RESEARCH PORTFOLIO

DR SHELLEY EDWARDS

EVIDENCE OF RESEARCH ACTIVITIES
2015 - 2022

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1 PERSONAL RESEARCH ACTIVITIES

Website link

Research skills and techniques:

- Molecular biology laboratory techniques (DNA extraction, PCR, gel electrophoresis)
- Phylogenetic analyses (including molecular clock dating)
- Phylogeographic analyses (including population genetics techniques)
- Morphometric techniques (traditional morphometrics; geometric morphometrics on 2D and 3D data)
- Functional trait analysis techniques (analyses of locomotion, bite force analyses, dietary analyses)
- Statistical analysis using the program R (descriptive statistics, comparative statistics, multivariate analyses, ordination, phylogenetic analyses, linear modelling, Bayesian modelling).

I am a herpetologist and an evolutionary biologist, with an interest in *how* and *why* species evolved in the way that they did. I conduct multi-disciplinary research to investigate which environmental conditions have led to specific phenotypes (essentially how an organism looks and functions) evolving. I have a keen interest in understanding the phenomenon of convergent evolution – how completely unrelated species have evolved the same phenotypes due to inhabiting similar environments; basically, a study of selective pressures leading to particular phenotypes. I utilize genetic sequencing to investigate the taxonomic level of various populations and species, and back up the genetic evidence of species delineations with investigations of the morphology and functional traits (such as running speed, bite force, dietary aspects) of the study species. This type of research involves fieldwork (to collect individuals, specimens and tissue samples), labwork (to produce genetic data and to produce functional trait analyses), and write-up of papers and book chapters, as well as dissemination of the research through conference attendance and community engagement activities.

Biological science is by its nature a collaborative endeavor – Nature itself is complex and to best investigate the various aspects present in Nature requires a wide range of knowledge and skills, so collaboration between scientists with the requisite knowledge is important for biological research. Very few biologists publish single author papers. I am the research head of the molecular laboratory (ZEML) in the Department of Zoology & Entomology and have supervised a number of undergraduate and postgraduate projects thus far (see sections below). My skill-set is varied and includes field work, laboratory work, and statistical analyses. Having received two research grants from the NRF (South African National Research Foundation) and the FBIP (Foundational Biodiversity Information Programme) in 2017, I have initiated research

projects that investigate the phylogenetic relationships within (and between) snake species, lizard species, and spiders. These projects are in collaboration with researchers at local museums (Port Elizabeth Museum and Albany Museum) and at international institutes. In addition to the projects that I am lead on, I have also been involved in and have co-supervised projects focussing on algae, insects, birds, and mammals. I have had the privilege of visiting various laboratories and museums, both locally and in Europe, including the Laboratoire de Biogéographie et Ecologie des Vertébrés (Montpellier, France), the Muséum National d'Histoire Naturelle (Paris, France), the Berlin Natural History Museum (Berlin, Germany) and a number of local museums (Ditsong Museum, Port Elizabeth Museum, Albany Museum, Amathole Museum, Iziko Museum). These collaborations not only allow for interaction and communication between different research groups across the continents, but also facilitate new skills being introduced into South African academia, and for my students to experience new and different perspectives in our field. As an added bonus, collaborative work between institutions allows for the advertisement of our institution to perspective postgraduate students, and also allows for an avenue of communication for our students who wish to broaden their horizons by studying at a different institution.

As a product of my research, I have published six articles as first author at present and sixteen as a co-author, with three manuscripts currently submitted for review. I have many more manuscripts in preparation; some that are collaborations between myself and researchers at University of the Western Cape, University of the Free State, CIBIO (Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado; Portugal), Universidade do Porto, Port Elizabeth Museum, South African Institute for Aquatic Biodiversity (SAIAB), South African National Biodiversity Institute (SANBI), Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB); amongst others. I have also published a book chapter entitled “Convergence in morphology is preceded by convergence in performance in lizards”. I have been an associate editor for the journal Cogent Biology and am still an associate editor for the African Journal of Herpetology (2017-present). I have attended and presented at a number of local and international conferences, including the World Congress of Herpetology, in Vancouver, Canada (2012), in Hangzhou, China (2016) and in Dunedin, New Zealand (2020). These products are tangible evidence of the quality of the research that I have conducted, but more than that, they are the culmination of years of study and enquiry. By no means are they the end-points of my research career, as each paper or conference presentation is merely a prelude to more intensive, and hopefully more applicable, research to be conducted by myself and my research group.

My research interests are varied, as evidenced by some of the publications that I have produced and that come out of the ZEML lab. My first publication detailed the results of my Masters work, and I published chapters from my PhD before being awarded the degree, as well as writing up a book chapter. I published a few papers before being employed as a lecturer at Rhodes University, when I initiated the Zoology & Entomology Molecular Lab (ZEML). I am the Research Head of the ZEML, and I supervise a number of postgraduate students that conduct their research in the lab. The lab is utilized by a number of students from other research groups, and sometimes I am included as co-author/co-supervisor on these projects too.

My publications show examples of my research interests, which for the most part aim to investigate the evolution of animals and determine the factors that drove their speciation. In collaboration with Mr. Conradie and Mr. Busschau, we investigated the species level divergence in the legless skinks, some populations that had been genotyped for the first time. This work revealed two new species, new to science, and we backed up the genetic evidence with

morphological analyses (Conradie et al., 2018). I have co-authored two papers in collaboration with colleagues from other institutions: the first is a paper on the evolutionary investigations of monkey-beetles and the second is the phylogenetic investigation of two species of Psammophiinae snakes from Angola (see below for description). As part of his PhD work, Chad Keates led the authorship of a paper on the taxonomy of the *Psammophylax* grass snake genus, and the resultant publication used a multi-disciplinary approach to name a new species and a new genus (*Kladirostratus*) from Tanzania. For that paper, I conducted the morphological analyses, but mentored Chad in the phylogenetic methods used in the paper.

I am currently busy with a phylogeny of the slug-eater snakes (genus *Duberria*), with individuals caught from across Africa (in collaboration with Mr. Conradie). The phylogenetic tree has revealed that subspecies of *Duberria lutrix* are in fact divergent at a species level, and in the upcoming paper we will be raising these subspecies to full species status. We will also utilize molecular-clock dating to investigate when the species diverged from one another and link these speciation events with environmental changes that occurred in the African region at those times.

A past student, Ms. Cassandra Barker, conducted a third-year project on how the Eastern Cape dwarf chameleon (*Bradypodion ventrale*) reacts to mammalian predators (namely vervet monkeys), and we are busy writing up that paper. In 2016, I began investigating the source of the invasive populations in the Eastern and Western Cape Provinces of the tropical house gecko, *Hemidactylus mabouia*, and these preliminary analyses formed the basis for Ms. Alungile Jeme's Masters project in 2020. In 2017, I began researching the evolution within the pisaurids spider family (the fishing spiders), and each year, I put together an Honours/undergraduate project that investigates a different part of the project. Currently, there are three students that will coauthor the paper with me by the end of this year. While I have many more projects on the go, I have highlighted the ones mentioned above to give examples of the type of research that I conduct.

2 ZEML (Zoology & Entomology Molecular Laboratory)

I initiated the Zoology & Entomology Molecular Laboratory (ZEML) in 2015, and the main research focus of the lab has been to investigate evolutionary questions in animals. As research head (and lab manager) of the lab since its inception, I have initiated projects that include the investigation of the evolution of various snake, lizard, frog, and spider species. In addition to my own students, various other research groups within the department, and other departments (such as Botany), utilize the lab to produce genetic sequences for their own research on insects, mussels, plants, and birds. My primary role is to be the research head (manage students, produce research ideas, and to teach lab members lab and analysis techniques); however, I also obtain funding for the research undertaken, manage the finances for the lab, and manage the stock of the lab consumables, reagents, and equipment.

The ZEML aims to conduct research investigating evolutionary biological questions, innovating through development of new techniques and software for use in the field. Please see ***Appendix A1*** for the Strategic Plan for the lab. The methods that will be initially used in these investigations include molecular techniques, morphological analyses, and functional analyses; however, it is anticipated that new skills brought into the group by the researchers hired (e.g., machine learning, software development, different analysis techniques) will expand the range of research methods used at the group in the future.

- **Molecular techniques:** Use of DNA genetic data (single genes and whole genomes) to delineate species, investigate evolutionary history of species, to investigate population structuring and processes, and provide base information about species and communities for conservation decision makers.

- **Morphological analyses:** The study of body shape of species to identify the factors that are underpinning evolutionary processes. These studies can determine whether evolution in groups is due to genetic history, or is being driven by the environment; i.e., the driving factors behind evolution in groups.

- **Functional analyses:** Studies of the functional aspects of an organism; for example, their bite force, their running speeds, their locomotion pattern (how they run), their diet preferences, their mode of foraging, amongst others. These aspects are often tightly linked with the organism's morphology, and give information about how they interact and function within a particular environment.

The research goals of the group include the production of scientific journal articles, but ultimately, we aim to be a group of innovation through the production of new analysis techniques and software. We also aim to improve on the knowledge of species and add to the conservation information for the resident species in their regions.

ZEML members have published papers resultant from their research, and I have supervised a number of undergraduate and postgraduate students (who have either submitted their theses for examination, or they have graduated). Publications produced in the biological sciences are no longer generally authored by a single researcher, as the sourcing of samples and the inclusion of multi-disciplinary analyses in the papers leads to collaborative production of papers. The very nature of the taxonomic work, for example, requires analysis of multiple aspects of an organism's biology and ecology (such as its genetic, morphological and behavioural aspects), necessitating the collaborative work between multiple researchers with knowledge of analysing the various aspects.

