Within Mojave National Preserve, catclaw flowers from the late spring to mid-summer, sometimes with a second flowering in early fall of wet years. Its flowers are yellow, forming a cylindrical spike, and quite fragrant. It sets seed in the late summer, producing bean-like pods containing fingernail-size seeds. Its common name is derived from the recurved spines on its stem and branches that resemble the claws on a housecat.

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Studying plant movement requires multiple levels of observation and experimentation. Unlike animals, plants are sedentary and depend on both seeds and pollen to disperse their genetic information. This complicates research as seeds and pollen can travel through completely separate abiotic (i.e. wind or water) or biotic (i.e. insects, rodents, grazers) dispersal mechanisms. Catclaw has been identified as an insect pollinated plant. However, no previous study has surveyed which pollinator species visit catclaw or how they move its pollen across the landscape. The major dispersal mechanism of catclaw's seeds is unknown. Animals, such as rodents, can transport seeds in desert areas like the Mojave. However, because rodents use these seeds as a food resource, the seeds are often eaten or damaged during transport. This makes rodents a costly or ineffective dispersal vector. It is therefore likely that catclaw and similar species rely on separate seed dispersal mechanisms for reproductive success.

Figure 2. Images of catclaw acacia in a typical dry-wash habitat (upper-left), developing seeds in early August (upper-right), an Africanized honeybee (*Apis mellifera scutellata*) pollinating catclaw (lower-left), and fully-developed pods with the seeds extracted (lower-right).

To determine the pollinators of catclaw acacia, I have conducted a survey of flower visitors over several summers. During this survey, I walked from tree to tree recording the observed pollinators and capturing unknown species by net for later identification in the lab. I found that although catclaw hosts a diverse community, over 80% of the insect pollinators were *Apis mellifera scutellata* (Figure 3), the so called Africanized honeybee, or "killer bee" (Figure 2). This finding is interesting, as the Africanized honeybee is an introduced species that moved into the US in the last 30 years. The remaining pollinators I observed were an assortment of bee, wasp, butterfly and fly species (Figure 3), including such notables as the hairstreak butterfly and the intimidating tarantula wasp (Figure 1). The dispersal distances of these observed species vary. Honeybees have been recorded travelling over 10 km (*6*), but many smaller solitary bees forage in less than a 600 m radius (*7*). Having identified the pollinators, my next goal is to determine the pattern of pollen-mediated gene movement across the landscape.

Genetic analysis enables a researcher to indirectly track the movement patterns of a species. This approach works by examining areas of DNA classified as neutral (also called non-coding DNA). Often times, when a change occurs in a functioning area of DNA (also known as coding DNA), it results in some physical difference that, more times than not, is bad, and causes the individual to die. Thus, changes in functioning areas of DNA do not often remain in populations of an organism across generations. In contrast, there are neutral areas of the DNA that essentially hold space and don't actually make anything or affect the organism's physical characteristics. Changes in neutral areas of the DNA are neither good nor bad and, thus, remain in the DNA, getting passed on from generation to generation. Consequently, if one examines individuals in two populations that have been closely associated over a long period of time (i.e. there has been lots of movement and breeding events between them), they would be more similar in this neutral area of the DNA than individuals in two populations that have been less closely associated (i.e. have had infrequent movement and breeding between them).

Therefore, I can examine multiple populations of a species and identify geographic areas with greater or lesser connectivity based on the genetic similarity between them.

Using this genetic approach, I am evaluating how much catclaw has moved across the Mojave, accounting for seed and pollen flow together. To do this, I sampled trees in 23 sites within and near the Mojave National Preserve (Figure 4). Within each of these sites, I have collected leaf tissue from 20 individuals. I then extracted DNA from this tissue to compare individuals at 10 neutral DNA regions. If there has been limited movement between sites historically, I will see decreasing genetic similarity between individuals as distance between them increases. I can use this information to infer global landscape and climate effects on plant movement by modeling how much of the variation in genetic relatedness between individuals can be explained by the landscape and climate between them.

The next part of this project is to explicitly distinguish the dominant landscape variables directing movement and to differentiate how they affect seeds and pollen.

Seeds: As mentioned before, seed dispersal is not well understood in catclaw. Work I have done with this species has shown that catclaw requires seed-coat abrasion and a large amount of water for germination to occur. These requirements are common of many desert seeds because a thick outer layer protects the seed inside from desiccation in the harsh desert environment. Mojave rainfall events are more common in the fall, just after late summer catclaw seed production. As catclaw occurs predominantly within or along dry-washes, water may serve as the primary seed dispersal mechanism. Even if animals do disperse seeds of this species, those seeds dispersed along

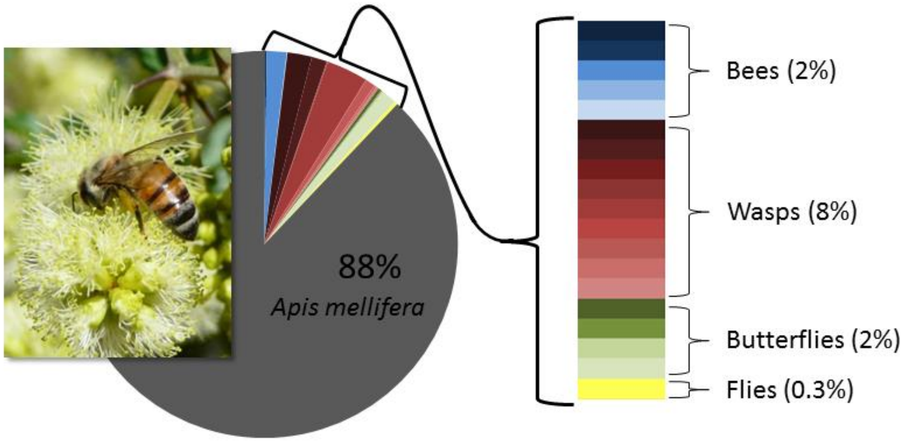

Figure 3. Pollinator community of catclaw acacia in the Mojave National Preserve. Each color shade represents a separate species.

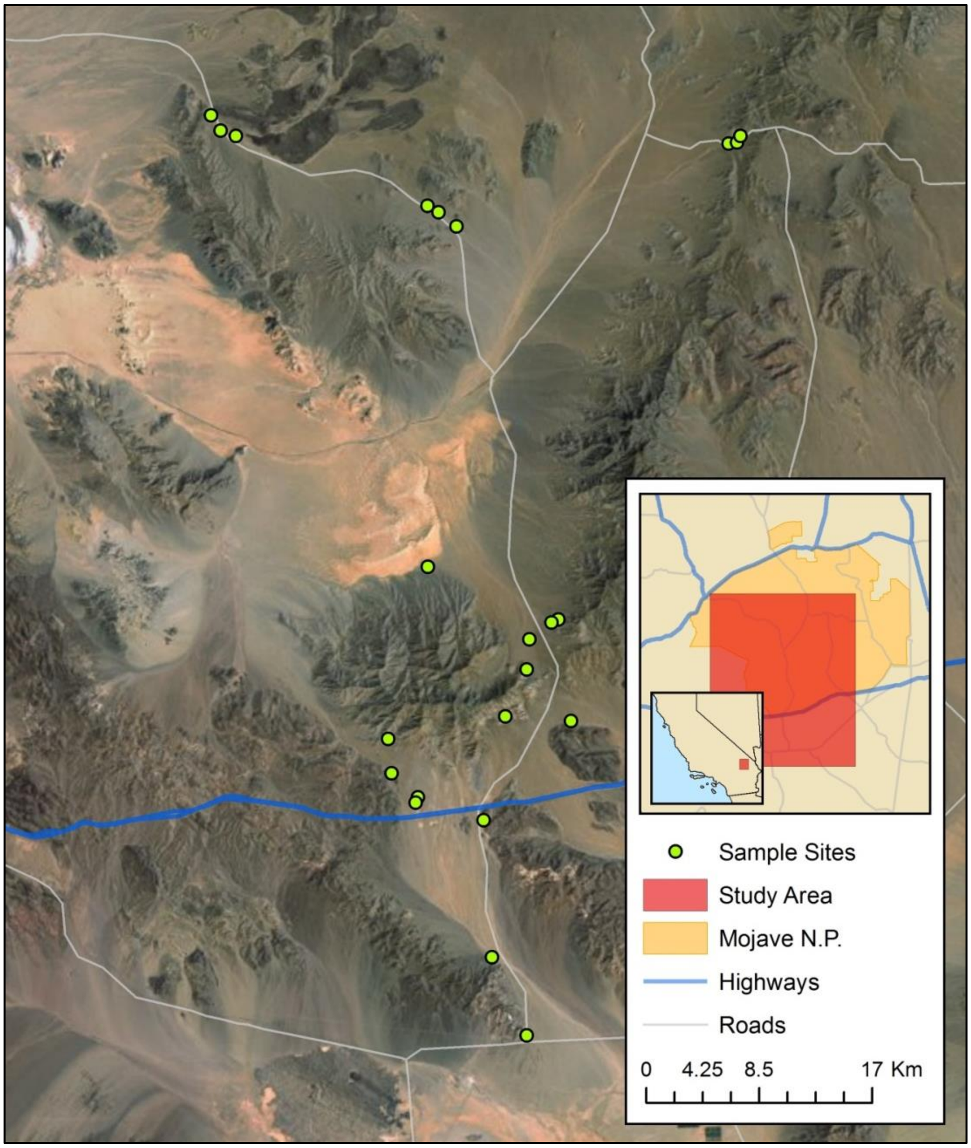

Figure 4. This is a map of 23 regional sample sites. I genotyped 20 catclaw acacia trees per site to identify historic movement patterns.

washes during rainfall have a greater likelihood of germinating and contributing to the next generation.

