Systematics of the Namib day geckos (Squamata: Gekkonidae: *Rhoptropus*)

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Under the Direction of
Dr. Aaron M. Bauer

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Lastly, I would like to dedicate this thesis in memory of Margarita Metallinau. Margarita was a dear friend and cherished mentor. The time and effort she put into her research was matched by the thoughtfulness and patience we all experienced

BIOGRAPHICAL SKETCH

Arianna was born in Whitehall, Pennsylvania, not far from Villanova where her involvement in herpetologically-based research science began. Although she had always been interested in the pursuit of an academic career, her experiences at Villanova University from 2008 to present were integral in the development and execution of this goal.

Arianna initiated her research career during her undergraduate education at Villanova University, where she was fortunate enough to work on the project 'Phylogeny and Evolution of the Geckos of the World' (DEB1234890) with renouned gecko specialist Dr. Aaron Bauer. This project primarily focused on the morphological and molecular evolution of various gecko groups at both broad and shallow time scales, resulting in several important contributions to the herpetological field. Through a Villanova Undergradute Research Fellowship, she was able to independently conduct the complementary project, 'A species level phylogeny of South African Flat Geckos (Gekkonidae: *Afroedura*) and the description of ten new species,' the results of which have since submitted to Zootaxa. She has had the opportunity to present these results at the World Congress of Herpetology VII in Vancouver and the Annual Society for the Study of Evolution meetings in Ottawa. Her undergraduate thesis concerning phylogenetics and reproductive evolution of the scincid genus Trachylepis received the Lawrence G. Gallen O. S. A. award from Villanova and has resulted in interesting discoveries, achieved through collaboration with South African, German, and Portuguese colleagues. She presented these findings at the 2013 meeting of the Herpetological Association of Africa through support from a travel grant awarded by the Association of Women in Science. This project led to her first exposure to collection-based fieldwork, as she traveled to South Africa in the summer of 2013 to collect these and other lizards in the Western Cape.

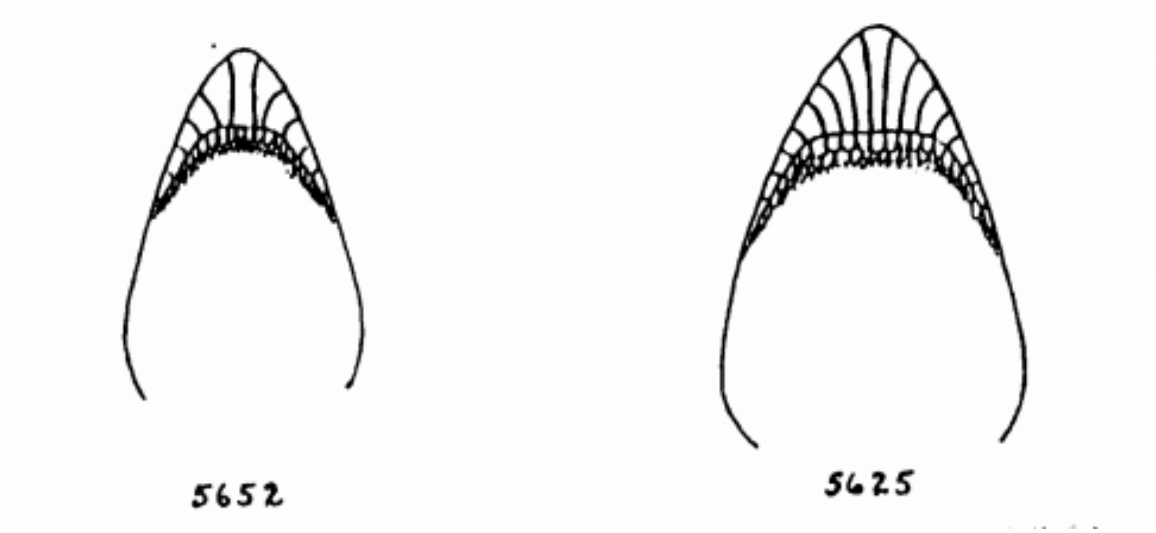
During her Master's studies at Villanova, she was supported by a Villanova Graduate Fellowship as well as a Teaching Assistantship. Her Master's work presented hereafter involved an excursion to Angola in November of 2014 where she gained valuable field and museum experience in a largely unsampled region of Africa. The trip also involved local instruction of best practices for collecting and databasing museum specimens at the National Museum of Natural History in Luanda. Her participation in the field of African herpetology has resulted in an enduring fascination with the unique biodiversity and geographic history of the continent, and a desire to continue this work at the doctoral level. Arianna is now a partner student of the Richard Gilder Graduate School at the American Museum of Natural History through the City University of New York Graduate Center where she is studying speciation and historical demography of Malagasy snakes under the direction of Associate Curator of Herpetology, Dr. Frank Burbrink.

ABSTRACT

The Namib day geckos (genus *Rhoptropus*) are a specialized group of rupiculous gekkonids endemic to the arid regions of western Namibia and southwestern Angola. Previously, nine species and subspecies have been recognized on the basis of morphological, mitochondrial, and/or allozymic data. Until recently, political strife in Angola, where the majority of species have either partial or endemic distributions, has prevented a comprehensive examination of the genus. Whereas most desert species are extreme outliers of mostly non-arid groups, *Rhoptropus* is one of the few vertebrate genera autochnothous to the Namib Desert Biome. The age of desert-adapted groups is of particular importance to disentangling the temporal onset and progression of aridification in what may be the world's oldest desert. Herein, a phylogenetic analysis incorporating all representative lineages using multilocus data and extensive intraspecific sampling is presented. All nine described lineages as well as two new putative lineages, one from the coastal Huab Region of the Kunene Province and one from the Angolan Escarpment, are recovered with good support in concatenated and mitochondrial analyses. Support is also found for the elevation of two lineages, *R. boultoni benguellensis* and *R. boultoni montanus* to full species status. Macroecological results suggest that species may be diverging ecologically although the niche of this group as a whole is largely conserved. Collectively, these findings augment contemporary knowledge of squamate diversity in southwestern Africa, and highlight the importance of ongoing investigations of Western Escarpment fauna. Divergence estimates indicate a minimum age of 36 Ma for *Rhoptropus* and younger than 28 Ma for all included lineages with the majority of diversification taking place from 6–17 Ma. These results suggest *Rhoptropus* may have originated in the early Oligocene subsequent to the progression of sub-humid conditions in southwestern Africa. Subsequently, the group radiated in the Miocene as the onset of hyper-aridity and a winter rainfall regime provided novel habitat for xeric-adapted lineages. The diversification of this group provides insight into the impact historical climate change has had in shaping regional biodiversity in the Namib Desert.

CHAPTER 1

Systematics of the genus *Rhoptropus*



"*Fragments of the natural method*
must be sought with the greatest care...
Nature makes no jumps.
All taxa show relationships on all sides
like the countries on a map of the world."

— Carolus Linnaeus
Philosophia Botanica, 1751
[Illustration: chin shields of *R. boultoni,* from Schmidt 1933]

I. Introduction

A. Biodiversity of Southern African

1. Sub-Saharan Africa

The family Gekkonidae has a global distribution, and is the most speciose gekkotan family to occur on mainland Africa. Gekkonid species richness and diversity is highest in subSaharan Africa, particularly the horn of Africa and the southwestern regions of Namibia and the Northern Cape Province (Fitzsimons 1943, Loveridge 1947, Bauer 1993, Branch 1999a, Bauer et al. 2006). Since the Cretaceous, southern Africa has been characterized by arid conditions until the late Miocene or early Pliocene (Lancaster 2002, Senut et al. 2009). Past climatic changes and variation in geology have resulted in the diversification of various substrate types and geological structures. Precipitation and temperature shifts in combination with extremely diverse topography throughout southern Africa have provided ideal conditions for exceptional gekkonid diversification, particularly so in the western arid region (Bauer 1993, Branch 1999a).

2. Significance of systematic studies on Southern African reptiles

In comparison to other squamate groups, geckos include the greatest number of known undescribed species in southern Africa (Kluge 1967, Joger 1985). Historical habitat subdivision and substrate diversity in southern Africa has provided a unique opportunity for substrate-specific gekkonid cladogenesis (Bauer 1993). Because many of these gecko groups have only been cursorily studied in the past and may contain high cryptic diversity,

the number of groups in need of taxonomic revision remains high (Herbert et al. 2001, Smith et al. 2008). Lack of adequate phylogenetic understanding causes gross underestimation of the region's biodiversity, especially in hotspots with high levels of endemism. A well-resolved taxonomic understanding of the aforementioned taxa is critical to conservation assessment for southern Africa, especially the southwestern coast. Many species are restricted to small rocky outcrops in isolated montane habitats of the escarpment mountains, and may be threatened by habitat loss due to mining, poor land use management, and other anthropogenic effects (Branch 1999a, Lubke 2013, see Figure 5).

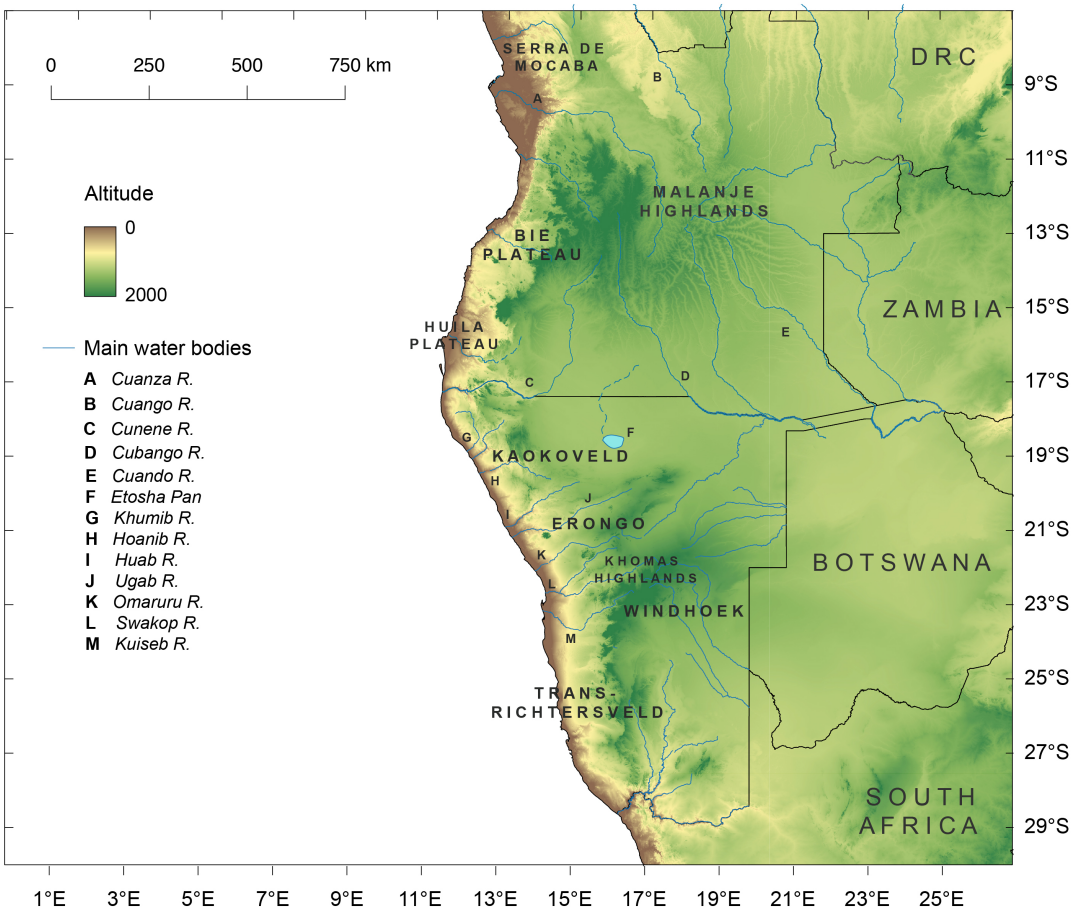


Figure 5. Topography of Namibia and Angola, major Escarpment sections are labeled. Major rivers indicated with letters A–M.

3. Phylogenetics and conservation

Phylogenetics can be used to address several questions related to evolutionary biology, biogeography and historical geological processes associated with the aforementioned taxa (Brian & Meester 1964, Matthee & Flemming 2002, Makokha 2006, Tolley et al. 2006, Swart et al. 2009, Tolley et al. 2009, Niet & Johnson 2009, Verboom et al. 2009). Specifically, the patterns observed amongst the species in question can be compared with various studies of phylogeography in other Southern African vertebrates to search for common patterns of speciation, areas of endemism, and historical geography (Van Zinderen Bakker & Mercer 1986, Lancaster 1989, Coetzee 1993, Branch 1998). The resulting species level phylogenies can provide a framework for studying the interesting evolutionary adaptations of these genera as well. This allows for a reconstruction of the evolution of habitat shifts and the morphophological adaptations that accompany these shifts. The data generated can also be used to identify cryptic species, which are especially common among the morphologically conserved but often genetically distinct lizard genera of this region (Lamb & Bauer 2002, Bauer et al.. 2006, Heinicke et al. 2011). It is important to note that the restrictive habitats and morphologically conserved characters prevalent in many rupiculous sub-Saharan herpetofauna contribute significantly to endangerment of certain species. Should phylogenetic studies identify previously unrecognized species located in increasingly small, select populations, attention can be drawn to particular lineages and biogeographic regions that may require closer supervision in the future (Griffin et al. 1989, Herrman and Branch 2010).

B. The genus *Rhoptropus*

1. Morphology

Rhoptropus geckos exhibit elongate slender limbs relative to snout-vent (SNV) length, four normal sized toes with an expanded tip containing 5-13 individual scansors, and a fifth rudimentary toe (Branch 1998). Minute claws are seen on rudimentary digits of most females, but never on males. Dorsally, scales are overall small and granular but may be lightly keeled or tuburcular. Head morphology is particularly distinct: a sloping concave snout gives rise to elevated, swollen nostrils dorsally, with elongate chin shields found on the ventral aspect (Peters 1869). All *Rhoptropus* are strictly diurnal but display vertically pupilled eyes, a trait more commonly attributed to their nocturnal relatives (Kluge 1967, Rieppel & Haller 1973, Werner 19777). Eyelids, as in most geckos, are immobile and completely fused around the eye. These geckos are small to moderately sized ranging from 46–75 mm, but males and females display no size-dependant sexual dimorphism. Femoral pores are absent in males, but the number and placement of pre-cloacal pores for some species have been considered a distinguishing characteristic in previous species descriptions. Body coloration varies in this group but can be distinctive for certain taxa (Figure 2). Unique apomorphies of the group include (1) a reduced number of presacral vertebrae (24 for *R. afer*, 25 for all other *Rhoptropus* versus an average 26 in other gekkonids), (2) parall binding of metatarsals II and III, (3) ventrolateral fat deposits, and (4) an elongate series of podial elements (Wellborn 1933, Russell 1979, Bauer & Good 1996). The intense selection pressure exerted by the arid conditions of the Namib and pro-Namib region occupied by these geckos has likely played a role both in their distinction from other sub-Saharan gekkonids as well as the somewhat convergent

evolution in behavior, body plan and locomotion between these animals and more distantly related desert squamates (Bauer et al. 1996, Aerts et al. 2000, Melville et al. 2006, Johnson & Russel 2009, Collins 2015).

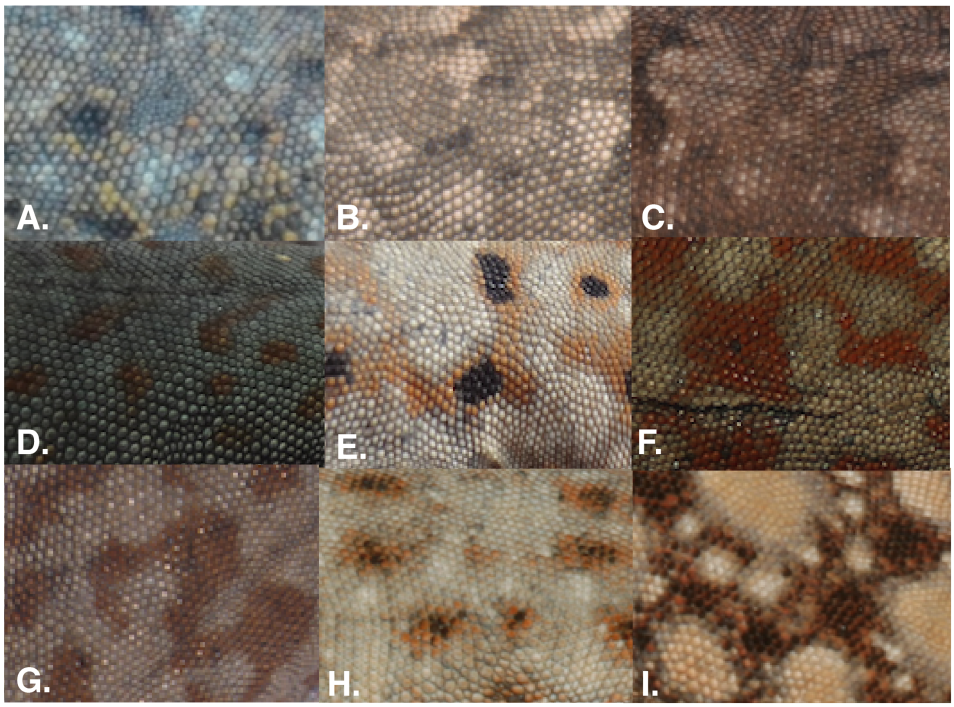


Figure 2. Representative dorsal color pattern for the following species (A-I): *R. afer*, *R. bradfieldi* (inland form), *R. diporus*, *R. montanus*, *R. taeniostictus*, *R. benguellensis*, *R. boultoni, biporosus*, *R. barnardi*

2. Ecology

Species of the genus *Rhoptropus* are almost entirely rock-limited; this restriction to a particular type of substrate tends to promote fragmentation in other rupiculous squamates (Figure 3). While other rock-dwelling groups in southern Africa (i.e., *Cordylus*, *Pachydactylus* and *Ptyodactylus*) seem to have allopatric distributions and high regional endemism, overall ranges for *Rhoptropus* tend to be sympatric and continuous with similar levels of endemism (Branch et al. 1995, Werner 1996, Bauer 1999, Lamb & Bauer 2000, Stanley et al. 2011, Figure 4). Other gekkonid taxa co-occuring in the western arid zone

are generally found on vertical rock faces, rough sands, or fragmented boulders. Because similar habitats are preferred by *Rhoptropus* (Figure 3), it has been hypothesized that the evolution of diurnality in this group may be a result of niche partitioning with other rupiculous desert geckos (Bauer & Good 1996, Figure 5).

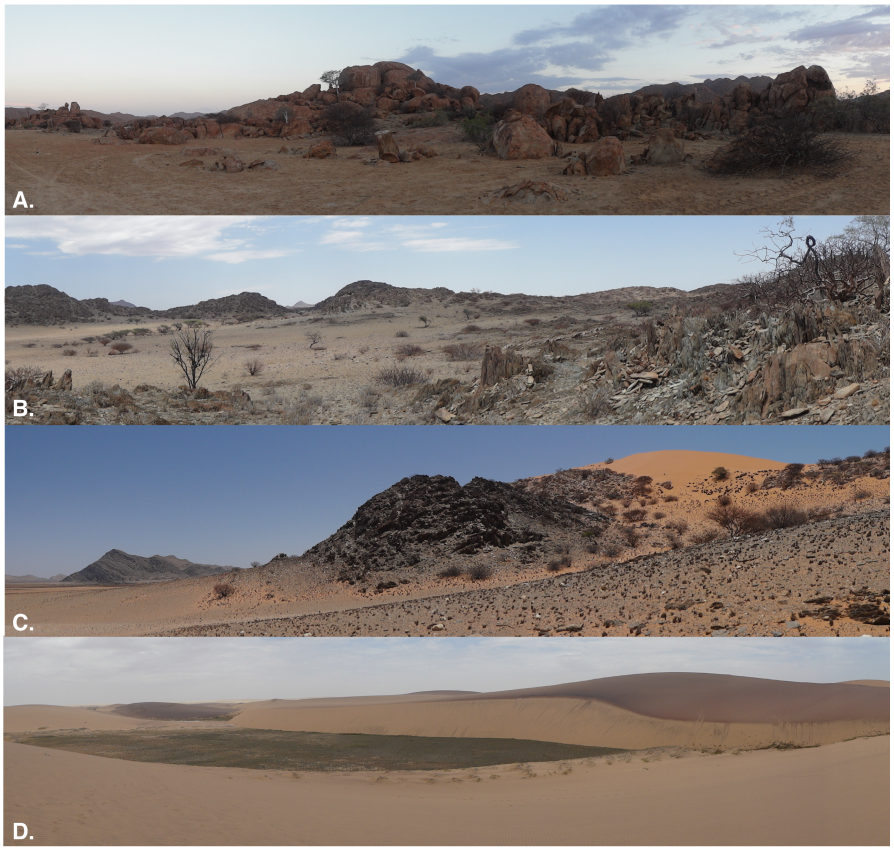


Figure 3. Representative habitat of (A) Angolan *R. boultoni* (Iona National Park, Namibe District, Angola), (B) Angolan *R. barnardi/biporosus* group animals (E Mangueiras. Namibe District, Angola), and (C) the contrasting habitat of the true Namib dune region, from which *Rhoptropus* species are absent (Coastal dunes near Praia do Navio, SSW Angola), as well as (D) semi-dune rocky habitat, suitable only for the terrestrial constituent *R. after (*Namibe-Lubango Rd, Namibe Province, Angola*)*.

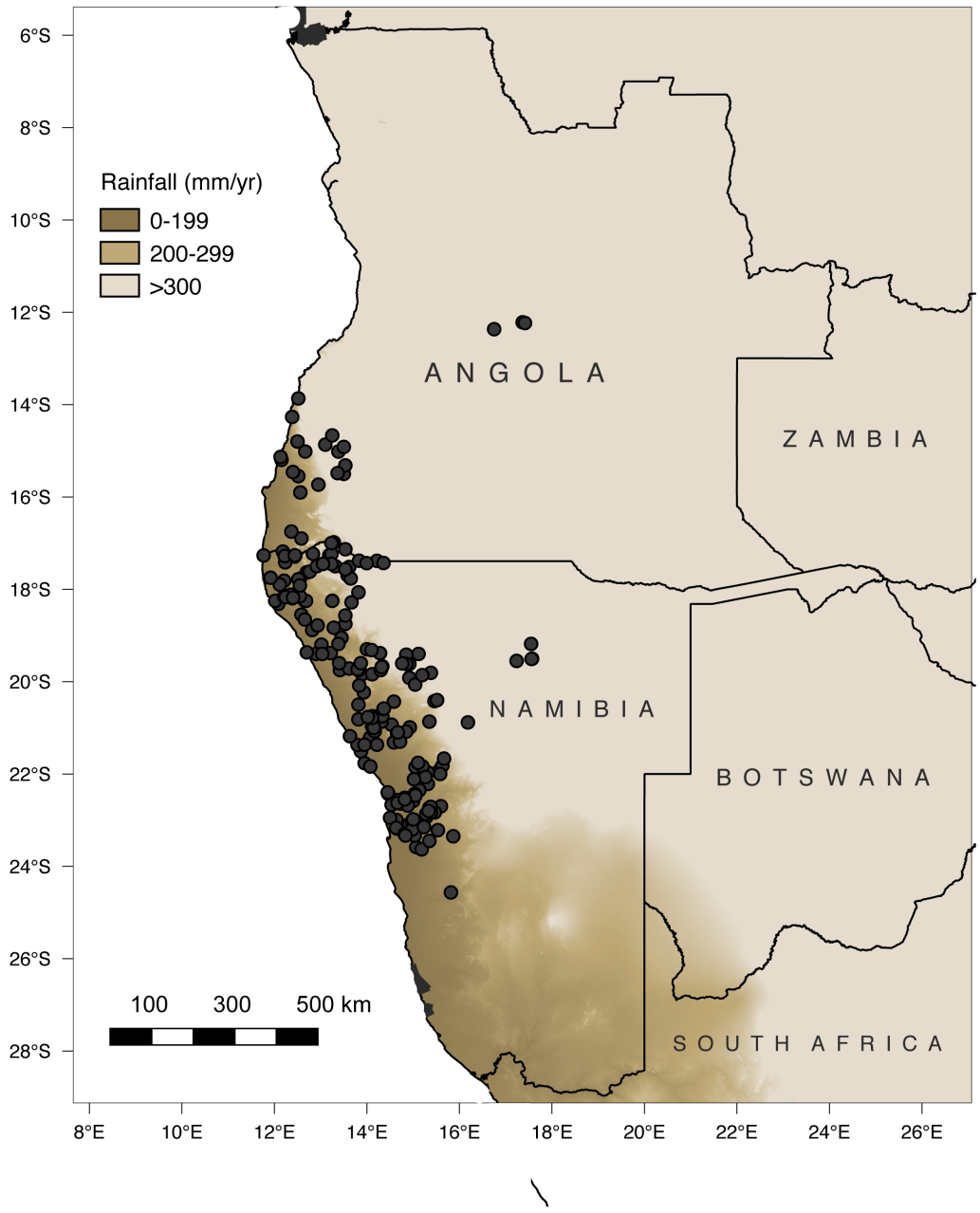


Figure 4. All unique georeferenced *Rhoptropus* localities obtained from global museum records for Namibia and Angola (117 total) are represented with black closed circles. Annual precipitation is plotted to show 300 mm rainfall zone–roughly correspondent to the Western Escarpment and the majority of *Rhoptropus* distribution range.

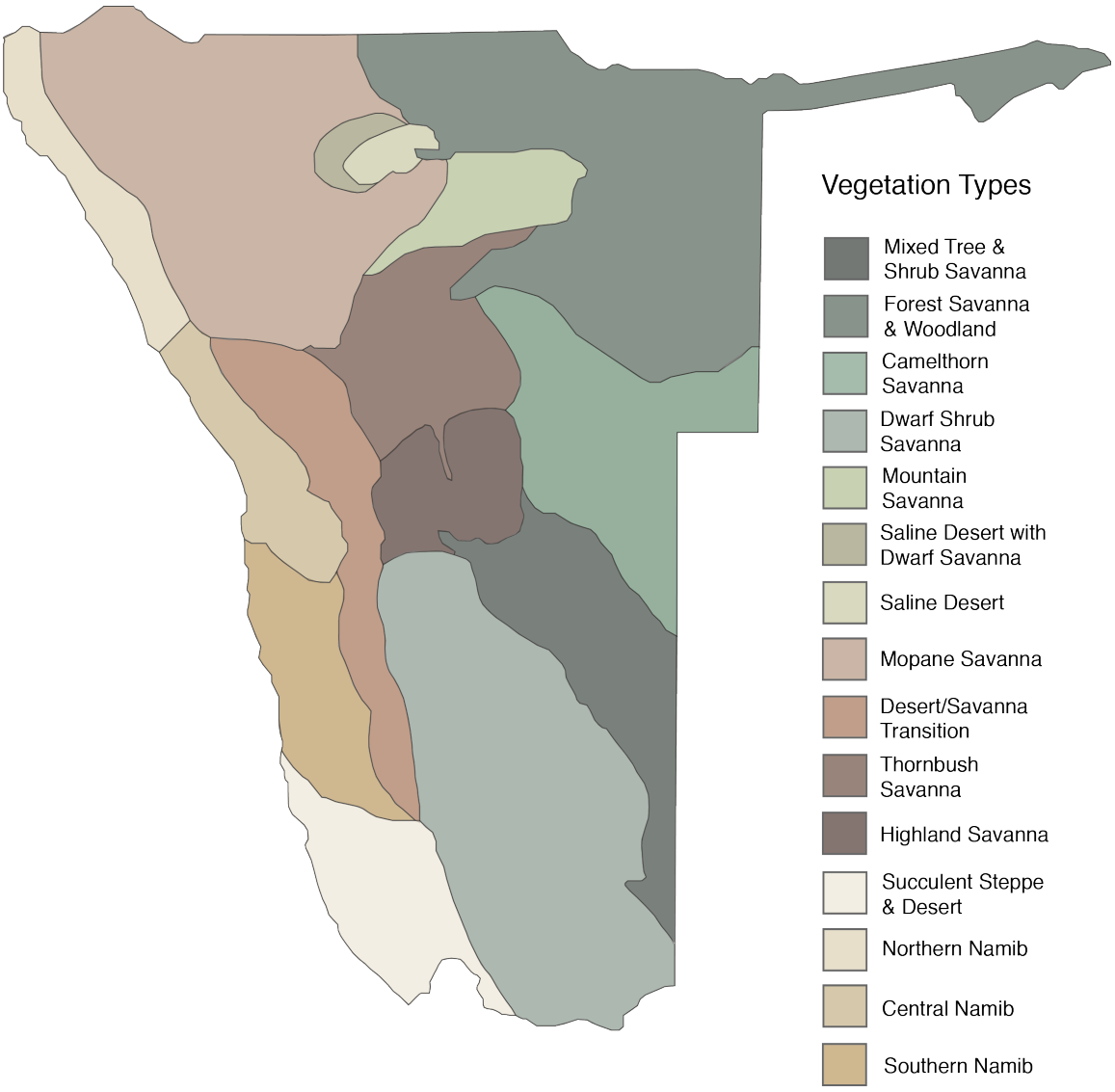


Figure 5. Vegetation types of Namibia as outlined by Giess 1971.