ZEML members also attend conferences to disseminate our research. I attended and presented at the World Congress of Herpetology (held in China) in 2016, presenting my research on sand-diving lizards. ZEML students (Dr Chad Keates and Mr. Luke Kemp) attended the Herpetological Association of Africa (HAA) conference in January 2017, presenting their research on snake diversity and snake phylogenetics to leading experts in the field of herpetology. As the Chair of the organizing committee for the 2019 HAA conference, I facilitated the organization of the conference and four ZEML students were the conference helpers. We all presented talks at the conference. In January 2020, myself and my PhD student (Dr Chad Keates) attended the World Congress of Herpetology (held in Dunedin, New Zealand) and presented talks at the conference.

Our lab is also involved with community engagement activities and have begun a research project using data collected during those activities (primarily the snake callouts). As our department provides students the opportunity at third-year (undergraduate) and Honours level to conduct research projects, much of our main research has been informed by the data collected by previous students during these short-term projects. Hereafter, I will describe our activities as a lab, and detail the products of our activities.

3 POSTGRADUATE PROJECT SUPERVISION

Students graduated:

MSc (main supervisor)

Mr. Anthony Evlambiou (2020)

MSc (co-supervisor):

Mr. Clarke Van Steenderen (2019)

Ms. Cassandra Barker (2020)

PhD (main supervisor):

Dr Chad Keates (2020)

PhD (co-supervisor):

Dr Krista Oswald (2018)

Current students:

MSc (main supervisor):

Ms. Alungile Jeme

Mr. Bruce Roestof

MSc (co-supervisor):

Mr. Johnathan Balmer

Ms. Asante Msimang

Postdoctoral fellow:

Dr Jessica Comley (2020-2021)

The wonderful thing about molecular biology is that the underlying principles of genetic labwork can be applied across multiple taxonomic groups, and the analyses are standard enough that once you learn the techniques, you can apply these techniques to investigate any organism, from vertebrates (like reptiles, frogs, birds, and mammals) to invertebrates (like insects, spiders, snails) to plants to bacteria. DNA is a molecule that is the coding molecule in most living organisms and the techniques to isolate and genotype DNA are standard enough to allow for investigations of all taxonomic groups. As such, I am able, as a supervisor, to guide students in producing genetic sequences, regardless of the taxonomic group being studied. After receiving the Foundational Biodiversity Information Programme (FBIP) small research grant (1-year grant), and the NRF Thuthuka young researchers research grant (3-year grant), both in 2017, I utilized the funds to initiate and supervise research on four main projects: (a) snake phylogenetics, (b) spider phylogenetics, (c) legless skink (lizard) phylogenetics, and (d) reptile morphometrics. Other projects are being funded through funding obtained by the students for their projects.

Dr Chad Keates has completed his PhD (after upgrading to PhD from Masters in 2018), in which he investigated the taxonomic grouping within the Psammophiidae (grass) snakes. He has produced a paper from his first chapter of his PhD dissertation, investigating the genetic relationships between the skaapsteker snakes (*Psammophylax*) (Keates et al., 2019). This paper named a new species distributed in Kenya, split off from a currently described species – named after the person who found the animals, Dr Chris Kelly, and a new genus *Kladirostratus* from Tanzania. This genus was named after the late Prof Bill Branch – a leading herpetological taxonomist in South Africa and a treasured friend and colleague. He has conducted a project paid for by National Geographic, doing labwork to obtain genetic barcodes for reptile and amphibian (frog) individuals caught in Angola; the results of which are likely to reveal new species previously unknown to science (Conradie et al., 2020a; Conradie et al., 2020b). He has also conducted the labwork and phylogenetic analyses for a paper that was co-authored by Ms. Ninda Batista, myself, and Prof Bill Branch, in which we raise the subspecies *Psammophylax rhombeatus ocellatus* to full species status and verify that *Psammophis ansorgii* is a valid species (Branch et al., 2019). We have also coauthored a paper on red toads *Schimaderma* (Batista et al., 2021) and one on geckos *Afrogecko* (Lobon-Rovira et al., 2022). Chad and I attended the World Congress of Herpetology in 2020, where he presented his PhD work. His PhD dissertation investigated species concepts from a species, genus and family level (family: Psammophiidae). See his website for more information on his activities.

Mr. Anthony Evlambiou's Masters research involved the investigation of the morphological adaptations of the legless skink lizards, the genus *Acontias*. These lizards are interesting as they are primarily fossorial (burrowers), and have very conserved morphologies, in that they tend to mostly have very similar head shapes in response to the same kind of selective pressures exerted on the individuals as they burrow into soil. He will utilize three-dimensional (3D) images, created from CT-scanning whole individuals (Fig. 1), to not only investigate the cranial shapes of the species, but also to identify whether vertebral number can be a useful species delineation character in this group. I look forward to seeing what he produces from his Masters and am glad to be one of a very few researchers in South Africa who can conduct 3D geometric morphometric analyses, and to pass on this knowledge to Anthony.

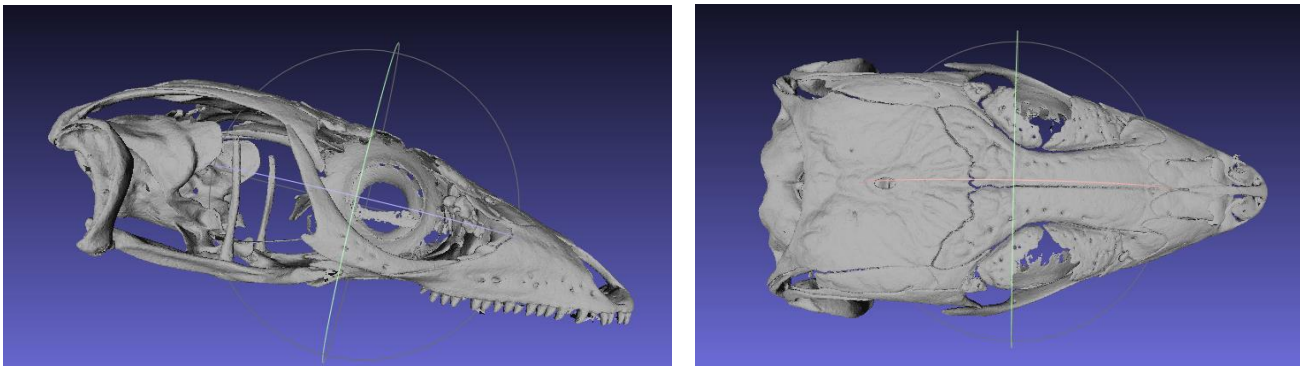

Figure 1: Three-dimensional images of the skull (cranium) of a lizard.

After doing an NRF internship within our department, Ms Alungile Jeme began her Masters work with me, investigating the source of an invasive gecko species, the Tropical House Gecko *Hemidactylus mabouia*. This species is endemic to southern Africa and has been invasive around the world, being a prolific competitor to local gecko species. Recently, this species has been found in the Eastern Cape and is assumed to have been introduced sometime in the 1990s. Ms. Jeme is using genetic analyses to investigate the geographic source of these introduced populations, so that we can begin to understand the potential mode of introduction.

Mr. Bruce Roestof is a Masters student working on the taxonomic relationships in the African Mantodea (praying mantises). Many of the African representatives have never been genotyped and have only very superficially been described using morphological characters. Mr. Roestof is producing an identification key for the African representatives of this order and using genetic analyses to identify whether morphological characters chosen as identifiers are useful and congruent with genetic designations.

I am also co-supervisor to a Masters student; Mr. Jonathon Balmer. Mr. Balmer is currently investigating the conservation status of two owl species, both of which have disjunct populations: populations in the northern parts of South Africa and in the southern parts of the Eastern Cape province. Once he has conducted field work to identify the localities of local populations, he will begin his labwork to genotype the different populations, in an effort to identify whether the disjunct populations represent subspecies or indeed full species.

I was co-supervisor to a Masters student; Mr. Clarke Van Steenderen. Mr. Van Steenderen investigated the genetic relationships in the biotypes of a biocontrol insect agent (cochineal insects) on cacti and conducted these analyses in the ZEML lab. He graduated in 2019, and produced a stellar Master's thesis, including producing a GUI in the program R to work with cochineal insects' genetics for future researchers and has published his work!

I co-supervised a Masters student, Ms Cassandra Barker, who investigated the genetic structuring and reproduction in an invasive mussel, *Perna perna*, along the South African coastline. Ms Barker used phylogenetic analyses and population genetic techniques to identify the phylogeographic break in this species along the south coast.

I was the co-supervisor to a doctoral student, Dr Krista Oswald, who investigated one of the oldest groups of birds – the rockjumpers. She utilized genetic analyses to investigate the taxonomic relationships between populations of the Cape rockjumpers and the Drakensburg rockjumpers. The unique bird species are taxonomically unique and the use of phylogenetic analyses will give insights into their evolution and possibly elucidate how they came to be the only surviving species in their lineage. Dr Oswald graduated in 2019 and is currently working on her publications.

I was the advisor to Dr Jessica Comley during her post-doctoral fellowship (2020-2021), in which she used genetic analyses to identify brown hyena *Parahyaena brunnea* individuals in the Eastern Cape region (funded by the Rufford Foundation). These analyses will contribute towards conservation decisions regarding the species introductions into nature reserves, as this species appears to be genetically depauperate due to a recent bottleneck occurring in the species.