To determine if dry-washes are directing the movement of catclaw seeds, I am examining a sub-region of the Mojave National Preserve. I identified three parallel washes running out of the Providence and Granite Mountains. Each of these washes has an independent headway and a potentially separate seed source. I collected leaf tissue from 217 catclaw trees in these washes and extracted DNA to compare them at neutral DNA regions and estimate relatedness (Figure 5). If washes are directing movement, then trees within the same wash will be more genetically similar to each other than trees in different washes, even if those washes are relatively close to each other.

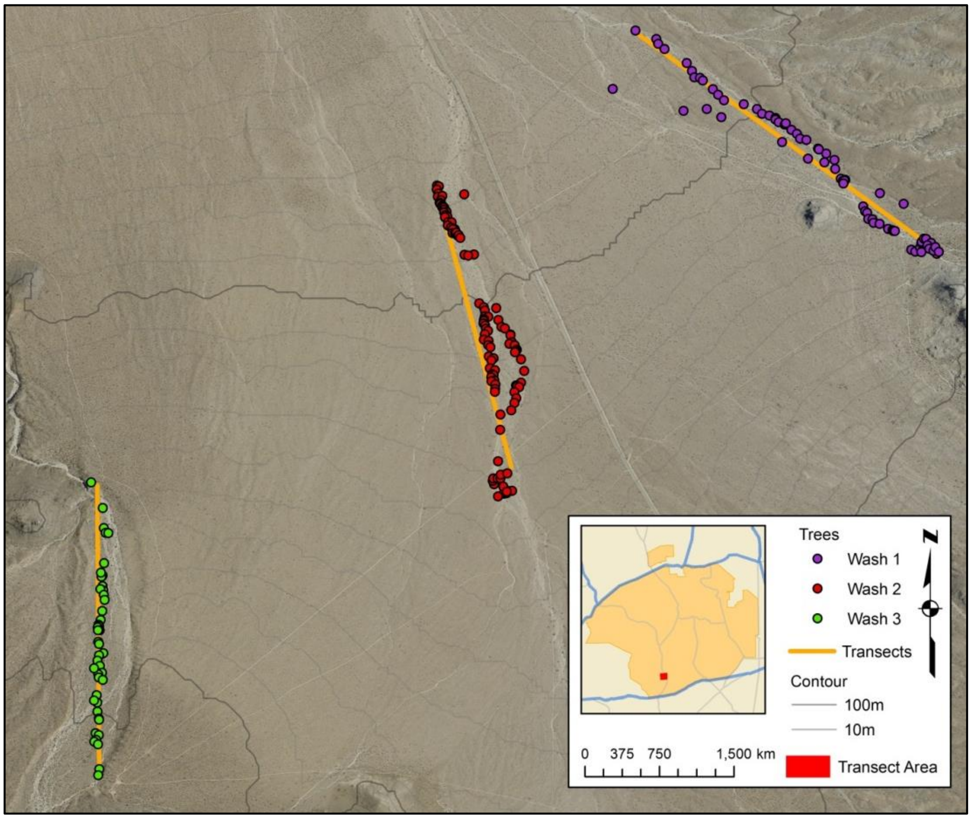

Figure 5. This is a map of the 217 catclaw acacia trees sampled along three parallel washes to determine the effect dry-washes have on directing seed and pollen flow.

Pollen: Next, I am investigating the landscape features influencing pollen movement. During its flowering period, catclaw is the dominant floral resource for pollinators in many areas of the Mojave. Numerous publications indicate that animal species (*8*), including pollinators (*9*), will direct their movement along the major pathway of a resource. Because catclaw is restricted to areas within or along washes, pollinators are less likely to travel outside of a given wash to find other resources. This predicts pollen flow should also be constrained within dry-washes. Nevertheless, there are other ecological effects that predict pollinators might move between washes. Over two years of floral survey throughout the Mojave Preserve, I have seen a strong correlation between elevation and flowering time in catclaw. In this species a 100 m drop in elevation translates to a five day difference in peak flowering (*10*). Dry-washes run along an elevation gradient – therefore there is a limited area along a wash where trees will be flowering at the same time. This limitation in resource availability might force pollinators to travel between washes to forage. Thus, even though there are forces to constrain pollen flow within washes, there is also pressure for movement to occur between them.

Using genetics to identify pollen flow is a bit complicated. One approach matches the DNA of a seed to its father. Just as with animals, half of the genetic information in plants comes from its mother and the other half from its father. So, if one knows what the DNA of the mother looks like, one can subtract the mother's contribution to the seed. The remaining portion of the DNA will have come from the father. By comparing this identified paternal DNA in the seed to the DNA of potential fathers within an area, one can match a seed to its father and know exactly how far a pollen grain traveled to reach a mother. I used this method to identify pollen flow in the Mojave. For this study I subsampled 20 mothers in the eastern two transects, collecting 12 seeds from each. If dry-washes don't direct movement, then there will be no difference in the number of detected movement events within, compared to between, washes. If dry-washes do direct the movement of pollen, then the majority of detected pollen dispersal events will occur within washes (Figure 6).

This study will inform conservation practices in this area by identifying the general movement patterns for plants and pollinators. Catclaw is a representative species for this zone, with other shrubby species exhibiting a similar pattern of distribution (button brittlebush (*Encelia frutescens*), smoke tree (*Psorothamnus spinosus*), spiny senna (*Senna armata*), etc.). If I find that movement in catclaw is limited and that its dispersal is directed along washes, it will give an indication that there is concern for it and similar species in the Mojave. The establishment of roadways often acts to divert or redirect dry washes. With development increasing and roadways expanding, there might be a significant change in the movement pathways for catclaw, leading to isolation of existing populations. Studies like these help to not only inform us of the general ecology of species, but make informed decisions to manage populations that are at risk due to human disturbance and environmental damage.

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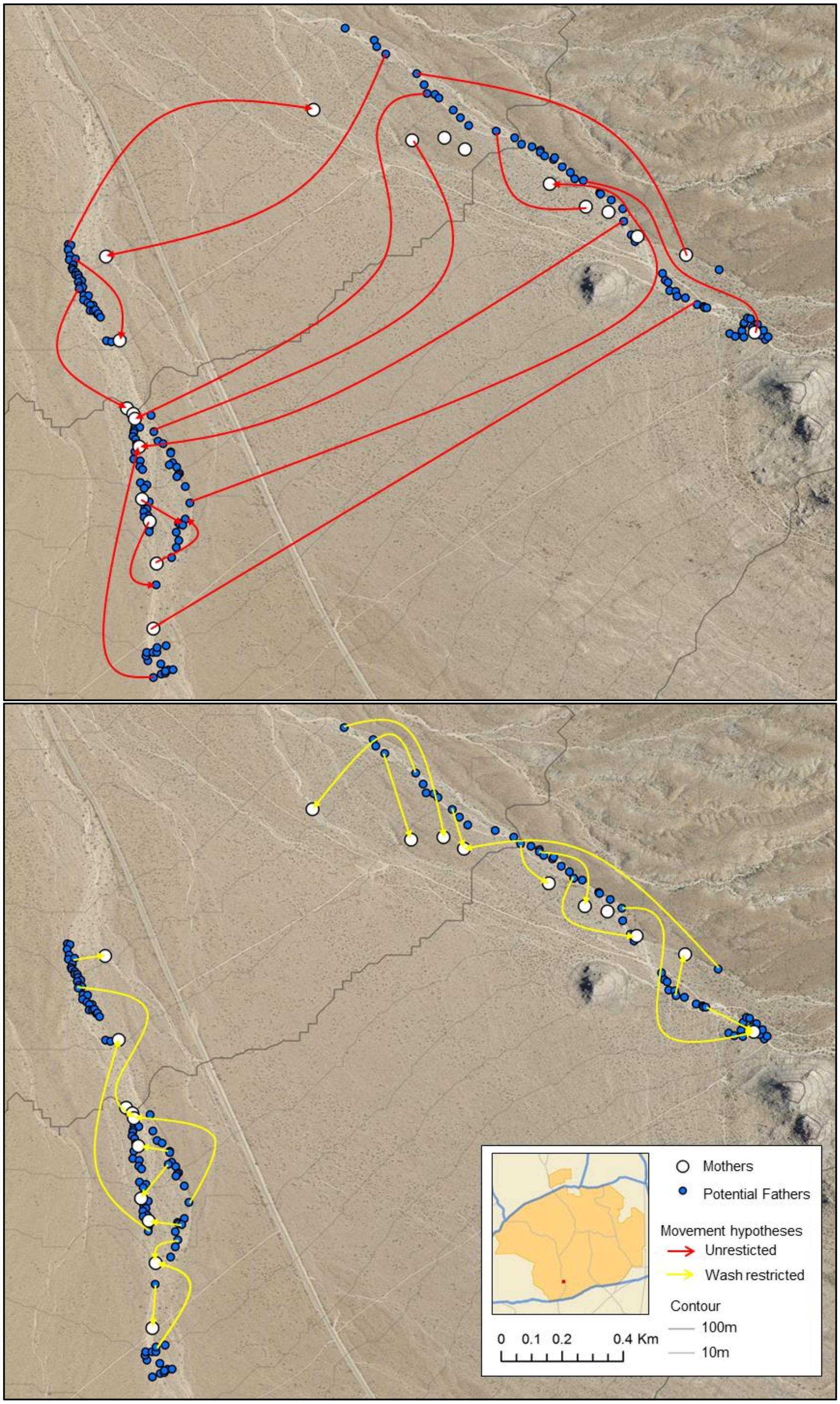

Figure 6. This is a map of potential pollen dispersal events of catclaw acacia between two parallel dry-washes in the Mojave National Preserve under alternative hypotheses: movement is not restricted by dry-washes (top), or movement is restricted by dry-washes (bottom). The white dots represent the maternal trees from which we collected seeds. The blue dots represent all the potential fathers we genotyped.