In regards to reproduction, Namib Day geckos utilize communal egg-laying sites and produce 2 hard shelled eggs per clutch in protected rocky sands or rock crevices 1-2 times per breeding season (Branch 1998). Their diet largely consists of small insects such as ants and flies that are obtained by ambush-style hunting. In general, these geckos are locally abundant in suitable, arid regions of the West Coast of southern Africa from the Kuiseb River to southwestern Angola (Figure 4). As many as three different species may occur

within a given area, and intrageneric niche partitioning is often seen with such sympatric distributions (Gorman & Hillman 1977, Vitt & de Carvalho 1995, & Rocha 1996, Dias & Rocha 2004, Stanley et al. 2011). Stamina and speed has been shown to vary amongst species depending on the preferred substrate type of the animal (Haacke & Odendaal 1981, Garland & Losos 1994, Russell & Johnson 2013).

When examined ecologically, the members of this genus do not possess a great deal of niche overlap, despite frequent sympatry (Haacke & Odendall 1981, Higham & Russell 2010). Clear variation exists with respect to substrate preferences and associated morphological and behavioral constraints (Odendall 1979, Johnson et al. 2005). *R. afer* are the only members to occupy horizontal rock sheets, have low in-field metabolic rates and fast, long distance escape mechanisms (Odendaal 1979, Nagy et al. 1993, Autumn 1999). *R. boultoni*, *R. barnardi*, and *R. bradfieldi* have some distributional overlap, but vary in substrate preferences. These species are strictly associated with large boulders in koppies or baobab trunks, small rocks, and large isolated boulders, respectively (Mertens 1955). Unlike *R. afer*, these members employ escape mechanisms with quick, short distance retreats to rocky crevices for protection (Bauer et al. 1996). On the other hand, it appears that *R. biporosus* and *R. barnardi* type animals have some distributional overlap in the northeast Kunene region of Namibia, and the substrate preference of these two animals of small granite or sandstone koppies as well as their similarity in body size clouds the mechanism behind their clearly divergent evolutionary histories. It is apparent that while *R. barnardi* can be found as inland as the Grootfontein region, such localities may be too wet (>400 mm ppt. annually) for *R. biporosus*, which remains restricted in

Namibia to the Kunene and Erongo Regions. Whereas previous studies have addressed the evolutionary context of these behavioral, locomotor and adhesive adaptations, the necessary sampling depth to adequately evaluate these traits and determine their role in the evolution of this group has not been provided phylogenetically (Haacke & Odendall 1981, Autumn 1999, Johnson et al. 2005, Highnam & Russell 2010, Russell & Johnson 2013, Collins 2015).

3. Species level introduction

***Rhoptropus afer* PETERS 1869**

Dactychylikion braconnieri — THOMINOT 1878
Dactychilikion braconnieri — BOULENGER 1885
Rhoptropus afer — BOULENGER 1885
Rhoptropus braconnieri — HEWITT 1910

Lectotype: ZMB 6149A, Zoologisches Museum Berlin, Germany (Bauer & Gunther 1991)

Type Locality: "Damaraland"

Rhoptropus afer prefers rocky desert habitats in the coastal regions of the Namib Desert from the Kuiseb River to southwestern Angola and probably has the most unique morphological distinctions of any other *Rhoptropus* (Bauer et al. 1996, Figure 50). Only *R. afer* exhibit a single row of enlarged mid-ventral caudal scales and 24 presacral vertebrae. Dorsal coloration is pale grey to fawn with light grey splotching or patches, often, the underside of the tail is yellow (-). This gecko has been shown to employ quick bursts of high speed across sandy substrates in comparison to sympatric sister taxa, *R. bradfieldi* (Highham & Russell 2010). This rapid escape behavior and substrate preference is reflected in the limb and digit morphology of the animal—*R. afer* have stout toes with short setae, a small subdigital pad, and considerably elongate hind limbs in comparison to

the front limbs (Bauer et al. 1996, Russell 2009, Johnson & Russell 2009). It has been postulated that the large number of apomorphic traits this species exhibits may be due to a recent ecological shift from climbing to running on flat surfaces (Werner, 1977). These geckos are average in size, reaching a maximum of about 53 mm (Visser 1984). *Rhoptropus afer* occur in the true desert of Namibia and Angola, where desert plains reach high mid-day temperatures and shelter is sought out between exfoliating rocky outcrops (Branch 1998, (Haacke & Odendaal 1981). The occupied microhabitat includes areas affected by coastal fog but does not extend beyond areas of sheetrock into the northern sand sea (Haacke & Odendaal 1981). Because so much of its range falls within the boundaries of the Skeleton Coast National park, previous studies have included poor sampling of this species with the exception of *R. afer* from northern Swakopmund. The terrestrial nature of these geckos in comparison to their more rupiculous-restricted congeners (Figure 3) makes them an interesting target for deeper phylogeographic analyses, highlighting the need to obtain collection permits within the often poorly sampled national park boundaries.

The furthest inland record for all *Rhoptropus* is that of R. *braconnieri.* The holotype (MHNP 294 [1411B], Museum National d'Histoire Naturelle, Paris, France) is recorded as having been collected from South Ngami Lake, Bechuanaland, Botswana, north of the Kalahari Desert. Previously considered a putatively separate species (Thominot 1878, Fitzsimons 1943, Kluge 1993, Welch 1994), *R. braconnieri* has since been synonomized with *R. afer* (Boulenger 1910). Controversy in regards to the status of this taxon still remains ambiguous due to insufficient holotype examination in recent morphological and

molecular studies (Bauer & Good 1996, Bauer & Lamb 2001). It has been suggested that the associated type locality information may be an inaccurate artifact of data obtained during specimen acquisition from a museum rather than true *in situ* collection due to the isolated, distant nature of this potential range and the lack of any additional specimens collected or observed since this species was described in 1878. Examination of historical climatic data of the region does not indicate any eastern extension of current suitable desert habitat to this more inland locality, further supporting the claim that such a dispersal of Namibian *Rhoptropus* was historically unlikely. Because this taxon is intermittently referenced in the literature despite its lack of validity, (Boulenger 1885, Hewitt 1910, Loveridge 1947, Auerbach 1987, Kluge 1993, Rösler 2000) confirmation of species status would be useful in preventing future confusion.

***Rhoptropus barnardi* HEWITT 1926**

Rhoptropus barnardi — LOVERIDGE 1947

Syntypes: SAM 16639, South African Museum, Cape Town SA

Type Locality: "Eriksson's Drift, Kunene River Region, Angola"

Rhoptropus barnardi is the smallest species of the genus, reaching a maximum size of approximately 46 mm (Bauer & Good 1996). Although the majority of *Rhoptropus* are extreme arid specialists, the regions occupied by *R. barnardi* tend to receive slightly higher rainfall. This species can be found occupying medium-sized boulders as well as small rocky hills and ridges. Back scales are both slightly keeled and tuberculated. Color varies from light to dark bands with irregular pale and dark spots, possibly in relation to

habitat variation (Figure 2). Competition for suitable habitat may have historically influenced present-day distributions, as this species rarely occurs in sympatry with several larger rupiculous species. Communal nesting sites with up to 200 eggs at a time have been encountered for this species (Branch 1998). Previous analyses have indicated a sister relationship between *R. barnardi* and *R. biporosus (*Bauer & Good 1996, Lamb & Bauer 2001). .Some variation in preferred habitat is seen, but these animals remain largely rupiculous from Solitaire in central Namibia to Novo Redono in Angola (Haacke & Odendaal 1981). The Angolan extent of this species range is still fairly tentative. Until recently, the only record for *R. barnardi* in Angola was from the type locality of *R. taeniostictus*, on the road from Namibe to Lubango (Laurent 1964a). Field surveys of the Namibe Province and surrounding areas conducted over the past few years have confirmed a tentative northern extent for this species through Namibe to Huila, however the identity of these constituents as true R. barnardi or a new but morphologically similar taxon remains to be seen (Ceríaco et al. 2016). Within *R. barnardi*, isolated populations in the easternmost extent of its range in the Otavi-grootfontein region are only minimally divergent from Namib and pro-Namib populations inland of the coastal fog-belt despite apparent geographic barriers physically separating these groups for a considerable amount of time (Figure 52). As *R. braconnieri* is disregarded as a discrete species, *R. barnardi* has the most inland distributions known for this genus.

***Rhoptropus boultoni* SCHMIDT 1933**

Rhoptropus boultoni — WERMUTH 1965 160

Holotype: FMNH 5624-15.46, 12.4, Carnegie Museum of Natural History, Pittsburgh, USA

Type Locality: “Pico Azevedo, Namibe Province, Angola”

Rhoptropus boultoni occurs in the southwestern parts of Angola through Damaraland in Namibia (Figure 51). These are the largest of all *Rhoptropus* that have been extensively examined morphologically, reaching a maximum SVL of around 74 mm (Bauer & Good 1996). The build of these geckos is robust, but toes are long and slender with 13 undivided scansors beneath the dilated toe-tip. Slight tuberculation of the dorsal scales is seen, and coloration involves unique maroon to orange blotches appearing against a dull grey background (Figure 2). Because color variation in association to habitat type (dark grey on basalts, lighter grey on granite rocks, Figure 6) has been observed in nature, it has been hypothesized that at least some *Rhoptropus* are able to change coloration to match their preferred substrate (Zug et al. 2001). Variation in size, skull morphology, nostril scales, and dorsal patterns were identified early on amongst *R. boultoni* from Epupa Falls on the Kunene River in comparison to more southern-distributed taxa (Bauer & Good 1996). Recent sampling from northern Namibia near the Kunene River has helped fill in the gaps for distributional data of *R. boultoni*, however *Rhoptropus* collected form this region with never before sampled localities present an interesting opportunity to expand known ranges for this animal. *Rhoptropus boultoni* has been collected from the Namibe Province in Angola, up through the type locality at Pico de Azevedo to just northeast of Namibe on the road to Lubango (Figure 51). To date, recent surveys into the more northern provinces have not yielded a more northern extent for this species range (Ceríaco et al. 2016). Because these animals can occupy large, isolated boulders and outcrops (Figure 18), clade-based genetic variation may be recovered across the longitudinal range of this

organism, making it another potential target for deeper intraspecific sampling and phylogeographic analysis. Two subspecies are currently recognized in this group, and appear restricted to the area north of the Kunene River: *Rhoptropus boultoni benguellensis* Mertens 1938 described from Buenguella Province, and *Rhoptropus boultoni montanus* Laurent 1964 described from Huila Province (Figure 18). Meaningful evaluation of their taxonomic status and true distributional extent has been limited by the unstable political state of Angola.

Figure 6. (A) Representative habitat of *R. boultoni* from Iona National Park, Namibe District, Angola (B) Adult *R. boultouni* with characteristic dorsal patterning of thick, dull rust to maroon dorsal latticework that typically begins post-orbitally until the base of the tail over a medium to light grey background, limbs and tail may contain lighter grey splotches, but no other markings. Picture credit Aaron M. Bauer. (C), *R. boultoni in situ* occupying large-sized boulders at the type locality, Pico de Azevedo, Namibe Province, Angola. Picture credit Luis M. Ceríaco.

***Rhoptropus bradfieldi* HEWITT 1935**
Rhoptropus bradfieldi — LOVERIDGE 1947

Syntypes: PEM R15874-75, Port Elizabeth Museum (formerly Albany Museum)

Type Locality: "Messum River, Erongo Region, Namibia"

Rhoptropus bradfieldi is entirely restricted to the semi-desrt coastal regions of central Namibia with no Angolan constituents. Specifically, the current known range of this species extends north along the coast to the Cape Cross region inland to the Brandberg (Figure 50). Like *R. afer*, *R. bradfieldi* lacks enlarged postmental chin shields, precloacal pores, and and large gular scales. Early observations of *R. bradfieldi* allied this species as closely related (Hewitt 1935, Fitzsimons 1938) or synonymous with (Parker 1936, Mertens 1938) *R. boultoni*. This day gecko has a grey to blueish ventral portion, but variable dorsal coloration has been observed between inland and coastal populations (Figure 2). This species is the only member of the genus observed vocalizing, possibly in a territorial context (Branch 1998). *R. bradfieldi* are diagnosable by the absence of precloacal pores and 11 undivided scansors beneath digit IV. Nearly all well-supported phylogenies estimate a close sister-relation between *Rhoptropus bradfieldi* and *Rhoptropus afer* (Bauer & Good 1996, Lamb & Bauer 2001, Gamble et al. 2008, Gamble et al. 2015, Heinicke et al. 2016). The evolutionary significance of melanistic variation seen amongst inland and coastal Southern populations remains unclear without deeper intraspecific sampling across a more continuous representation across the range of *R. bradfieldi* (Bauer & Lamb 2001). It is possible that this color variation may be related to thermoregulation in regions with cool advective fog as shown in cordylid, scincid and

Pachydactylus lizard populations occurring along the western coast of Africa (Baedenhorst et al. 2002, Mouton 1987, Mouton & Oelofsen 1988, Branch 1998, Mouton & van Wyk 1990, Portik 2010, AMB, per obs).

***Rhoptropus boultoni benguellensis* MERTENS 1938**
Rhoptropus boultoni benguellensis — LOVERIDGE 1947

Holotype: SMF 25275, Naturmuseum Senckenberg, Frankfurt am Main, Germany

Type Locality: "Cubal, Benguella Province, Angola"

Although *R. b. benguellensis* has been affiliated with *R. boultoni* in previous morphological assesments, the habitats and distributions of *R. b. benguellensis* and *R. boultoni* are remarkably different (Figure 3, Figure 7). The range of this animal appears substantial, with known localities in the Benguella, Huambo, Cuanza Sul and Malanje Provinces of Angola, making it the most northernly distributed Rhoptropus with localities as remote as the Cuanza River (Figure 51). Much like other *Rhoptropus*, *R. b. benguellensis* is strictly rupiculous, occupying large to moderate sized boulders near streams, although this range spans the undifferentiated woodlands and grasslands and deciduous forest and grass ecoregions of Angola, with considerably higher humidity and lower temperatures than more southwestern Angola (Ceríaco et al. 2016, Figure 18). *Rhoptropus b. benguellensis* is distinguished form *R. boultoni* by a reduced SVL and only 2 enlarged mental sublabial scales in comparison to the 3 or 4 seen in *R. boultoni* (Mertens 1938). Because *R. b. benguellensis* has never been included in any molecular analyses, the genetic distinction and species level relationships between true *R. boultoni* occurring in Angola and this sublineage is unclear. Additional sampling for any ambiguous Angolan

taxa is a critical target of this study and the taxonomic standing of *R. b. benguellensis*.

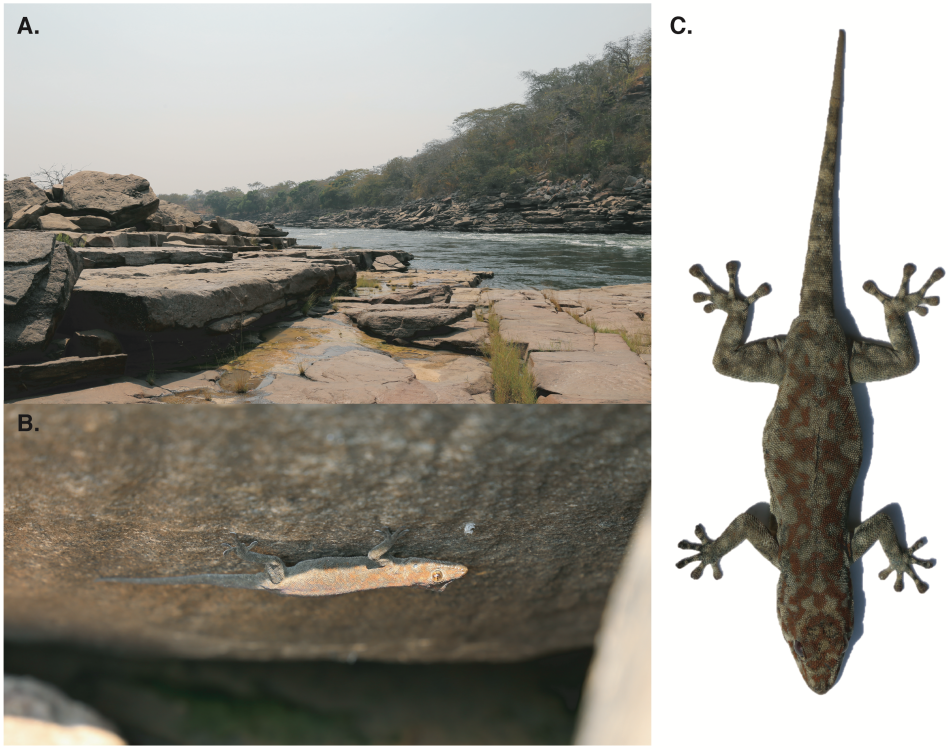


Figure 7. (A) Representative habitat of *R. benguellensis* from Lauca, Malanje Province, Angola (B), *R. benguellensis in situ* occupying large boulders near streams (C) Adult *R. benguellensis* with characteristic dorsal patterning of thick, bright orange-red dorsal latticework that typically begins the post-nasal and fade towards the pelvic region or base of the tail. Background color is medium grey, limbs and tail display pale grey blotches but no orange or red.

***Rhoptropus biporosus* FITZSIMONS 1957**

Rhoptropus biporosus — WERMUTH 1965

Holotype: TM 24198, Ditsong Museum of Natural History (formerly Transvaal Museum)

Type Locality: "Orupembe, about 120 miles West of Ohopoho, Kaokoveld Region, Namibia"

Rhoptropus biporosus are the second smallest Rhoptropus geckos, with maximum SVL of 49 mm. The build and external characteristics of this gecko are superficially similar to that of *R. barnardi*, and for this reason misidentification of these two species is fairly common

(Bauer, pers. obv.). Upon detailed inspection, *R. biporosus* has a more pointed and less sloping snout as well as longer, narrower limbs and tail, and slightly variant coloration from that of *R. biporosus*, although sympatric overlap exists at several known localities in the northern Namib region (Figure 2). This gecko also has fewer digital lamellae than *R. barnardi*. Early descriptions of *R. boultoni* included specimens of *R. biporosus*, highlighting morphological affinities, such as limb length relative to body size, despite the size differentiation evident in larger comparative samples (Schmidt 1933). It is clear that sampling from the southernmost extent of this range near Sesfontein is true *R. biporosus*, but multiple *R. cf. biporosus* collected from Orupembe appear distinct in form and require molecular investigation (Figure 52). As implied by the specific epithet, closer examination of this often misidentified gecko reveals only two precloacal pores arranged in a single row are found on males of this species, although studies have shown this character to be variable within and among populations for other *Rhoptropus* geckos (Bauer & Lamb 2001). The toes and tail of this gecko are elongate and thin, but not as extreme as seen in *R. afer*, with 11 undivided scansors beneath digit IV. Coloration is somewhat variable within this species, but tends to display irregular dark or medium grey bars and splotches on a light grey or fawn background with mildly tuberculated dorsal scales. The habitat preference for this gecko is low boulders and flat rocky outcrops as seen in the semi-desert region in the Kaokoveld region across the Cunene River into adjacent southwestern Angola (Figure 52). Taxonomically, this species tends to fall within a group containing *R. barnardi* and *R. boultoni* (Bauer & Good 1996, Bauer & Lamb 2001). Preliminary field observations for unidentified *Rhoptropus sp.* from northern Gai-as (Namibia) appear intermediate in form between *Rhoptropus biporosus* from the

Khomid River region and *Rhoptropus barnardi* south of Epupa Falls. Angolan surveys have been historically sparse, and until recently the only published record of this species from the region was from Pico Azevedo (Bauer & Good 1996). *R. biporosus* has also been collected from across southern Namibe and Cunene Province near Otchinjau, and recently published field surveys have revealed more northern records near Camucio below the Serra da Neve (Wulf Haacke, Ditsong National Museum of Natural History, Ceríaco et al. 2016). These latest field surveys have highlighted the possibility that *R. biporosus* populations from the Escarpment region of southern Angola appear morphologically distinct from those below the Escarpment. Investigations of other taxa with distributions that span the Escarpment have revealed cryptic species on the highland plateau that are genetically distinct from their lowland congeners thus highlighting the need for closer investigation of the relationship these Escarpment *Rhoptropus* have to other *R. biporosus* (Brennan et al., in prep).

***Rhoptropus taeiniostictus* LAURENT 1964**

Rhoptropus taeniostictus — KLUGE 1993

Holotype: MD 1967, Museu Dundo

Type Locality: "km 60 on roadd from Mossamedes to Sá da Bandeira (Lubango), Mossamedes district, Angola"

Rhoptropus taeiniostictus are distributed at lower elevations exclusively on moderate to large-sized isolated boulders and koppies in the Namibe Province, Angola. Maximum SVL is approximately 65 mm (Bauer & Good 1996, 8). Initial descriptions of *R. barnardi* included *R. taeiniostictus* from Mucungo (Schmidt 1933) and even after the species was described by Laurent (1964) on the basis of a single specimen, close affinities between the

two species remained consistent. This may be attributed to the similarity in dorsal color patterning of the two species–light rust clouding with black or charcoal spots or blotches with a light grey background–although size disparity in adult specimens is apparent (Figure 2, 8). Throughout the taxonomic history of the genus, *R. taeiniostictus* has been estimated as sister to the larger monophyletic clade including *R. boultoni* + (*R. biporosu*s + *R. barnardi*) in morphological analyses (Bauer & Good 1996), but locality data has been relatively limited. Like *R. b montanus* and *R. b. benguellensis*, its taxonomic placement within *Rhoptropus* has never been evaluated molecularly due to the limitations of Angolan tissue sampling north of the Kunene River (Lamb & Bauer 2001). To date, samples have not been obtained outside the Namibe province, but within this region it can be relatively abundant at given localities when adequate boulder outcroppings of moderate size are available (Ceríaco et al. 2016, Ditsong National Museum of Natural History Collections, Figure 52).

8. (A, C) Representative habitat of *R. taeniostictus* from West of Caraculo off Namibe-Lubango Road, Namibe District, Angola, Namibe District, (B) Adult *R. taeniostictus* with characteristic dorsal patterning of 4-5 rows of dorsal 3-4 distinct black spots that extend post-orbital to caudal over a light rust lattice with pale grey background; limbs and tail contain variable grey blotches but no rust or black markings. (D), *R. taeniostictus in situ* occupying vertical surface of large boulders.

***Rhoptropus boultoni montanus* LAURENT 1964**
Rhoptropus boultoni montanus — WERMUTH 1965

Holotype: MD 1854, Museu do Dundo, Dundo, Angola

Type Locality: "Boca da Humpata, Huila Province, Angola"

A large series of *R. b. montanus* has been collected near Lubango, Huila Province and more recently from the Namibe Provincial side of the Leba Pass region of Boca da Humpata, the type locality (Ditsong Museum of Natural History, Ceríaco et al. 2016, Figure 51). These animals have a clearly divergent niche from *R. boultoni*, and were observed basking on moist, granite rocks covered in bryophytes with pools of collected water on the edge of the cliff face at elevations as high as 1850 meters (Fig. 9). The climate of the region is more affiliated with the upper plateau of Angola with increased humidity, lower temperatures and dense vegetation in comparison to the arid and sparsely vegetated lowland (Figure 18). Physically, these geckos have a rounded snouth, robust bodies and limbs with large granular scales and darkly pigmented olive grey dorsals covered in rust spots while the ventral side is a lighter bluish grey or white (Figures 13, 21). Max SVL is recorded as 72 mm, which is not considerably smaller than *R. boultoni*, although the type description indicates that its smaller size and a reduced number of digital plates (5–8 instead of 9–13) with more proximal subdigital scales than plates are diagnostic (Laurent 1964). The decision to group *R. b. montanus* with *R. boultoni* has more to do with geographic closeness than morphological affinity, as *R. b. montanus* also shares a number of scale features with *R. barnardi* (Loveridge 1964). The relationship of morphological distinction and habitat for *R. b. montanus* has been observed in a number of other montane endemics of lower elevation squamates (Janse van Rensburg, Mouton &

van Niekerk, 2009, Leaché, Helmer & Moritz, 2010, Jambrich & Jandzik 2012, Portik et al. 2013, Figure 51), it is possible that *R. b. montanus* represents a highly derived, endemic lineage of montane adapted *Rhoptropus*. This species has never been included in a molecular analysis therefore the relationship of this taxon to true R. *boultoni* from Angola and the taxonomic standing of this sublineage awaits evaluation.

Fig. 9. (A), *R. montanus in situ* occupying the rocky outcrops and crevices of the cliff face, at 1845 meters elevation. (B) Representative habitat of *R. montanus* from the high plateau outlook at Leba Pass, Huila Province, Angola. (C) Adult *R. montanus* with characteristic dorsal patterning of small, bright orange to red spots that typically begin post-orbitally and extend to the base of the tail over a dark grey background, limbs and tail are typically solid grey with no blotches or spotting, body is robust.

***Rhoptropus diporus* HAACKE, 1965**

Rhoptropus bradfieldi diporus — BAUER et al. 1993
Rhoptropus diporus — BAUER & LAMB 2001

Holotype: TM 28238, Ditsong National Museum of Natural History (formerly Transvaal Museum)
Type Locality: "Farm Twyfelfontein, Namibia"

The elevation of subspecies *R. bradfieldi diporus* to full specific rank in 2001 by Bauer & Lamb has been the most recent taxonomic revision of the genus. The range of this species occurs as far north as the Huab River (Farm Vrede) and southwards through Twyfelfontein to the Ugab River near Brandberg (Bauer et al. 1993, Bauer & Lamb 2001, Haacke 1965; van den Elzen 1983, Figure 50). The presence of enlarged precloacal scales with pores was considered diagnostic by Haacke (1965) and can be observed in the type series specimens. Additional morphological examination of *R. diporus* revealed that the presence of this character is inconsistent; additionally, coastal *R. bradfieldi* do not seem to have this feature, but inland *R. bradfieldi* show variation. More broadly applicable diagnostic features include small, round thigh and precloacal scales on the ventral side (Bauer & Lamb 2001). Because genetic differences between *R. bradfieldi* and *R. diporus* are relatively shallow (9.7%–11.6%, cytochrome b, Bauer & Lamb 2001) in comparison to other intrageneric *Rhoptropus* (19%-27%, cytochrome b) investigation of ecological diversification and habitat preferences may lend insight into the mechanistic driver of divergent evolution in these two lineages. At present, it can only be observed through their distribution that geological speciation with subsequent dispersal into sympatry may explain the contemporary differentiation and distribution of these taxa (Grünert 2000). Alternatively, as *R. bradfieldi* prefers large isolated boulders while *R. diporus* appears to

ccupy granite and sandstone koppies and rock walls, it is possible that ecological speciation *R. diporus* and *R. bradfieldi* comprise the only two known Namibian endemics of the genus *Rhoptropus*, but cryptic variation that has been observed in *R. barnardi* groups may challenge this distribution of endemism (Figure 50).