I also mentor students from other institutions. The first student, Ms Ariella Rink, completed a Masters investigating a beetle and used geometric morphometric techniques to investigate body shape differences between the sexes (and aspect that I mentored her in); she has published her research. The second student, Ms Faith Masilive, produced novel DNA primers used in sequencing red algae and produced a phylogenetic tree for the South African group of marine algae (her submitted manuscript is currently in review).

Although I am primarily a herpetologist, there is an enormous paucity of knowledge about southern African spiders, and in particular there are very little published phylogenetic studies on southern African spiders, so I have expanded my set of study species to include spiders. A past Honours student, Mr. William Rawson, and a past third-year student, Ms. Khanyisile Buthelezi, have investigated the phylogenetic relationships between spiders from the Pisauridae family – a fascinating group of spiders that 'fish' for prey such as frogs and fish, sometimes up to three times their own size! I am interested in finding out whether this fishing behaviour, seen in one genus of pisaurids from South Africa and in a related genus distributed in Australia and Japan, is one that evolved convergently, or whether this is an ancestral trait in this group.

4 UNDERGRADUATE RESEARCH PROJECT SUPERVISION

As a department, we provide students at undergraduate and Honours level the opportunity to conduct research projects. I have been fortunate to be supervisor to a number of students each year since 2016 as they conduct projects (see list below) on a wide range of subjects, from phylogenetic analyses of frogs, snakes and spiders, to investigating anti-predator responses in chameleons, to dietary choice experiments in frogs, to species distribution predictions of an invasive gecko species. Each of these projects are intended to be short projects, investigating a single research question; however, I have taken the opportunity to structure these projects as 'pilot studies' to inform my future research efforts.

The Department of Zoology & Entomology requires third-year undergraduate (Zoology and Entomology) and Honours students to conduct year-long research projects. As these projects are the first foray into the world of biological research for the students, we (supervisors) create the project idea and design the project for the students, and guide the students in conducting the research activities and the write-up of the results. We do not expect that the end product will result in a publication, but those that do, obtain high marks for this component of the course. ***Appendix 2*** contains a list of undergraduate and Honours projects that I have supervised.

5 FIELDWORK

Much of the above-mentioned research being conducted by myself and the students at the ZEML begins with an acquisition of animal specimens. In order to genotype an individual's DNA, one needs some tissue from that individual. For small specimens, such as insects, mostly the whole specimen is used to extract DNA, but larger specimens (such as vertebrates) require only a small (~ $1cm^3$) piece of tissue, or some blood. To obtain these specimens, we go on field trips around the country (Fig. 1) to catch live specimens to measure (body length etc.) and to sample a small piece of tissue. We then release the animals back at the site of their capture. Once we have the tissues, we return to the lab to conduct genetic labwork to obtain the genetic sequences required for each project.

Figure 1: Field work takes us to remote parts of Africa. Photos of Dr Chad Keates, Mr Luke Kemp, Mr Anthony Evlambiou and Dr Shelley Edwards (top right).

In Grahamstown/Makhanda, we are very fortunate to be within a biodiverse region, which is relatively rural, with large expanses of surrounding regions being protected in nature reserves. Due to this natural setting, wildlife is often encountered by the populace of the town. We are called by the public to their residences and workplaces to remove snakes that have made their way into populated areas. Dr Chad Keates instigated a research project (in addition to his postgraduate work) in which he collects data on humidity, barometric pressure and other climatic variables to investigate which climatic factors are leading to the movement of snakes within urban areas. With every snake-callout, we not only engage with the public about snakes and try to reduce the public's negative perception of snakes, but we also collect data for research, and in the process save a snake's life! Once we have the snake 'in hand' (so to speak), we bring the individual back to the lab to take measurements, check the condition of the snake's health, administer any first-aid on the snake (if necessary), provide the snake with a meal (if it appears to be emaciated), and take a small piece of the tail for use in future genetic analyses (Figs. 2 and 3).

This is a set of actions that are performed by many herpetologists (professional and amateur) around the country, and as such many herpetologists have a collection of tissues of various snake species. It is thus that we are able to put out a call to our colleagues for tissues of our study species, and we are able to obtain tissues for our species from a variety of localities around the country (and in fact, around Africa), without having to conduct the field work ourselves. Snakes are notorious for being difficult to find, and in fact most of the sampling of snakes are usually done after chance encounters with snakes, so obtaining tissues from colleagues that have encountered snake species allows us to have a good spread of samples for our analyses. This informal sharing of tissues has resulted in many new species being discovered and range extensions have been noted. Much of the distributional data has been continuously collated by the University of Cape Town (UCT) Animal Demographic Unit (ADU), and members of the public can submit their finds (via photos) on their website (http://vmus.adu.org.za), and our lab has contributed to the various animal atlases listed on the website with our findings.

Figure 2: Processing some live snakes for various research projects conducted by ZEML. Left: Dr Shelley Edwards holding a rinkhals (*Hemachatus haemachatus*), in a tube to prevent bites; Right: Dr Chad Keates and Mr Anthony Evlambiou (ZEML Masters students) prepare to 'tube' a small puffadder (*Bitis arietans*), seen curled on the ground in front of them.

Figure 3: During snake callouts, we remove snakes from the public's homes and workplaces, and in the process collect data on environmental factors that are driving snake movements in urban areas. Dr Chad Keates (pictured left) is a ZEML Masters student that initiated the research project connected with the snake callouts, and we are often called out multiple times a week. Left: Chad is holding the snakes (in plastic containers) that had been collected in one week in May 2018. Right: a male boomslang (*Dispholidus typus*) caught during a snake callout.

6 PUBLICATIONS

Please see ***Appendix 1*** for a complete list of my publications. I will highlight eight papers that I have authored/co-authored here (Table 1 includes the reference for the papers and their abstracts).

The select set of papers that I would like to highlight show the utility of using genetic data to identify new species and taxonomic groups, and also how useful it is to test different algorithms to find the most accurate taxonomic structure in animals. These methods can be applied to any number of organisms, as DNA is present in all living organisms, from bacteria to plants to invertebrates (e.g., insects) and vertebrates (e.g., reptiles). Many of these papers include comparisons of genetic structuring with morphological shape and functional aspects of the species (such as bite force, locomotion, dietary aspects). These comparisons were done to identify whether there is congruence between genetic and phenotypic traits (i.e., that ancestry plays a role in the phenotypic traits of species) or whether there is a link between phenotypic traits and the environment (i.e., showing that evolution of phenotypic traits is shaped by the environment).

Table 1: *Select list of publications (in chronological order). Reference, with the abstract below, given for each.*

van Steenderen, Clarke**;** Paterson, Iain; **Edwards, Shelley**; Day, Michael. (2020). Addressing the red flags in cochineal identification: The use of molecular techniques to identify cochineal insects that are used as biological control agents for invasive alien cacti. *Biological Control*. 152: 104426. (*Impact factor: 2.754)*
Abstract: Invasive Cactaceae cause considerable damage to ecosystem function and agricultural practices around the world. The most successful biological control agents used to combat this group of weeds belong to the genus *Dactylopius* (Hemiptera: Dactylopiidae), commonly known as 'cochineal'. Effective control relies on selecting the correct species, or in some cases, the most effective intraspecific lineage, of cochineal for the target cactus species. Many of the *Dactylopius* species are so morphologically similar, and in the case of intraspecific lineages, identical, that numerous misidentifications have been made in the past. These errors have resulted in failed attempts at the biological control of some cactus species. This study aimed to generate a multi-locus genetic database to enable the accurate identification of dactylopiids. Genetic characterization was achieved through the nucleotide sequencing of three gene regions (12S rRNA, 18S rRNA, and COI) and two inter-simple sequence repeats (ISSR). Nucleotide sequences were very effective for species-level and *D. tomentosus* lineage-level identification, but could not distinguish between the two lineages within *D. opuntiae* commonly used for biological control of various *Opuntia* spp. Fragment analysis through the use of ISSRs successfully addressed this issue. This is the first time that a method has been developed that can distinguish between these two *D. opuntiae* lineages. Using the methods developed in this study, biological control practitioners can ensure that the most effective agent species and lineages are used for each cactus target weed, thus maximizing the level of control.
Keates, Chad; Conradie, Werner; Greenbaum, Eli; **Edwards, Shelley.** (2019) A snake in the grass: Genetic structuring of the widespread African grass snake (*Psammophylax* Fitzinger 1843), with the description of a new genus and a new species. *Journal of Zoological Systematics and Evolutionary Research.* 57(4): 1039-1066. (*Impact factor: 2.154)*
Abstract: *Psammophylax* (Fitzinger 1843) is a widespread yet poorly studied genus of African grass snakes. A genetic phylogeny of six of the seven species was estimated using multiple phylogenetic and distance-based methods. To support the genetic analyses, we conducted morphological analyses on the body (traditional morphology) and head (geometric morphometrics) separately. Phylogenetic analyses recovered a similar topology to past studies, but with better resolution and node support. We found substantial genetic structuring within the genus, supported by significantly different head shapes between *P. a. acutus* and other *Psammophylax*. *Psammophylax a. acutus* was recovered as sister to its congeners, and sequence divergence values and morphometrics supported its recognition as a new genus. Increased sampling in East Africa (Tanzania, Kenya, and Ethiopia) revealed that *Psammophylax multisquamis* is polyphyletic, necessitating the description of a new, morphologically cryptic species from northern Tanzania. The distribution of *P. multisquamis* sensu stricto is likely restricted to Kenya and Ethiopia. The study has further resolved multiple aspects of *Psammophylax* systematics, including the taxonomic validity of two central African subspecies, *P. variabilis vanoyei* (Laurent 1956) and *P. tritaeniatus subniger* (Laurent 1956). Inclusion of specimens from the more remote parts of Africa, in future analyses, may result in the recovery of additional diversity within *Psammophylax*.