New Poppies from the Mojave

Shannon M. Still [1]

Two new species of *Eschscholzia* were recently described (*1*) from the Mojave Desert and surrounding lands. While many people might think that the discovery of a new species means traveling to a distant land, hiking an area never before traveled, and stumbling upon a plant that is instantly recognizable as new to science, it is rarely this direct. The path to discovering a new species can be long, winding and not always obvious. Botanists can hope to collect something that is distinctly new, but that is rarely the case. New species are often collected long before they are recognized as something previously unknown. The differences between species can be cryptic and clear only once more work has been completed. The discovery of a new species often entails pouring over thousands of plants and trying to re-imagine how the species could be categorized. This was the case with these two *Eschscholzia* from the Mojave.

The path to discovery of these two poppy species began with a phone call to Jim André, Director of Sweeney Granite Mountains Desert Research Center. I had just started a dissertation at the University of California Davis, where I would study the molecular relationships of the genus *Eschscholzia*, the group of plants that includes the California poppy, *Eschscholzia californica*. The purpose of the call that day was to ask permission to collect *Eschscholzia* from the Granite Mountains, one of the 38 ecological reserves in the University of California Natural Reserve System. I was hoping to collect some specimens from the Mojave and I thought this would be a good area in which to start. For this activity, I needed permission and support from André. This simple phone call snowballed into a several-years effort to correctly identify and categorize the desert *Eschscholzia*.

What I did not realize at the time is that what seemed to be a well-studied group of plants was, in fact, a group rife with problems. I learned from Jim that the plants were much more variable than described by previous botanists. The best way to understand this variation was to observe the plants in their natural setting - in the desert, not the herbarium. An herbarium is a place where plant specimens are stored for research and reference. While herbaria are extremely important to taxonomic and conservation research, the act of pressing the plants changes our perspective of leaves and flowers. Foliage is often distorted as three-dimensional leaves are pressed into two dimensions and flowers often change color when desiccated. When I first spoke with André, I had looked at several hundred herbarium specimens of *Eschscholzia* and thought I knew the plants and their identifying traits. Admittedly, I had no idea when I spoke to him that day that I was about to embark on a lengthy road to discovery. But, as you'll read in the following text, once I started to look more closely at these desert poppies, I realized that the problem was even more complex than originally suspected.

The Jepson Manual (*2*) reference for the California flora lists 14 *Eschscholzia* taxa. A taxon (pl. taxa) is a group of organisms at any rank, such as subspecies, species, genus, family, or higher level. The word taxa is often used to simplify the discussion when describing the total number of recognized names when they are at different hierarchical levels. Of the 14 poppy taxa, six are common to the Californian deserts: *E. californica* ssp. *mexicana* (Greene) C. Clark, *E. glyptosperma* Greene, *E. minutiflora* ssp. *minutiflora* S. Watson, *E. minutiflora* ssp. *covillei* (Greene) C. Clark, *E. minutiflora* ssp. *twisselmannii* C. Clark & Faull, and *E. parishii* Greene. In reading through the key, one might think that the desert taxa have very distinct morphological characteristics. While two of these taxa, *E. californica* ssp. *mexicana* and *E. glyptosperma*, are fairly easy to distinguish, the others are not so discernable. The results of my research indicate that, in fact, there are eight taxa present in the desert, two of which were recently described (*1*). The remainder of this article will focus on the more problematic species, *E. minutiflora* and *E. parishii*, as well as the two new species.

In order to understand the problems within the desert taxa, one must have a better understanding of their history and morphological traits. Previous to this study on the genus, the species *E. minutiflora* (where the second part of the species name, the specific epithet, literally means 'small-flowered') was considered to have three subspecies: *E. minutiflora* ssp. *minutiflora*, *E. minutiflora* ssp. *covillei* and *E. minutiflora* ssp. *twisselmannii*. Curtis Clark placed all three as subspecies of *E. minutiflora* in 1991 (*3*). However, further examination of herbarium specimens during my research showed that it was difficult to distinguish two of these subspecies from *Eschscholzia parishii* (Parish's poppy), which is a large-flowered poppy (20-50 mm wide). The small flowered variety, *E. minutiflora* ssp. *minutiflora*, on which the entire flower ranges 6 to12 mm wide (*4*), is easy to distinguish from *Eschscholzia parishii* based on flower size alone. However, the other two subspecies of *E. minutiflora* have a range of flower sizes that overlap with *E. parishii*. In addition, all subspecies of *E. minutiflora* have been described as having overlapping geographic ranges with *E. parishii*. Due to this difficulty, many herbarium specimens

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are misidentified.

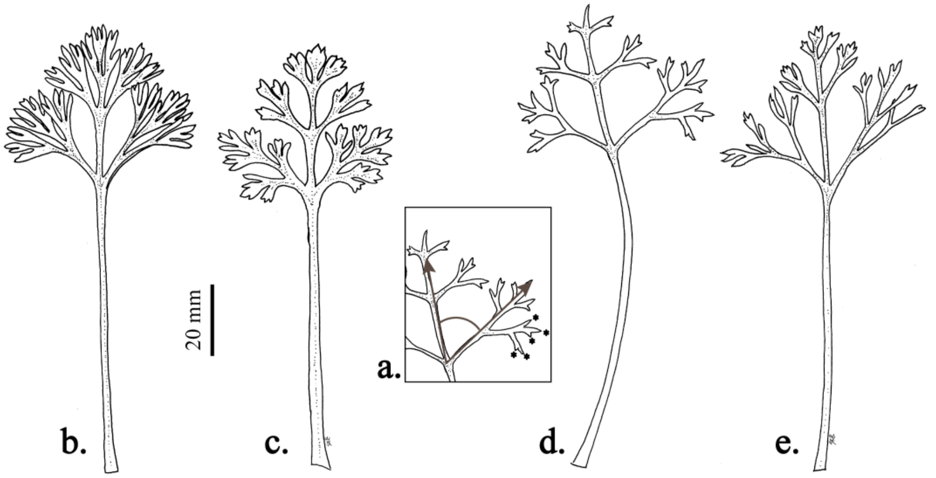

Figure 1. Illustrations of measurements (a) and typical basal leaves for *E. min.* ssp. *minutiflora* (b), *E. androuxii* (c), *E. parishii* (d), and *E. papastillii* (e). The angle of leaf divergence is shown in (a). The ultimate leaf segments are represented by an asterisk (*) in a portion of the segments in (a).

The species misidentification is largely due to morphological plasticity. This refers to the adaptability of an organism to change in its environment, for example, between various habitats. Among the *Eschscholzia*, the flower size and leaf morphology are highly plastic. Flower size can vary greatly depending on the environmental conditions (e.g. microhabitat and/or precipitation) for the individual plant. For this reason, it is important to utilize a suite of traits that, in combination, can help distinguish the taxa. For example, based on my research, there are several leaf morphological traits that can be used to distinguish the three *E. minutiflora* subspecies from *E. parishii* (Table 1, Figures. 1 & 2):

1. The angle that the side petiolules diverge from the rachis (the continuation of the petiole past the point where the petiolules are attached to the petiole, seen in Figure 1a), is usually wider in *E. parishii* than in *E. minutiflora*.
2. The number and shape of the terminal leaf segments (the leaf "tips", which are the numerous, small, terminal sections of the poppy leaf), have been important characters for identification. Asterisks in Figure 1a represent these terminal leaf segments.
3. The length of the bud tips in relation to the entire bud length is also an important diagnostic character (Figures 2c and 2f).