4. Taxonomic history

Systematics of the genus *Rhoptropus* have been particularly difficult, due in part to lack of adequate sampling and unclear species boundaries (Lamb & Bauer 2001). Initial delineation of various *Rhoptropus* species involved recognition of scale character variation (Fitzsimons 1938, Laurent 1964, Haacke 1965). *Rhoptropus afer* is by far the most distinct member of the genus in terms of behavior and morphology, and for this reason no taxonomic confusion concerning this group has arisen historically. The only exception to this is *R. branconnieri*, described by Thominot (1878), and synonymized with *R. afer* by Boulenger (1910). Conversely, the remaining members of the genus are somewhat less distinctive superficially and many occur sympatrically. This significant overlap in distribution is made more confounding by the lack of complete knowledge concerning ecological specificity and niche partitioning within sympatric sites (Collins 2015). *R. boultoni* initially was described from a type series that incorporated its smaller relative *R. biporosus* due to inadequate sample size and poor representation of intraspecific variation (Schmidt 1933). *R. bradfieldi*, R. *boultoni* and *R. barnardi* in particular have been subject to the greatest affect of synonymy and presumed affinity both historically and at present (Hewitt 1935, Fitsimonz 1938, Parker 1936, Mertens 1938, FItsimonz 1957, Laruent 1964, Bauer pers. obs.). The earliest attempt to evaluate these

affinities phenetically was done by Russel (1997a). He reviewed scalation and other external features for the entire genus with the exclusion of *R. biporosus* and Angolan forms (*R. taeniostictus*, *R. b. benguellensis*, *R. b. montanus*), grouping together *R. afer* + *R. bradfieldi* and *R. barnardi* + *R. boultoni*. Visitation of outstanding taxonomic problems using 16 allozymic and morphological characters (Bauer & Good 1996, Fig. 10) identified two well-supported clades for 6 of the 9 known species and subspeices: a monophyletic clade consisting of *R. afer* + *R. bradfieldi* and reciprocally monophyletic clade consisting of *R. taeiniostictus* (*R. boulton*i + (*R. barnardi* + *R. biporosus*)). These relationships, with the exception of *R. taeiniostictus,* were re-evaluated with additional data from the mitochondrial markers 16s and cytochrome b (Lamb & Bauer 2001, Fig. 10) with increased support for the aforementioned topology and confirmed the identity of *Pachydactylus* as the sister group to *Rhoptropus*. The most recent revision of this genus was done in 2001 (Bauer & Lamb, Fig. 10), elevating the subspecies *R. bradfieldi diporus* to full species status on the basis of molecular and morphological data (see Table 1 for complete type specimen data).

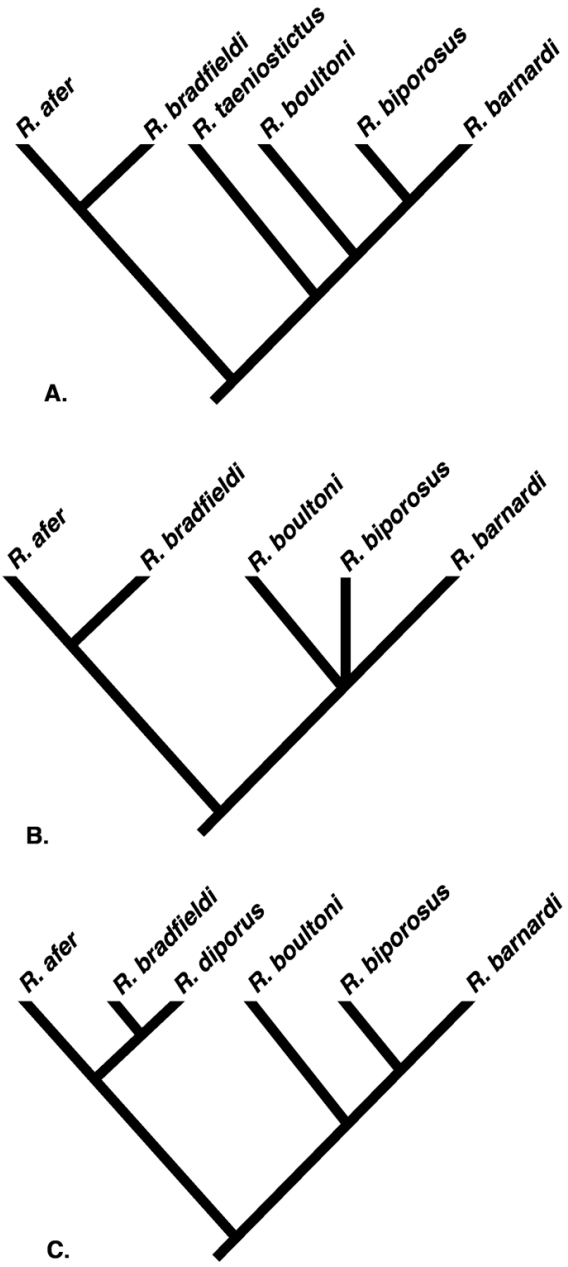


Fig. 10. Previous hypothesis for the phylogenetic relationships of *Rhoptropus* geckos. (A) Majority rule consensus of three equally parsimonious trees estimated using 16 morphological characters; topology displayed also corresponds to the majority rul consensus of three trees estimated using morphological and allozymic (B) characters. *R. diporus*, *R. b. montanus*, and *R. b. benguellensis* were not included in this analyses. (B) Strict consensus of two trees estimated using six allozymic characters; *R. diporus*, *R. b. montanus*, *R. b. benguellensis* and *R. taeniostictus* were not included in these analyses (Bauer & Good 1996). (C) Single most-parsimonious tree estimated using cytochrome b and 16S mitochondrial loci both individually and concatenated (Lamb & Bauer 2001). *R. b benguellensis*, *R. b montanus* and *R. taenioustictus* were not included in these analyses.

Table 1. List of type specimen information for previously described *Rhoptropus* species and subspecies. Coordinates are represented in Figures 10-12 as stars. Asterisks indicate uncertainty regarding the precise origin of the type; for these records, coordinates have been approximated as accurately as possible using the locality string provided in the original species description.

Species	Museum ID	Type	Locality	Latitude	Longitude	Reference
Rhoptropus afer	ZMB 6149A	lectotype	Damaraland, Namibia*	-20.369189	14.014363	Peters, 1869
Rhoptropus braconnieri	MHNP 294 (1411B)	holotype	S Ngami Lake, Bechuanaland, Botswana*	-20.502236	22.791307	Thominot, 1878
Rhoptropus barnardi	SAM 16639	syntype	Eriksson's Drift (Vau do Coloeque), Kunene River Region, Angola	-17.26944	14.525	Hewitt 1926
Rhoptropus boultoni benguellensis	SMF 25275	holotype	Cubal, Benguella Province, Angola*	-13.033858	14.206055	Mertens, 1938
Rhoptropus boultoni montanus	Museu Dundo 1854	holotype	Boca da Humpata, Huila Province, Angola	-15.066711	13.247912	Laurent 1964
Rhoptropus boultoni boultoni	FMNH 5634	holotype	Pico Azevedo, Namibe Province, Angola	-15.534	12.49197222	Schmidt 1933
Rhoptrpous biporosus	TM 24198	holotype	Orupembe, ~120 m W Ohopoho, Kaokoveld Region, Namibia	-18.160093	12.562074	FitSimons, 1957
Rhoptropus taeniostictus	Museu Dundo 1967	holotype	km 60 on rd from Mossamedes to Sá da Bandeira (Lubango), Mossamedes district, Angola	-15.036446	12.653005	Laurent 1964
Rhoptropus diporus	TM 28238	holotype	Farm Twyfelfontein, Namibia	-20.616669	14.333335	Haacke, 1965
Rhoptropus bradfieldi	PEM R15874-75	syntypes	Messum River, Erongo Region, Namibia*	-21.390538	13.917725	Hewitt, 1935

C. Angola

1. Current conditions

a. Geography

The majority of the country is comprised of a high plateau, reaching elevations of 1000-2000 meters, the central portion of which consists of forest terrain. Several distinct highlands associated with this plateau are of biological importance –The Angolan Escarpment (Figure 5). These areas are known to harbor extreme plant and avian diversity, but have been poorly surveyed for other vertebrate taxa. At the western border of this plateau, there is a sharply contrasting drop into rolling hills and scattered mountain highlands, and a final leveling off at 0 m elevation along semi-desert Atlantic coastal plane 50 km inland near Benguela to 200 km inland near Luanda to the oceanic border which extends into Namibia (Pickford et al. 1992; Klopper et al. 2009; Mills 2010). In the east, rocky, tropical habitat transitions into Kalahari Desert sands via a more gradual elevational drop-off. A number of prominent rivers can be found in Angola, contrasting the intermittent majority of water bodies in Namibia. Several Congo Basin Tributaries as well as the Zambezi River flow through Angola through its northern and eastern borders. The Kwanza River drains the central portion of Angola, the Congo River drains the northern section, and the Kunene River drains the southwest into the Atlandtic Ocean, while the east drains to the Etosha Pan of Namibia, the Okavango Swamps of Botswana, and the Zambezi. A substantial number of intermittent rivers exist as well, and tend to drain various portions of Western Escarpment regions during the rainy season (Figure 5).

b. Climate

Angolan climate is classified as tropical with a discrete dry season and can be further subdivided into three main zones: The arid coast, the sub-tropical plateau, and the tropical north. The cool arid climate of the coastal plane south of Benguela into Namibia is attributed to the cold, northward flowing Benguela Uplift System (BUS). Arid to semi-arid conditions persists along this narrow strip of coastal plain up to Luanda in the north (~2–35 cm annual rainfall, see Figure 11). As this lowland region sharply transitions into the west central highlands, the rainy season becomes longer and more consistent, which is evidenced by the denser green vegetation of this zone. These mountains also serve to shield the inland plateau from the aridifying effect of the BUS. As a result, the plateau receives consistent precipitation (~80–160 cm annually) and a moderate rainy season with creating an overall flat savannah biome. Further still to the east this plateau slopes into the Congo and Zambezi basins, returning to arid conditions near the Kalahari. Temperatures become more tropical closer to the equator, reaching averages of about 20-5^{o}C n the north, and 10–15^{o}C in the south-central region, however the weather on the coast is unpredictable and can spike when winds pass over from the interior (see Figure 3).

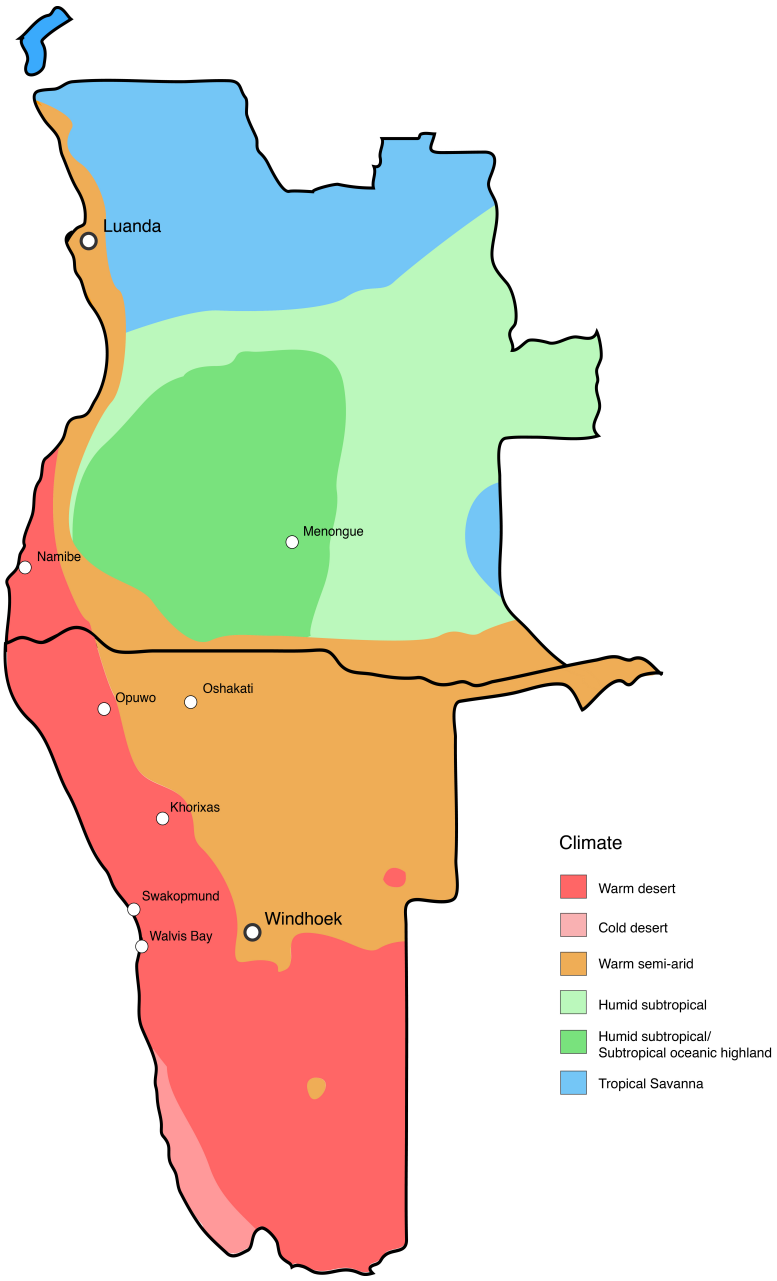


Figure 11. Climatic classification for Namibia and Angola. Estimates are based on annual and monthly averages of temperature and precipitation (McKnight 2000).

c. Landscape

In the north, the vegetation is dominated by tropical evergreen and semi-deciduous rainforest, transitioning centrally to miombo woodland and afromontane forest-grassland

mosaics. Towards the eastern extent the high plateau forest is replaced by Kalahari Highveld shrublands and Nama-Karoo semi-desert in the south. Extending north from Namibia, the true Namib portion of Angola is contained in the far southwest with arid sandy coastland environment up through Benguela (Huntley and Matos 1994; Dean 2001; Dombo et al. 2002). The Great Escarpment spans the African Plateau beginning in northwestern Angola passing through Namibia in the south into South Africa and east and north-east through South Africa, Lesotho and Swaziland into eastern Zimbabwe and adjacent Mozambique (Figure 5). Within Angola, the Escarpment region is approximately 1,000 km long but harbors a wide variety of habitat types. The substrate of this region is highly variable in comparison to neighboring countries, which in concert with climatic variation may be responsible in part for the unique fauna of the region.

d. Biodiversity

Biodiversity assessments of Angola have been relatively limited due to an intense liberation war (1961–1975) and followed by civil war spanning the time of independence in 1975 until 2002. The majority of the available data on Angola biodiversity dates back to the second half of the nineteenth century and first half of the twentieth century. Only recently has political stability augmented enough to allow for preliminary biodiversity surveys into poorly explored and assessed regions. The Angolan Escarpment harbors known endemic hotspots for avian, fish and floral diversity, however the region has not been formally documented as a biodiversity hotspot due to lack of sufficient documentation and considerable gaps regarding specific taxa (Myers 2000, Figueiredo et al. 2009, Darwall et al. 2009 Clark et al. 2011). At present, frog and reptile endemism

appear pronounced but detailed exploration of the diversity and species richness of these groups in the Escarpment region is still underway (see Ceríaco et al. 2016). In comparison to other Escarpment regions, the Angolan portions harbor the highest endemic biodiversity second only to South Africa. More specifically, one of the most poorly studied but critical portions of the country's Escarpment regions, the Bie´ Plateau, has the steepest moisture gradients and most extreme elevational isolates of all the Western Escarpment sections (Huntley & Matos 1994, Dean 2001, Dombo et al. 2002). Where the arid coastal plane and the high plateau meet, the Bie plateau serves as a climatic buffer with unique plant diversity in comparison to other nearby endemism zones (Hall 1960, Pickford et al. 1992, Dean 2001, Sekercioglu & Riley 2005, Klopper et al. 2009). Discretely specialized microhabitats can be found here such as the Escarpment woodlands, montane brushwood, and cloud forest, (Airy Shaw 1947, Olson & Dinerstein 1998, Van Zinderen Bakker 1962, White 1983, Meadows & Linder 1993, Dupont & Behling 2003). In addition to the Bie plateau, the Malanje Highlands, Huila Plateau and other potential high elevation isolates may reveal diversity on par with the centers of endemism documented in South Africa, Lesotho and Swaziland given additional biodiversity survey work and assessment due to the expansive terrain and unique climate diversity of these Escarpment sections (Van Wyk & Smith 2001, Figueiredo 2010, Clark et al. 2011)

II. Materials & methods

1. Taxon sampling

Extensive tissue collections for *Rhoptropus* are available in main herpetological museum and university collections (incl. CAS, MCZ, PEM). A few have been included in previous

molecular and morphological analyses (Bauer & Good 1996, Bauer & Lamb 2001, Lamb & Bauer 2001), but putatively new taxa, their close relatives, and Angolan material will require reexamination for accurate diagnosis. Two hundred and fifty two tissues were procured from the aforementioned institutions and collected in the field for all 7 recognized species and 2 described sublineages of *Rhoptropus* (Table 1, see Figures 12–14*)*. Although the northern and eastern extents for *Rhoptropus* are still unclear, collections specifically targeted the southwestern portion of Angola where the greatest density of Rhoptropus are known from historical collections (Figure 4) providing comprehensive geographical coverage throughout the confirmed distribution. To avoid overlooking cryptic species, sampling depth was increased within the *R. barnardi*, *R. biporosus* and *R. boultoni* groups where preliminary morphological data has indicated the potential for novel taxa. Following dissection in the field, tissues were preserved in 95% ethanol, and subsequently stored between 20 and 80^{o}C. Older tissues obtained from museum collections were preserved in 90–95% ethanol and soaked in water prior to DNA extraction. Multiple systematic studies have confirmed *Pachydactylus* geckos as sister to *Rhoptropus*, therefore representatives of this sister as well as other individuals from a Pachydactylus radiation (Pachydactylus, Chondrocdactylus) and closest sister groups (*Afroedura, Goggia*) from a South African gekkonid radiation were chosen as outgroup taxa for the purpose of rooting the phylogeny (Lamb & Bauer 2001, Bauer and Lamb, 2005, Gamble et al. 2012, Gamble et al. 2008, Gamble et al. 2015, Heinicke et al. 2016, in prep).

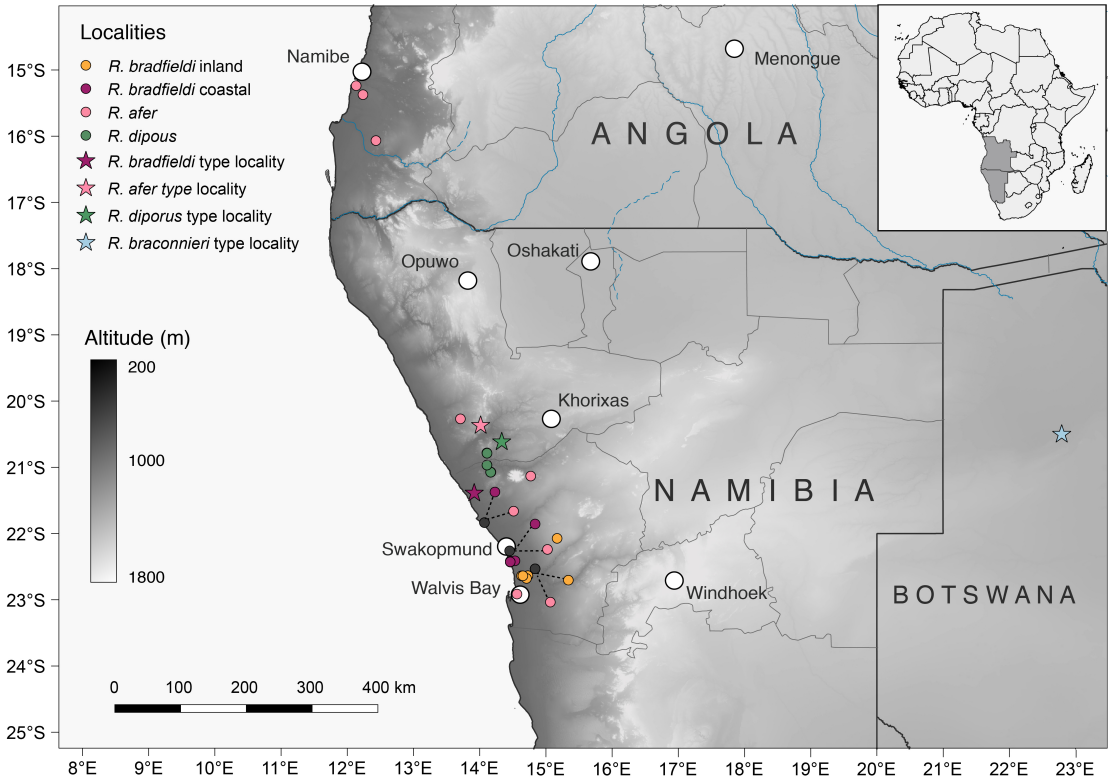


Figure 12. Map of west central Namibia and southwestern Angola showing the localities of specimens examined in the *afer* group and relevant landmarks. Genetically sampled *Rhoptropus* localities are indicated by closed circles, approximated type specimen localities are indicated by stars. City reference points are labeled and designated by white circles. Only samples included in this study have been plotted, however the map encompasses the entire range of *R. afer* (Kuiseb River to southwestern Angola), *R. diporus* (Brandberg and north to the Huab drainage), *R. bradfieldi* (Kuiseb River north at least as far as the Messum River), and the putative *R. braconnieri* (near Lake Ngami, Botswana).

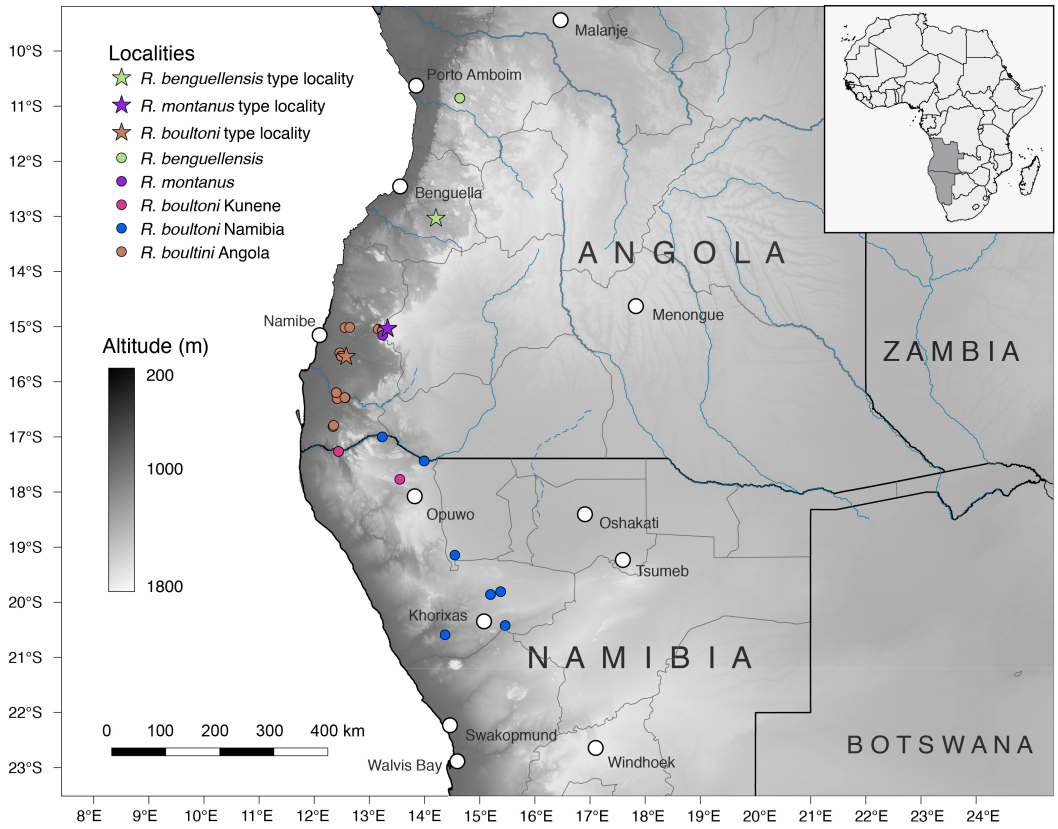


Figure 13-. Map of west central Namibia and southwestern Angola showing the localities of specimens examined within the *boultoni* group and relevant landmarks. Genetically sampled *Rhoptropus* localities are indicated by closed circles, approximated type specimen localities are indicated by stars. City reference points are labeled and designated by hollow circles. Only samples included in this study have been plotted, however the map encompasses the entire range of *R. boultoni* (southwestern parts of Angola through Damaraland in Namibia) *R. montanus* (Known only from the High Pass of the Leba Plateau, Huila Province), and the partial range of *R. benguellensis* (known from Benguella and Cuanza Sol Provinces, but may range as far northeast as Malanje).

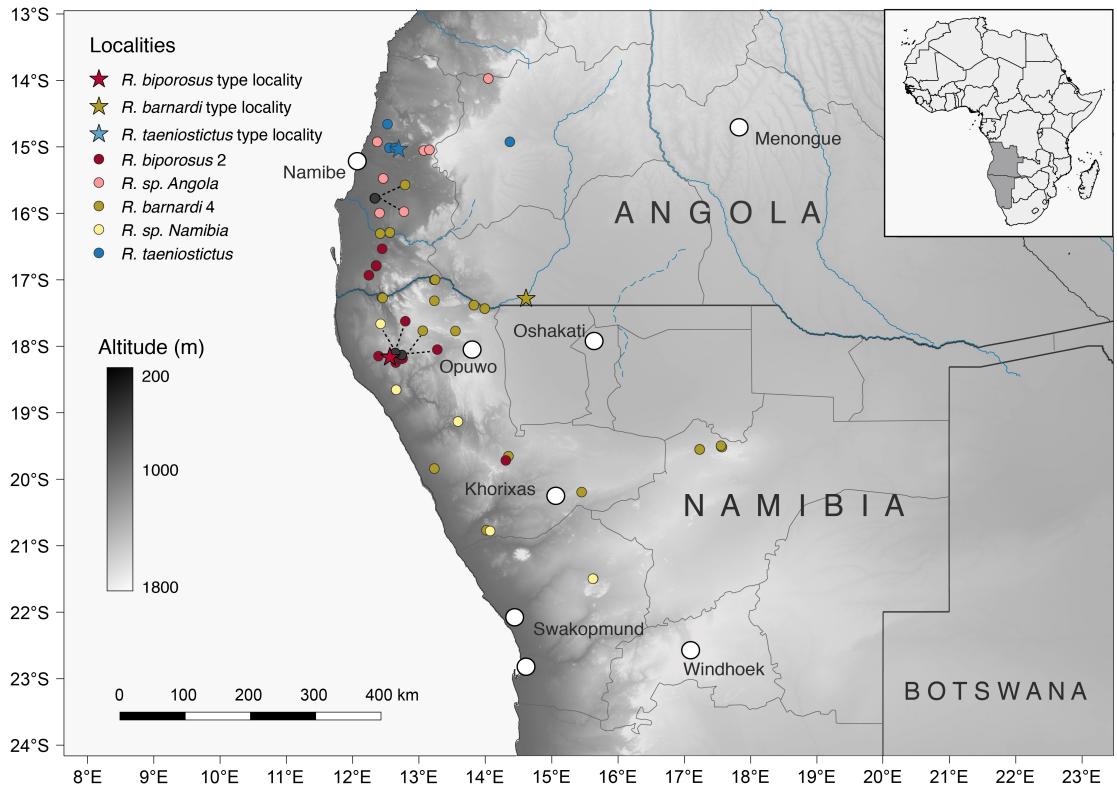


Figure 14. Map of west central Namibia and southwestern Angola showing the localities of specimens examined within the *barnardi/biporosus* group and relevant landmarks. Genetically sampled *Rhoptropus* localities are indicated by closed circles, approximated type specimen localities are indicated by stars. City reference points are labeled and designated by hollow circles. Only samples included in this study have been plotted, however the map encompasses the entire range of *R. barnardi* (southern extent near Solitaire, central Namibia to easternmost extent at the Otavi mountains to northern extent Novo Redono, Angola) *R. biporosus* (Kaokoveld region [Sesfontein] into adjacent southwestern Angola), and *R. taeniostictus* (Namibe Province only, low elevation).