Conradie, Werner; Busschau, Theo; **Edwards, Shelley.** (2018) Two new species of *Acontias* (Acontinae, Scincidae) from the Mpumalanga Highveld escarpment of South Africa. *Zootaxa*. 4429 (1): 089–106. (*Impact factor: 0.949)*

Abstract: The African genus of fossorial legless lizards (*Acontias* Cuvier) currently comprises 26 species and subspecies. In a recent study on the two disjunct populations of *Acontias breviceps* Essex, the presence of cryptic species was discovered. Here, we increase the sampling size and describe these disjunct populations from the Mpumalanga Escarpment of South Africa as new species. The new species differ from congeners based on a combination of factors, including the number of midbody, ventral, and subcaudal scale counts, ventral pigmentation, allopatric distributions, and genetic divergences. The new species are genetically distant from nominal A. breviceps, with which it shares overall pigmentation and scalation. The new description adds to the growing number of Mpumalanga escarpment endemic reptiles, and highlights the area as a biodiversity hotspot. The use of vertebral counts as a distinguishing character between species is briefly discussed.

Edwards, Shelley; Tolley, Krystal; Measey, John. (2017) Habitat characteristics influence the breeding of Rose's dwarf mountain toadlet *Capensibufo rosei* (Anura: Bufonidae). *Herpetological Journal* 27: 287–298. (*Impact factor: 0.662)*

Abstract: Direct anthropogenic factors (e.g., habitat loss, fragmentation, and degradation) threaten many amphibian populations, however some declines have occurred in supposedly pristine environments with no obvious causes. These enigmatic declines may be due to shifts in environmental factors influencing development and ultimately adult survival. Rose's mountain toadlet *Capensibufo rosei* has undergone such an enigmatic decline, with several populations presumed to be locally extinct at historic breeding sites. The two remaining breeding sites (Silvermine (SILV) and Cape of Good Hope (CGH)) on the Cape Peninsula of South Africa were monitored for three years (2012-2014) for life history traits and ecological requirements. Males congregate at ephemeral pools during the middle of the austral winter, with females arriving to lay eggs and then immediately leaving. Breeding only occurs in a few of the available pools. We hypothesised that larval development in colder, deeper pools would result in smaller-bodied tadpoles, and ultimately in relatively smaller adults. Pools at SILV were significantly deeper and colder compared to CGH, with breeding occurring in pools that were 27.05±10.21 mm and 21.55±6.95 mm deep at SILV and CGH, respectively. Contrary to expectations, breeding adults and developing tadpoles at SILV were larger than CGH individuals. The percentage of non-developing eggs at CGH was high compared to SILV and other anuran species. Development within this threatened species may be influenced by pool characteristics, which could provide clues as to the factors that influenced local extinctions in historical populations.

Edwards, Shelley; Herrel, Anthony; Vanhooydonck, Bieke; Measey, John; Tolley, Krystal. (2016) Diving in head first: trade-offs between phenotypic traits and sand-diving predator escape strategy in *Meroles* desert lizards. Biological Journal of the Linnean Society. 119(4): 919-931. (*Impact factor: 1.961)*

Abstract: Survival, in part, depends on an individual's ability to evade predators. In desert regions some lizard species have evolved head-first sand-diving strategies to escape predators. To facilitate this behaviour, a distinctive head morphology that facilitates sand-diving has evolved. This specialised head morphology may, however, come at a cost to other ecologically relevant functions, particularly bite force. Here, we investigated the relationship between morphology and function in a southern African lacertid lizard genus, *Meroles*, which consists of eight species that utilise different escape strategies, including sand-diving and running for cover. It was hypothesized that the specialised head

morphology of diving species would negatively affect bite force capacity. We found that species from each escape strategy category differed significantly in head shape, but not bite force performance. A phylogenetic tree of the genus was constructed using two mitochondrial and two nuclear genes, and we conducted phylogenetic comparative analyses. One aspect of the head shape differed between the escape strategies once phylogeny was taken into account. We found that bite force may have co-evolved with head morphology, but that there was no trade-off between biting capacity and escape strategy in *Meroles*.

Edwards, Shelley; Tolley, Krystal; Vanhooydonck, Bieke; Measey, John; Herrel, Anthony. (2013) Is dietary niche breadth linked to morphology and performance in Sandveld lizards *Nucras* (Sauria: Lacertidae)? Biological Journal of the Linnean Society.110: 674–688 (*Impact factor:1.961)*

Abstract: The functional characteristics of prey items (such as hardness and evasiveness) have been linked with cranial morphology and performance in vertebrates. In lizards particularly, species with more robust crania generally feed on harder prey items and possess a greater bite force, whereas those that prey on evasive prey typically have longer snouts. However, the link between dietary niche breadth, morphology, and performance has not been explicitly investigated in lizards. The southern African genus *Nucras* was used to investigate this link because the species exhibit differing niche breadth values and dietary compositions. A phylogeny for the genus was established using mitochondrial and nuclear markers, and morphological clusters were identified. Dietary data of five *Nucras* species, as reported previously, were used in correlation analyses between cranial shape (quantified using geometric morphometrics) and dietary niche breadth, and the proportion of hard prey taken and bite force capacity. Dietary niche breadth and the proportion of hard prey eaten were significantly related to cranial shape, although not once phylogeny was accounted for using a phylogenetic generalized least squares regression. The proportion of evasive prey eaten was a significant predictor of forelimb length when phylogeny was taken into account. We conclude that, in *Nucras*, the percentage of evasive prey taken co-evolves with forelimb morphology, and dietary niche breadth co-evolves with cranial shape. However, although head width is correlated with the proportion of hard prey eaten, this appears to be the result of shared ancestry rather than adaptive evolution.

Edwards, Shelley; Branch, William; Vanhooydonck Bieke, Herrel, Anthony; Measey, John; Tolley, Krystal. (2013) Taxonomic adjustments in the systematics of the southern African lacertid lizards (Sauria: Lacertidae). *Zootaxa*. 3669 (2): 101–114 (*Impact factor: 0.949)*

Abstract: Molecular phylogenetic analyses of southern African lacertid lizards (Eremiadini) using mitochondrial and nuclear markers revealed two examples of generic assignments incompatible with monophyletic clades. *Australolacerta* Arnold 1989, a genus endemic to South Africa and to which two isolated species have been referred, is paraphyletic at the generic level. In addition, the species *Ichnotropis squamulosa* Peters 1854 was found to be embedded within the genus *Meroles.* To resolve the paraphyly in *Australolacerta* we erect a new genus, *Vhembelacerta* Edwards, Branch, Herrel, Vanhooydonck, Measey, & Tolley, **gen. nov.**, to accommodate *Lacerta rupicola* FitzSimons 1933. To maintain a monophyletic *Ichnotropis* Peters 1854, *Ichnotropis squamulosa* Peters 1854 is transferred to *Meroles* Gray 1838, now named *Meroles squamulosus* **comb. nov.** Where necessary the genera affected by these actions are re-characterized.

Edwards, Shelley; Vanhooydonck, Bieke; Herrel, Anthony; Measey, John; Tolley, Krystal. (2012) Convergent evolution associated with habitat decouples phenotype from phylogeny in a clade of lizards. *PLoS-One* 7 (12): e52636. DOI: 10.1371/journal.pone.0051636. (*Impact factor: 2.740)*
Abstract: Convergent evolution can explain similarity in morphology between species, due to selection on a fitness-enhancing phenotype in response to local environmental conditions. As selective pressures on body morphology may be strong, these have confounded our understanding of the evolutionary relationships between species. Within the speciose African radiation of lacertid lizards (Eremiadini), some species occupy a narrow habitat range (e.g. open habitat, cluttered habitat, strictly rupicolous, or strictly psammophilic), which may exert strong selective pressures on lizard body morphology. Here we show that the overall body plan is unrelated to shared ancestry in the African radiation of Eremiadini, but is instead coupled to habitat use. Comprehensive Bayesian and likelihood phylogenies using multiple representatives from all genera (2 nuclear, 2 mitochondrial markers) show that morphologically convergent species thought to represent sister taxa within the same genus are distantly related evolutionary lineages (*Ichnotropis squamulosa* and *Ichnotropis spp*.; *Australolacerta rupicola* and *A. australis*). Hierarchical clustering and multivariate analysis of morphological characters suggest that body, and head, width and height (stockiness), all of which are ecologically relevant with respect to movement through habitat, are similar between the genetically distant species. Our data show that convergence in morphology, due to adaptation to similar environments, has confounded the assignment of species leading to misidentification of the taxonomic position of *I. squamulosa* and the *Australolacerta* species.

7 Impact of Research

The study of evolutionary biology really does form the basis of many other fields of investigations; because evolution is the underpinning of how species interact and function in environments, an understanding of how species come about allows for further study into conservation science, ecology, medical science, physiology of organisms, agricultural science, to name a few. In the excellent review by Losos et al., (2013), Jonathan Losos states that: “Much human activity, however, is changing Earth's climate and habitats, with uncertain but potentially severe environmental stresses on many other species … and the solutions to the many resulting problems may well require understanding evolutionary interactions among species and their mutual dependencies”.