These traits seem clear when reading a species description, but are often difficult to measure and can be variable due to normal plasticity and environmental conditions. For example, in my effort to study hundreds of herbarium specimens, I found that many plants had morphological traits, indicating that hybridization may be occurring between *E. parishii* and *E. minutiflora*. To further the confusion, Tasha La Doux, Assistant Director at the Sweeney Granite Mountains Desert Research Center,

Table 1. Morphological traits for the confusing desert *Eschscholzia*; species are in columns and traits in rows. A) Traits described in the *Eschscholzia* treatment in the Jepson Manual (*2*). B) Traits described in the dissertation (*4*).
*** *E. androuxii* and *E. papastillii* have NA values for the Jepson Manual descriptions because they were not considered in that treatment; they are species recently described (*1*).**

	E. minutiflora* ssp. *minutiflora	***E. minutiflora* ssp. *covillei***	***E. minutiflora* ssp. *twisselmannii***	***E. androuxii****	***E. parishii***	***E. papastillii****
A) Jepson Manual description						
Bud tip	short-pointed	short-pointed	short-pointed	NA	long-pointed	NA
Petal length (range)	3-10 mm	6-18 mm	10-26 mm	NA	8-30 mm	NA
Terminal leaf segment shape	rounded to acute	rounded to acute	Rounded	NA	Acute	NA
Range	to s NV, sw UT, w AZ, nw Mex.	n & c Mojave Desert	ne Kern Co. of Mojave Desert	NA	s Mojave Desert, Sonoran Desert	NA
B) New circumscription						
Bud tip (mean % total bud length)	< 20% (short-pointed)	< 20% (short-pointed)	< 20% (short-pointed)	20% (short-pointed)	> 25% (mid- to long-pointed)	> 30% (long-pointed)
Petal length (median & range)	5 (2-10) mm	9 (4.5-12) mm	16 (9-19) mm	16 (10-23) mm	14 (5-20) mm	16 (6-24) mm
Terminal leaf segment shape	rounded to acute	rounded to acute	rounded	rounded to acute	acute	Acute
Receptacle rim width	0.06 mm	0.06 mm	0.11 mm	0.04 mm	0.07 mm	0.28 mm
Angle of petiolule divergence from petiole	< 35°	< 35°	< 35°	< 35°	> 40°	> 35°
No. terminal leaf segments	45 (20-90)	54 (20-90)	38 (30-60)	55 (30-90)	30 (15-50)	45 (20-75)
Range	to s NV, sw UT, w AZ, nw Mex.	n & c Mojave Desert	ne Kern Co. of Mojave Desert	s Mojave Desert and n Colorado Desert	w Colorado Desert and Baja California	c & s Mojave Desert, Sonoran Desert

informed me of an interesting poppy she had collected in Joshua Tree National Park (JTNP). According to La Doux, this plant looked most like *E. parishii*, but it had a receptacle rim resembling *E. californica* (the California poppy), a defining trait for *E. californica*. Could *E. californica* be in JTNP without previous mention or collections during the preceding century? It seemed unlikely.

Needless to say, from initial study of herbarium specimens and plants in the field, as well as seeing the anomalies suggested by both André and La Doux, it became very clear to me that the morphological traits used to define the desert poppies, while appearing clear in the Jepson Manual, were not quite so lucid in reality.

As discussed above, relying on the current morphological descriptions to identify the desert poppies is misleading, at best. This is not to say that previous research on the group was not good science, as Curtis Clark, the author of the treatment on *Eschscholzia* in the Jepson Manual (*2*) and the Flora of North America (*5*), did a good job describing the similarities and differences between the taxa, as they are currently known. However, Clark started his work in the genus before molecular methods were widely used and it was difficult to identify defining morphological characters in the group. Molecular methods can help to verify the defining characters between taxa.

Examining the molecular differences among species can shed additional light on the evolutionary history of a group, including circumscribing taxa. The goal of this *Eschscholzia* research was to examine both the morphological and molecular relatedness of the desert poppies and attempt to reconstruct their evolutionary history to see if the morphological differences were corroborated by the molecular differences.

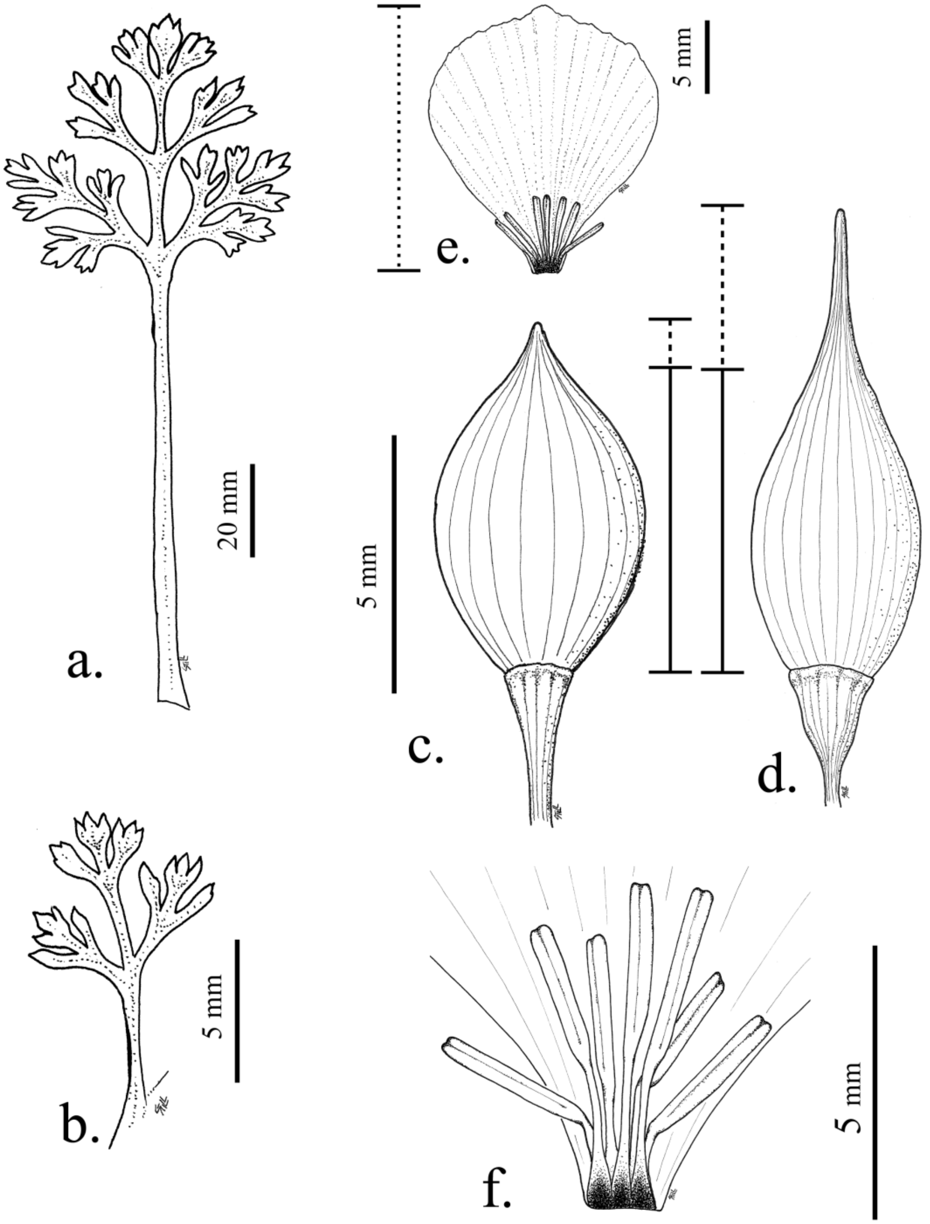

Figure 2. Illustrations of key characters for *E. androuxii*: typical basal leaf (a), cauline leaf (b), bud (c), petals with attached stamens (c), and close-up of the base of the stamens (e). Bud for *E. papastilli* (f) is shown for comparison. The bars between (c) and (f) represent the length of the main bud (solid) and the bud tip (dashed) for both new species.

There are several benefits to utilizing molecular phylogenetics in botanical studies, including the ease of access to DNA on herbarium sheets. It is possible, and commonplace among taxonomic work, to solely utilize plant material collected from the dried, pressed herbarium specimens in estimating phylogenies. Sampling of herbarium specimens can be done quickly and the sampling effort can span a much wider geographic range than a person could possibly cover in the same amount of time collecting fresh samples. This type of sampling can also be useful for studying the more ephemeral groups of plants, such as herbaceous bulbs or annuals (e.g. *Eschscholzia* spp.). This was exemplified by my own research in the desert - where it didn't rain for the first two years of my project (making it difficult to collect *Eschscholzia* in the field).

However, there are serious cautions and limitations to any taxonomic study if fieldwork has been eliminated. Herbarium samples are obviously not alive nor in their natural environment. Observing the plants in their natural environment facilitates correct identification by experiencing firsthand the morphological variation among and within species, as well as habitat preferences that you simply cannot learn in a laboratory, or from a book or herbarium specimen. If herbarium specimens are being relied upon to determine taxonomic relationships, it is essential that the specimens be labeled correctly.

My own research demonstrates this point. In retrospect, I can safely say that many of the *Eschscholzia* specimens I looked at in the herbarium were incorrectly labeled, including many used for the initial molecular phylogenetic work in this study. However, I did not recognize this at the time because I had not been into the field to discover firsthand the variation and problematic taxa. Furthermore, as I learned later, some species are not well defined in the Jepson Manual, and the current key to the genus does not work well for the desert taxa. Hence the rampant misidentification on herbarium sheets.

So, while it was thought possible to morphologically distinguish the different species, the molecular evidence was indicating otherwise. In the molecular phylogenies, individuals from the same species were not resolving together. For example, some *E. minutiflora* collections were resolving as part of the *E. parishii* group and vice versa. In other words, herbarium specimens assigned like names were not necessarily most closely related to one another. Having multiple individuals of a given species resolve closer to a different species is a problem and indicates either an error in identification or in the description of the species.

The problems experienced with the identification of desert species of *Eschscholzia* converged during a visit to the Sweeney Granite Mountains Desert Research Center. I traveled into the field with André and La Doux to look at the mysterious poppies they had told me about earlier. Despite my initial molecular analyses showing such unresolved relationships among and within the desert species, I was not focused on the idea that new species might be awaiting discovery. However, I was stymied by some plants at the base of the Old Dad Mountains, which lie along the southern boundary of Mojave National Preserve (MNP). As André had warned me, there were plants that I could not identify; in other words, I was looking at a new species to science. The leaves on these interesting specimens looked similar to *E. parishii*, but there was something different about the plants. The receptacle appeared to have a slight torus (Figure 3a), or rim, which is the common identifying characteristic of the best-known species *E. californica*. As it turns out, this was the same entity that La Doux had seen in JTNP.