2. DNA extraction, amplification and sequencing

For each individual, genomic DNA was extracted from ~2–5 mg of liver, toe or tail tip tissue using a using a Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA). Using this isolated genomic DNA, portions of one mitochondrial (mt) gene (ND2), and two nuclear (RAG1, MAP1A) were amplified for all individuals. New sets of genus-specific internal primers were designed from sequences obtained with universal primers using molecular data from two divergent lineages, *R. afer* and *R barnardi* using the Primer3 primer

design tool in Geneious v6.1 (see Table 2 for complete molecular locus information). All reactions were performed in 25 µl volumes and included the following: 9.82 µl dH20, 2.5 µl 10X Qiagen PCR Buffer, 2.5 µl 5X TaqMaster PCR enhancer, 2.5 µl of 2 mM dNTPs, 0.18 µl Taq polymerase (5 units/µl), 2.5 µl of template genomic DNA (at 12-50 ng/µl), and 2.5 µl of both forward and reverse 8 µM primer. PCR reactions were executed on an Eppendorf Mastercycler gradient thermocycler. PCR conditions varied for each gene, but typically amplification consisted of an initial denaturation step at 94^{o}C for 3–5 min, 35 cycles of extended denaturation at 94^{o}C for 30–45 seconds, annealing at 50–60^{o}C for 30–45 seconds, and extension at 72^{o}C for 30–60 seconds. Details of PCR amplification regimes and specific primer sequences are provided in Table 2. Prior to sequencing, amplified products were treated with Ampure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) to remove residual dNTPs and primer sequences.

Table 2. Mean ages (in Myr) and the corresponding 95% highest posterior density ranges (HPD) for major *Rhoptropus* lineages, obtained using nonparametric rate smoothing (node labels shown in Figure 24).

Name	Origin	Gene	Length (bps)	Primer Name	Sequence (5' to 3')	Reference
KIF24	nuclear, protein coding	*kinesin family member 24*	590	KIF24F1	5'-SAAACGTRTCTCCM AAACGCATCC-3'	Portik et al. (2012)
MAP-1A	nuclear, protein coding	*Microtubule Associated Protein 1A*		MAP-1APF1	5'-SAACAGYATMCCT TCCTCTCGRAC-3'	Jacobsen et al. (2014)
				MAP-1APR1	5'-CCTCTGGAAACCA CACTTTCTTCTCA-3'	Jacobsen et al. (2014)
				MAP-1ARhopF378	5'-GAGCCCTGACGAC AGCACCG-3'	This paper
				MAP-1ARhopR850	5'-CSTGCAAGTTCCTC CCACCC-3'	This paper
ND2	mitochondrial	*NADH dehydrogenase sub- unit 2*	1027	METF1 L4437	5'-AAGCTTTCGGGCCC ATAC-3'	Macey et al. (1997)
				ND2R102	5'-CAGCCTAGGTGGGC GATTG-3'	Greenbaum et al. (2007)
				CO1R1	5'-AGRGTGCCAATGTC TTTGTGRTT-3'	Macey et al. (1997)
				ND2RhopF450	5'-RCCGGMCTAAACC AGACACAAACRCG-3'	This paper

				ND2RhopR475	5’-TCGYGTTTGTGTCTGGTTTAGKCC-3’	This paper
				ND2RhopF32	5’-MGCCTGACTYGGMTAGAACTWAAYAC-3’	This paper
				ND2RhopR915	5’-YATGGTTGGTTTTTCAYTTKTGTTCA-3’	This paper
TrptRNA	mitochondrial	*tryptophan transfer RNA*	220	TRPR3 H5540	5’-TTTAGGGCTTTGAAGGC-3’	Macey et al. (1997)
RAG-1	nuclear, protein coding	*recombination activating gene 1*	1078	RAG-1F700	5'-GGAGACATGGACACAATCCATCCTAC-3'	Bauer et al. (2007)
				RAG-1R700	5'-TTTGTACTGAGATGGATCTTTTTGCA-3'	Bauer et al. (2007)
				RAG-1F396	5’-TCTGAATGGAAATTCAAGCTGTT-3’	Groth & Barrowclough (1999)
				RAG-1R397	5’-GATGCTGCCTCGGTCGGCCACCTTT-3’	Groth & Barrowclough (1999)
				RAG-1PF1	5’-YAWGAAATTTKCTGGAAATTCAAGCT-3’	Portik et al. (2013)
				RAG-1PR1	5’-GTCTYGGTCGGCCACCTTTGTT-3’	Portik et al. (2013)

Sequencing analyses were performed using a 3730 Capillary Electrophoresis Automated prism sequencer (Applied Biosystems Inc.) and the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). Sequenced gene products were either single set (1 forward, 1 reverse) or dual set (2 forward, 2 reverse) to ensure the quality of overlapping contigs and prevent false insertions and heterozygous base calls. All sequences will be deposited in GenBank (Supplemental 1. Additional sequence data for analytical purposed were obtained from GenBank and incorporated in ND2 and RAG-1 analyses (Acces. No. JX041431, JX041432, JX041430, JQ945336, JQ945337, EF534810).

3. Sequence alignment, partitioning and pairwise distances

Raw electropherograms of forward and reverse sequences were de novo assembled into contigs using Geneious v8.1 and manually inspected for sequencing error and read quality. Edited contigs were aligned and manually edited to account for codon deletions and sequencing error. Resulting chromatograms were translated to check for premature stop codons using MacClade v4.08 (Maddison & Maddison, 2005). Initial Geneious alignments with free end gaps were performed with Geneious v8.1 (Drummond et al., 2012). All nuclear genes were be scanned for potential heterozygous individuals. Alignments were further compared to pre-existing datasets (Gamble et al. 2016), and translated to check for substitutions leading to stop codons or frameshifts using Geneious v8.1 (Maddison &

Maddison 2000).

The best models of sequence evolution for the mitochondrial and nuclear datasets were determined using PartitionFinder v1.1.1 with penalization imparted for the number of parameters used in each model (Lanfear et al. 2012). The 'ALL' PartitionFinder model used was used, meaning that all parameterization schemes specifically employed for different downstream analyses, such as BEAST or RAxML were explored. Because certain tree estimation programs can apply only a limited number of sequence evolution models, partition finder was run an additional time under the 'RAxML' setting, which allows for only two possible models: GTR+G and GTR+I+G. The Bayesian Information Criterion (BIC) was used for model selection and the comparison of different partition schemes, branch lengths were linked, and the greedy heuristic search algorithm was selected to search for the best partition scheme. Sets of sites were defined by the partition scheme or data blocks grouped by gene and by codon for the RAG1, ND2 and MAP1A concatenated mitochondrial and nuclear datasets. PartitionFinder results suggested the data should be divided into six partitions employing three distinct models: The GTR+I+ Γ model for ND2 position 1, ND2 position 2, and ND2 position 3; the GTR+ Γ model for ND2 tRNAs and MAP1A position 3, and the HKY+I+ Γ model for RAG1 positions 1 + 2 + 3 and MAP1A positions 1 + 2. Under the RAxML settings, the following partitions were recovered: The GTR+I+ Γ model for ND2 position 1, ND2 position 2, and ND2 position 3; the GTR+ Γ model for ND2 tRNAs and MAP1A position 3, and the GTR+I+ Γ model for ND2 position 1, ND2 position 2, RAG1 positions 1 + 2 + 3 and MAP1A

positions 1 + 2. The GTR+ Γ model was the best fit for ND2 position3, ND2 tRNAs, and MAP1A position 3 (summary in Table 3).

Table 3. Characteristics of the six sequence data partitions estimated by PartitionFinder. Ambiguously aligned positions were removed from all analyses and are not included in these calculations. Calculations were performed on the ML and BI data alignment which includes only focal ingroup taxa and immediate outgroups.

Partition	Model	Genes (Codons)	Base Pairs
1	HKY+I+G	RAG pos1, RAG1 pos2, RAG1 pos3	1-1068\3, 2-1068\3, 3-1068\3
2	GTR+I+G	ND2 pos1	1069-2008\3
3	GTR+I+G	ND2 pos2	1070-2008\3
4	GTR+I+G	ND2 pos3	1071-2008\3
	GTR+G	tRNA	
5	HKY+I+G	MAP1A pos1, MAP1APpos2	2009-3551\3, 2010-3551\3
6	GTR+G	MAP1Apos3	2011-3551\3
		Scheme lnL:	-22381.66429
		Scheme BIC:	47630.3738
		Number of params:	877
		Number of sites:	3551

Theoretically, the HKY designation refers to the nucleotide substitution model outlined by Hasegawa-Kishino-Yano 1985 (HKY85). This model allows for differences in substitution rates for transitions and transversions (2 parameters, in essence, the Kimura 2-parameter 1980 model [K80]) while allowing for differences in nucleotide frequencies (4 parameters, in essence the Felsenstein 1981 model [F81]). This model is relatively simplified in comparison to the General Time Reversable nucleotide substitution model (GTR, Lanave et al. 1984, Tavare 1986, Rodriguez et al. 1990), the most general, neutral, independent, finite sites, time reversible model for nucleotide substitution. This model takes into account the frequency of each base at each site as well as the frequency of each replacement resulting in six total substitution rate parameters, calculated from the

probability of four possible basepairs plus four base frequency parameters (again, the F81 model). The aforementioned models describe rates of nucleotide substitutions, however other models exist which explain rate variation among sites across a sequence: the gamma distribution (designated '+G') and the proportion of invariant sites (designated 'I'). When a gamma distribution incorporated, all DNA sites will be modeled under a distribution defined by a scale parameter and a shaping parameter. This distribution covers a wide scale of possible rates that are binned accordingly and estimated rates can be drawn varying distributional shapes depending on the shape parapmeter (e.g. exponential, uniform). The "I" designation accounts for sites that do no change, this parameter allows for a more flexible gamma distribution. This estimation accounts for known invariant sites to be excluded from gamma calculations, so only variable sites are considered.

Distance based methods assume knowledge of the true evolutionary distances between a pair of taxa, defined as the average number of substitutions per site in a DNA sequence. When computing these values, the distance between any two taxa is the sum of the lengths (Evolutionary distances) of all the branches on the path between those two taxa. These distances can then be used to infer the true phylogeny. Pair-wise distances are a class of distance-based methods that measure the degree of difference between two tips on an evolutionary tree (the proportion of charactesr for which two taxa have a polymorphic character state). The limitation of this method is that it is too general —
pair-wise distances accumulate more slowly than true evolutionary distances, as silent mutations will cause discrepancy between observed and actual sequence divergence. Although distance based methods for phylogenetic inference may not be an advantageous

approach, pair-wise distance calculations can be useful in quantifying the amount of genetic differentiation between known independent lineages. When examining closely related cryptic species, knowledge of true species distances can be a useful line of evidence for independent evolutionary trajectories. Although these distances as well as formal morphological and ecological evidence have already been examined for a number of *Rhoptropus* species (Bauer, Russell & Powell 1996, Lamb & Bauer 2001, Bauer & Lamb 2010), the genetic distinctiveness of Angolan taxa and the instraspecific variation that exists for this group has not yet been determined. Estimates of evolutionary divergence between species were conducted in MEGA7 (Kumar et al. 2015). Corrected analyses were conducted using the General Time Reversable model (Lanave et al. 1984, Tavare 1986, Rodriguez et al. 1990) across all mitochondrial ND2 sequences, and again separately for all RAG1 sequences. Codon positions considered were $1^{st}+2^{nd}+3^{rd}$+Noncoding. All positions containing gaps or missing data were excluded. For comparative purposes, uncorrected pairwise distances were also calculated. A total of 1009 positions were evaluated in the final ND2 dataset, and a total of 1058 positions were included in the final RAG1 dataset. Mean distances and ranges were calculated within species groups for evaluation of genetic distinctiveness of putatively new taxa (Figures 14 & 15).

4. Maximum Likelihood

Whereas character based estimations (e.g., parsimony, Fitch 1971, Swofford 1993, Swofford 1996) assume equivalent character state changes along both long and short branches, likelihood and distance methods consider such a change to be more probable

along longer branches (Hillis et al. 1996). Since outgroup taxa or deeply divergent lineages often have long branches, parsimony analyses may provide an incorrect topology (Siddall &Whiting 1999). Additionally, longer periods of evolutionary time subject such datasets to increased mitochondrial saturation. This is more problematic in deep-time divergences, however, and less relevant when considering recent speciation events. Model based methods do not suffer from long-branch attraction (LBA) so long as the model fits the data relatively well (Felsenstein 1978). Likelihood represents a quantity that is proportional to the probability of the data given specific values for all parameters in the model. Maximum likelihood, in particular, searches for the tree topology that is most likely given the data and model assigned a priori (Edwards 1972). This algorithm searches for the tree that has the highest probability of giving rise to the observed data. The likelihood is the probability that the data would be observed under a hypothesis. In phylogenetic inference, the hypotheses are all of the possible trees. The aim is to determine the probability of the data arising under each tree, and that the tree with the highest likelihood is the best estimate of the true tree, and a model of DNA sequence evolution must be specified. Models are selected rather than assumed based on the site-to-site variation, composition, and rate matrix of the given data (Palumbi 1989). Models differ in their free parameters, and the more free parameters implemented without over-constraining the data, the better the model will be able to model evolutionary events and fit the data (Felsenstein 1981). For this method, a particular tree, parameters and branch lengths are set, and the likelihood of each character is determined by summing over all possible combinations for that site. The log-likelihoods of each of these sites are multiplied to get an overall likelihood value for that particular tree. After this, the iteration

will optimize branch lengths and parameters again. This process is repeated performed over all possible trees.

In summary, there are several advantages to using likelihood methods: (1) branch lengths and different tree topologies are taken into account (2) robust to many violations of the assumptions in the evolutionary model (3) data can be fit to desired evolutionary model and molecular clock theories (4) all sequence data, including distantly related sequences, can be utilized in an efficient and powerful way (Felsenstein 2004). For large data sets, however, a single heuristic search can be incredibly time consuming for a modern computer to complete, yielding only a representative point estimate of an entire phylogeny (Stewart et al. 2001, Holder & Lewis 2003). To quantify nodal support, Maximum Likelihood nonparametric bootstrapping – a measure of accuracy for estimated relationships – can be used. Despite the complexity and high computational cost of ML, significant progress has been achieved with the onset of fast and accurate programs such as PHYML (Guindon and Gascuel, 2003), GARLI (Zwickl, 2006) and RAxML (Stamatakis et al., 2005). All Maximum Likelihood estimations were implemented in RAxML v8.2.4 with 1000 nonparametric bootsrap replicates (Stamatakis 2014). Because all ML programs implement the same mathematical function, likelihood scores should be comparable amongst runs performed under the same sets of parameters for equivalent datasets. For this reason, likelihood scores, topoplogies, and branch lengths of runs executed under varying parameter or sequence datasets were compared between trees.

5. Bayesian Inference

An alternative method for estimating branch lengths and tree topologies using a model-based approach is Bayesian Inference. This method combines the prior probability of a phylogeny with the tree likelihood to produce a posterior probability distribution on hypothesized realtionships (Huelsenbeck et al. 2001). Overall topology and branch support for Bayesian analysis are expressed as posterior probabilities, (Karol et al. 2001, Lutzoni et al. 2001, Murphy et al. 2001), approximated by Markov chain Monte Carlo (MCMC) algorithms, sampling technique where at each step a new set of parameters is simulated and the likelihood ratio and prior ratio is calculated relative to the current state. If the product is better the parameters are accepted and a next step is proposed. The stationary distribution of this sampling is the desired posterior distribution, computed using the likelihood and the priors to infer the phylogeny, and expressed as a consensus tree (Yang & Rannala 1997). A set of samples from the beginning of MCMC in Bayesian inference prior to chain stability can be allocated as 'burn in'. This is the parameter space explored before a chain has found a region with high posterior probability and is essentially sampling in less probable tree space. These suboptimal states are usually discarded from further analysis. In a reasonable computational time, Bayesian analysis of sequence data is able to infer phylogenetic topology and estimate node uncertainty directly as substitutional models, branch lengths, and topological variables (Huelsenbeck et al. 2001, Holder & Lewis 2003). It has been argued that this evaluative method proves more time effective than Likelihood-based approaches, however in this era of increasing computational resources, the difference between these methods is negligible for sub-genomic datasets (Heled & Drummond 2010, Huelsenbeck et al. 2002, Huelsenbeck et al. 2001, Huelsenbeck & Rosenquist 2001). Discrepancies frequently exist between

nonparametric bootstrap support values and Bayesian posterior probabilities, which may lead to strongly conflicting interpretive results (Huelsenbeck et al. 2002). More recently, phylogenetic studies have been published relying solely on Bayesian analyses, and a number of crucial species delimitation, biogeographic, diversification, and phylogeographic programs implementing BI methods are available (Arkhipova & Morrison 2001, Henze et al. 2001, Lutzoni et al. 2001; e.g. BP&B, Yang & Rannala 2010, BioGeoBEARS, Matzke 2013, BAMM, Rabosky et al. 2013, IMa, Hey et al. 2012). Although certain simulations predict Bayesian support values to be closer estimates of the true probabilities of recovering clades, (Wilcox et al. 2002) other cases recovered high support values for conflicting hypotheses (Buckley et al. 2002, Douady et al. 2002). Although small model misspecification may largely impact the accuracy of this approach, Bayesian inference still offers an efficient method of estimating substitution model parameters, branch lengths, and topology under complex evolutionary change (Huelsenbeck et al. 2001, Huelsenbeck 2002, Heled & Drummond 2010).

Bayesian methods produce a posterior probability distribution, which intrinsically has credibility intervals. This is produced through an application of Bayes theorem, which essentially applies a likelihood function to a prior distribution (constructed from a priori knowledge). The prior distribution is shaped by the likelihood function to produce a distribution proportional to the posterior distribution (by a factor of the marginal distribution). Since this is computationally intractable for most phylogenetic problems, the posterior distribution is typically estimated through sampling methods such as Markov chain Monte Carlo (MCMC) simulations. Specifically, MCMC simulations produce

multiple runs through a Markov chain process in order to search parameter space for convergence to the posterior distribution (Lemey et al. 2009, Huelsenbeck et al. 2002, Huelsenbeck and Ronquist 2001, Nylander et al. 2004). Since this process is centered on probability density functions, the representation of the data in distribution form naturally allows for uncertainty intervals, represented by credibility intervals.

Maximum likelihood (ML) methods produce a point estimate (i.e. best tree) as a result of evaluating trees using a probability function (i.e. inferring the likelihood, or the chances, of the data fitting the tree). Since there is naturally an unknown error distribution, the uncertainty of the ML tree can be expressed through support measures, particularly resampling methods such as bootstrapping or jackknifing. Generally speaking, these methods randomly reorder the data multiple times and test for fit of the tree with the randomly generated data. Furthermore, although a most optimal tree is inferred, there are still likelihood values for suboptimal trees. These ML values can be used to create credible sets of tree topologies or for model selection tests, which arguably is a form of expressing uncertainty; these methods of expressing uncertainty however are not specific to ML trees as these are also used for Bayesian inferred trees (Lemey et al., 2009).

Given the potential for discrepancies between the quantification of phylogenetic uncertainty between Bayesian and Likelihood estimation, both methods were used for phylogentic tree estimation. The BI analysis was implemented in BEAST 1.8.2 (Drummond et al. 2012) using a Yule tree prior and uncorrelated lognormal relaxed clock. Four replicate analyses were run for 100 million generations sampled every 10000 generations. Burn in was set at a conservative 25% (the first 2500 generations), resulting

in 7500 total trees. Effective sample sizes were estimated in Tracer 1.5 (>300 for all parameters in each run) to confirm adequate chain length and mixing. Convergence was assessed using Gelman & Rubin's r statistic (Gelman et al. 1995). Independent runs were conducted to ensure parameters estimates were not the result of the algorithm being stuck on local optima. Adequate convergence was confirmed by a standard deviation of split frequencies between chains was <0.01 with r values approach values of 1.0 for all parameters.

7. Concatenation vs. species tree estimations

Even when a gene phylogeny is correctly inferred from input sequence data, the phylogeny itself may be misleading when trying to elucidate true evolutionary relationships between taxa. Evolutionary phenomenon such as paralogy, hybridization, introgression, and incomplete lineage sorting may influence the gene's individual evolutionary history, thus correspondence between the gene phylogeny and the hypothetical phylogeny of the entire genome does not always persist (Brower et al.1996, Page & Charleston 1997, Cao et al. 1998, Pollard et al. 2006). In comparison to nuclear genes, mitochondrial genes have relatively fast evolutionary rates. For this reason, utilizing only mitochondrial gene sequence to infer a phylogeny may exacerbate the impact of long branches, incomplete lineage sorting, selection, and introgression for a particular node, leading to an incorrect phylogeny for the species (Fisher-Reid & Wiens 2011).

In attempt to partially resolve these issues, concatenation and coalescent approaches have

been developed as alternatives to single or limited gene analyses. When overall agreement in topology is found between multiple nuclear and mitochondrial gene trees, the input sequence data for these separate trees can be combined and analyzed as a single large "gene" with partitions allowing for separate models of nucleotide substitution per locus. Simulations have shown that this concatenation approach can yield more accurate trees in comparison to consensus tree methods ML and BI analyses by increasing the number of informative sites (Gadagkar et al. 2005). This is advantageous because it allows for the inclusion of taxa and genes from various prior studies in combination with new data to potentially reveal novel relationships and mechanisms that would not be separately traceable. Increasing the genetic sampling also provides better resolution and support for difficult relationships, in instances such as polytomies, incorrect paraphyly, and weakly supported branches may have resulted—

either from speciation events such as rapid radiations or from evalution of poorly informative genes (Pollard et al. 2006, Peters et al. 2007, Graybeal 1998, Zwickl & Hillis 2002). It has been observed that increased sampling of loci may also augment the quantity of missing data in an alignment. Missing data has been shown to yield inaccurate estimations of node support, branch lengths, and tree topology (Lemmon et al. 2009). However, many empirical studies have also shown that within a certain threshold, this may not always be the case (Weins et al. 2008, Weins & Morrill 2011 Roure & Baurain 2013).

The caveat of concatenation methods is the incompatibility of independent gene histories in the estimation of a single consensus tree. Although mutation rates and models of

sequence evolution are allowed to vary, the resulting topology does not necessarily reflect potential gene discordance, but rather the signal of more informative loci. This can be particularly problematic when the selection of loci is biased (limited), and evolutionary forces such as selection have produced an alternative evolutionary trajectory. Simulation studies have shown that inferring species-level relationships from concatenated gene trees are often misleading due to the difficulties of assessing multiple possible evolutionary scenarios that could be used to fit any given tree (Degnan & Rosenberg 2006). Coalescent-based approaches emphasize evolutionary history at the level of species, which may differ form the genealogical pathway of individuals or gene trees (Maddison 1997). Such Species-tree methods have been proven to provide relatively comprehensive phylogenies, uncovering relationships and modes of evolution that would otherwise not be available through gene-tree methods (Waters et al. 2009, Drummond and Rambaut 2007). Accurate reconstruction of evolutionary relationships using species-tree methods may be impeded via several demographic and mutational processes. One demographic process is incomplete lineages sorting (ILS): when independent alleles fail to coalesce into a single ancestral copy at a deeper time than species coalesce. Large historical populations sizes increase the genetic variation in a population, making it more difficult for genes to sort into their respective independent lineages. Similarly, short timing between coalescent events leaves little time for genes to sort, making ILS more common in both of these scenarios. Species trees may also be confounded by introgression and hybridization, resulting in a greater estimation of population sizes and branching times due to the greater than expected degree of variation in the demographic samples, which is interpreted as resulting lack of lineages sorting. With hybridization, inference may predict that two

species are non-independant when in fact they are, but genetic material has been recently exchanged in the past or is still being exchanged amonst a limited number of individuals in the population (Edwards, 2008).

Mutational processes that may impede the inference of species trees are gene duplication or insertions and deletions. Species trees may be inaccurate if duplication of genomic regions and subsequent extinction of various copies has occurred. In such instances, it will be unclear if copies being compared are, in fact, homologs. In reality, the two genetic copies may follow different trajectories where one eventually becomes extinct and the other continues, but in the individuals for which they are sampled, different stochastic pathways will produce differential variation in each, such that the gene copies are orthologous and not paralogs. Therefore, the species tree and the gene tree in such a circumstance will not agree. Long branch heterogeneity may cause issues with species tree inference, as mutations will accumulate in divergent lineages at a greater rate than they will accumulate in less divergent lineages, thus such lineages may seem more similar than by random chance, when in reality such insertions and deletions may impede species inference as well, as they prevent homologous comparisons to different genetic regions, and can result in frame shift mutations. As a result, such regions may be under selective pressures, violating the assumptions of species tree inference, that all variation is the result of genetic drift (neutrally evolved).

Despite the limitations of concatenation methods, phylogenies based on gene-tree toplogy are still published (e.g., Smid et al. 2015, Brennan et al. 2016, Medina et al. 2016, Skipwith et al. 2016, Welton et al. 2016). Concatenation methods are still widely used

given accurate quantities of genetic information and lack of conflict between loci (paper examples). When larger, sub genomic quantities of data are made available, studies are often published with concatenation methods regardless of individual gene tree conflict, although this could cause inaccurate estimation of coalescent parameters such as historical population size and branch length. In the absence of confounding evolutionary processes, studies have shown that at least 10 loci are required to approach the true species tree toplogy, and 25-50 or more loci are required to estimate accurate species tree topologies, (Ruane et al. 2015). However, other published works have also found close agreement between genomic and subgenomic dataset phylogenies estimated under concatenated and coalescent methods and mitochondrial phylogenies (e.g. Leache et al. 2015).

In addition to the assumptions of the analytical method, both concatenation and species tree methods assume a priori that input sequence data and alignments are both correct, that homology has been determined, and that phylogenetically relevant similarity exists between the sequences. Common instances of introduced human error, missing data, and the absence of critical lineages can greatly alter final results. A probable solution to this problem is to increase sampling of taxa and loci (Weins 2005). By increasing the number of genes examined, a greater number of informative characters can be incorporated into final phylogenentic results, and decrease the possibility of gene tree and species tree incongruence (Degnan & Rosenberg 2006, Maddison & Knowles 2006).

Given the coalescent assumptions that are violated by mitochondrial data, the ND2 data should not theoretically be included in any species tree analyses. The exclusion of this

dataset, however, would result in only two nuclear loci used in estimating phylogenetic relationships. This dataset would be inadequate to inform unbiased coalescent analyses. To account for the potential variation between nuclear and mitochondrial data, independent trees generated from single loci were run and compared prior to concatentation. For the ML and BI analyses, tree estimates were generated for all independent loci and for a concatenated dataset. Partitions for this dataset were based on PartitionFinder results and parsed by gene and codon into the following for the concatenated datasets: ND2 position 1, ND2 position 2, ND2 position 3, ND2 tRNAs, RAG 1 positions 1+2+3, and MAP1A positions 1+2 and MAP1A position 3. For independent datasets, the same codon partitions and models (see 3) were used.

8. Niche modeling

a. Approaches

With increasing availability and depth of global environmental data (WorldClim) geography, climate, geology, and locality information can be used through Geographic Information Systems (GIS) to construct a spatial model of distribution given a set of sample occurrences and their respective environmental values (Rotenberry et al. 2006). Requirements of such analyses include: some knowledge of habitat requirements, data on species occurences in geographic space, maps of environmental variables for remote sensing, a model to link these habitat requirements to the environmental variables, a resulting map of predicted species occurences and habitat requirements, and statistical data to validate these predictions (Peterson 2001).

As seen in most satellite images and scanned maps, geographic information can be stored as continuous fields – measurements across an area that are continuous but also vary substantially within that field. This information can be contained in grids with fixed resolution where each cell in the grid contains a unique value, such as soil type, altitude, and precipitation. The advantage of representing the data this way is the inclusion of indistinct boundaries, satellite information, and aerial surveys all use raster-based scanners, thus allowing for ease of transfer and availability of geographic information. Using spatial interpolation, it is possible to determine the climatic and geographic data for unsampled areas between sampled localities to create a continuous field of useable raster data. This information has a wide variety of applications with respect to understanding the climatic and geographic variables which are currently, have historically, or potentially may influence biotic distributions (Peterson 2001, Kozac et al. 2008, Losos et al. 2008). This can be done by obtaining current distributional data and modeling this information back onto environmental layers in true geographic space using Geographic Information Systems (ArcGIS v10.0) and other empirical modeling software (i.e., GARP, Stockwell & Peters 1999, MAXENT, Phillips et al. 2006).

In addition to phylogenetic distinction, the level of differentiation in niche between genetically distinct groups may provide additional lines of evidence for the evolution of independent lineages, especially when obvious morphological differentiation is absent (Losos et al. 2008). Ecological niche models (ENM) can be an important tool in understanding these patterns of biodiversity by assessing niche overlap between

popualtions or determining environmental tolerance differences between putative sister taxa, which may indicate a potential avenue for reproductive isolation (Carstens & Richards 2007, Warren et al. 2008, Myers et al. 2013).