Nature is a web of interacting species within communities, and extinction of certain groups within that web will off-balance the delicate interplay between the species, sometimes causing community collapse.

- The first step to knowing what needs to be conserved is knowledge about what species are present in those communities – **species delineation (taxonomy and systematics)**.
- In order to understand the ecology of species that exist today, we need to look to the past to understand the evolutionary paths that these species took, and what factors drove the species to diverge – **speciation factors (evolutionary biology)**.

- By understanding what factors underpin evolution, we can start to look to the future and determine what factors need to be conserved in order for the current species to survive – **conservation science**. In this way, having knowledge about the evolution of groups, and the constituent species in communities, we can identify conservation actions that need to take place to conserve our biodiversity.
- Lastly, identifying the common factors in the evolution of species (**comparative evolutionary biology**) provides basic information for medical science (e.g., for vaccine development; development of CRISPR technologies), for agricultural science (e.g.; pest control using biocontrol; increasing crop yields), for technological advancements (e.g.; production of bio-computers; development of bio-fuels), amongst many others.

The primary aim of research conducted at ZEML is to investigate the evolution of animals and plants (namely investigating the taxonomy and systematics of groups, investigating the speciation factors and drivers, and applying them for conservation purposes). Much has been discovered about the mechanisms underpinning the evolution of organisms, and the factors that drive evolution. However, much is still left to discover. The advancement in technologies and analysis techniques has driven the field of evolutionary biology into new territory and allowed for better understanding of the processes involved in the evolution of organisms. Research conducted at the ZEML uses molecular techniques to investigate the genetic structuring of populations, the taxonomic structuring of groups, and to estimate the likely evolutionary path of the groups over the course of their speciation. We use research into the phenotype (morphology, behaviour, functional traits) to support the molecular analyses, with comparisons to environmental variables (like biome, rainfall, soil type) helping to identify what factors are driving the evolution of phenotypic traits.

8 FUNDING

Date	Institution	Type of Training or Qualification
2016-2022	Research grant: Rhodes University	Funding for laboratory consumables and research costs
2019	Travel Grant: Rhodes University	World Congress of Herpetology 9, Dunedin, New Zealand
2017-2019	Research grant: NRF/Thuthuka	Funding for herpetofaunal phylogeography projects
2017	Research grant: NRF/FBIP	Funding for herpetofaunal phylogeography project.
2016	Travel Grant: Rhodes University	World Congress of Herpetology 8, Hangzhou, China
2014	Travel Grant: NRF/KIC	Herpetological Association of Africa conference 12, Gobabeb, Namibia
2012	Scholarship: Erasmus Mundus Scholarship	Scholarship for ten-month research at University of Antwerp, Belgium
2012	Travel Grant: NRF/SABI	Student Workshop and travel to Richards Bay
2012	Travel Grant: SABI	World Congress of Herpetology 7, Vancouver, Canada
2011	Research grant: International Foundation of Science (IFS)	Research Grant for field equipment and publication costs
2011	Bursary: NRF/SABI Innovation Doctoral Scholarship	National Research Foundation NRF/SABI PhD Bursary
2010	Bursary: NRF Grantholder-linked Bursary	NRF Grantholder-linked Bursary
2008	Bursary: NRF/DST Masters Grant-Holders Bursary	NRF/DST Grant-Holders Masters Bursary

9 CONFERENCES

I regularly attend conferences and forums, with the aim of establishing collaborations and to disseminate my own research. I have attended 23 conferences and forums (see ***Appendix 3***), and two conferences posters were presented by students, that I co-authored. This list includes four international conferences (the World Congress of Herpetology (Fig. 4-6) and the Benelux Congress of Herpetology). I have met researchers from all around the globe and connected with colleagues resulting in plans for future collaborations.

Figure 4: Presenting a portion of my doctoral work at the World Congress of Herpetology in Vancouver, Canada (2012).

Figure 5: South African delegates at the World Congress of Herpetology 2020. Left to right: Dr Mike Bates (National Museum, Bloemfontein), Dr Chad Keates (ZEML), Dr Shelley Edwards (ZEML), Prof Alan Channing (UWC), Mr Werner Conradie (PE Museum, Gqeberha).

Figure 6: Other South African delegates at the World Congress of Herpetology. From Left to right: Dr Mike Bates, Mr Gary Nicolau (ZEML), Mr Werner Conradie, Dr Chad Keates (ZEML), (Dr Stuart Nielsen photobombing), Mr Warren Schmidt, Ms Emily Jackson (Rhodes University).

10 TRAINING AND WORKSHOPS

I have attended a number of training courses and workshops, in order to be well-prepared as an evolutionary herpetologist. The most important course thus far was the snake-handling course, presented by Johan Marais, during which we learned safe handling techniques for venomous snakes, and first-aid in the case of snake bites (Fig. 7). This course has prepared me for my current work on venomous snakes and has enabled my lab (and more specifically myself and my students) to become the ones to call for snake removals in the Grahamstown/Makhanda area. I have also twice attended a 4x4 training course, learning how to properly handle off-road terrain and get better acquainted with how a 4x4 off-road vehicle handles in various terrains (Fig. 8). This has been invaluable on field trips and allowing us to effectively access areas that have been historically under-sampled in terms of reptiles.

Figure 7: Snake handling course 2014 – learning how to apply first aid in case of a snakebite.

Figure 8: 4x4 driving course at Killarney, Cape Town (2014).

11 ZEML IN THE NEWS!

Research featured in newspapers

"A snake named Kelly"

- https://www.grocotts.co.za/2020/07/14/a-snake-named-kelly/

"Eastern Cape researchers discover new snake species"

- https://www.dispatchlive.co.za/news/2020-06-20-eastern-cape-researchers-discover-new-snake-species/
- https://www.therep.co.za/2020/06/21/eastern-cape-researchers-discover-new-snake-species/
- https://www.heraldlive.co.za/news/2020-06-20-eastern-cape-researchers-discover-new-snake-species/
- https://www.talkofthetown.co.za/2020/06/21/eastern-cape-researchers-discover-new-snake-species/
- https://www.ru.ac.za/latestnews/easterncaperesearchersdiscovernewsnakespecies.html

"Mind the toads… you need them!"

- https://www.grocotts.co.za/2020/03/16/mind-the-toads-you-need-them/#prettyPhoto

"The snake charmer"

- https://nextgenherpetologist.co.za/2019/08/07/rhodos-2018-19-the-snake-charmer/

"A leap into the frog world"

- https://www.talkofthetown.co.za/2019/06/22/a-leap-into-the-frog-world/

"Aspiring herpetologist advocates for reptiles"

- https://nextgenherpetologist.co.za/2019/04/13/oppidan-press-aspiring-herpetologist-advocates-for-reptiles/

"Slithery signs of possible danger"

- https://nextgenherpetologist.co.za/2018/03/15/daily-dispatch-newspaper/

Article in the Annual Research Report 2018 for Rhodes University.

See article on the next page or at this link:

https://www.ru.ac.za/media/rhodesuniversity/content/research/documents/RRR_2018.pdf

Mr Chad Keates and Dr Shelley Edwards. *Credit: Chris Marais*

Dr Shelley Edwards and Chad Keates
Department of Zoology and Entomology

Reptile Detectives

At the top of Rhodes University's Life Sciences Building is a laboratory that would have completely astounded the father of modern taxonomy, Carolus Linnaeus.

When Swedish naturalist Linnaeus began bringing systems and order to the classification of animals and plants roughly 280 years ago, there was only one tool available: careful observation and description of species.

By the time he died in 1778 his great book *Systema Naturae* was 2 300 pages long, spread over three volumes, giving succinctly descriptive Latin names to over 13 000 organisms.

Taxonomy has variously been described as a science, an art, and a battleground. Disagreements over classifications among scientists are legendary and bitter. They can and have raged for years.

Complicating things immeasurably is the fact that members of identical species can look quite different. The domestic dog is perhaps the most vivid example, ranging in size and appearance from the tiny Yorkshire Terrier to the gigantic Irish Wolfhound.

The converse is also true. Members of completely different species can look exactly the same.

"There are thirty different species of lizards around the world, from seven different families, that all have black and yellow striped bodies

with blue tails," points out Dr Shelley Edwards, Senior Lecturer of Evolutionary and Molecular Biology at the University's Department of Zoology and Entomology.

Taxonomy and Taxidermy

Adjoining her office is the laboratory that Linnaeus would so have envied - where this kind of conundrum can be sorted out through genetic analysis of DNA.

Most of the work here is being done on reptiles. Back in the days of Linnaeus, this would have entailed studying actual samples of these animals, usually stuffed to preserve their appearance.

And that in turn relied on explorers such as Francois Levaillant, William John Burchell and Joseph Banks who would go on expeditions around the world to bring back samples. These collections had immense value to natural history museums.

When Francois Levaillant set off on his expeditions around South Africa in 1781, he was considered one of the best taxidermists in the world, thanks in part to his secret recipe of arsenic soap that made a dramatic difference in preserving specimens for longer, including their sheen and colouration. Some of his stuffed birds are still in the archives of French museums today.

Later on, natural history museum curators would set out and acquire specimens themselves. For centuries, the job entailed a certain handiness with rifles, an unflinching devotion to stuffing and mounting animals, and a gift for arranging these in helpful dioramas that gave visitors an idea of their habitat and behaviour.