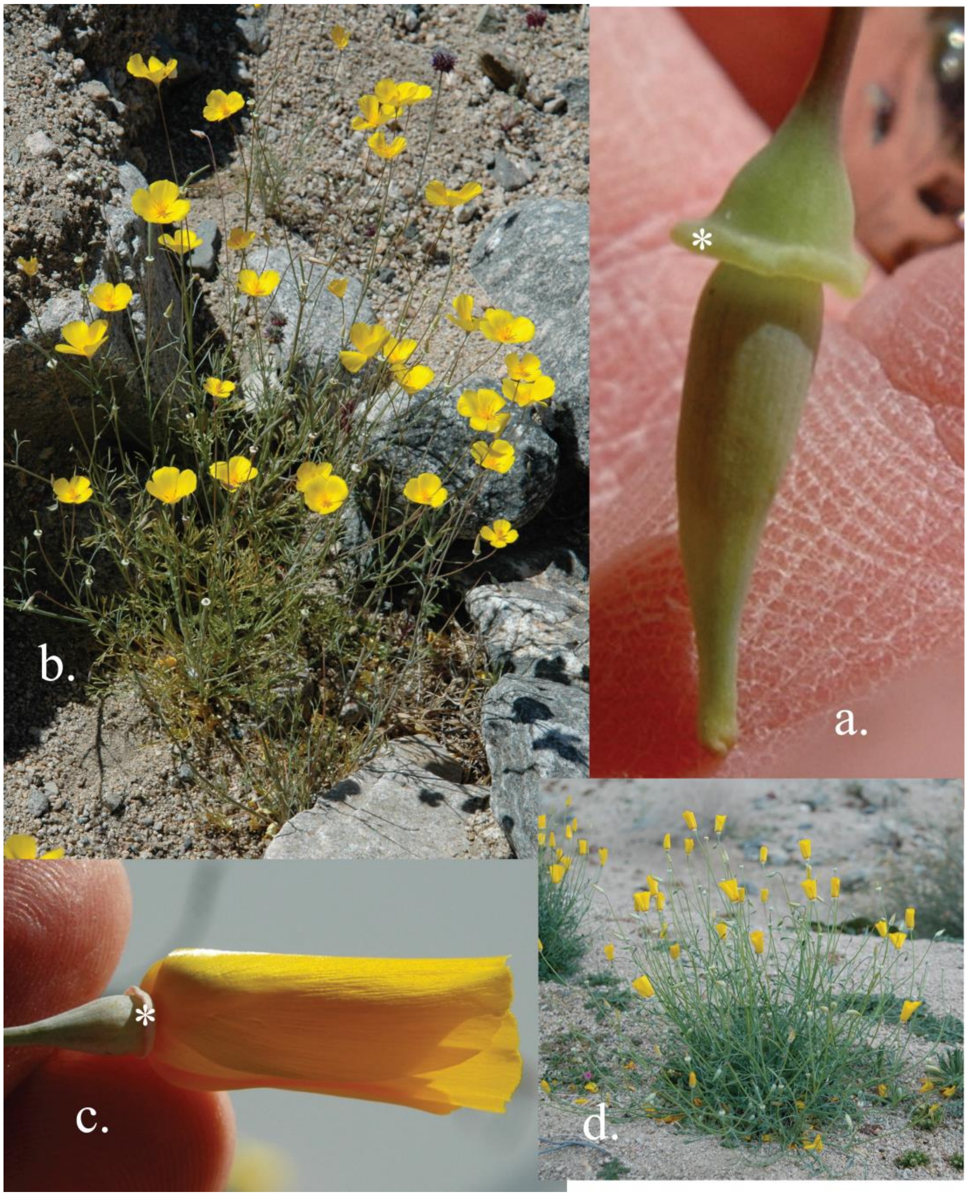

Figure 3. The new species, *Eschscholzia papastillii* (aka, the cryptic poppy), is distinguished from *E. parishii* by the large receptacle rim (torus) shown in (a) and (c), but it resembles *E. parishii* due to the large flower (b-d). Notice the receptacle rim resembles small, white doughnuts at the base of the fruit in (b). The upright, highly branched habit for this species is shown in (b) and (d).

On that same trip, I was stymied again by plants that were collected from JTNP with leaves that looked most like *E. minutiflora* but had flowers as large as *E. parishii*. These specimens had shorter bud tips than *E. parishii* and had black spots at the base of the filaments. Although I didn't know it then, I was looking at yet another new species to science. After seeing these interesting specimens, along with all the variation within the species, I was eager to get back to the lab to see whether I could make sense of the morphological variation I witnessed in the field.

The answer to these questions came after I extracted DNA from the specimens I had collected fresh from the field. The unusual plants that appeared morphologically to be a hybrid between *E. minutiflora* and *E. parishii*, but with a slight receptacle rim, ended up resolving together as a close relative to *E. parishii* (Figure 4). This included plants from the Old Dad Mountains, JTNP, and other locations around the Mojave Desert. The other anomalous plants found in JTNP that appeared to be a large-flowered *E. minutiflora* resolved together as a distinct group, but as a close relative to *E. minutiflora* ssp. *minutiflora* (Figure 4). Ultimately, the results of my combined morphological and molecular analyses sparked a moment of clarity: there were new taxa to be considered. Now it was necessary to begin the process of determining how to best describe and identify the new taxa. In other words, more focused work on these interesting desert species was needed.

Next, it was important to complete morphological analyses to see if these data would support the molecular findings. I needed to identify the characters that unite the new taxa and tease apart the differences between these new species and those already described. While several traits have been used in the past to distinguish the taxa (Table 1A), new traits would also be measured to help determine the differences (Table 1B). Once this work was completed, it was clear that there are morphological characters that could be used to differentiate the species.

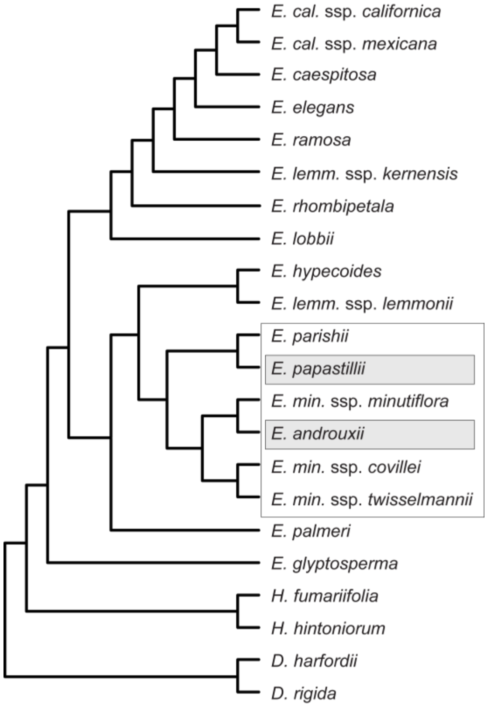

Figure 4. Cladogram illustrating the relationships of the 22 taxa of the tribe Eschscholtzieae as inferred from two nuclear and two chloroplast gene regions (6). Gray boxes outline the new species, *E. papastillii* and *E. androuxii*. Closely related species are indicated with a white box around the group. Dendromecon and Hunnemannia, the two other genera in the family, are also represented in the phylogeny.

It is clear that both new species are molecularly different from the other *Eschscholzia* (Figure 4). The molecular traits are consistent among many individuals of each species (*4*). While the molecular differences do not necessarily merit new species description, when considered in combination with morphological characteristics, the two new taxa *E. androuxii* and E. *papastillii* are conceptually strong.

The first new species, *E. papastillii* (Figures 3 & 5), appears similar to *E. parishii* in that the foliage seems to have pointed tips and the buds have very long tips. But there are important differences from the other taxa that warrant the description of a new species.

Two new species

Two new species of *Eschscholzia* were recently described (*1*) and both morphological (*4*) and molecular (*1, 4*) analyses were required to identify the new taxa. Both species, *Eschscholzia androuxii* Still and *Eschscholzia papastillii* Still, are found in the Mojave Desert.