In this study, all analyses and comparisons were performed using contemporary climatic variables interpolated at 30 second arc resolution (WorldClim, Hijmans et al. 2005, Table 8. These bioclimatic variables were augmented with categorical information for Angola and Namibia regarding land cover (0.5 km scale, Broxton et al. 2014, Figure 5), soil type diversity (0.5 km scale, Atlas of Namibia Project, 2002, Figure 15), and annual maximum green vegetation fraction (30 arc second resolution, Broxton et al. 2014, Table 4). Occurrence points used in this analysis were derived from confirmed-identity samples used in this study and morphologically determined museum specimens from Ceríaco et al. 2016. Analytical models and approaches employed are described below.

Table 4. Bioclimatic and physical geographic variables used in ecological niche modeling (Figure 7) derived from continuous monthly temperature and rainfall values for representative seasonality, annual trends, and potentially limiting environmental factors (WorldClim) as well as categorical land cover (Broxton 2014a) and soil type (Atlas of Namibia, 2002).

ID	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter
BIO20	land cover type, colleceted from 2001–2010 at 0.5 km scale
BIO21	soil type, covering the highest percentage of each mapping unit surveyed at 0.5 km scale
BIO22	annual maximum green vegetation fraction collected from 2001–2012 at 30 arc second resolution

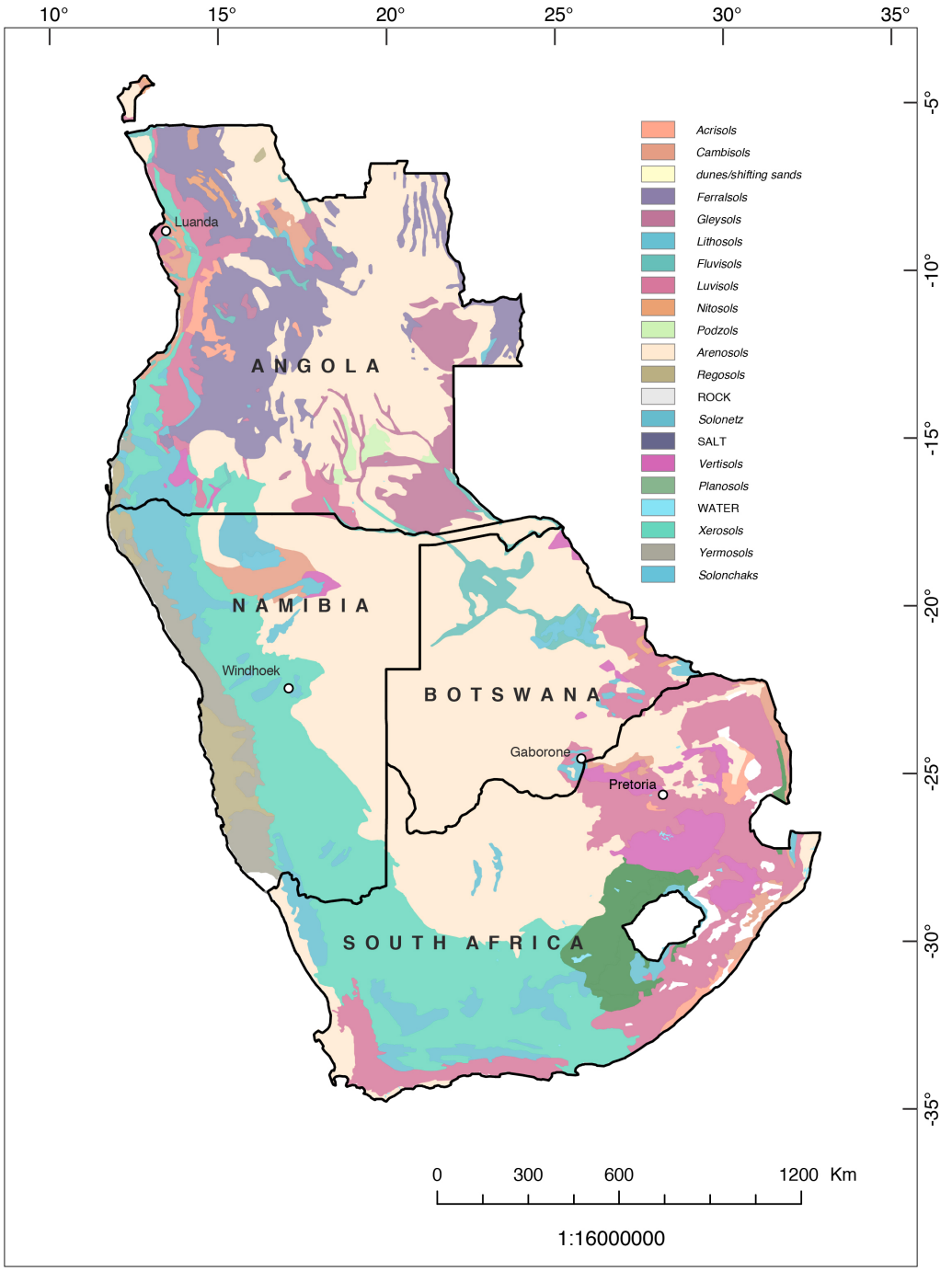


Figure 15. Digital soil map for Namibia, Angola, Botswana and South Africa. Relevant landmarks are indicated by white circles.

b. Analytical models

GIS data can be used to understand species distributions to predict the occurrence of species for locations where survey data is lacking. This is useful for a variety of applications, including conservation planning, species status assessment, projections of the effects of climate change, ecological restoration, and environmental impact and risk analysis (Carstens & Richards 2007, Rissler & Apodeca 2007). However, the ability of this information to make accurate predictions largely depends on the type of modeling methodology used (i.e., Generalized linear models [GLMs], Generalized additive models [GAMs], Classification trees [CTs], Random Forests [RFs]). In this study, the algorithm MAXENT v3.1 (Phillips et al. 2006, 2008), a presence-only modeling method that uses background environmental data rather than absence data, will be implemented. This method focuses on how the environment where a species is known to occur relates to the environment of the rest of the study area to find the probability distribution of maximum entropy subject to constraints imposed by information regarding species presences and environmental conditions across the study area (Phillips et al. 2006, Elith et al. 2011). For MAXENT v3.1, default convergence threshold (10^{-5}) and 500 iterations were performed with 25% of all localities used for model training. Suitable regularization values and functions of environmental variables were estimated by MAXENT based on sample size. Using this maximum entropy, relative habitat suitability was scored by MAXENT as a continuous probability value ranging from 0 (unsuitable) to 100 (highly suitable).

The generation of a niche model for *Rhoptropus* using all species point localities was used

to estimate a range prediction for the genus as a whole as well as the potential independent ranges of individual lineages. Major advantages of using this method are the ability to use presence-only data, which is typically more accurate than absence data, and the availability of new modeling methods, such as MAXENT (Elith et al. 2006). The drawbacks of using this method, however, include the inability to understand and interpret predictions in the absence of adequate historical biogeographic and species-specific limitations, and sample selection bias. With proper a priori phylogenetic and historical knowledge and a sufficient number of records, area coverage, sample bias correction, cross validation of model fit, and sound statistical interpretation, this method can be an incredibly informative and robust technique for understanding species distributions and degree of niche overlap.

c. Statistical interpretation

Because ecological models are subject to a significant source of error, predictions will always contain a degree of uncertainty. To maximize the raliability and usefulness of model predictions, several steps must be taken to eliminate misleading models and interpretations. Multiple Maxent runs were performed and cross-validated, and these initial results were compared in ArcView, with subsequent alterations of the initial model and input layers and locality points being made as necessary to minimize misleading data. For bioclimatic layers, information regarding isothermality and temperature annual range was excluded due to correlation with other variables (BIO3 and BIO7, respectively). Of the 315 locality points initially assessed, 18 were removed due to lack of species identity confirmation. Duplicate records were also eliminated, resulting in a total of 135 unique

occurrence points. Prediction accuracy was evaluated by examining the area under the curve (AUC) of receiver operating characteristic (ROC) plots, which compare a probabilistic prediction with a binary outcome. This assumes that the proportion of times a prediction of presence is seen will be higher than the prediction of absence for a true presence, ranging from a value of 0.5 (random) and 1.0 (perfect discrimination).

Multivariate environmental niche overlap between taxa was quantified using the PCA-env approach outlined in Broennimann et al. 2012. This practical tool applies gridded kernel smoother and spatial environmental factors and an ordination test based on PCA calibrations to the occupied region of the two groups being compared. Nice overlap within the first two PC axes is quantified through the use of occurrence data and spacial environmental data obtained through bioclimatic and land cover data with Schoener's D statistic (Schoener 1997). This continuous statistic ranges from values of 0 to 1, where one represents complete niche overlap and zero represents no niche overlap. This statistic can be used to asses niche similarity and niche equivalency between sister species pairs. Niche equivalency tests assess whether environmental niches between species are effectively identical (Warren et al. 2008, Graham et al. 2004). On the other hand, similarity tests assess the ability of one ecological niche model from a given taxon to predict the niche other another taxon better than what would be expected under a random null hypothesis where the ecological niche model contains no information about the distribution of another taxon (Warren et al. 2008). Null models were used to asses the significance of niche equivalency and niche similarity by comparison observed Schoener's D to values simulated from background points in southwestern Africa (Broennimann et al. 2012).

III. Results

A. Tree comparisons

The most complete taxon sampling is represented in the ND2 dataset (Figure 16), incorporating a total of 1074 basepairs of which 687 sites are variable and 454 are parsimony-informative. The RAG1 dataset includes 1069 total basepairs of which 208 sites are variable and 134 are parsimony informative (Figure 27). The MAP1A dataset contained 1024 total basebairs with 714 variable sites, 353 of which were parsimony informative. ML and BI analyses of these datasets were highly concordant and strongly support *Rhoptropus* as monophyletic and sister to *Pachydactylus* geckos (ND2 dataset, 98% BSS, RAG1 dataset, 95% BSS, concatenated dataset, 99% BSS). Between BI and ML analyses, interspecific relationships for *Rhoptropus* are fully congruent. All species previously described in the literature appear monophyletic with the exception of *R. bradfieldi*, where the coastal population is more closely related to *R. diporus* than to inland populations of *R. bradfieldi* in the ND2 and concatenated analyses (coastal *R. bradfieldi* + *R. diporus* relationship, 99% BSS in the concatenated dataset, >95% BSS in the ND2 dataset, Figures 16, 17). Any differences between *R. bradfieldi* and *R. diporus* in the RAG1 and MAP1A nuclear datasets were not recovered (Figures 216, 17). Paried-down mitochondrial and RAG1 datasets incorporating few individuals recovered the previous described topology for *Rhoptropus* relationships, with *R. afer* sister to *R. bradfieldi+R. diporus*, and this clade as reciprocally monophyletic to all other *Rhoptropus*. The larger RAG1 and MAP1A datasets also recovered this relationship, but with low

support (39% BSS RAG1, 48% BSS MAP1A, Figures 27, 28). Larger datasets with increased intraspecific sampling and appropriate model partitions for ND2 as well as the ND2+RAG1+MAP1A concatenated dataset only partially recover previously published patterns of relationship for *Rhoptropus*, with *R. afer* sister to all other *Rhoptropus* (>95% BSS in the ND2 dataset, 100% BSS in the concatenated dataset, Figures 16, 25, 26). Furthermore, in concatenated analyses, the group containing *R. bradfieldi*+*R. diporus*, the only described clade of Namibian endemic *Rhoptropu*s, is sister to all other *Rhoptropus*, but with low support in the ND2 tree (35% BSS, Figure 16) and higher in the concatenated tree (100% BSS, Figure 17). The support for the clade containing *R. afer*+*R. bradfieldi*+*R. diporus* in the nuclear datasets was moderate (72% BSS RAG1, 68% BSS MAP1A, Figures 27, 28).

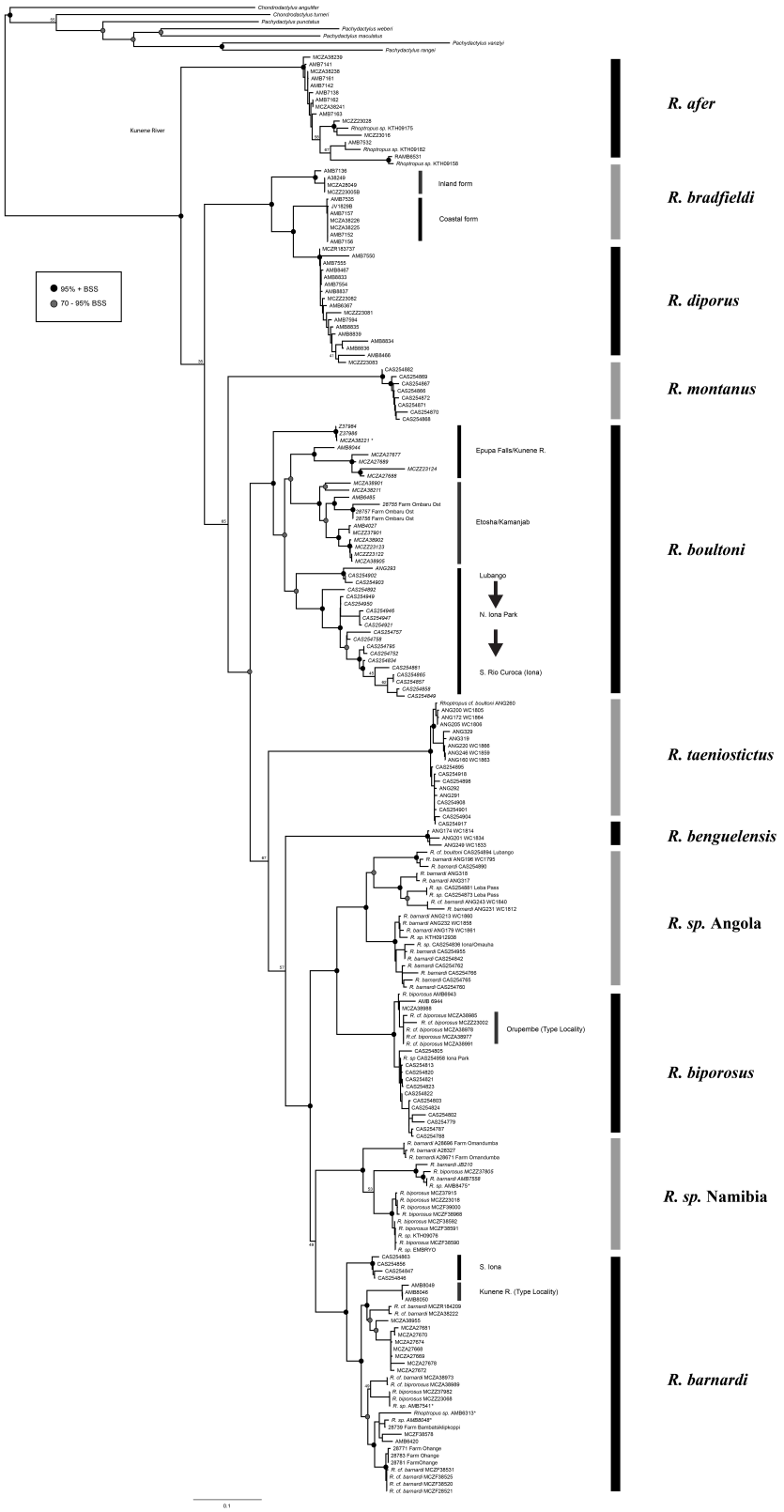


Figure 16 . Maximum likelihood phylogram of *Rhoptropus* relationships derived from mitochondrial data only (ND2). Solid circles indicate >90% MLBS/1.0 BPP at the node, and open circles indicate 70–90% MLBS/0.9–0.99 BPP.

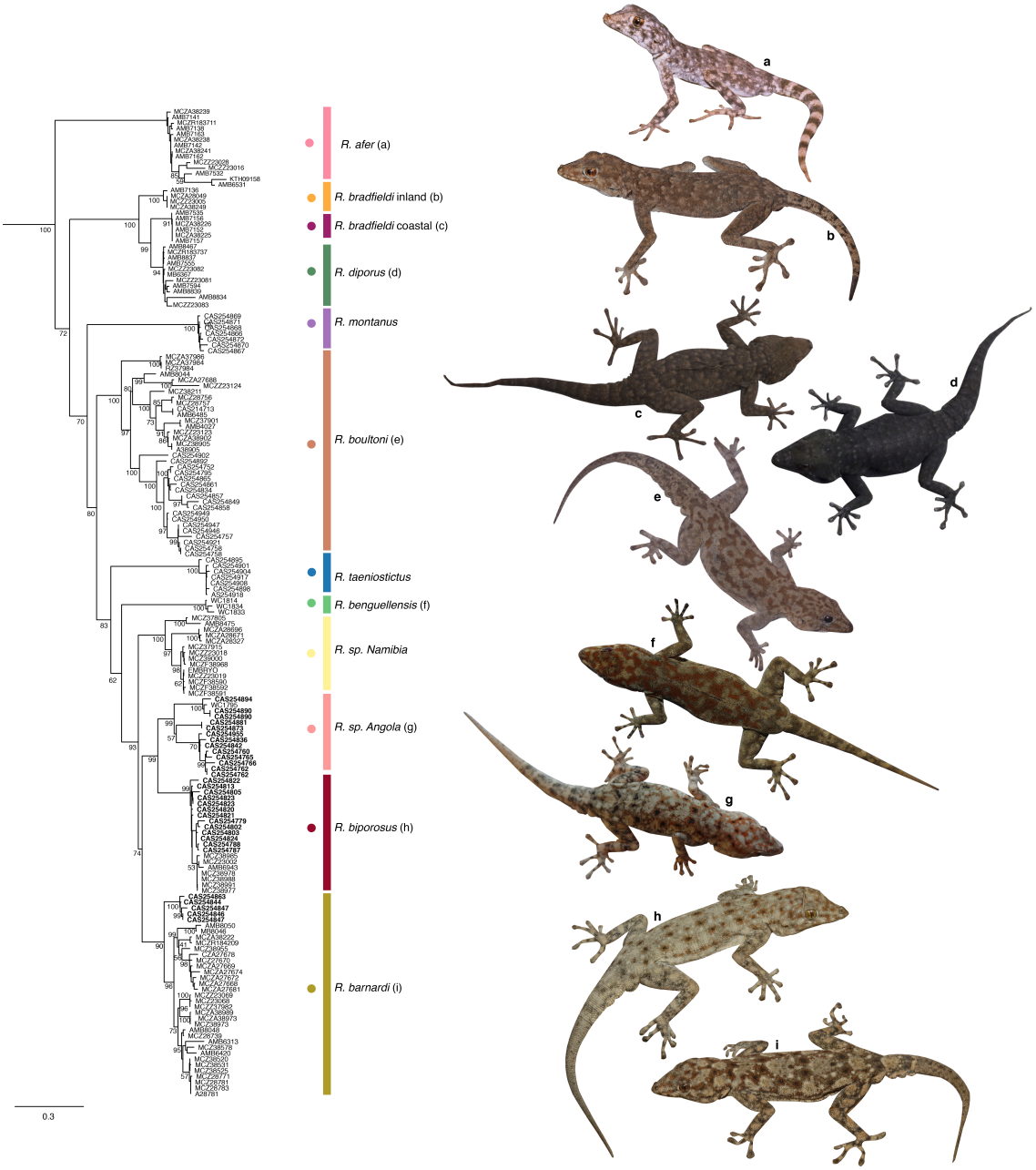


Figure 17. Maximum likelihood phylogram of *Rhoptropus* relationships derived from three concatenated genes (ND2, RAG1, MAP1A). Solid circles indicate >90% MLBS/1.0 BPP at the node, and open circles indicate 70–90% MLBS/0.9–0.99 BPP. Images (top to bottom) of representative *Rhoptropus* species are as follows from top to bottom: *R. afer*, *R. bradfieldi* from the coast, *R. bradfieldi*from Rossing Mountain (inland), *R. diporus*, *R. boultoni* from Namibia, *R. benguellensis* from Malanje, *R. barnardi*, and *R. biporosus*.

The other major instances of incongruence had to do with the placement of Angolan endemics *R. taeniostictus* and *R. montanus*. In the nuclear datasets, *R. montanus* and *R. taeniostictus* are grouped as sister species with moderate support (72% BSS RAG1, 70% BSS MAP1A, Figures). This group containing *R. montanus* and *R. taeniostictus* was well supported as sister to all other *Rhoptropus* (93% BSS RAG1, 88% BSS MAP1A). The topology of the ND2 and concatenated datasets, on the other hand, estimated the placement of *R. montanus* as sister to the group containing *R.boultoni+R. buenguellensis+R. taeniostictus+R.barnardi+R. biporosus* was poorly supported in the ND2-onlydataset (65% BSS, Figure 16) and better supported in the concatenated dataset (70% BSS, Figure 17). Support for *R. boultoni* as sister to all other *Rhoptropus* excluding *R. afer*, *R. diporus*, *R. bradfieldi*, and R. montanus or *R. montanus+R. taeniostictus* was moderate across all datasets (72% BSS RAG1, 70% BSS MAP1A, 75% BSS ND2, 80% BSS concatenated, Figures16, 17).

Intraspecific structure recovered for *R. boultoni* in the ND2/concatenated tree was not well supported in the RAG1 and MAP1A trees with the exception of *R. boultoni* from the basal Kunene being sister to all other *R. boultoni* (100% BSS across all datasets, Figures 25-28). Support for intraspecific clades of *R. boultoni* in Angola and Namibia were recovered with good support (>95 % for both clades in the ND2 dataset, 80% for the Angolan group and 100% for the Namibian group in the concatenated dataset, Figure 17). Support for a sister relationship between these two clades was also well supported when recovered (80% BSS ND2, 100% concatenated, Figures 25, 26).

Support for *R. taeniostictus* as sister to all remaining *Rhoptropus* (*R. barnardi* group + *R. benguellensis*) was not found in the nuclear datasets and variably supported in datasets incorporating mitochondrial information (67% in ND2, 83% concatenated, Figures 25, 26). The relationship of *R. benguellensis* to the *R. barnardi/R.biporosus* group was poor (63% concatenated, 57% ND2, Figures 25, 26), but sampling for this group was minimal given the extent to which this species can occur and the likelihood of additional genetic variation that has not been incorporated here.

The clade containing *R. barnardi* and *R. biporosus* animas is always recovered as monophyletic with good support, which agrees with all previous systematic investigations for *Rhoptropus* (>95% BSS ND2, 93% concatenated, 95% BSS RAG1, 95% MAP1A, Figures 25-28). Substructure within this group, however, was not found for the RAG1 dataset and was less supported in the MAP1A dataset than in the mitochondrial and concatenated trees. Relationships within the group are moderately consistent, with both ND2 and the concatenated trees finding a sister relationship between *R. biporosus* and *R. sp.* Angola (>95% BSS ND2, 99% BSS concatenated, Figures 25, 26). Variation at less well supported nodes exists for other relationships within this group: in the concatenated analysis, the clade containing *R. biporosus*+*R. sp.* Angola is sister to *R. barnardi* (90% BSS, Figure 17) and this grouping is sister to *R. sp.* Namibia (74% BSS). For the ND2 dataset, the *R. biporosus*+ *R. sp*. Angola group is sister (95% BSS) to a clade containing *R. barnardi* + *R. sp.* Namibia. The relationship in the ND2 phylogeny of *R. barnardi* to *R. sp.* Namibia, however, is poorly supported (49% BSS, Figure 16).

The 3-gene concatenated dataset had some missing data – importantly, nuclear sequences for *R. benguellensis* were not obtained (Supplemental 1, but nonetheless recovered a nearly congruent topology to the RAG1 and ND2 datasets (Figures 27, 28). The preferred topology from the dataset with the least amount of missing sequence data, the concatenated dataset, was used as the reference tree for species relationships within *Rhoptropus (*Figure 17*)*. In some cases, this expanded nuclear and mitochondrial phylogeny was able to provide greater support for certain relationships than the single gene mitochondrial and nuclear phylogenies, for example, the relationships within the *R. barnardi*/*R. biporosus* group. Other nodes deeper in the phylogeny were poorly supported in both datasets, such as the placement of *R. taeniostictus*.

B. Molecular systematic results

a. *Rhoptropus afer*

Rhoptropus afer appears to be the most morphologically and ecologically divergent species within the arid constituents of this genus (Bauer et al. 1996, Russell 2009, Johnson & Russell 2009, Figure 3). Despite an extensive range throughout Namibia and southwestern Angola, genetic distances within this group are conservative in comparison to those observed within other species of *Rhoptropus*. This species occupies rocky sand habitat in the Namib proper, but distributions can reach more inland localities of the pro-Namib as populations likely follow the rocky riverside habitat of Namibia and Angola's temporary and permanent water systems despite the surrounding sandy (Figure 2)

substrate otherwise associated with these localities (Figure 50). Although divergence with distance is often observed in vagile organisms in comparison to rupiculous-restricted conspecifics on isolated boulders, this pattern is not observed for *R. afer*. Divergence between individuals from the Brandburg, Swakopmund regions appear substantial but (13.4%-20.7%). Sampling is relatively sparse for areas in between the Erongo Region of Namibia and the Namibe Province of Angola, although the divergence between individuals fmor these regions does not currently imply cryptic species may be present (Figure 50). Deeper sampling from areas within park boundaries and the southwest of Angola will be beneficial in determining the northern extent of this species and the validity of this pattern of population panmixia in this taxa.

b. *Rhoptropus bradfieldi* and *Rhoptopus diporus*

Phylogenetic results indicate with high support (>95% BSS) that *R. bradfieldi* is paraphyletic with respect to its previously designated sister taxa *R. diporus*. Lineages designated as *R. bradfieldi* have two main distributions corresponding to discrete phylogenetic clades. Coastal localities include individuals occupying large, black boulders less than 1 kilometer from the ocean, and inland localities include individuals that tend to occupy boulders and rock faces on the side of mountains, where climate is distinctly warmer and receives higher rainfall than the cool foggy but arid habitat of the true Namib coastal region. Phenotypically, individuals from these inland localities are fawn to grey in color with cloudy patterning whereas individuals from the coastal population are nearly solid charcoal to black with occasional small grey spots (Figure 2). The variation in color pattern may be due to the higher number of fog days encountered on the coast in

comparison to inland localities as a mechanism for thermoregulation or it could have arisen as a means of substrate camouflage on the dark boulders found on the coastal region near Walvis Bay and Swakopmund (Zug et al. 2001). The use of color as an evolutionary character may be ambiguous as ancestral polymorphism in pigmentation can be the result of a relatively simple and often neutral mutation. The adaptive significance of this variation remains unclear, however regardless of the adaptive significance of the mutation, and the lingering presence of individuals with darker pigmentation could indicate reproductive isolation between inland populations and coastal populations that ancestrally possessed this mutation (Baedenhorst et al. 2002, Mouton 1987, Mouton & Oelofsen 1988, Branch 1998, Mouton & van Wyk 1990, Portik 2010). This melanism could also be the results of local adaptation or a locally plastic trait as many populations of *Rhoptropus* that are not genetically distinct contain both dark and light colored individuals, and this color can sometimes shift with respect to habitat, at least in *R. boultoni* (Branch 1998, Cox & Chippendale 2014). While color polymorphism is extensive in squamate reptiles and has been shown to impact genetic structuring of populations (Sinervo & Svensson 2002, Gray & McKinnon 2006, Corl et al. 2010, Hugall & Stuart-Fox 2012). Melanism within populations can also influence sympatric reproductive isolation through speciation mechanisms such as disruptive selection or assortative mating (Avise et al. 1992, Elmer et al. 1999). Population divergence in sympatric taxa has been observed more frequently as the direct result of sexual selection, however, the resultant variation can still be manipulated through the impact of the aforementioned non-sexual selection (Smith 1962, West-Eberhard 1986, McMillan et al. 1999, Pryke and Griffith 2006, West-Eberhard 1986). In the case of R. bardfieldi, however, popoulations appear significantly divergent

and either allopatric or parapatric through the sampled portion of the known range. Although no localities contain both color variants, in order to determine the distinctness of the inland and coastal populations as they relate to *R. diporus,* a more through examination of specimens from both localities and the incorporation of more inland genetic samples is necessary (Bauer & Lamb 2001).