It was those highly prized specimens that helped taxonomists define the often-disputed boundaries between species.

The Species Sleuths

These days Dr Edwards and Doctoral candidate Chad Keates analyse genetic samples in the Zoology and Entomology Molecular Laboratory (ZEML) from a tiny piece of tail - the lizard or snake escapes with its life - or a liver sample harvested from an animal caught for science.

They both had unlikely beginnings as reptile species sleuths. When Dr Edwards began her BSc at Stellenbosch University her ambition was to become a conservation veterinarian. It was only while doing her PhD on the genetics of Lacertid lizards that her direction changed irrevocably.

"I fell in love with reptiles, anything scaly and awesome - they've become the highlight of my career thus far. I realise that every biologist feels their study species is top notch, but the fact that these lizards seem to be so good at adapting to their environments truly fascinates me."

It was when Dr Edwards began supervising Chad Keates' doctoral studies on *Psammophiinae* (grass, sand and whip snakes) that the world of serpents began to intrigue her too. This sub-family of snakes is mildly venomous and as Keates describes them, "slender, gorgeous and lightning quick".

Keates never envisaged a career path in science. While at school, he was an average learner.

"I remember very clearly the day the deputy headmaster told me I lacked the academic capabilities to pass high school science."

He stubbornly persisted though, studied journalism at Rhodes for his undergraduate degree and then switched to Zoology for his Honours. He excelled, graduating with distinction.

"That's when I became really mad about snakes."

Keates began his Masters by studying the phylogenetics of the spotted skaapsteker snake (*Psammophylax*). Halfway through, his studies were upgraded to PhD, expanding to include the *Psammophiinae*.

Evolution and Speciation

"This country's snakes are very under-studied," says Keates. "Just last year we found a new snake species. There might even be a new family of frogs coming out of this lab. South Africa is the most sampled place in Africa. Southern Africa is home to around 660 species of reptiles, with approximately 165 species of snakes. Yet we're still finding new ones.

Brown house snake (*Boaedon capensis*). *Credit: Chris Marais*

"We are all working on genetics, because there is no point in studying an animal if you don't know what it is yet. Taxonomy first, then ecology."

Dr Edwards explains: "We're interested in how something became a species, the driving factors or speciation events that led to one group becoming different enough to be a new species. A speciation event, although it sounds like quite a sudden thing, is usually millions of years in the making. These are environmental or habitat changes, some kind of geological event, a mountain being pushed up, the course of a river changing, something that splits populations so that they stop interbreeding and evolve separately.

"Africa is a fantastic continent to be studying this simply because evolution was not interrupted by any glaciation processes during the last Ice Age. It has just undergone changes in rainfall and elevation. Over millions of years, half of Africa was pushed up by the magma in the mantle underneath the Earth and this uprising led to a change in the rainfall patterns and the reason why we have savannah.

"The rising of the Drakensberg range now intercepts the rain-bearing clouds that used to bring moisture to the Karoo, once an inland sea. Since the mountains have contributed to the drying out of the whole Karoo basin, species have responded in various ways.

"If we look back five million years ago and see what has happened, we can possibly predict which species will survive climate change. Perhaps a population will contract, or expand."

Hadeda ibises, once limited to forests and wetlands, are now widespread throughout South Africa, Dr Edwards points out. Vervet monkeys have also expanded their populations along dry and wet rivercourses through the Karoo. Another area of Dr Edwards' studies includes the spread of the house gecko (*Hemidactylus mabouia*) in the Eastern Cape province.

"What we find could help conservation efforts, giving baseline information that safeguards vulnerable species."

Pressure and Change

"We're trying to see signals of changes in the genetics of various reptile species. So we do single species genetics and look at their evolution and the times that they split and then do another species, another and another - we use multiple lines of evidence to look into the past and we can then start to try to predict how species are going to possibly survive climate change in the future."

If conditions are constant, a species could remain the same for millions of years, adds Keates.

"But if there is pressure, the rapidity of the change depends on its generation times - how many times a year it reproduces. So if you've got something like an insect that can reproduce in a week, with 52 generations in a year, it can evolve quickly.

"But if you have a tortoise, say, that lives for 150 years, and produces an egg every two years, it will take some time for that species to change. Those with mutations that give an advantage for survival are the ones that will carry on."

In reptiles, habitat change has forced speciation, which often begins with morphology (appearance).

Dr Edwards brings up two images of South African chameleons on her computer screen.

"Genetically, these are very nearly identical. But this one lives in forested areas, has that bony crest on its head, and is brightly coloured. It's much bigger than this one that lives in open fynbos areas, has dull colours and a small head with no crest. They've adapted to the habitat they're in, which is why there are these morphological differences. Theoretically, if they become physically separated, they would stop interbreeding and become completely separate species one day."

Snakes and Lizards

In fact, Dr Edwards points out, snakes evolved from lizards millions of years ago. They began to burrow because something must have changed in their habitat. Limbs became a hindrance, and eyes were superfluous in the dark.

"These resulted in the primitive blind snakes."

Even so, the ancient snakes retain the vestiges of limbs, including the pelvic girdle. Keates picks out a specimen from a box he brought in. It looks like a giant millipede without the feet.

"You can barely tell the back from the end. But the tail does have a sharp spine it uses for self-defence."

The more recently evolved snakes, he explains, include the boomslang, which has huge eyes and dangerous venom.

"So snakes are just glorified lizards."

Threats, Pets and Roads

One of the biggest threats to reptile populations is the pet trade. Lizards and snakes are in huge demand, especially the rare, charismatic and endemic ones with tiny distribution ranges like the Albany Adder, the Plain Mountain Adder, the Sungazer lizard and many kinds of tortoises.

Keates says he is contacted by people all the time, wanting to know where he found this or that species.

"Collectors have offered me money. They'll follow people like me on *Facebook* or *Instagram*, and try to find out where the photos were taken. I take the geo-tags off my photographs before I post them on my website *www.nextgenherpetologist.co.za*.

"If you look at *YouTube* videos on the pet trade, you'll see warehouses of people with tortoises in boxes so small they can't move.

"But the problem generally isn't with the reptiles you see, it's the ones you don't. It's the rare, illegal to trade ones that sell for a fortune on the black market. They end up far from home, kept in secret enclosures, their valuable genes lost to nature.

"But habitat destruction and roads are even more of a threat. Hundreds die on the roads of South Africa every day."

Horny Devils and Technicolour Warfare

Both Edwards and Keates marvel at the ingenuity and variety among reptiles.

There are swimming lizards (iguanas) in the Galapagos, an Australian lizard called the *Horny Devil* that can shoot blood from its eyes, and South Africa's own flat

lizards that fight with competitors by flashing their technicolour stomachs at one another. Koggelmanders meanwhile, show their fitness to mate by turning their heads bright blue and doing press ups.

It's not always habitat that determines changes in species. Dr Edwards explains:

"Those 30 different lizard species that all have striped bodies and blue tails have all found the same solution to an ecological problem - in this case predation.

"In nature, blue is a strange colour, but seems to be quite attractive to certain birds and mammals. So if you have a lizard with the ability to break off its tail and leave it wiggling behind it, then the predator is distracted and that will give the lizard an advantage. The stripes are also a way to confuse the predator. It is disruptive colouration. While the lizard is running, the predator cannot focus properly on it. Zebras use the same trick."

Keates shares his passion for reptiles in outreach, taking snakes and lizards to schoolchildren and interested groups. He also offers demonstrations and 'critter walks' as well as a snake removal service.

When not working on his thesis, side projects or environmental awareness, he roams the country "in search of weird and wonderful reptiles and amphibians. I've photographed all the species I've encountered and uploaded them to my website so that others can enjoy Southern Africa's amazing diversity."

But he also loves being in the laboratory.

For Keates, the dusty traditions of taxonomy have acquired a whole new glamour through the research coming from the Zoology and Entomology Molecular Laboratory.

"Dr Edwards has elevated five new slug-eating snakes to species level. We've got two new grass snakes from Tanzania. A new pygmy toad from Angola. A whole new gecko genus from Angola too, plus a new skink from Mozambique. There are lots of cool things happening in this lab," says Keates.

"It's like CSI, except with reptiles."

Julienne du Toit

Mr Chad Keates with a Rock Monitor.
Credit: Javier Lobon Riviera

12 FUTURE PLANS

My plans for research in the coming years include the phylogenetic investigations of various herpetological and arachnid species, and the inclusion of three-dimensional investigations of reptile skeletons in relation to their lifestyles (Fig. 9). I would like to further investigate other cases of convergent evolution in reptiles, and in particular in snakes, and to produce novel analyses methods for evolutionary biology.

I would also like to explore the use of Single Nucleotide Polymorphisms (SNPs) as a set of markers for phylogenetic analyses – a set of analyses that will see our lab moving away from single gene sequencing to explorations of whole genome sequencing. In addition, I would like to explore new techniques in DNA fingerprinting.