The major trait that segregates *E. papastillii* from previously described desert taxa is the presence of the receptacle rim (Figures 3 & 5), often called a torus in the literature. The presence of a torus, even just 1/4 mm in size, indicates that the species is the new cryptic poppy, *E. papastillii*. While not as large as that of a typical *E. californica*, where the torus can be 2 to 10 mm wide, the rim of *E. papastillii* is usually present and distinguishes this species from the other desert taxa to which it appears morphologically similar. This new taxon typically has fewer terminal leaf segments

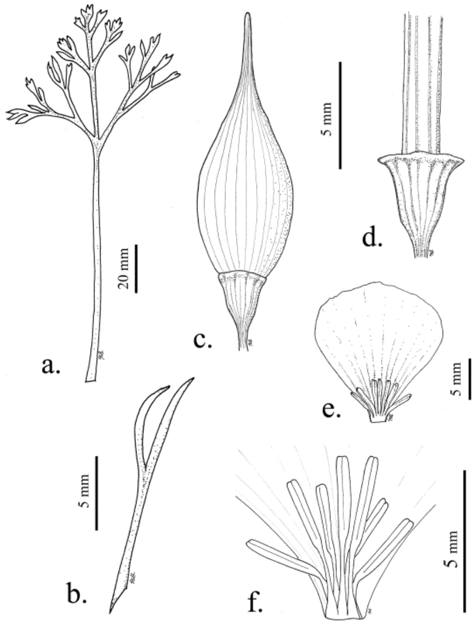

Figure 5. Illustrations of key characters for *E. papastilli*. Typical basal leaf (a), cauline leaf (b), bud (c), receptacle rim (d), petal (e), and close-up of the base of the stamens (f).

on the basal leaves than any of the subspecies of *E. minutiflora* or the new *E. androuxii* (Table 1B; Figure 1). This species, *E. papastillii*, has large yellow flowers and each petal might be up to 24 mm long, the upper limit for flower size within the desert poppies. In the past, these plants were typically called *E. parishii* due to the leaf morphology and the long bud tip. However, the first couplet in the *Eschscholzia* key in the Jepson Manual (*2*), which discusses the torus, could also send a botanist to the conclusion that they are looking at *E. californica*. This species can be seen at its best in sandy washes at the base of the Old Dad Mountains, adjacent to the Granite Mountains Desert Research Center, and at Sheephole Pass on the road from Amboy to Twentynine Palms. In both locations, this new species grows with both *E. glyptosperma* and the small-flowered *E. minutiflora* ssp. *minutiflora*. Most plants that are collected from the Mojave Desert and identified as *E. parishii* are likely this new taxon. The species range (Figure 7) extends from just south of Death Valley National Park (DVNP), south into Imperial County, and possibly down the eastern shore of the Sea of Cortez. To the west, the species might not extend much past Barstow. The species also extends east into Arizona, but further work is necessary to define the eastern extent of its range.

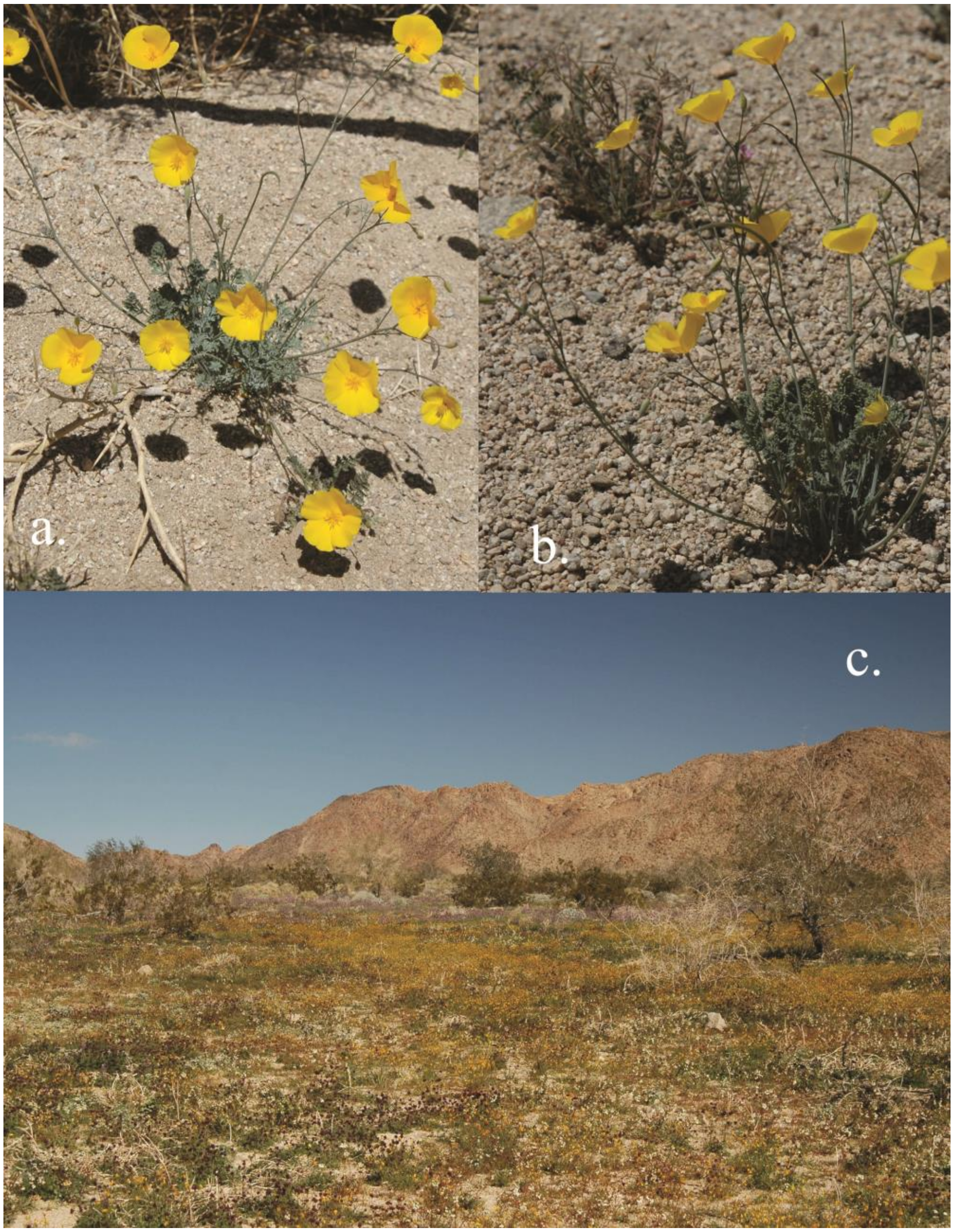

Figure 6. The new species, *Eschscholzia androuxii*, is common throughout Joshua Tree Tree National Park (JTNP). This new taxon usually has nodding buds, a shorter bud tip, and more compact basal foliage than E. papastillii (a and b). It also has black spots at the base of the filaments, which can be seen by the naked eye. *Eschscolzia androuxii* becomes an abundant groundcover on wet years, shown here south of Cottonwood Pass in JTNP (c).

The second new species to be recognized, *E. androuxii* (Figures 2 & 6), has been observed in JTNP and the surrounding landscape. Due to the large flower size and overlapping ranges, this species was often called *E. parishii*. However, the bud tips for this new species are too short, and the flowers are nodding in bud, resembling *E. minutiflora*. The basal leaves (Figure 1c) more closely resemble *E. minutiflora* (Figure 1b) than the other species (Figure 1d-e), but the flowers are too large for the subspecies. The range for both *E. minutiflora* ssp. *covillei* and *E. minutiflora* ssp. *minutiflora* is larger. While this new taxon resembles *E. minutiflora* ssp. *twisselmannii* in flower, the terminal leaf segments are more acute and narrow, and the species is disjunct from the range of *E. minutiflora* ssp. *twisselmannii*. Also, the new species has a black banding at the base of the filaments unlike the other desert taxa. The results of my morphological and molecular analyses indicate this is also a new taxon.

These findings mean that the genus will not only have two more species, but that the ranges and defining characters for other species change as well. *Eschscholzia parishii* has a smaller range than previously thought and many specimens currently attributed to this taxon will be considered one of the two new taxa. The range for *E. parishii* is a fairly narrow band extending from the north side of San Jacinto Mountain in San

Diego County to the north, and then south down the Peninsular Range into Baja California. *Eschscholzia parishii* likely does not occur much east of this range and is not found along the coast. The ranges for both new species overlap (Figure 7) as nearly the entire range for *E. androuxii* is within the range for *E. papastillii*.

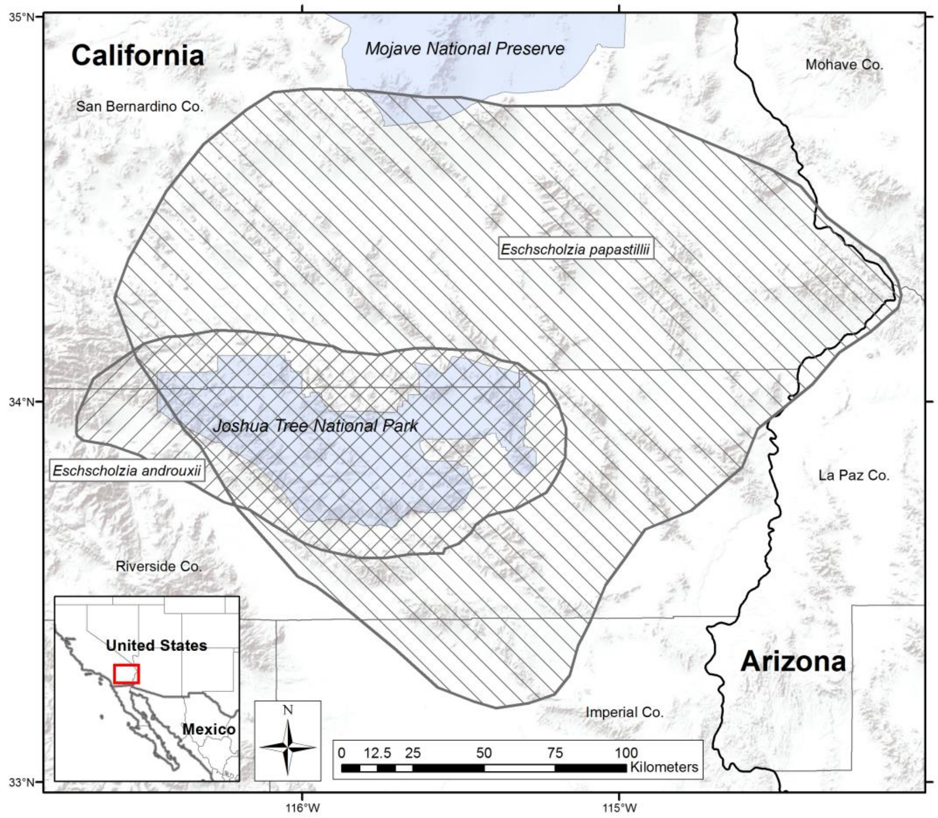

Figure 7. Estimated distribution for the two new *Eschscholzia* species.