c. *Rhoptopus boultoni* group

i. Intraspecific variation

Within *R. boultoni* the degree of sequence divergence between clades is comparable to divergence between recently described taxa. A clade from the northern Kunene Region in Namibia that is not comprehensively sampled is distinctly divergent from a sister clade containing two discrete clades, one endemic to Namibia and the other endemic to Angola. Within the Namibia clade, divergence appears to increase with distance, possibly due to a lack of admixture near population borders due to habitat restrictions. Because the Kunene River flows at the border of these two countries year round and drains into the Atlantic ocean, it may serve as a potential barrier promoting speciation between Angolan and Namibia taxa. In other gecko groups and for other *Rhoptropus* with distributions that span this potential barrier, this River does not seem to play a role in enforcing reproductive isolation; rather, the sharply contrasting habitat turnover reached near the Angola escarpment from the Namib Desert in this country seems to be more influential in enforcing reproductive isolation between lineages. With more sampling throughout the extent of this region, the mechanism of isolation between this clade and its sister clade

populations may be discernable.

ii. Subspecies of *Rhoptopus boultoni*

It is clear that these two species are not only distinct from one another and from all other *Rhoptropus* (mean 22.4%, range 17.9%-30.5% ND2 sequence divergence between *R. benguellensis* and all other *Rhoptropus;* mean 25.1%, range 21.5%-27.4% ND2 sequence divergence between *R. montanus* and all other *Rhoptropus)*, but also any phylogenetic affinity with *R. boultoni* as suggested in previous morphological assessments is not supported. *R. benguellensis* appears to be sister to all other *Rhoptropus* and *R. montanus* appears to be sister to *R. boultoni*+*R. b. benguellensis*+*R.taeniostictus*+*R.barnardi* group. The branches for *R. b. montanus* and *R. b. benguellensis* are long in comparison to other lineages, which is expected given the degree of isolation and genetic distinction of these groups. In the nuclear phylogeny, however, *R. taeniostictus* appears sister to *R. b. montanus*, which may arguably be an equally likely relationship given the lack of resolution of this tree. Whereas *R. taeniostictus* occupies more lowland habitat, Present knowledge of the range of *R. b. montanus* does not indicate the extent to which this animal occupies the Huila Plateau, therefore the diversity recovered at Leba Pass may not be representative (Figure 18). For *R. b. benguellensis*, ongoing herpetological surveys for Angola indicate an expansive range for this animal, with known localities in the Benguella, Huambo, Cuanza Sul and Malanje Provinces, making it the most northernly distributed *Rhoptropus* with localities as remote as the Cuanza River. Preliminary examination of more diffuse localites, have tenativeyl identified a lack of genetic divergence between populations from Cuanza Sol and Buenguella populations. Because

the climate and habitat of Angola shifts dramatically as the Escarpment region is approached, but it is possible that the more remote populations at the extent of this species' range are cryptically divergent and require closer examination. The habitat occupied by these two species is also remarkably distinct from all other *Rhoptropus*, which is generally considered a Namib and pro-Namib endemic. While *R. benguellensis*, habitats and distributions of *R. b. benguellensis* and *R. boultoni* are remarkably different (Fig. 9, Figure 6). While *R. b. benguellensis* strictly rupiculous like other *Rhoptropus*, and occupies large boulders near rocky inland streams, the habitat of its range encompasses regions with much higher annual rainfall and lower annual temperatures at high elevations (Ceríaco et al. 2016, Figure 18, Figure 7). *R. b. montanus,* on the other hand, is only known from a restricted portion of the Huila Plateu, which spans the eastern border of the Namib Province where it meets the Huila Province with elevations as high as 1850 meters. Geographically, this area is much closer to the known range of *R. boultoni*, possibly lending to the conservative affinity of *R. b. montanus* with this taxon. Climatically, however, this region is much cooler, more densely vegetated and wet with overall habitat that is truly representative of the lower Angolan Escarpment where it starkly meets with the contrastingly arid and sparsely vegetated coastal plain (Figure 18). The body of *R. b. montanus* is robust and dark charcoal to olive-grey, the snout is rounded, and the scales are lightly tuberculated (Fig. 9). *R. b benguellensis* has a more slender body with longer limbs and smoother scales which is more typical to that of *R. boultoni* and *R. taeniostictus* with bright orange coloration cloudy patterning on a dark grey background (Figure 7). A number of important morphological characters outlined in the descriptions of these organisms holds true as well. *R. b. benguellensis* has 2 enlarged mental sublabials with

rounded edges in comparison to the number seen in *R. boultoni*, although the body size variation between these two species should be reinvestigated as a distinctive character (Mertens 1938). *R. b. montanus*, on the other hand, clearly shows a reduced number of subdigital plates in comparison to *R. boultoni* as well as an increased number of proximal subdigital scales (Laurent 1964). Given the molecular, ecological and morphological evidence highlighted above, it is suggested herein that *Rhoptropus boultoni benguellensis* and *Rhoptropus boultoni montanus* be raised to full species status.

Figure 18. Type locality habitat of (A) *R. boultoni*, and the contrasting habitat of previous proposed boultoni subspecies, (B) *R. montanus*, Leba Pass, Huila province, Angola and (C) *R. benguellensi*s, Lauca, Malanje Province, Angola. Picture credit Luis Ceríaco

e. *Rhoptropus barnardi* group

The group containing the previous described *R. barnardi* and *R. biporosus* is recovered as

sister to *R. benguellensis*. This relationship is not well supported, however, in the mitochondrial dataset (<80% BSS ND2, Figure 16). Support for relationships within this group are well defined, and may harbor a wealth of cryptic evolutionary diversity. Specifically, *R. biporosus* from below and above the escarpment appear distinct. The relationship to *R. sp* from Angola and *R. biporosus* is well supported (99% BSS ND2, Figure 16), but divergences between these two populations are substantial (avg. sequence divergence for ND2 15.82%, range 13.2-17.1%) in comparison to other recently elevated subspecies (*R. bradfieldi* and *R. diporus*, 10.5% sequence divergence for ND2). This pattern of diversity has been recovered in a number of other taxa with distributions in the southwestern portion of Angola and those collected from the Benguella Province (i.e., *Pachydactylus oreopholis*, *Pachydactylus punctatus,* Brennan et al. 2016, in prep.). This putatively new species clade from the escarpment region and sister species, true *R. biporosus*, correspond with the morphological groupings of Ceríaco et al. 2016 for *Rhoptropus sp.* and *Rhoptropus biporosus* from Angola. Although some degrees of superficial morphological variation has been noted in this novel group (Ceríaco et al. 2016), and overall body plan and color pattern appears intermediate between *R. biporosus* and *R. barnardi* (AMB, pers. comm.). Regardless, formal morphological evaluation is necessary to fully identify and describe this lineage.

The recognition of individuals sampled from within true *R. barnardi* is additionally supported by the morphological examination of Angolan material (see Ceraico et al. 2016). For individuals from Namibia assigned to *R. barnardi*, only cursory in-field examination of specimens has been performed at this time. Regardless, the close

phylogenetic affinity of confirmed between *R. barnardi* from Angola and tentative *R. barnardi* from Namibia (90% BSS) supports the validity of these two geographic clades both corresponding to true *R. barnardi*. This clade is sister to the clade containing *R. biporosus* and *R. sp*. from Angola with moderate support (74% BSS), which agrees with previous phylogenetic estimations although no Angolan material had been incorporated in this assessment to date. Far inland populations of *R. barnardi* are less divergent from coastal populations in comparison to divergence between Angolan and Namibian populations. Although the further inland habitat of Namibia where some *R. barnardi* have been collected in the northern Otjozondjupa Province receives higher rainfall than the Kaokoveld Region where a portion of their distribution is found (500-550 mm/yr vs. <200 mm/year), substrate, rather than clime, may be more important in dictating the distribution of this species. The coincidence with riverine systems and *R. barnardi* distribution, much like *R. afer*, probably has more to do with an allied movement of organisms up the river system. As these animals move inland, they likely stay closely affiliated with water bodies, as preferred rocky outcrop formations are allied with riverine habitat despite the surrounding woodland soil habitat that becomes more ubiquitous inland. *R. barnardi* do not appear to be found at southern locations beyond the Kunene Province, and although they do span the Kunene River, northernmost localities have not been recorded far beyond Namibe-Lubango.

Aside from the clear identification of a clade that corresponds to true *R. barnardi,* support is also found for a clade distributed in the northern Erongo and Huab Regions of Namibia that is sister to the clade containing true *R. barnardi*+*R. biporosus*+*R. sp* Angola (93%

BSS). Relationships within this group are additionally well supported (98-100% BSS ND2, Figure 16), however the presumed affinity between *R. barnardi* and this parapatric clade is not found (15.6% ND2 nucleotide sequence divergence). Morphologically, individuals from the Gai-As region of the Kunene Province are intermediate in form between *R. biporosus* and *R. barnardi* (AMB, pers. comm.) with intermediary sharpness of the rostrum, length of the limbs, and patterning of the body. The overlap in distribution between *R. bipororus*, *R. barnardi*, and *R. sp* Namibia near Orupembe, the type locality for true *R. barnardi*, makes identification of the mechanism for reproductive isolation between these One possible explanation for this distributional overlap and genetic distinction could be different historical distributions under alternative climatic regimes that were isolated due to desertification and retreat to less arid habitats that have since returned to sympatry.

Radiocarbon dating of trees and buried sediment during the Little Ice Age (15-1800 yrs ago) indicate increasingly aridified conditions in the Damaraland/Kaokoveld region. Contemporarily, this region actually receives more rainfall today than it did during that time period, therefore it is likely that conditions fluctuated during the quaternary in contrast to the presupposed continual natural progression of aridification that is often assumed for the Namib (Eitel 2005, Eitel et al. 2002). During intensified arid conditions, these geckos could have moved inland to escape extreme aridity, and distributions could have shifted eastwards as the climate become more tolerable after the Little Ice Age.

Another possible explanation sympatric speciation, as the habitat between these geckos

does not seem partitioned with both groups of individuals found on koppies of similar rock types and equivalent size, which is hybridization. A hybrid zone can exist where two population of species interbreed, producing offspring of mixed parentage. Although parent populations are genetically distinct, they are not entirely isolated reproductively. The degree of hybridization between species that are not geographically isolated is a proxy for the amount of behavioral and genetic isolation of the two populations, and how far along the speciation continuum these populations are under the biological species concet (de Quieroz 2007). These zones are usually a product of secondary contact between populations or species that have differentiated previously in allopatry. When no measurable differences can be found between hybrid and purebred offspring, parental populations are expected to coalesce and differences between them decrease. Hybrid zones can develop in regions termed "ecotones," where different habitats meet. If the hybrid is better suited for this intermediate habitat than either of the parental species, a stable hybrid zone can form. Hybrid zones will occur when there is a cline in the genetic composition of parent taxa (Doebeli & Dieckmann 2003). These populations are closely related but genetically distinct. Parent species must be genetically similar enough, however, so that the compatibility of the genomes is still maintained to produce a fit hybrid. This compatibility is dependent mainly on the genetic divergence between the two species (Moore 1977). The habitat encountered between these taxonomic groups may represent a plausible ecotone, and the intermediate forms of this endemic Namibia clade could be indicative of a new species as the results of historical, but not ongoing hybridization (Hewitt 1988). Either way, this is unlikely to be a simple case of isolation by distance confounding population structure, as genetic distances between geographically clustered

individuals from different populations is greater than that seen in geographically distant individuals from the same population (Wright 1940). Without knowledge of historical demography of these lineages in a temporal context, the underlying mechanism for the reduction in admixture between these clades is not discernable.

f. *Rhoptopus taeniostictus*

Previous analyses of the relationships within *Rhoptropus* have identified a sister relationship between *R. taeniostictus* and the larger monophyletic clade containing R. *boultoni*, *R. biporosus*, and R. barnardi (Bauer & Good 1996). These investigations were solely based on morphological characters, therefore this is the first time R. *taeniostictus* has been evaluated in a molecular context with complete sampling across the entire genus. The distribution of this species at present appears to be lower elevations exclusively found in the dune fields of the Namibe Province of Angola and possibly as far inland as the Huila province at lower abundances (Ceríaco et al. 2016, Ditsong National Museum of Natural History, 8). Support for the previously estimated placement for *R. taeniostictus* was not recovered in any of the molecular analyses. However, this morphological estimation was based on a limited number of samples, and the recovered relationship in this study as sister to the monophyletic clade containing *R. benguellensis*, *R. barnardi* and *R. biporosus* is not well supported (<70% BSS ND2, Figure 16). This placement is not unreasonable, however it is possible that this group could fall out else where given additional molecular data and species-tree analyses. Regardless of its taxonomic placement, this group is clearly distinct from all other *Rhoptropus* (mean 22.5% ND2 nucleotide sequence divergence) including those with which it shares some distributional

overlap (*R. biporosus*, *R boultoni*), and morphological distinction observed in individuals from the type locality was always observed in individuals collected from Namibe (Ceríaco et al. 2016, Figure 8).

Table 6. Corrected (bottom left) and uncorrected (top right, bold) mean pairwise genetic distances for *ND2* mitochondrial locus of *Rhoptropus* lineages.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	*R. afer*		**0.27**	**0.26**	**0.27**	**0.26**	**0.24**	**0.24**	**0.24**	**0.23**	**0.23**	**0.23**	**0.24**	**0.24**	**0.25**
2	*R. taeniostictus*	0.34		**0.28**	**0.24**	**0.27**	**0.26**	**0.25**	**0.22**	**0.22**	**0.22**	**0.21**	**0.24**	**0.23**	**0.23**
3	*R. diporus*	0.33	0.35		**0.28**	**0.27**	**0.11**	**0.13**	**0.23**	**0.22**	**0.22**	**0.23**	**0.25**	**0.25**	**0.24**
4	*R. benguellensis*	0.34	0.3	0.35		**0.27**	**0.24**	**0.24**	**0.22**	**0.2**	**0.2**	**0.19**	**0.22**	**0.21**	**0.22**
5	*R. montanus*	0.33	0.33	0.34	0.34		**0.24**	**0.24**	**0.25**	**0.23**	**0.23**	**0.25**	**0.25**	**0.27**	**0.27**
6	*R. bradfieldi* coastal	0.29	0.32	0.12	0.3	0.29		**0.12**	**0.21**	**0.2**	**0.2**	**0.21**	**0.22**	**0.22**	**0.22**
7	*R. bradfieldi* inland	0.29	0.31	0.15	0.29	0.29	0.14		**0.21**	**0.19**	**0.19**	**0.21**	**0.23**	**0.24**	**0.22**
8	*R. boultoni* Cunene	0.29	0.27	0.28	0.26	0.31	0.25	0.24		**0.11**	**0.11**	**0.19**	**0.2**	**0.19**	**0.21**
9	*R. boultoni* Angola	0.26	0.28	0.25	0.25	0.28	0.22	0.22	0.13		**0.12**	**0.17**	**0.18**	**0.19**	**0.19**
10	*R. boultoni* Namibia	0.28	0.27	0.27	0.24	0.27	0.24	0.22	0.13	0.13		**0.18**	**0.19**	**0.19**	**0.21**
11	*R. barnardi*	0.27	0.26	0.29	0.22	0.3	0.24	0.25	0.22	0.2	0.21		**0.15**	**0.15**	**0.15**
12	*R. biporosus*	0.29	0.3	0.3	0.26	0.31	0.26	0.27	0.23	0.21	0.22	0.17		**0.16**	**0.14**
13	*R. sp.* Namibia	0.3	0.28	0.31	0.26	0.34	0.26	0.3	0.23	0.23	0.22	0.17	0.18		**0.16**
14	*R. sp.* Angola	0.3	0.28	0.29	0.26	0.34	0.26	0.26	0.25	0.22	0.25	0.18	0.15	0.18	

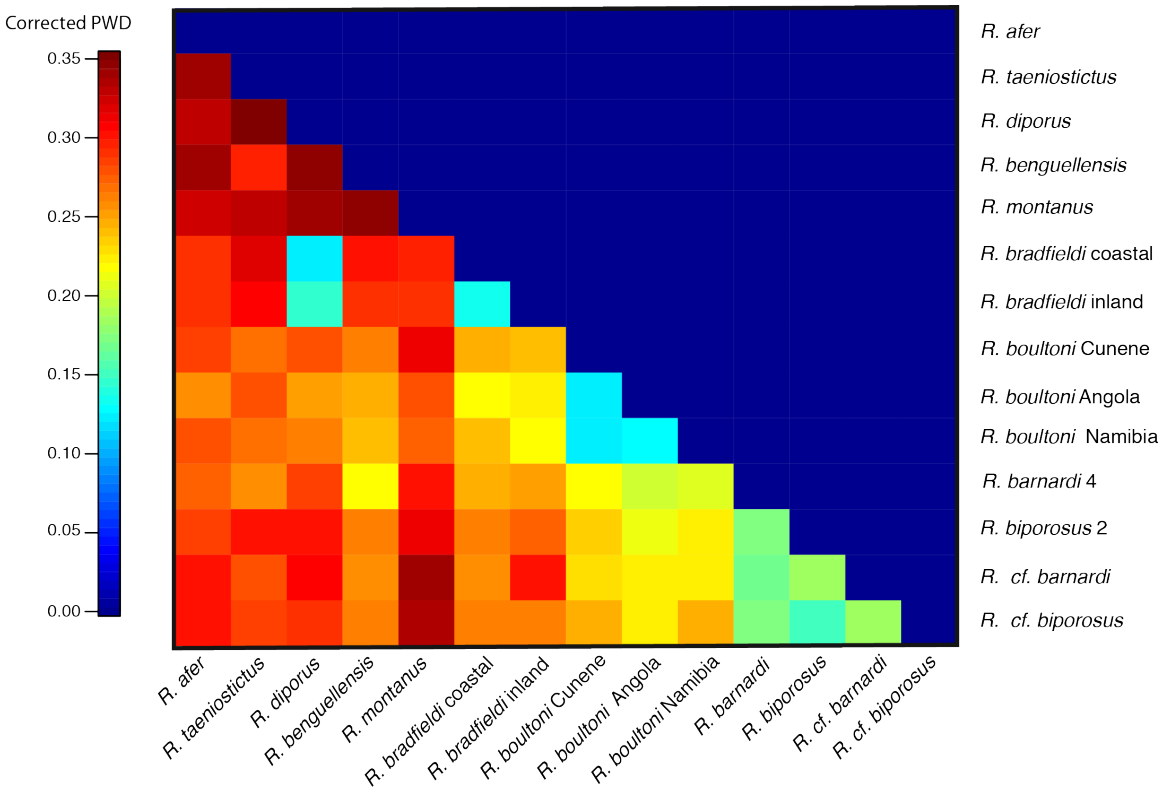


Figure 19. Heatmap of corrected (K2P) mean pairwise genetic distances for *ND2* mitochondrial locus of *Rhoptropus* lineages.

Table 5. Corrected (bottom left) and uncorrected (top right, bold) mean pairwise genetic distances for *RAG1* nuclear locus of *Rhoptropus* lineages.

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*R. afer*		**0.03**	**0.03**	**0.03**	**0.02**	**0.03**	**0.03**	**0.04**	**0.03**	**0.03**	**0.03**	**0.03**	**0.03**
2	*R. taeniostictus*	0.03		**0.02**	**0.02**	**0.02**	**0.03**	**0.03**	**0.03**	**0.02**	**0.02**	**0.02**	**0.02**	**0.02**
3	*R. diporus*	0.03	0.02		**0.02**	**0.02**	**0.03**	**0.02**	**0.03**	**0.02**	**0.01**	**0.01**	**0.01**	**0.01**
4	*R. montanus*	0.03	0.02	0.02		**0.03**	**0.03**	**0.03**	**0.03**	**0.02**	**0.02**	**0.02**	**0.02**	**0.02**
5	*R. bradfieldi* coastal	0.03	0.03	0.02	0.03		**0.01**	**0.03**	**0.03**	**0.03**	**0.02**	**0.02**	**0.02**	**0.02**
6	*R. bradfieldi* inland	0.03	0.03	0.03	0.03	0.01		**0.03**	**0.03**	**0.03**	**0.03**	**0.02**	**0.02**	**0.02**
7	*R. boultoni* Cunene	0.03	0.03	0.02	0.03	0.03	0.03		**0.01**	**0.01**	**0.02**	**0.02**	**0.02**	**0.02**
8	*R. boultoni* Angola	0.04	0.03	0.03	0.03	0.03	0.03	0.01		**0.01**	**0.03**	**0.03**	**0.02**	**0.02**
9	*R. boultoni* Namibia	0.03	0.02	0.02	0.03	0.03	0.03	0.01	0.01		**0.02**	**0.02**	**0.02**	**0.02**
10	*R. barnardi*	0.03	0.02	0.01	0.02	0.02	0.03	0.02	0.03	0.02		**0.01**	**0.01**	**0.01**
11	*R. biporosus*	0.03	0.02	0.01	0.02	0.02	0.03	0.02	0.03	0.02	0.01		**0.01**	**0.01**
12	*R. sp.* Namibia	0.03	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01		**0.01**
13	*R. sp.* Angola	0.03	0.02	0.01	0.02	0.02	0.02	0.02	0.03	0.02	0.01	0.01	0.01	

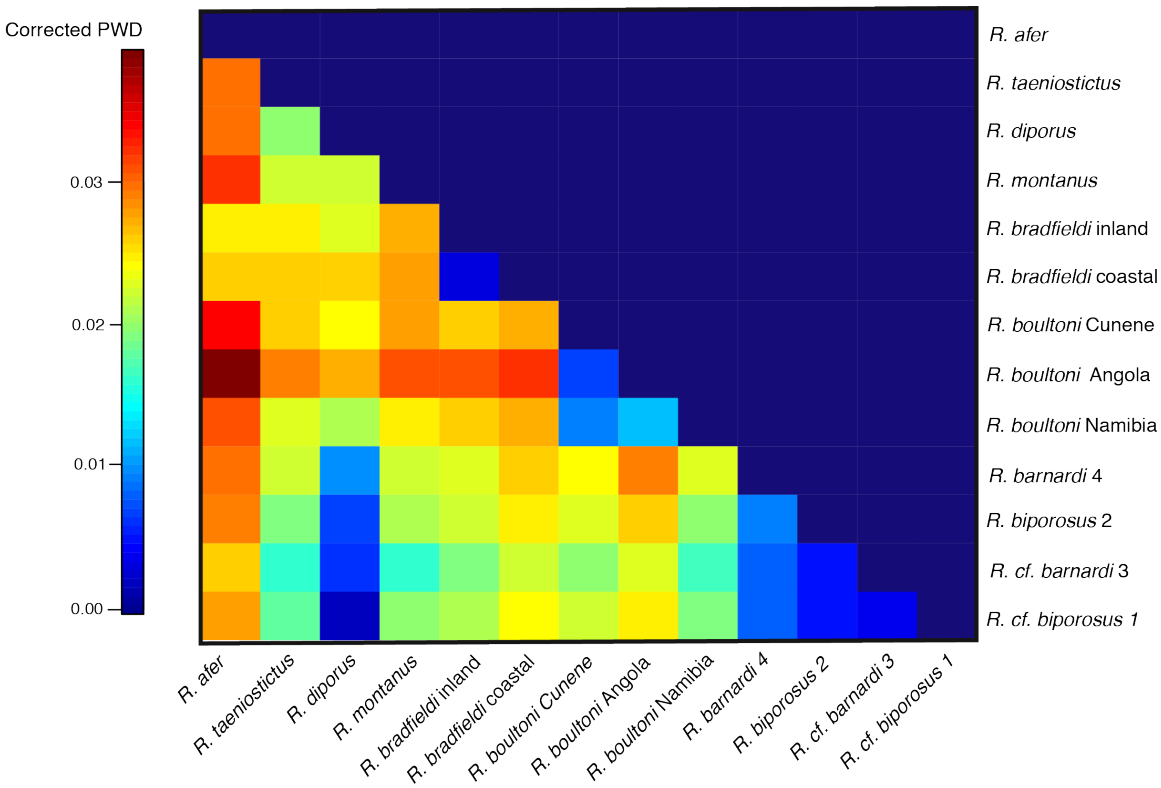


Figure 20. Heatmap of corrected (K2P) mean pairwise genetic distances for *RAG1* nuclear locus of *Rhoptropus* lineages

C. Environmental niche

a. *Rhoptopus braconnieri*

The Maxent model's internal jackknife test of variable importance showed that 'annual precipitation' was the most important predictors of *Rhoptropus*'s habitat distribution, closely followed by 'precipitation seasonality'. This was true for both *Rhoptropus* as a whole and individual iterations run for each species within the genus. Although geology and soil type were less important than precipitation, these variables were also informative in predicting suitable habitat for *Rhoptropus*. These variables showed the highest gain in comparison to other variables. Adaptation to extreme aridity may be in part an adaptation to extreme temperature variability in desert and montane habitats, whereas many Rhoptropus may still be functioning at their biological limits with respect to water availability. Although *R. benguellensis* and *R. montanus* occur in higher rainfall zones, these regions are still distinct from the interior of Angola, and temperatures are equally extreme due to altitude. Soil type as an important predictor reinforces the importance of substrate to the distribution of this group, as well as other groups of gekkonids. These bioclimatic results suggest that the species was ancestrally constrained by habitat availability rather than the aridifying climate of the Namib region (Pulliam 2000, Nattier 2013). The Maxent model predicted potential suitable habitat for *Rhoptropus* with low omission rates (Figure 7). Most suitable habitat for *Rhoptropus* was predicted along the Namib and pro-Namib portions of southwestern Angola and western Namibia just below the Kuiseb River (Figure 4, Figures 29-36). Moderate suitability can be seen in the north central Otavi region, from which, unsurprisingly, *Rhoptropus* have been collected recently

and in the past. The region beyond the predicted southern extent in the Sperrgebeit is nearly devoid of watersheds and even the intermittent riverine systems of northern and central-southern Namibia, and the soil types in non-suitable regions enclosing their distribution appear to be arenosols and dune sand. Whereas these geckos can find suitable rock habitat in a number of variable climatic regions, certain types of soil seem to constrain the distribution from reaching further regions of potentially suitable habitat more inland and in the south. Studies have found that a minimal threshold of samples exists for model prediction (Wisz et al. 2008, Williams et al. 2009, Costa et al. 2010, Figures 29-36), while other niche modeling investigations have argued that few, accurately distributed samples may still be sufficient in the estimation of suitable habitat (Pearson et al. 2007). In this study, despite the increased sampling depth relative to other *Rhoptropus* studies, a number of geographic gaps still exist, and the true extent of some species is still unclear. Ongoing work to georeference and examine all *Rhoptropus* from Namibia and Angola found in historical museum collections and definitive boundaries between the true number of species in this genus will allow for realistic, high quality constraints. Overall, the the high degree of biome-specific endemism of the Namib desert may apply to other groups with locally adapted constituents of a larger non-arid radiation, whereas for *Rhoptropus*, post aridification speciation might be the result of distribution of suitable substrate and rocky habitat as well as a certain range of precipitation seasonally

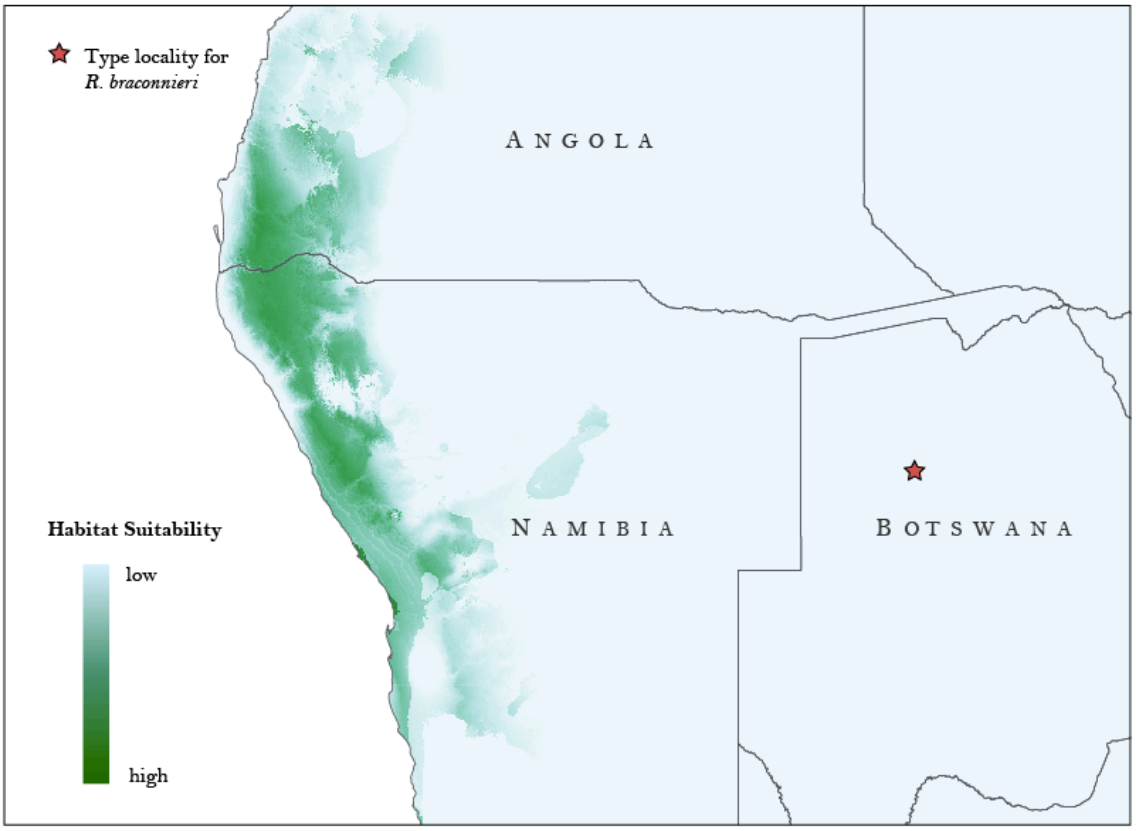


Figure 21. The predicted contemporary distribution of *Rhoptropus*. Projection is based on contemporary climate data using the bioclimatic variable layers indicated in Table 4 with the program MAXENT (Phillips et al. 2006). The darkest shading in the color-scale key indicates the highest predicted areas for the contemporary ecological niche model. Sampled localities are indicated by white circles. The published type locality for *R. braconnieri* Thominot 1978, South Ngami Lake, Bechuanaland, Botswana, is indicated by a red star, well outside the proposed contemporary range for *Rhoptropus*.