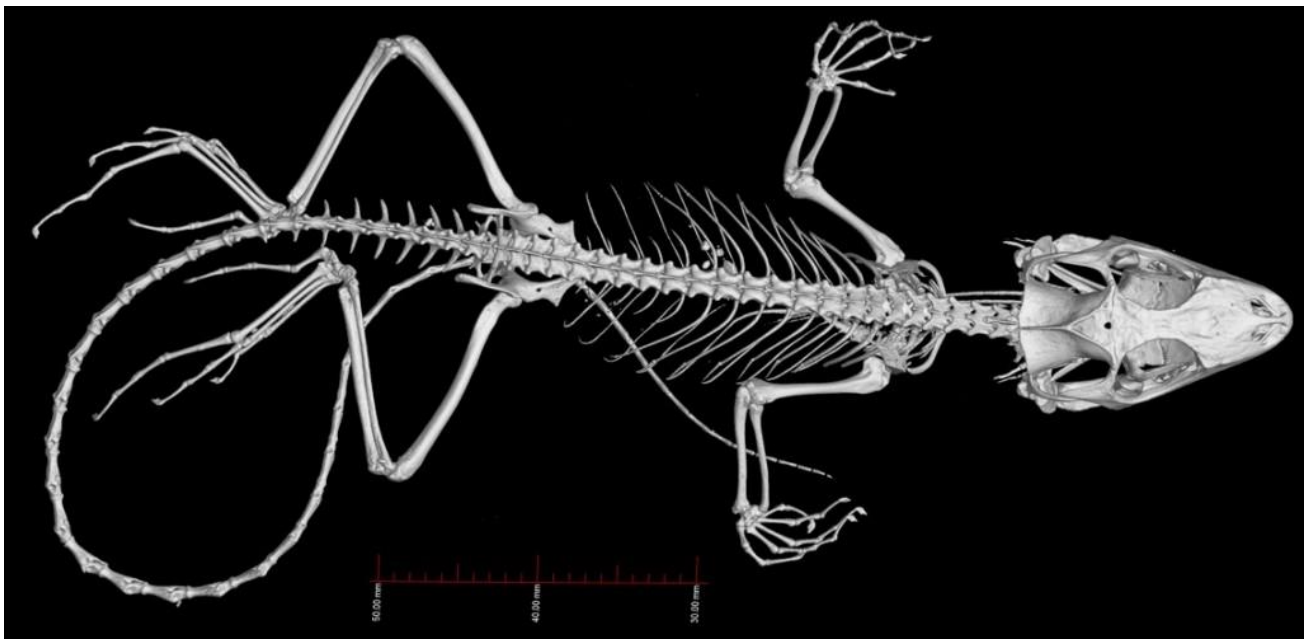

Figure 9: A three-dimensional reconstruction of a lizard body, used to investigate shape differences between species, and link the skeletal characteristics to particular lifestyles of the species.

Lastly, I envision ZEML as being a laboratory that is accessible not only for my students, but also for students and researchers from other research groups at Rhodes University that wish to include genetic investigations in their research. I would like the lab to be instrumental in snake-awareness initiatives within the local area and surrounds, and to attract students and the public alike to participate in the activities available at Rhodes University by creating opportunities to do so. In short, I would like to create a space where cutting-edge research is done to answer some of the oldest questions in biological science.

- ☙ * ❧ -

APPENDIX 1: LIST OF PUBLICATIONS TO DATE

Published articles – ZEML members in bold

Lobon-Rovira, Javier; Conradie, Werner; Vaz Pinto, Pedro; **Keates, Chad; Edwards, Shelley;** Du Plessis, Anthony; Branch, William. (2022) Systematic revision of *Afrogecko ansorgii* Boulenger, 1907 (Sauria: Gekkonidae) from western Angola. Zootaxa. 5124(4), 401-430.

Baptista, Ninda; Vaz Pinto, Pedro; **Keates, Chad**; **Edwards, Shelley**; Rodel, Mark-Oliver; Conradie, Werner. (2021) A new species of red toad, *Schismaderma* Smith, 1849 (Anura: Bufonidae), from central Angola. Zootaxa. 5081(3): 301-332

Villet, Martin; **Edwards Shelley**. (2021) Phylogenetic position of the African cicada genus *Tugelana* Distant, 1912 (Hemiptera: Cicadidae). African Invertebrates. 62(2): 399-410

Nicolau, Gary; Petford, Melissa; **Edwards, Shelley;** Busschau, Theo; Lynch, Keir; Kemp, Luke; Balmer, Jonathan; **Keates, Chad;** Hundermark, Courtney; Weeber, Joshua; Conradie, Werner. (2020) New insights into the geographical distribution, ecology and conservation status of South Africa's endemic Coastal Leaf-toed Gecko, *Cryptactites peringueyi* (Boulenger, 1910). *Herpetology Notes.* 14: 439-450.

Conradie, Werner; **Nicolau, Gary**; **Kemp, Luke**; **Edwards, Shelley;** Klein Snaken-Borg, S; Reeves, Brian. (2020). *Lygodactylus capensis*: New records for Makhanda area. *African Herp News*. 74: 78-82

van Steenderen, Clarke; Paterson, Iain; **Edwards, Shelley**; Day, Michael. (2020). Addressing the red flags in cochineal identification: The use of molecular techniques to identify cochineal insects that are used as biological control agents for invasive alien cacti. *Biological Control*. 152: 104426.

Keates, Chad; Conradie, Werner; Greenbaum, Eli; **Edwards, Shelley.** (2019) A snake in the grass: Genetic structuring of the widespread African grass snake (*Psammophylax* Fitzinger 1843), with the description of a new genus and a new species. *Journal of Zoological Systematics and Evolutionary Research*. 57(4): 1039-1066.

Rink, Ariella; Bowie, Rauri; Altweg, Res; **Edwards, Shelley;** Colville, Jonathan. (2019) Contest dynamics and assessment strategies in combatant monkey beetles (Scarabaeidae: Hopliini). *Behavioural Ecology*. 30(3): 713-723.

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Edwards, Shelley; Conradie, Werner. Phylogeny of the slug-eater snakes *Duberria*, with remarks on their evolution, and description of new species.

Jeme, Alungile; **Edwards, Shelley;** Conradie, Werner. Source of the invasive populations of *Hemidactylus mabouia* (Tropical house gecko) in the Eastern and Western Cape Provinces of South Africa.

Edwards, Shelley; Ntokozo Hlope; Rawson, William; Buthelezi, Khanyilise. Phylogenetic investigations of the convergent evolution of fishing behaviour in the spider family Pisauridae.

APPENDIX 2: LIST OF STUDENT SUPERVISION

Postgraduate projects in progress:

Masters projects

Main supervisor:

Bruce Roestof:	Taxonomy of the African Mantodea.
Alungile Jeme:	Geographic source of the invasive Tropical House gecko, *Hemidactylus mabouia*, in South Africa.

Co-supervisor:

Jonathan Balmer:	Phylogeography of two small owl species in South Africa.
Asante Msimang:	A fair drug development progress: Research ethics, animal sentience and the development of quinolone antibiotics as a potential model for the proposal of changes to the drug development and bringing novel antimicrobials to clinical use in human medicine.

Students graduated:

Masters projects

Main supervisor:

Anthony Evlambiou:	An evolutionary study of legless skinks' (*Acontias* Cuvier, 1817) head and vertebrae morphology.

Co-supervisor:

Clarke Van Steenderen:	Phylogenetic analysis and barcoding of *Dactylopius costa* (Hemiptera: Dactylopiidae): An important genus in the biological control of cactaceous weeds in South Africa. [Main supervisor: Dr I. Paterson]
Cassandra Barker:	Geographic stability in the phylogeography of the brown mussel, *Perna perna*, on the South African coastline. [Main supervisor: Prof Christopher McQuaid]

PhD (doctorate) projects

Main supervisor:

Chad Keates:	Integrative Systematic Structuring of the Widespread Psammophiid Snakes (Psammophiidae): A Multi-evidence Species Delineation Approach.

Co-supervisor:

Krista Oswald:	An integrative approach to understanding vulnerability of an alpine range-restricted bird to climate warming.

Postdoctoral projects:

Dr Jessica Comley:	Genetic variation in the Eastern Cape populations of brown hyena *Parahyaena brunnea*.

Undergraduate and Honours projects:

2015

No projects supervised during 2015, as I was hired as a temporary lecturer in February 2015, and only hired in a permanent capacity in September 2015.

2016

Undergraduate (3rd year Zoology) projects

Andrew Chen:	Evolution of webbing on the hind feet in *Hyperolius* frogs is linked to rainfall seasonality and levels. [morphometrics]
Benjamin Kirkaldy:	Is head shape in burrowing Squamata the result of convergent evolution? [morphometrics]
Carla Bint:	Abundance of *Hyperolius marmoratus verrucosus* in Grahamstown/Makhanda. [ecology]
Lauren Offord:	Hopping around Grahamstown/Makhanda: A diversity and abundance study of frogs (Anura). [ecology]
Luke Kemp:	The effect of grazing on reptile diversity. [ecology]
Nonjabulo Matomela:	The abundance and distribution of *Cacosternum boettgeri* in the Grahamstown/Makhanda Area. [ecology]
Yolokazi Ndobeni:	Bronze Dainty frog *Cacosternum nanum* abundance and distribution around Grahamstown/Makhanda, Eastern Cape. [ecology]

Honours projects

Main supervisor:

Benjamin Miller:	The trophic ecology and prey catching morphology of aquatic and riparian nursery web spiders (Araneae: Pisauridae) in Grahamstown/Makhanda (Eastern Cape, South Africa). [trophic ecology; morphometrics]
Chad Keates:	Phylogenetic analysis of *Psammophylax rhombeatus rhombeatus*. [genetic phylogeny]
Ella Morran:	Phylogenetic reconstruction of southern African ridged frogs (genus *Ptychadena*). [genetic phylogeny]
James Radloff:	Lizards with the blues: Investigations of environmental factors that may have resulted in phenotypic convergence. [genetic phylogeny]
Tessa Woollgar:	Head scale morphology of legless skinks: *Acontias* (Cuvier) (Scincidae: Acontinae). [morphometrics]