Finding new species is not a new phenomenon. Researchers are continually finding new plants in the field or on herbarium sheets. What was surprising to me is that neither of these plants (*E. androuxii* or *E. papastillii*) had been described in the past. At the turn of the 20th century, there were 105 species of *Eschscholzia* described (*7*). Most of these species are considered to be forms of *E. californica*, the common California poppy known and loved throughout the state. By the early 1920s, there were approximately 190 different taxa of *Eschscholzia* described (*8, 9*). Of these described taxa, only 10% were from the California deserts and only 16% were from US deserts. This illustrates the under-collection of plants from the region and helps to explain how these two taxa were not previously discovered or identified. In fact, *E. androuxii*, the new species found predominantly in JTNP, has been growing and has been collected in the area for more than 100 years. Many people have seen the plants, but they were not recognized as something different. These were not wallflowers in a seldom-traveled canyon. These plants would often grow in large quantities and they made quite a floral show (Figure 6c). Finding or recognizing new plants right under our noses demonstrates that more work is necessary to understand our desert flora. The preservation of desert habitat is important to this process.

The study of the desert *Eschscholzia* helps us to better interpret the ecology and evolution of plants in California. This understanding is important to better predict how the landscape, and the plants within it, may change in the future. But this work also provides a good example of how research is conducted and the importance of our natural areas in this pursuit.

It is probably not a coincidence that the new species to be described are largely from areas of the desert that have been protected. These protected areas are often chosen for their unique landscapes or high species diversity. To have Mojave National Preserve, Granite Mountains Desert Research Center, Joshua Tree National Park, and Death Valley National Park as sites for collection and study proved invaluable and each area provided a good laboratory to study the genus. Preserving areas of increased biodiversity is important. Desert parks and all the areas in between are important components of a continuous ecosystem.

Having many closely related species growing in the same range allows better species comparison. Differences in their morphological features can be recognized in the field because they are often growing in the same environment and therefore controlling morphological plasticity. Including the two new taxa, MNP has five species within its boundary and is the western extent for *E. cal.* ssp. *mexicana*. The new cryptic poppy, *E. papastillii* is found in the Old Dad Mountains and likely throughout parts of the MNP. *Eschscholzia minutiflora* ssp. *covillei* is found in a couple of places in the MNP and *E. minutiflora* ssp. *minutiflora* and *E. glyptosperma* are found throughout. Both JTNP and DVNP have several *Eschscholzia* species within their borders and are areas that have many previous collections. As the new taxon *E. androuxii* is found only in and around JTNP, this is an important region for the uncommon new species. The new taxon E. papastillii is also found throughout JTNP and, to the north, may sneak into the southern part of DVNP.

The Granite Mountains played an especially important part in the

Eschscholzia research, as it was possible to peruse their collections of specimens at the herbarium and talk with other botanists and ecologists that often stay at the research station. Most importantly, I spent many nights at the Granites while using the station as a base for collecting and studying the plants in MNP and surrounding lands.

So, a simple phone call started this entire process and led to an increase in understanding of one of the more iconic plants for the state of California. Without the initial phone call to ask permission to collect some poppies, the discovery of these new species may not have happened. Sure, it is possible that the same conclusions may have been reached, but it would have taken much longer with more obstacles. The research shows the value of collaborating with others and being open to seeing something different. More importantly, the results of this research demonstrate the need for fieldwork, protected pristine landscapes, and that the desert remains a place of discovery.

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Sweeney Granite Mountains Desert Research Center: a hub for research and learning in the Mojave Desert

Tasha La Doux[1] and James M. André[1]

The Sweeney Granite Mountains Desert Research Center (GMDRC) is part of the University of California (UC) Natural Reserve System (NRS), the largest university-affiliated network of field stations in the world. The GMDRC was established as the Granite Mountains Reserve in 1978 with the following mission:

> *"… to contribute to the understanding and wise management of the Earth and its arid environments by supporting university-level research, teaching, and public service within the Center's protected lands and throughout the California Deserts".*

In 1987 the University entered into a long-term cooperative agreement with the Department of the Interior, Bureau of Land Management, encompassing both University and federally owned public lands, which expanded the reserve to approximately 9,000 acres (2,300 acres UC-owned). The agreement provided the University with non-exclusive use of the federally owned lands for the purposes of conducting research and educational activities in accordance with the charter of the NRS. The 9,000-acre reserve was recognized in the California Desert Protection Act of 1994, which also transferred the federally owned lands to the National Park Service. In 1995, the University renamed the reserve as the Jack and Marilyn Sweeney Granite Mountains Desert Research Center.

The NRS consists of 39 reserves throughout the state of California, each of which is unique in the services it provides, its capabilities, and what is emphasized in its mission. What the GMDRC offers to visiting researchers and classes, as much perhaps as any field station in the western U.S., is a tremendous natural area, pristine, diverse, and expansive. The GMDRC is embedded within millions of acres of federal lands, much of it designated wilderness, where landscape-level ecological processes are still functioning. Without a doubt the quality of this natural area, including Mojave National Preserve, represents the single greatest asset of the GMDRC.

The GMDRC serves an important "gateway" role in California's eastern Mojave Desert by facilitating academic research throughout the region. About half of the research projects facilitated by the GMDRC are conducted on federal lands outside our boundary (including the Preserve). More importantly, by providing lands that are protected for the purpose of research, we offer a unique opportunity for scientists to establish long-term

[1] Sweeney Granite Mountains Desert Research Center, Kelso, California.

studies as well as providing protection for sensitive study sites and equipment. On-site weather data, GIS databases, species lists and other data maintained by the GMDRC are invaluable to researchers, as well as staff expertise and support. The data collected over the years becomes an invaluable source of information for future work.

Overall visitation to the GMDRC has steadily increased since its inception in 1978. The GMDRC now hosts, on average, 850 students and scientists annually, this includes approximately 20 classes per year. Having this kind of continuity and availability of land that can be used by instructors and researchers year after year is a powerful attribute of a field station. In addition, the long list of publications generated by research facilitated by the GMDRC is a great metric for assessing our contribution toward achieving our mission.

Over the last 35 years, more than 400 academic research projects affiliated with GMDRC have generated nearly 650 publications. Most of these are in the form of peer-reviewed journal articles (59%), however significant contributions have been made in the form of books, book chapters, conference proceedings, films/audiovisual media, and all forms of gray literature such as government reports, magazine articles, and natural history guides. In addition, GMDRC has a long history of supporting graduate student research, demonstrated by the 48 Ph.D. Dissertations and Master Theses completed as a result of research conducted on (or near) the reserve. In an effort to share the significant contributions being made toward a better understanding of the desert ecosystems, including the lands within Mojave National Preserve, this issue of the Science Newsletter is a collaborative effort between the National Park Service and the UC Natural Reserve System. The following are highlights of additional studies affiliated with the GMDRC.

Research Highlights

Timothy Higham, Assistant Professor at UC Riverside, and his students are broadly interested in how animals move in their natural environment in relation to ecological pressures. More specifically, the focus of their research at the GMDRC is part of an ongoing project examining muscle dynamics, biomechanics of locomotion, and predator-prey interactions of desert-dwelling lizards in California. Higham is expanding his research interests to include several lizard species from the Mojave Desert, including *Uma scoparia*, *Uta stansburiana*, *Callisaurus draconoides*, *Coleonyx variegatus*, *Aspidoscelis tigris*, *Phrynosoma platyrhinos*, *Crotaphytus bicintores* (shown in the photo above), and *Sceloporus magister*. By studying the relationship of ecology to biomechanics he hopes to gain a better understanding of how habitat structure acts as an underlying selective pressure on these animals, which will then allow him to predict impacts of future or current habitat modifications.

Meagan Mnich is a Ph.D. student working with **Benjamin Houlton** in the Department of Land, Air, and Water Resources at UC Davis. They are interested in isotopic constraints on ecosystem-scale nitrogen balances in the desert. This work is part of a larger project funded by a NSF-CAREERS grant, awarded to Houlton in 2012 and titled, “Large-scale nitrogen cycles and underrepresented groups: A plan for advancement”. Houlton and his students, including Mnich, use a range of natural isotopic techniques, models, and experimental approaches to advance our understanding of ecosystem responses to global environmental change. In particular, the research at the GMDRC focuses on nitrogen cycling within desert ecosystems by comparing isotopic measures of soil, plants, and rainfall deposition on a local and regional scale. Data collected at the GMDRC will be used to build better models for predicting global nutrient cycling.

Jacob Landis, a Ph.D. student of **Pamela Soltis** at the University of Florida, is studying the morphological and molecular evolution of flower color in Polemoniaceae. Specifically he is interested in species of *Leptosiphon* and *Linanthus*, as these two genera contain multiple examples of polymorphic flower color. He visited the GMDRC in April of 2013 as he was traveling throughout the southwest in hopes of collecting material for his phylogenetic analyses. Both Director Jim André and Assistant Director Tasha La Doux assisted his efforts by providing him with locality information, as well as collections of species they had encountered prior to his visit. This type of assistance from the GMDRC staff is of great value to researchers like Landis, who may have limited opportunities to be in the field (i.e. at the right place, at the right time). This is especially true in the case of desert annuals, a challenging group to study because they are both temporally and geographically ephemeral.