The type locality of *Rhoptropus braconnieri* and its validity as a species has been variable in the literature (Thominot 1878, Boulenger 1910, Fitzsimons 1943, Kluge 1993, Welch 1994, Bauer & Good 1996). Initial descriptions of a Rhoptropus-like animal from the Lake Ngami Region of Botswana would constitute the most inland locality for this genus (Thominot 1878). This locality is separated from other *Rhoptropus* distributions by high elevation aolian sediment beyond the central plateau and Kalahari Desert. This habitat is notably unsuitable for *Rhoptropus*, and has no connectivity to habitat that is identified as

suitable, therefore it is unlikely that *Rhoptropus* was ancestrally locality inland and dispersed and diversified in the Namib region, or that dispersal beyond this range took place historically (Figure 4). This intermittent region is not predicted by the genus-level distribution model, providing additional evidence that this locality data is an artifact of specimen acquisition rather than true biological data. For these reasons we formally reject the validity of *R. braconnieri* as a species of Rhoptropus, and show the support for Rhoptropus distributions further inland than the Otavi region to be unlikely.

b. Niche overlap

Niche equivalency can be rejected in three out of the six species pairs examined (Table 8). This suggests that clades within *Rhoptropus* that have more recently diverged do not have comparable environmental niches (Figures 30, 31, 33, 24). However, similarity tests were significant between 2 of the 6 taxon pairs (Table 9). This suggests that in less than half of the groups studied, one species' ENM is able to correctly model the distribution of another species that it is closely related to. Thus, support is found that the ecological niches of these other 4 species pairs are more similar than by chance (specifically, all but *R. barnardi*/*R. sp.* Namibia and *R. sp.* Namibia/*R. sp.* Angola). For these two excluded pairs, one groups ENM had no better ability to predict the niche model of its sister species than expected based on overall environmental similarity between the regions. The point estimate used to assess patterns of RI and evolution of ecological differentiation, Schoener's D statistic, ranged from 0.231 – 0.801 across this group, signifying a range of differences in the contemporary environmental niche for *R. barnardi* group geckos (Table

7).

Table 7: Schoener's D statistic values (ranging from 0 to 1) indicating the degree of niche overlap between species.

		1	2	3
1	*R. barnardi*			
2	*R. biporosus*	0.672		
3	*R. sp. Namibia*	0.67	0.231	
4	*R. sp. Angola*	0.184	0.801	0.448

Table 8: Tests of niche equivalency. Significant values for niche equivalency tests demonstrate that the species pairs are occupying distinct environmental niches.

		1	2	3
1	*R. barnardi*			
2	*R. biporosus*	0.048		
3	*R. sp. Namibia*	0.051	**0.034**	
4	*R. sp. Angola*	**0.0198**	0.061	**0.041**

Table 9: Tests of niche similarity. For the background similarity tests *p*-values are listed as "species y predicting species x, species x predicting species y". Statistically significant values ($p < 0.05$) indicate that species are more similar than expected under a null hypothesis of randomization.

		1	2	3
1	*R. barnardi*			
2	*R. biporosus*	0.014, 0.032		
3	*R. sp. Namibia*	**0.078, 0.293**	**0.04, 0.132**	
4	*R. sp. Angola*	0.019, 0.029	0.017, 0.019	0.019, 0.042

The terms Allopatry, Parapatry, and Sympatry are all defined by the role that geography plays on the formation of species. Whereas allopatry refers to a process of speciation whereby two daughter populations of an ancestral population become completely isolated from one another through geographic barriers, sympatry refers to populations in which geography plays no role at all in genetic divergence between sister groups. Species in sympatric populations diverge through isolation that results from behavioral and ecological isolation within a single, shared region. This process is often linked to Sexual Selection and Disruptive Selection. Parapatric Speciation represents the interplay between allopatric and sympatric extremes, and generally presents a more realistic view of how genetic isolation develops between populations. In parapatry, geographic, ecological, and behavioral changes act in concert to gradually cause populations to diverge from one another. Because the formation of barriers (such as mountain range formation) almost always occur on a slow, geological time scale, pure allopatry, the sudden complete separation of two populations is unlikely through geographic means, just as reproductive isolation in sympatry is difficult to tease apart from spatial varation within populations. All organisms are the product of the environment in which they live, and geography as well as ecology may a role influence speciation events, either directly through a physical barrier to gene flow, or indirectly though long term environmental stability clines that allow sympatric or parapatric species to form (Coyne and Orr, 2004).

Previous studies have demonstrated that the degree of environmental niche overlap may be biased by the degree of geographic overlap shared between species as bioclimatic data

can be limited (Warren et al. 2008). Of the species pairs examined (*R. barnardi*, *R. biporosus, R. sp* Angola, *R sp.* Namibia), niche equivalency is rejected ($P<0.05$) in three of the 6 taxon groups examined, *R. sp.* Namibia to *R. biporosus*, *R. sp.* Angola compared *to R. sp.* barnardi and *R. sp.* Namibia compared to *R. sp.* Angola. This indicates that at least for some groups, speciation events can be associated with differentiation in environmental niche. Given the variation in climate and landscape that can be seen throughout the distribution of these geckos despite their restriction to environments that are considered arid and rocky. Niche similarity, on the other hand, does not precisely correspond with niche overlap observations. Niche similarity is supported for more than half of the species clusters compared. *Only R. sp.* Namibia/*R. sp.* Angola and *R. sp.* Namibia/*R. barnardi* have niches that are not more similar than would have been expected from random given the environmental backgrounds in which species are distributed. This suggests that although environment may have played a role in the separation of species, overall niche is likely to be a conservative trait within certain lineages, especially when organisms are operating at the edges of their physiological limits.

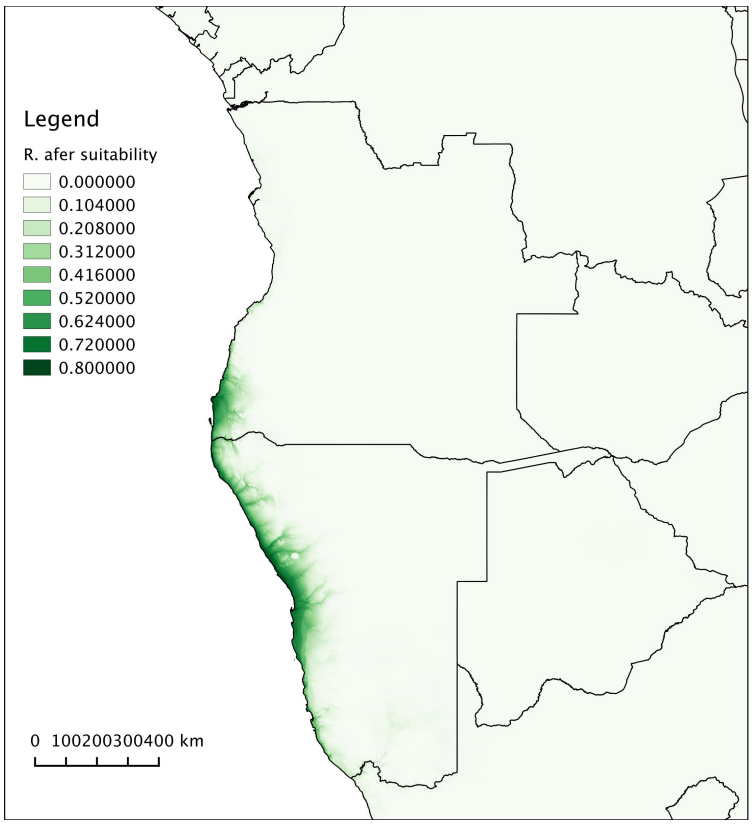


Figure 22. Niche model for *R. afer* generated using the MAXENT model.

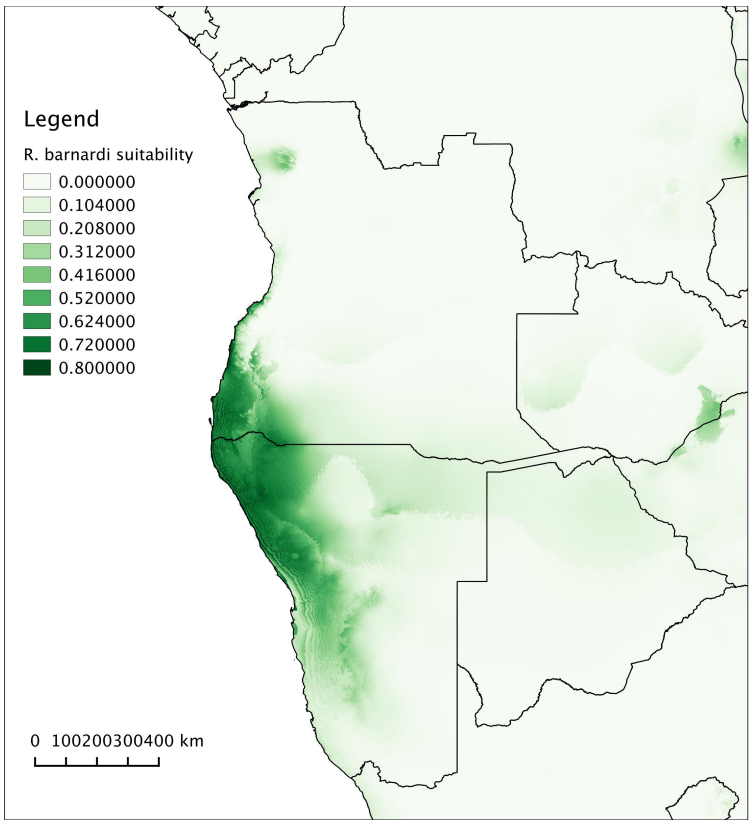


Figure 23. Niche model for *R. barnardi* generated using the MAXENT model.

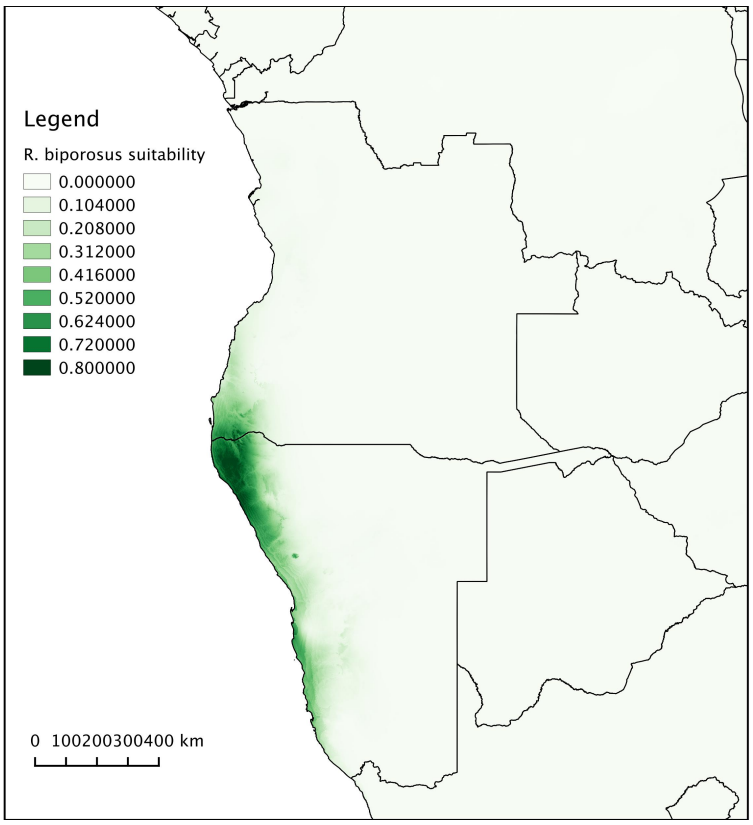


Figure 24. Niche model for *R. bipororsus* generated using the MAXENT model.

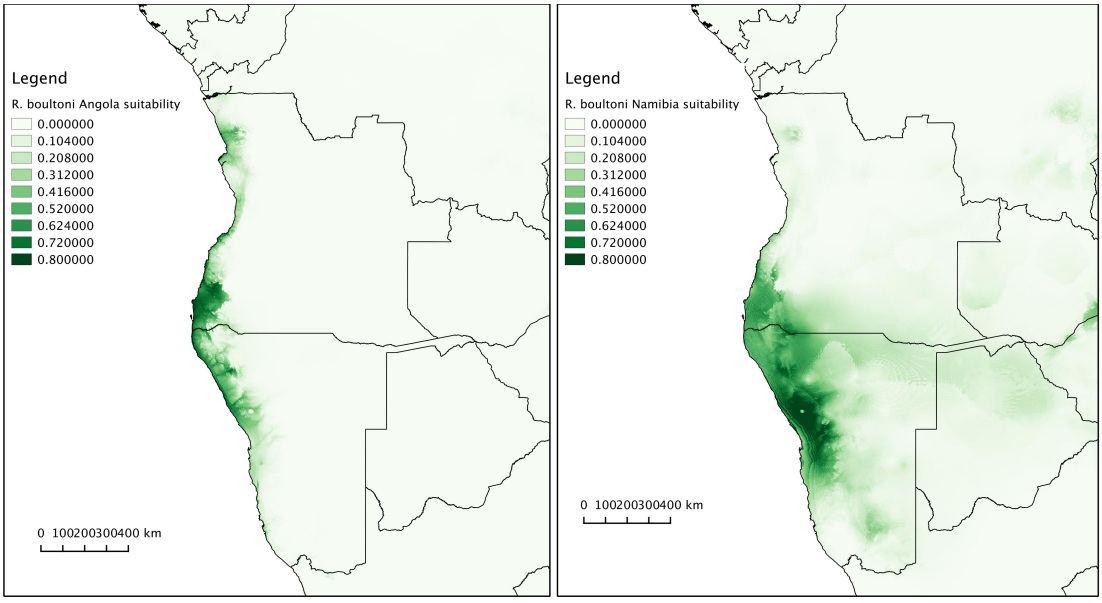


Figure 25. Niche model for *R. boultoni* (left) Namibian populations and (right) Angolan population generated using the MAXENT model.

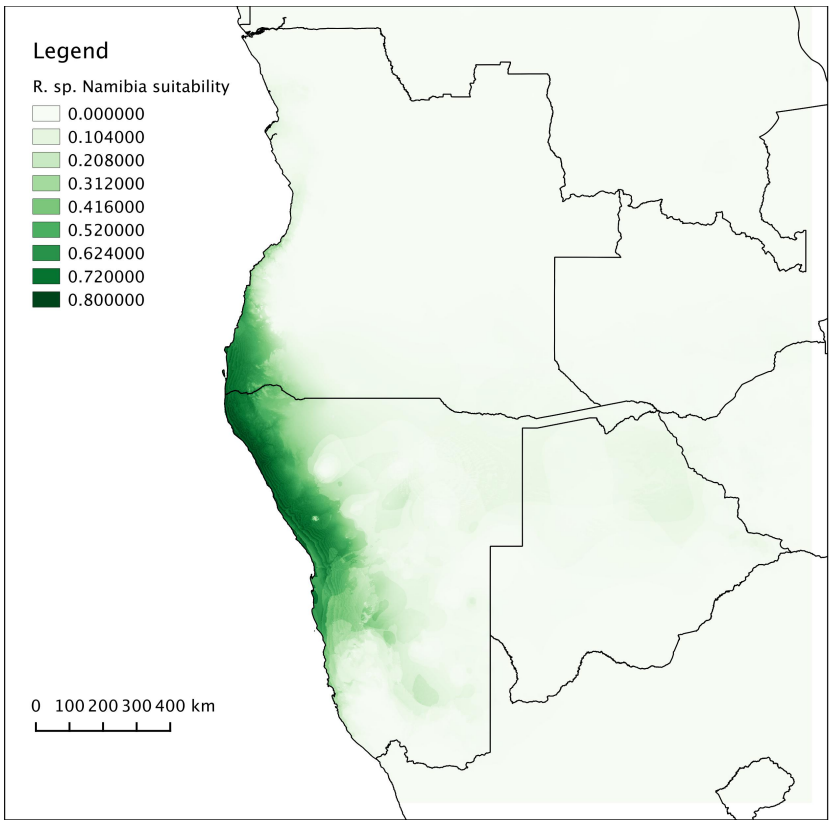


Figure 26. Niche model for *R. sp. Namibia* generated using the MAXENT model.

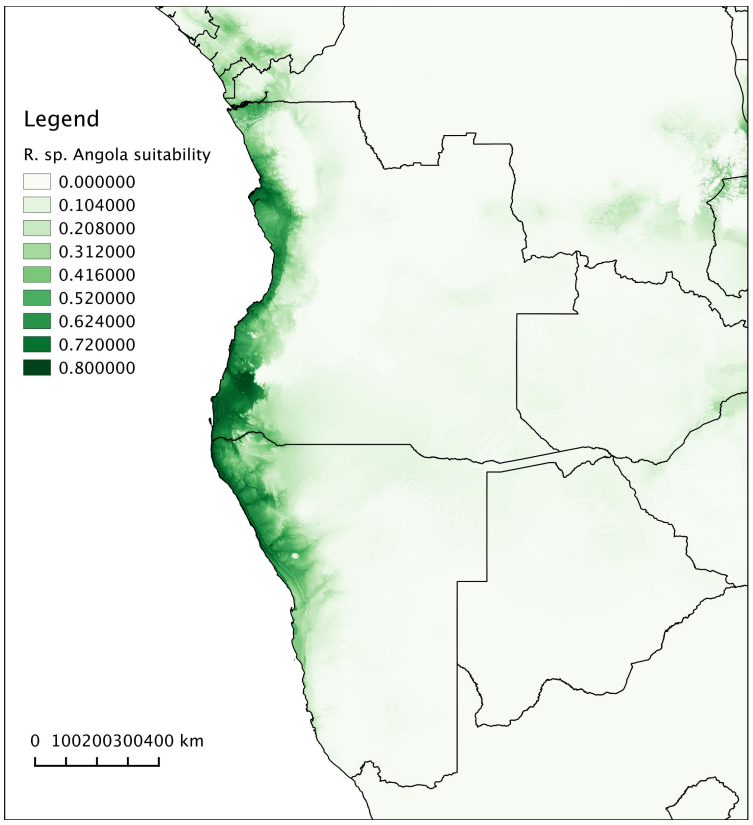


Figure 27. Niche model for *R. sp. Angola* generated using the MAXENT model.

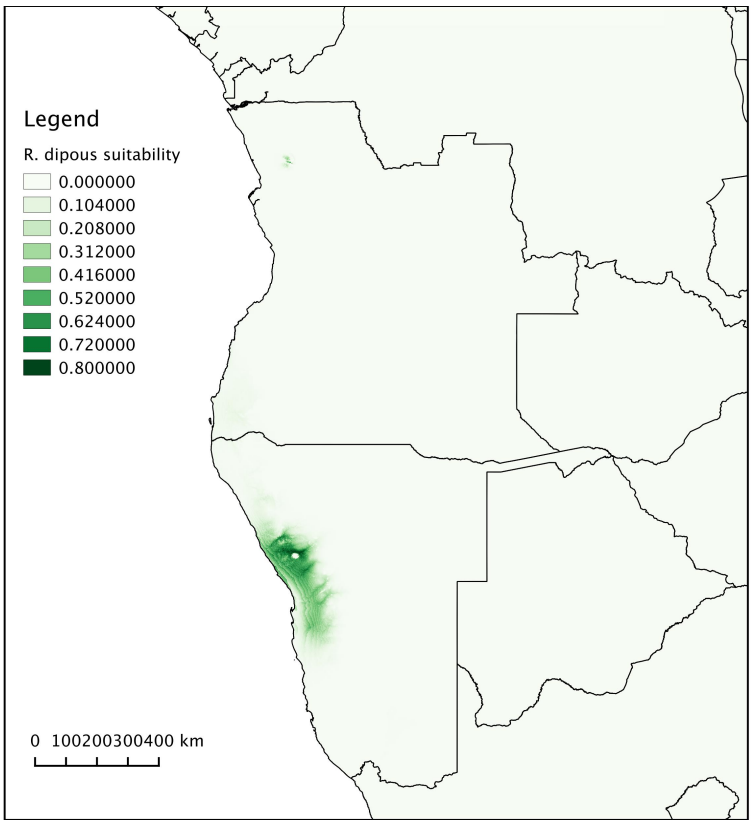


Figure 28. Niche model for *R. diporus* generated using the MAXENT model.

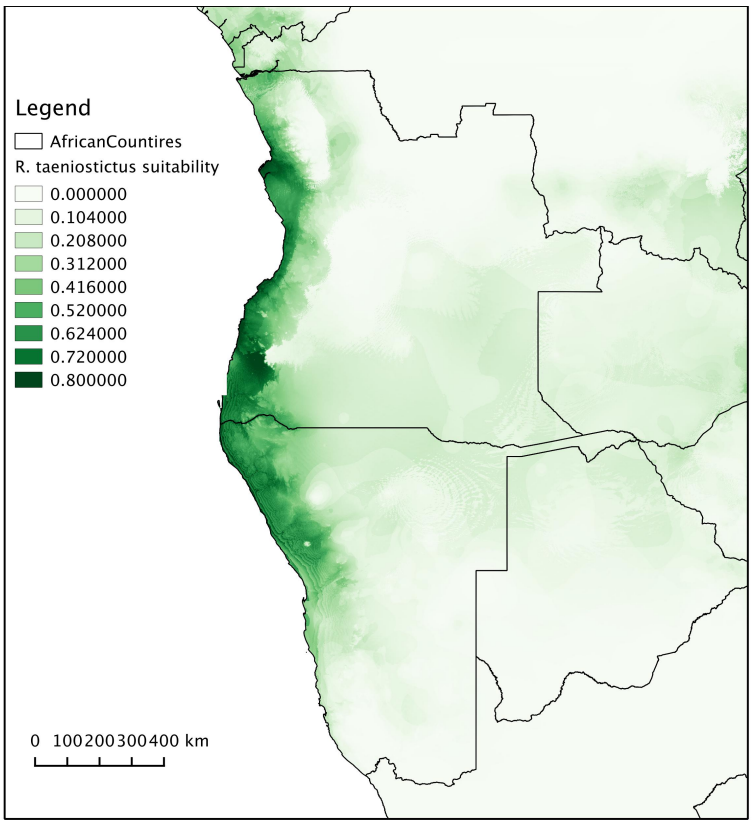


Figure 29. Niche model for *R. taeniostictus* generated using the MAXENT model.

IV. Discussion & broader impacts

Using estensive taxon sampling and multiple lines of genetic evidence, robust phylogenetic results have been used to estimate evolutionary patterns of relationships for Rhoptropus geckos. This data, in concert with collection-based macroecological approaches have been used to investigate genetic and ecological variation occuring accross the extensive latitudinal ranges of several taxa. This research will prove useful to the immediate field of evolutionary biology, but will also present the opportunity to breach the larger scientific sphere by offering other scientists a framework for making comparisons in parallel vertebrate systems (Dunham & Miles 1985).

Prior to this systematic evaluation, the genus *Rhoptropus* contained 9 described species and subspecies, one of which had never been evaluated in a molecular context and an additional two for which full species status had not been considered formally. Only two lineages were known Namibian endemics (*R. bradfieldi* and *R. diporus*), whereas three were considered Angolan endemics. The rest of the species in this group appeared to occupy ranges spanning both countries, long-term political unrest limiting access to necessary specimen collection zones has led to uncertainty regarding this extent and the potential cryptic diversity it might harbor (Bauer & Good, 1996) with little knowledge of the Angolan extent for several. Given the lack of attention and in depth range sampling throughout the systematic history of this group, intrageneric relationships have been elusive and subject to a considerable amount of uncertainty through their early history. Although the taxonomic relationships of these geckos has been hypothesized in the past,

studies have lacked the depth of species sampling and analytical methods necessary to fully understand relationships at the species level (Bauer, Russell & Powell 1996, Lamb & Bauer 2001, Bauer & Lamb 2010). Superficially, these animals are morphologically conserved and navigation amongst species identification is largely dependent upon minor differences in scalation, body size and coloration. This distinction in morphology varies amongst species as well, especially for those taxa with diffuse ranges across multiple landscapes and habitat types. Despite elevation of certain taxa to full specific level and attempts to resolve synonomy, difficult taxonomic issues persist due to misidentification resulting from the morphologically conserved characters and overlapping or unclear range distributions prevalent amongst species.

Through recent collaboration with Angolan Environmental ministries, museum collections, unsampled regions of Angola as well as undersampled inland localities from Namibia have now been relatively well investigated in a molecular context. With this increased sampling, the prospect of at least two undescribed species can be anticipated. Phylogenetic results indicate samples from the Huab Region of northern Namibia as well as well as a potentially distinct lineage from the Angolan Escarpment. Although this genus is not considered species rich in comparison to some of its southern African gekkonid relatives (i.e. *Afroedura*, Jacobsen et al. 2015, *Pachydactylus*, Heinicke et al. 2016), deep investigation of this group has highlighted the importance of further herpetological investigation of the Angolan Escarpment and its endemic biodiversity. Although Namibia may be considered better studied in respect to its biodiversity when compared to a number of other African countries, deeper sampling of groups such as *R. barnardi* as well as *R.*

boultoni has revealed that the true species richness of the Namib region may be underrepresented due to lack of evaluation of cryptic taxa.

A. Species concepts and taxonomic implications

Species concepts are difficult not only because of biological variation of taxonomic groups under consideration, but also because a number of concepts are untestable (Coyne and Orr, 2004). Early definition of species was based on the morphological species concept, which identifies distinguishing characters to define a species (Cracraft, 2000; Mayr, 1996), however theses characters can often be incredibly cryptic and historically overlooking for a topologically similar group of organisms (Buss and Yund, 1989, Winston 1999). This approach does not take into account population level variation that can often be obscured by plastic traits that may be characteristic of certain individuals in a population, but not all and not consistently from generation to generation (Cox 2014). These morphotypes can be indicative of metapopulations, or groups of individuals with lower migration rates due to local extinction and recolonization by the larger inclusive population, discrete populations undergoing speciation, or allelic variants that are adaptively neutral and unlinked to loci under selective pressures and therefore maintained in a population due to a lack of background selection removal (King 1988, Carney et al. 2007). The population level was later address as individuals that were reproductively isolated, otherwise known as the biological species concept (Mayr 1942). Historically, reproductive isolation with the exception of obvious morphological (e.g. body size or reproductive organ variation) or behavioral isolation characters was difficult to identify in museum specimens, therefore proof of this reproductive isolation was difficult to produce

(Mallet 1995, Wheeler 1999). With the onset of molecular and especially next generation sequence data, parameters such as admixture, the number of migrants per generation, and historical population size under a number of different models (i.e. island models, isolation migration models) can lend insight as to the allelic composition of individuals and the overall demographic history of the population. A number of other species concepts have been introduced that may be more taxonomically relevant such as the recognition species concept and the cohesion species concept (Patterson, 1985, Templeton, 1989). For a species oriented point of view, many of these concepts are useful, but say little regarding the evolutionary processes that generated species' separation. The phylogenetic species concept takes this maintenance of monophyly into consideration along with some portions of the biological species concept regarding reproductive isolation (Hennig 1966, Willman 1986). This concept is broad and can be interpreted differentially—in particular, identifications of monophyletic clusters can cause oversplitting of species with respect to the type of data used for phylogenetic estimation and sampling bias, where isolation by distance can be confused with population genetic structure (de Queiroz and Donoghue, 1988). Often, this phylogenetic concept is merged with morphological species concepts to designate monophyletic units with diagnosable charactesr as discrete species (Wheeler and Nixon, 1990), which still may be subject to the pitfalls of uninformative or cryptic characters. This monophyly can be considered more substantially as a group of organisms whose genes have more recently coalesced with one other relative to organisms outside that group (Baum and Donoghue, 1995). This coalescent species concept is particularly important when rates of coalescence amongst genes are variable, and the availability of genetic data lacks genomic coverage (Coyne and Orr, 2004). Often, such as in the case of

rapid radiations, the greater portion of genes examined have not yet sorted, yet the species themselves are unambiguously definitive due to adaptation to a number of novel conditions over an evolutionary period too short to allow for the sorting of all loci (Shaw 2001). The uncertainty of the phylogeny must also be considered in this case, as ILS can confound species tree estimation but not prevent absolute inference of species identity (Avise and Wollenberg, 1997).