Co-supervisor:

Chad Keates:	The effect of painted reed frog (*Hyperolius marmoratus verrucosus*) predation on the mass rearing of two biocontrol agents for water hyacinth (*Eichhornia crassipes*). [ecology]

2017

Undergraduate (3rd year Zoology) projects

Cassandra Barker:	Anti-predator response of the Eastern Cape Dwarf Chameleon, *Bradypodion ventrale*, to various stimuli of vervet monkeys, *Chlorocebus pygerythrus*. [behaviour] (in preparation)
Khanyisile Buthelezi:	Phylogeny of the family Pisauridae. [genetic phylogeny]
Kestrel Raik:	Utilization by *Hyperolius marmoratus verrucosus* of the biocontrol rearing tunnels at Waainek Mass Rearing Facility, Grahamstown/Makhanda. [behaviour]
Daniel Rogers:	A survey of the spiders found within the Grahamstown/Makhanda (Eastern Cape, South Africa) area. [ecology]

Undergraduate (3rd year Entomology) projects

Carol Munro:	Feeding preference of spiders on biological control agents of water hyacinth. [behaviour]

Honours projects

Main supervisor:

Benjamin Kirkaldy:	Is wing shape in Odonata the result of convergent evolution? [morphometrics]
Carla Bint:	Competition for shelter between *Otomys irroratus* (Muridae) and *Rhabdomys pumilio* (Muridae). [ecology]
Jonathan Balmer:	Spiders' tarsal claw structure in relation to hunting strategy, with specific reference to Fishing Spiders (Pisauridae: *Nilus* sp) and other pisaurids. [morphometrics]
Maruchelle Cilliers:	Resistance to routinely used anthelmintics in wireworm *Haemonchus contortus*, infecting domestic sheep. [medicine]
Luke Kemp:	Phylogeographic comparison of *Ptychadena porosissima* (Steindachner, 1867). [genetic phylogeography]

Co-supervisor:

Luke Kemp:	It's not all black and white: An overview of the Albany adder (*Bitis albanica*) (Hewitt, 1937) including an ecological niche model. [niche modelling; ecology]

Honours Review Articles

Kaeleah Andrew:	The magnitude of impact that cats have on biodiversity
Luke Kemp:	The effects of climate change on species with temperature-dependent sex determination.
Clarke van Steenderen:	A question of scale: Queens and the court jester as models for biotic and abiotic drivers of evolution.

2018

Undergraduate (3rd year Zoology) projects

Richard Carkeek:	A study into the invasive populations of the tropical house gecko, *Hemidactylus mabouia*, in the Eastern Cape. [genetic phylogeny]
Cara Trivella:	Ecotypes in the Eastern Cape dwarf chameleon (*Bradypodion ventrale*: Chamaeleonidae) are related to vegetation densities. [morphometrics]

Honours projects

Main supervisor:

Bruce Roestof:	Morphology of mantis raptorial forelegs in relation to diet. [morphometrics]
Kaylen Bowers:	The origin of South African invasive populations of tropical house gecko (*Hemidactylus mabouia*). [genetic phylogeny]
William Rawson:	Phylogeny of the Pisauridae (Araneae). [genetic phylogeny]

2019

Undergraduate (3rd year Zoology) projects

Emily Jackson:	Effects on sleeping perch site selection by environmental factors in the Eastern Cape Dwarf Chameleon – *Bradypodion ventrale* (Gray, 1845). [behaviour] (in preparation)

Bongekile Makhathini: Spider diversity (Arachnida: Araneae) in different habitats in Grahamstown/Makhanda, Eastern Cape. [ecology]

Camron Paul: The preference of four different shelter usage by reptiles. [ecology]

Bruce Roestof: A morphological comparison of the shell shape between two Lineages of Brown Mussel, *Perna perna* (Linnaeus 1785), in South Africa. [morphometrics]

Honours projects

Main supervisor:

Cara Trivella: Morphology and vegetation associations of the Knysna Dwarf Chameleon, *Bradypodion damaranum* (Boulenger, 1887). [morphometrics] (in preparation)

Janais Delport: The description of a new bristletail species (Archaeognatha: Meinertellidae) from Limpopo, South Africa. [taxonomy; genetic phylogeny] (in preparation)

Honours Review Articles

Tahnee Bennett: Does the fossil record contribute to our fundamental understanding of evolution?

2020

Undergraduate (3rd year Zoology & Entomology) projects

Projects cancelled due to the Covid-19 National Lockdown.

Honours projects

Main supervisor:

Emily Jackson: The natural history and strandings of the Yellow-bellied sea snake (*Hydrophis platurus*) along the South African coastline, using museum samples. [morphology; reproduction] (in preparation)

Liam Yell: Body size versus head shape: which is more important for a burrowing reptile? [morphometrics]

Honours Review Articles

Nicola Dreyer: Geomagnetic polarity reversals: Historical perspective, present assumptions and future consequences.

2021

Undergraduate (3rd year Entomology) projects

Gary Nicolau: Molecular phylogeny of the nursery-web spiders (Pisauridae: Araneae) with a focus on South African members. [genetic phylogeny] (in preparation)

Benjamin De La Fontaine: Fire and ant-termite interactions in a South African urban periphery – with a novel commensalism of harvester ants (*Messor capensis* Mayr) with termites. [ecology] (in preparation)

Honours projects

Main supervisor:

Rochelle Bessinger: Morphological variations of auditory bullae in otomyine rodents (Rodentia: Otomyini) in southern African biomes. [morphometrics] (in preparation)

Honours Review Articles

Cameron Amos: Why have we, as a global community, not achieved the Aichi Biodiversity Targets?

2022

Undergraduate (3rd year Zoology) projects

Deandra Goddard: Population genetics of grass frogs *Ptychadena porossisima* (Ptychadenidae). [genetic phylogeny]

Amahle Sifumba: Morphological shape variations of auditory bullae in otomyine rodents (Rodentia: Otomyini) in southern African biomes. [morphometrics]

Mateenah Barry: Head shape differences in yellow-throated plated lizards *Gerrhosaurus flavigularis*. [morphometrics]

Ntokozo Hlope: Molecular phylogeny of the nursery-web spiders (Pisauridae: Araneae) with a focus on South African members. [genetic phylogeny]

Honours projects

Main supervisor:

Gary Nicolau: Phylogenetics and taxonomy of *Afroedura* [phylogenetics, taxonomy].

Co-supervisor

Tinashe Mashayamombe: Testing for the most appropriate euthanasia substances for invertebrates [animal ethics; animal biology]

Takudzwa Mugiya: Testing for the most appropriate euthanasia substances for invertebrates [animal ethics; animal biology]

Honours Review Articles

Benjamin de la Fontaine: Satan or Saviour: Eugenics may be lurking behind CRISPR technology

Sbonisipho Manqele: Do animals have rights?

APPENDIX 3: CONFERENCE AND WORKSHOP ATTENDANCE

Date	Forum	Location	
During employment at Rhodes Univ.			
2021	SASSB 2021 Webinar Series	South Africa	Attended
2021	2nd Eastern Cape workshop on Ethics in Disaster Situations	Grahamstown, South Africa	Presentation
2020	World Congress of Herpetology 8	Dunedin, New Zealand	Presentation
2019	1st Eastern Cape workshop on Ethics in Disaster Situations	Grahamstown/Makhanda, RSA	Attended
2019	Herpetological Association of Africa (HAA) conference 2019	Cape St Francis Bay, RSA	Presentation
2018	FBIP forum (August 2018)	Cape St Francis Bay, RSA	Presentation
2017	Herpetological Association of Africa (HAA) conference 2017	Bonamanzi Game Reserve, KZN, RSA	Posters (co-author)
2016	Pan African Ornithological Congress (POAC)	Senegal	Poster (co-author)
2016	World Congress of Herpetology 8	Hangzhou China	Presentation
2015	Joint ZSSA/ESSA conference	Grahamstown/Makhanda, RSA	Presentation
Prior to employment at Rhodes Univ.			
2014	HAA conference 2014	Gobabeb, Namibia	Presentation
2013	Biodiversity SA conference	Cape Town, RSA	Poster
2013	4th Diamond Route conference	Johannesburg, RSA	Poster
2013	Presentation at the Erasmus Mundus scholarships Alumni event	Cape Town, RSA	Presentation
2012	19th Benelux Congress of Zoology	Brussels, Belgium	Presentation
2012	World Congress of Herpetology 7	Vancouver, Canada	Presentation
2012	SABI Forum	Richards Bay, RSA	Attended
2011	2nd Diamond Route conference	Johannesburg, RSA	Presentation
2011	Joint ZSSA/PARSA conference	Stellenbosch, RSA	Presentation
2011	Presentation to the Friends of Rietvlei Nature Reserve committee	Cape Town, RSA	Presentation
2011	HAA conference 2011	Cape Town, RSA	Presentation
2008	Joint SAAB/SASB conference	Drakensburg, RSA	Attended
2007	ZSSA/ESSA/SASQA conference	Potchefstroom, RSA	Attended
2006	Fynbos Forum conference	Rawsonville, RSA	Attended
2004	Progressive Realisation of Environmental Rights conference	Stellenbosch, RSA	Attended