John Regus, a Ph.D. student in the Evolution, Ecology, & Organismal Biology program at UC Riverside, is interested in the evolution of interspecific symbiotic interactions. For his dissertation he is studying a legume-rhizobia symbiosis using several annual species of the *Acmispon* (*Lotus*) genus. He is testing how variation in exogenous nitrogen can alter the cost and benefits of symbiosis for the host and symbiont, and more specifically, he is interested in how the host legume controls the spread of ineffective rhizobia. His research will shed light on how external sources of nitrogen, such as fertilizer and atmospheric deposition of NOx, will impact agronomic and natural systems.

Dylan Rood is a geomorphologist specializing in the use of cosmogenic nuclides and accelerator mass spectrometry to study the evolution of Earth surface processes, tectonic geomorphology, and paleoclimatology. He is a Research Fellow at the Scottish Universities Environmental Research Centre, as well as an Assistant Researcher at UC Santa Barbara's Earth Research Institute. His research in the Mojave Desert focuses on the timing, formation rate, and geomorphic development of precariously balanced rocks. The study site he is using at the Granite Mountains represents a region of low seismicity, which he then compares to another location with high seismicity near the San Andreas Fault. He will be using his data and analyses to directly test seismicity models, ground motion prediction equations, and hazard estimates associated with the 2008 USGS National Seismic Hazard Maps and Cybershake.

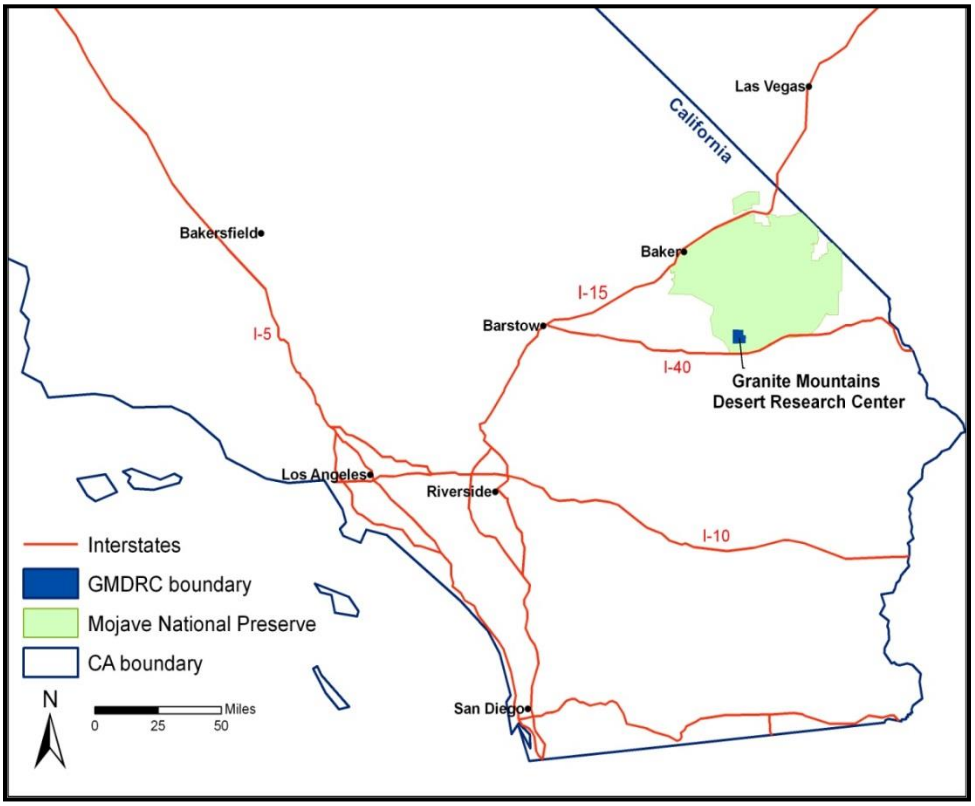
James E. Russell, Associate Professor of Biology at Georgia Gwinnett College, spent 3 weeks at the GMDRC last year collecting data and specimens for a long-term project that he started as a graduate student over 10 years ago. As a graduate student, Russell studied the ecological and evolutionary consequences of infection by the bacterial symbiont *Wolbachia* in parasitoid wasps of the genus *Trichogramma* (shown in the photo above). In his current position at Georgia Gwinnett College, he is leading several Student-Faculty Research Collaborations, which are required courses for undergraduates in the science disciplines, all of which revolve around the ecology of parasitoid wasps. In June of 2013, Russell and his team of students collected thousands of butterfly eggs in order to begin several studies addressing population structure, sex ratio selection, and *Wolbachia* infection rates among natural populations of *Apodemia mormo*, a butterfly that is host to several *Trichogramma* species. The data collected this year will be used to compare rates of parasitism and offspring sex-ratios in the *Wolbachia-Trichogramma* parasitoid system to data collected 15 years ago, but more importantly it will be used to launch additional Student-Faculty Research Collaborations.

Alex Filazzola, a Ph. D. student at York University, is working with **Christopher Lortie** to study direct and indirect effects of nurse plants on seedbanks and annual plant communities. Filazzola, along with two undergraduate students (**Amanda Liczner** and **Ally Ruttan**), established study plots that will allow them to test for biotic and abiotic effects of shrubs on germination and pollination rates for neighboring annual plants. They are employing an interesting method of monitoring pollinator visitation in which small video cameras are placed in and around each study plot to capture pollinator visitation rates. Apparently the cameras pick up amazing detail. Germination studies will be used to test for the effect of microhabitat (open canopy versus shrub canopy) and seed density.

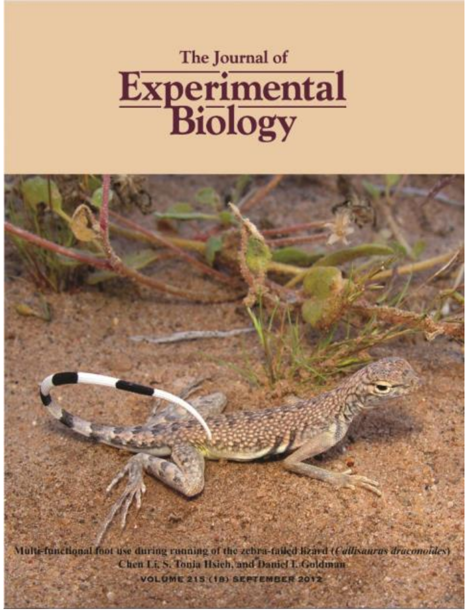
Terry Griswold is a research entomologist who runs the USDA-ARS Bee Biology & Systematics Lab, as well as being adjunct faculty for Utah State University. His research interests include systematics, biogeography, and biodiversity of native bees. Through his many years of research in the region he has made several discoveries of new species to science, as well as documented range extensions for a number of bee species. In addition, his studies have focused on floral preferences and spatial patterns in bee communities.

Jeffrey Jenkins is a Ph.D. student in the Environmental Studies Department at UC Santa Cruz. His dissertation research focuses on environmental policy of rare earth element extraction and life cycle analysis of minerals used for renewable energy applications and high-tech devices. He is exploring the relationship between government, private industry, and civil society in the development of policies for environmental impacts, mining, processing techniques, and sustainability of consumer demand. There are four rare earth element mines scheduled to re-open in the U.S. by 2015, one of which is located between the north and south units of Mojave National Preserve.

The results of a collaborative effort between **Tonia Hsieh**, Assistant Professor at Temple University, and **Dan Goldman**, Associate Professor at Georgia Tech, was highlighted on the front cover of the Journal of Experimental Biology in September of 2012. Their study on multi-functional foot use during running in the zebra-tailed lizard (*Callisaurus draconoides*) addressed how ecological parameters, such as habitat structure and substrate, influence locomoter behavior and control. The Goldman lab combines field studies of organism biomechanics with modeling of substrates in order to create mathematical and physical models of the



Sweeney Granite Mountains Desert Research Center is located in southeastern California.


The Journal of Experimental Biology

Multi-functional foot use during running of the zebra-tailed lizard (*Callisaurus draconoides*)
Chen Li, S. Tonia Hsieh, and Daniel I. Goldman
VOLUME 215 (18) SEPTEMBER 2012

organisms (i.e. robots). These robots are developed to hop, walk, climb, and burrow into a variety of substrates and have real-world applications such as exploration on Mars, search and rescue devices, and mechanical limbs.

The Sybil and Al A. Allanson Center and Library consist of residence and laboratory buildings located in Granite Cove.

The 900 square foot James E. Southard Conference Room can accommodate up to 30 participants for presentations and meetings.

To learn more about the Sweeney Granite Mountains Desert Research Center

please visit the website
http://granite.ucnrs.net

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About the Newsletter

The Mojave National Preserve Science Newsletter publishes contributions from researchers regarding in-progress or recently completed scientific work in Mojave National Preserve. Articles range from general interest stories intended for a broad audience to technical research reports. The reports are summaries of peer-reviewed journal publications. The interested reader should refer to the citations.

This May 2014 Mojave National Preserve Science Newsletter and past issues are archived at:

http://www.nps.gov/moja/naturescience/sciencenews.htm