Speciation occurs throughout a grey area over many generations – genes may become isolates before or after behavioral aspects prevent interbreeding, thus depending on the point in the process of speciation during which individuals are examined or sampled, a different interpretation may be derived on the isolation of those two lineages. This may also be taxon-specific, for example, subspecies are no longer regarded as valid in squamate studies but historical artifact continues to propagate this species designation in vertebrate groups such as birds and primates (Wilson & Brown 1952, Mayr 1982). In other fields such as diatomic studies, unique morphological characters still best explain divergent taxa as species numbers are high and molecular data is not available for new types identified in the fossil record (Mann 1991, Mayr 1996). Ultimately, because biological and ecological species concepts can conflict with one another depending on the context of the system being examined, for example ring species may be morphologically, geographically and genetically divergent and constitute many distinct lineages, when brought together from geographic isolation they may still interbreed, thus violating the biological species concept (Moritz et al. 1992).

Using secondary criteria or multiple lines of evidence for the identification of independent evolution of metapopulations (unified species concept, DeQuieroz 2007) may be the best approach to avoid incorrect or seemingly conflicting descriptions of delimitation criteria. These lines of evidence can be any mixture of the following concepts: ecological, where species occupy distinct niche space and are therefore diverging (Van Valen 1976, Andersson 1990), and may eventually become reproductively isolated; phylogenetic, where species are reciprocally monophyletic; reproductive, which identifies species due to a lack of hybridization or interbreeding (Hennig 1966, Ridley 1989, Meier and Willmann 2000, Rosen 1979, Donoghue 1985, Mishler 1985); morphological, with unique and divergent characters used to identify underlying genetic divergence (Mayr 1996, Cracraft 2000), or may have morphologically distinct genital morphology that prevents interbreeding; behavioral, species may have non-concertive mating signals, breeding areas or dial patterns, encouraging genetic divergence and hybridization; or genetic (Paterson 1985, Masters et al. 1987, Lambert and Spencer 1995), which states that species may hybridize but form infertile or unviable offspring, ultimately reducing fitness and resulting in a loss of hybrid genotypes and selection against interbreeding (Wright 1940, Mayr 1942, Dobzhansky 1950). The application of these concepts is important, as they lead to the under or over-estimation of biodiversity and therefore inaccurately applied conservation initiatives (Moritz 1994, Agapow 2004). Ultimately, the designation of species may be an anthropogenically-enforced concept to identify units for conservation efforts or to quantify and understand global patterns of biodiversity, whereas the differentiation between populations in reality exists on a continuum of variation across space and time (Cracraft 1983). Although all such lines of evidence cannot be collected

for all independent lineages, several instances of evidence provide strong support for species delimitation. Given this information, in this study the universal species concept is applied, incorporating ecological distinction along with phylogenetic and morphological information to identify independently evolving lineages (e.g., *R. benguellensis* and *R. montanus*). Because these same lines of evidence are not as clear or available for distinct populations of *Rhoptropus* in Namibia and Angola (*R. sp*.), accompaniment of morphological or additional genetic information indicative of reproductive isolation is suggested to confirm or refute the validity of these lineages as independent species.

A. Trait evolution and adaptation

The genus Rhoptropus contains a small but moderately diverse group of species that are both relatively common and accessible due to their diurnal nature and preferred habitats. In addition to being an iconic constituent of the Namib, Rhoptropus has become a model organism for studies of gecko locomotion and adhesion, and the collection and scientific observation of the biology, natural history, physiology and behavior of *Rhoptropus* has been relatively well-studied (Odendaal 1979, Nagy & Seely 1993, Bauer, Russell & Powell 1996, Autumn 1999, Higham & Russell 2010, Gamble et al. 2012, Russell & Johnson 2013). Because past phylogenetic investigation of the group has been limited, however, such studies have been restricted in their understanding of trait evolution and adaptations, which require a well-supported phylogenetic context (Bauer, Russell & Powell 1996, Lamb & Bauer 2001, Bauer & Lamb 2010). This study will therefore prove useful to the immediate field of evolutionary biology, but will also offering other scientists a framework for making comparisons in parallel vertebrate systems and an opportunity to

explore the evolution of morphological and physiological traits in *Rhoptropus* and the adapative evolution of desert taxa (Dunham & Miles 1985).

B. Cryptic species & conservation

The data presented here is also useful in the identification cryptic species, which are especially common among morphologically similar genera such as *Rhoptropus* (Bickford et al. 2007). It is important to note that the restrictive desert habitats and morphologically conserved characters of many *Rhoptropus* geckos contribute significantly to endangerment of certain species. Characterizing the true biodiversity of this region will therefore be important to future conservation evaluation with respect to future anthropogenic land use change (Herbert et al. 2004, Robertson et al. 1998).

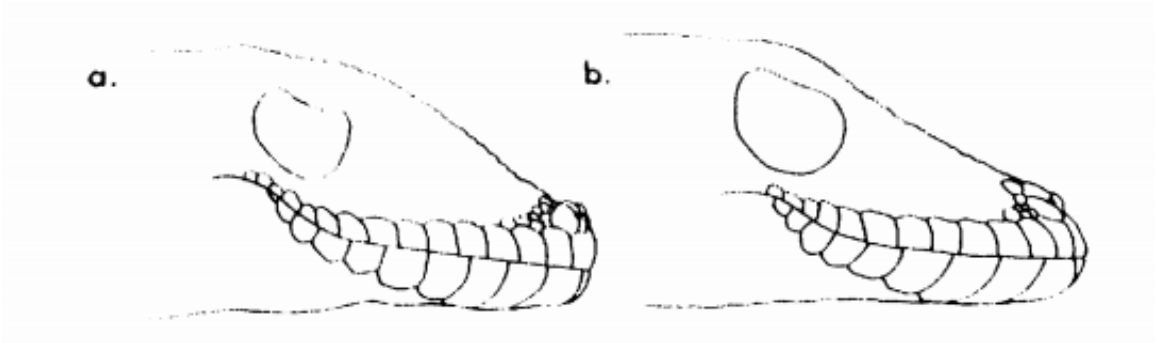
Preliminary studies have revealed that the taxonomic composition of the Escarpment region in Angola is incredibly unique with respect to the more xeric, lowland groups present in southwestern Angola (Brennan et al. 2016, in prep., Ceríaco et al. 2016). As the political state in Angola has prevented field collection during the advent of progressive molecular phylogenetic techniques, many described and putatively new species have never been included in a molecular phylogeny to date. For this reason, the unknown genetic distinctiveness and distribution of these organisms prevents adequate conservation assessment. Although a few studies have lent insight to the potential for extreme endemism in the Escarpment region, total vertebrate diversity remains unclear (Huntley & Matos 1994, Dombo et al. 2002, Cowling, Hilton-Taylor1994, Figueiredo 2010, IUCN 1990). Many Namibian taxa reach their northernmost extent in Angola, and the possibility for parapatric speciation at the edges of these ranges has never been investigated. While

habitat loss is less of a concern in the sparsely populated regions of the country, areas adjacent to major cities have been subjected to substantial deforestation and anthropogenic desertification. Angola is particularly rich in mineral and petroleum reserves, and as the country continues to stabilize, mining and prospecting are predicted to increase (Huntley and Matos 1994). Unlike the southwestern extent of the Namib in Angola, that falls partially within the extent of Iona National Park, the escarpment region as well as important central and southern forests are entirely unprotected to date (Huntley and Matos 1994, Dean 2001, Cohen et al. 2004, Sekercioglu & Riley 2005). There has also been a scarcity of research conducted on the Namibian Escarpment and associated pro-Namib fauna (Simmons et al. 1998), and many portions of this habitat remain unprotected. Communitiy conservation initiates in Namibia are relatively well established, however a number of critical areas such as the Kaokoveld Escarpment still require attention (Barnard 1998, Van Wyk & Smith 2001). Private Game Reserves offer protection for a number of isolated habitats, however this form of protection is only tentative and unstable without implementation of conservation initiates and agreements with the community (Barnard et al. 1998). Although portions of this region may not boast the endemic diversity seen in the Angolan Escarpment, the conservation activity of this country is important along another thread. Namibia conservation initiatives also serve to protect the biodiversity of neighboring Angola. For Escarpment and desert endemics shared between the two countries, only Namibia has the resources at present to prevent land use change. Until the protection network of Angola is better better developed, it is important to assess and update regional biodiversity in Namibia for these shared habitats (Simmons et al. 1998). Already, it can be seen that investigation of the position of previously unsampled Angolan

taxa has revealed the specific status of *R. benguellensis* and *R. montanus* as well as a putatively new lineage from the escarpment related to *R. barnardi group* animals. The assessment of taxa from northern Namibia has identified a putatively distinct lineage as well, lending support to the wealth of unrecognized biodiversity in the Namib Desert.

CHAPTER 2

Diversification of the genus *Rhoptropus*



"Look closely at nature.
Every species is a masterpiece,
exquisitely adapted to the particular environment
in which it has survived.
Who are we to destroy or even diminish biodiversity?"

— Edward Osborne Wilson

[Illustration: labial scales of *R. diporus* (a) and *R. boultoni* (a), from Schmidt 1933]

I. Introduction

A. The Namib Desert

1. Current conditions

a. Geography

The Namib Desert covers nearly 135,000 square kilometers and stretches along some 2,000 km from the Carunamba River of the Namib Province in southern Angola across the length of Namibia to the mouth of the Orange River in the Cape Province of South Africa. Covering just 15% of Namibia's total land area, it is bounded in the west by the cool Atlantic ocean, but the eastern extent is more arbitrary and roughly coincides with the 1000 m altitude or 100 mm rainfall zone, although pro-Namib conditions persist further inland. Despite its great longitudinal expanse, the width of this desert rarely exceeds 100 m, bordering the Great Western Escarpment in the northeast and gradually transitioning into the Kalahari and Karoo Deserts in the southeast.

b. Climate

Rainfall is scarce in the Namib (5–85 mm/yr); potable water is found only as sub-flow beneath streambeds chiefly of streams that rise in the rainy plateau east of the escarpment (Sharon 1981) but coastal fogs resulting from interactions between waters of the offshore Benguella Current and warmer desert air supply a small degree of consistent moisture (Olivier & Stockton 1989; Olivier 1995). The advective fog does not persist further than

30 km inland and marks the narrow strip between the cold Atlantic Ocean and the hot inland desert. This current also moderates the desert's climate to some degree; temperatures of the coastal region are generally mild, ranging between 14–20^{o}C in the warm season and 7–13^{o}C in the cool season (Olivier, 1995). Inland, continental conditions take precedence, with summer temperatures reaching around 25^{o}C on average during the day and may drop near or below freezing at night. The air is often near saturation point, with humidity at 100 percent for 19 hours/day in the warm season and 11 hrs/day in the cool season (Goudie 2002). The southern portions of the Namib (Lüderitz and south) are subtropical and under a winter rainfall regime, while the central and northwest escarpment region is a semi-arid transition zone (Pickford 2000, Pickford & Senut 1997, 1999, Senut et al. 2009, Ward et al. 1993; see Figure 3).

c. Landscape

Within the Namib, several distinct types of terrestrial habitats prevail: continual flat gravel and bedrock plains, transitional savanna in regions in the eastern-most regions, coastal wetlands, bare rock mountains, linear oases supported by temporary rivers, and an extensive "sand sea" south of the Kuiseb River with island of dark rocky outcrops and inselbergs along the coast between Walvis Bay and Swakopmund (Logan 1969). With the exception of the Cuenen and Orange Rivers at the northern and southern extent of Namibia, respectively, most rivers in this region are intermittent, flow underground, and do not drain oceanically (however the Swakop Omaruru Rivers do occasionally). Overall vegetation is sparse, but low succulent bush habitat is intermittently found in the heavy fog zone near the hyper-arid coast where rainfall is nearly absent and temperature

fluctuations are extreme (Olivier, 1995). Along the eastern border, a thin to moderate cover of annual grasses appears in most years (Van Damme 1991). The desert is primarily contained on a broad plateau eroded into bedrock that slopes gradually from the coastline to the Great Western Escarpment around 900 meters (Figure 5), coinciding roughly with the 300 mm rainfall zone (Figure 4). Subtropically, the landscape largely consists of undulating sandy slopes with the highest sand dunes found in the world (up to approx. 250 m). In the southern and central portions, the terrain is overtaken by steep montane isolations (Logan 1969, Figure 5).

d. Biodiversity

Despite its seemingly harsh landscape, the Namib Desert provides a considerable scope of climatic and ecological variation throughout its extent (Craven & Marais 1992). This variety has allowed for an explosion of speciation across many taxonomic lineages occupying discrete areas of endemism (Simmons 1998, Maggs et al. 1998, Griffin 1998, Barnard 1998, Craven & Voster 2006, Figure 30). In particular, one group that has done exceptionally well in the Namib environment is the family Gekkonidae. Within this family, an upwards of 40 species of gecko are currently known from the Namib Desert region, and many new species still await description (Branch 1999a, Cumulative Effects Analysis 7.7, A. M. Bauer unpbl.). Perhaps the most impressive diversity is found in those groups which normally are cryptic yet display remarkable adaptations for survival in the Namib (Brain 1963, Figure 30). Because many gekkonids exhibit highly derived substrate specificity and the Namib Desert offers a unique array of habitat types, niche partitioning has largely influenced this species richness seen today (Bauer 1999). In addition to its

impressive diversity, the number of endemic reptiles in this region exceeds that of other vertebrate groups (Griffin 2000, 2003). Having the second lowest human population in the world (approx. 2 million, 2015 Human Development Report), anthropogenic influence on these desert species has been relatively low in the past (Martinez et al. 2013). Despite this, some species have recently become conservation priorities on the basis of endemicity and rarity as mining activities, bush encroachment, and climate change all pose potential threats to Namib biodiversity (Griffin et al. 1989, Herrman and Branch 2010).

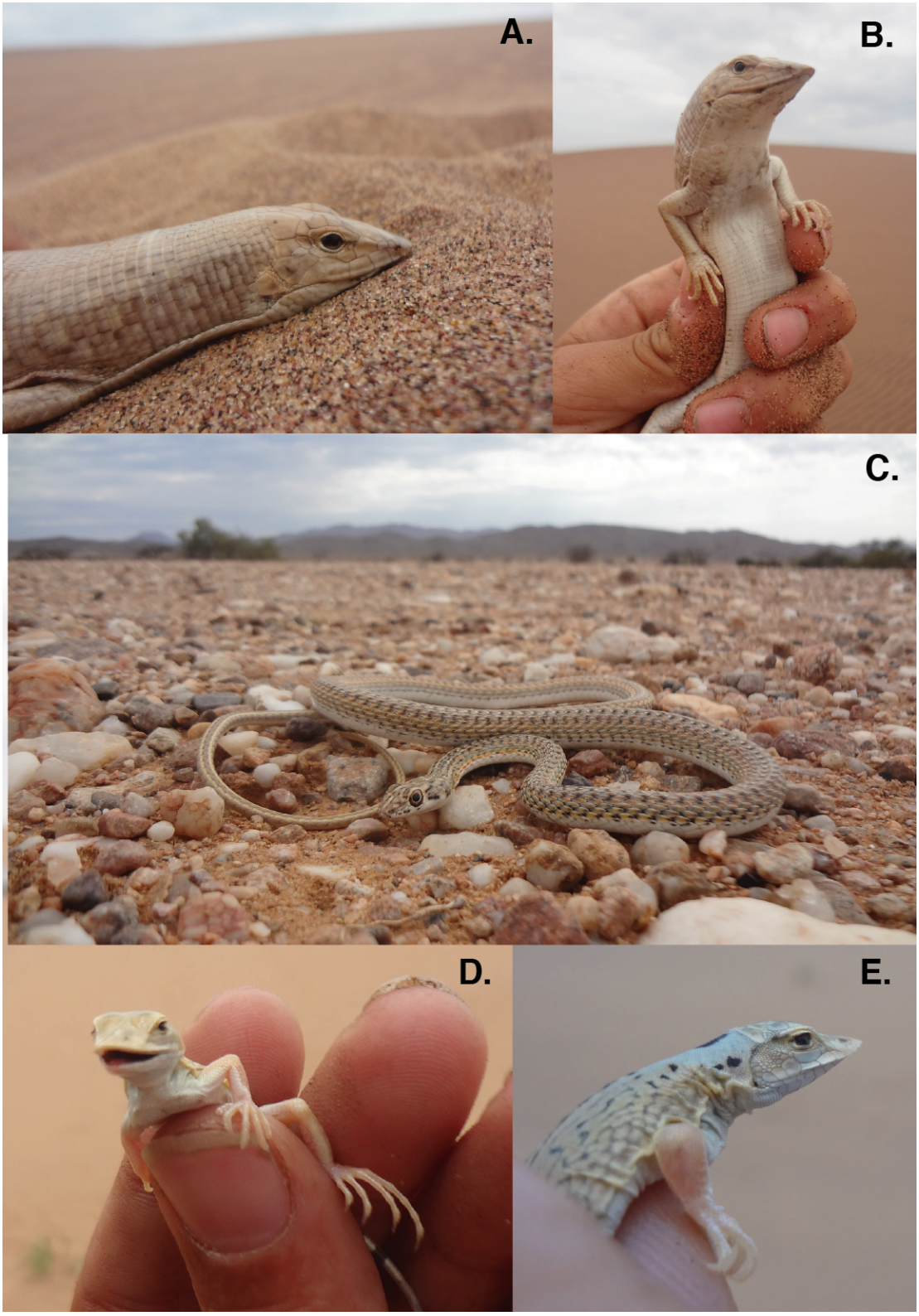


Figure 30. Representative squamate Namib specialists (A-B) *Angolosaurus skoogi,* (C) *Psammophis cf. namibensis,* (D-E*) Meroles anchiete.*

2. Historical content

a. Historical climate of the Namib

Long since considered to be one of the oldest deserts in the world, the actual age of the Namib Desert remains somewhat ambiguous (Hartley et al. 2005, Ward et al., 1983). Different parts of the southern African continent became arid at different times, with desertification beginning in the Namib as early as 17–16 Ma, much older than present-day Sahara and other African deserts, where aridification began around 7–8 Ma and Plio-Pleistocene, respectively (Senut et al. 2009, Schuster et al. 2006, Sepulchre et al. 2006, Zhang 2014, Figure 31). As a result, the fauna of the Namib had a long period of time to adapt to arid, unstable climate. When new arid habitat became available in other regions of southern and eastern Africa in the Late Miocene and Plio-Pleistocene (8–7 Ma, Schuster et al. 2006), several Namib lineages expanded into these developing arid niches before local fauna could fully adapt (Senut et al. 2009). This explains the degree of impact the Namib has had on the overall biodiversity of Africa, with a specific emphasis on old lineages with long standing arid adaptations (Pickford & Senut 1999).

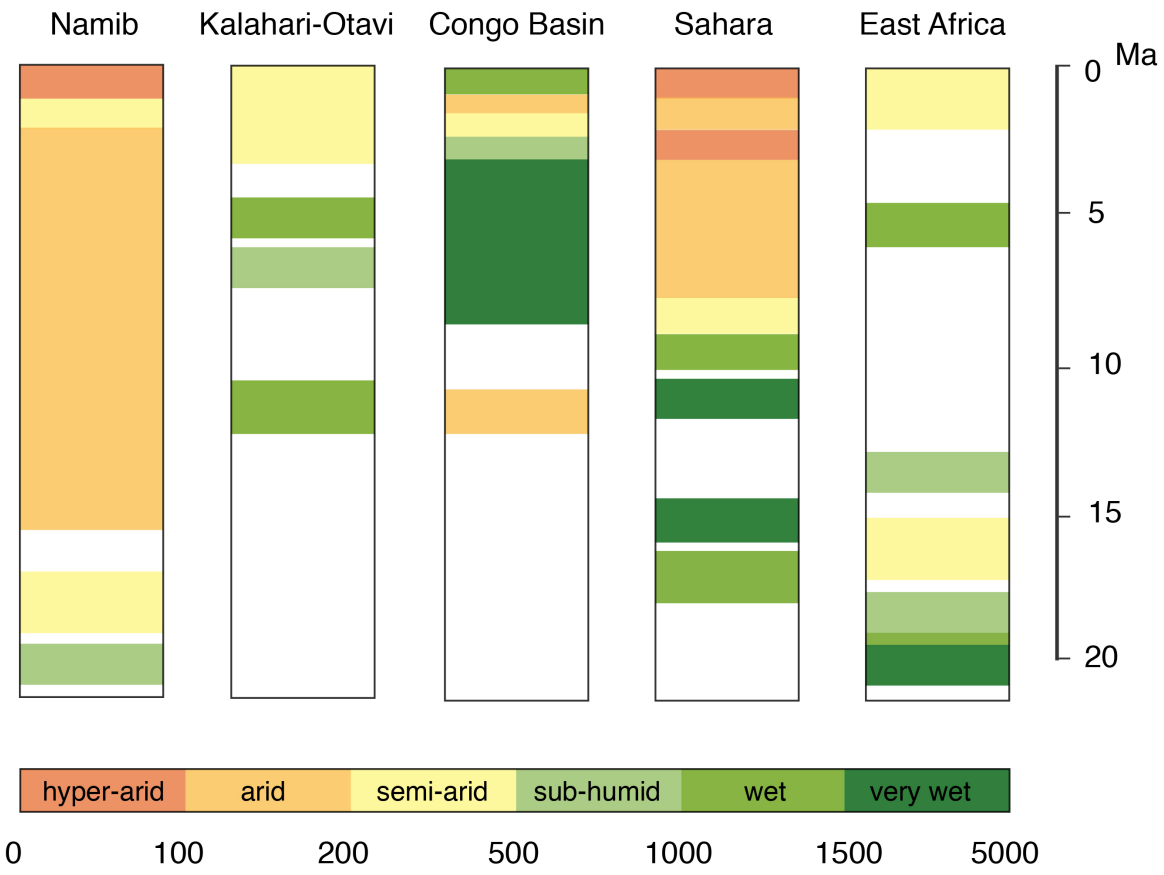


Figure 31. Complex history of desertification in Africa based on fossil record evidence; note earliest evidence of arid conditions in Africa in the Namib, with comparatively few fluctuations in this climatic progression, as well as the progression of tropical climate in certain zones neighboring regions that were progressing at the same time towards aridity. Numerical values represent estimated mm of rainfall for given classifications of climatic conditions, white zones indicate a lack of fossil data available for climatic estiamtion (modified from Senut et al. 2009).

Present xeric conditions seen along the coast of southwest Africa are maintained by the cold Benguella Current, aridification by the South Atlantic anticyclone, southeast trade wind divergence, and cold Atlantic Central Water upwelling (Vincent 1972, van Zinderen Bakker 1975). Although it appears that at least semi-arid conditions have ultimately persisted over time, the extent of the hyper-arid zone has undergone a northwards shift and the pro-Namib region may have been subject to increased moisture (van Zinderen Bakker

1955). During glacial times, temperatures in general for this region were dramatically lower, causing the Benguella Current to shift northwards, subsequently causing an invasion of these arid conditions in the north, but never reaching as far as the Sahara (van Zinderen Bakker & Desmond Clarck 1962, Koch 1960, van Zindeen Bakker 1963). These colder periods also brought increasing rainfall to inland areas, possibly impacting gekkonid populations occurring living on rocky mountain isolates related to more eastern mesic taxa (W. D. Haacke, Pickford et al. 2006). Because such reptiles occurring inland that are related to strict arid-adapted constituents may date back to the last glacial period, and the importance of temporal relationships for these groups is critical in understanding the approximate age of the Namib Desert Biome using such bioclimatic indicators (Balinsky 1962, Volk 1964, Koch 1960, Mertens 1955, Korn & Martin 1937, Foissner 2002).

b. The age of the Namib

i. Controversy

The true age of the Namib Desert, and likewise its placeholder as the oldest desert in the world, has been historically debated in the literature. Although these two main lines of thought are still frequently referenced, new geological and paleontological findings are continually being evaluated to better hone in on the true sequence events that have produced present day conditions. The earliest arguments regarding the age of the Namib were based on present day diversity of plants and beetles. To procure this vast diversity

and species richness, it has been proposed long periods of evolutionary time must have been necessary (Koch, 1961, 1962). The other side of this debated a much younger age for the Namib—mid-Miocene at the oldest—on the basis of geomorphological evidence (Patridge and Maud, 1987). Intermediate sides of this argument have also been taken, proposing Eocene origins of progressive aridification (Ward & Corbett 1990). Geomorphological evidence has been known to mislead the approximation of these dates in the past (Rust 1974, 1988b), but overall paleontological evidence of the fauna and flora of the region and surrounding ocean coupled with sound geomorphological finds have proven useful in the estimation of desertification events (e.g. Ward et al.1993, Pickford 2002, Pickford & Senut 1999, Dupont et al. 2005, Senut et al., 2009). Previously solidified approximations are continuously challenged with new findings, such as the discovery that climate within the early Quaternary did not progress continuously towards present day conditions but rather experienced fluctuations in northwest Namibia (Eitel 2005, Eitel et al. 2002). Because of the uncertainty that still surrounds understanding of these aridification events, contemporary biological studies of diversification events of endemic desert lineages can be used to reinforce or refute previous approximations (Richardson et al. 2001, Steckel et al. 2010). See Table 10 for a summary of key aridification events in the Namib region.

Table 10. Key southern African climatic events and timeline associated with the aridification of the Namib Desert region

Event	Region	Date	Evidence	Reference
Progressive decrease in regional humidity	NW Namibia	Holocene, ca. 3800 cal yr BP	Fossilized rock Procavia capensis dung middens provide stable nitrogen isotope data	Chase et al. 2010
Precipitation fluctuation	Damaraland & Kaokoveld regions	Late Pleistocene, 19000 cal yr BP	radiocarbon dating of trees and luminescence dating of sediments buried endoreic sediment shows a decrease in sediment runoff indicating increasingly aridified conditions	Eitel 2005, Eitel et al. 2002
Dessication and more winter rainfall	SW Africa	Early Pleistocene, 2.2 Ma	fossil pollen data	Dupont et al 2005
Cooling of Indian Ocean surface temperature and glacial/interglacial cycles leads to spreading of grassland	SW Africa	Early Pliocene, 5-3 Ma	global historical sea temperature data	Cane and Molnar 2001, deMenocal 2004
Increased rainfall and humidity	Western Escarpment	Early Pliocene, 5 Ma	uplift of the East African escarpment (rift system)	Sepulchre et al 2006, Cerling et al 1997
Conversion of woodlands to grasslands	North and South	Late Miocene, 8-6 Ma	isotope studies, atmospheric CO2 decrease	Cerling et al 1997
Benguella Upelling System causes summer drought in southern namibia, Start of southern desertification in the Namib, Benguela Current was forced northward along the southwest African	North and South	Middle-Late Miocene, 16-7 Ma	diversification of cape floristic fauna determined from fossil pollen data + terrestrial flora data as well as dated diversification evens	Senut et al. 2009. Dupont et al 2011
Global oceanic cooling, expansion of the Antarctic Ice cap, hyper arid conditions in the north	Northern Namib	Early Miocene	global paleoclimatic data from ice sheet and sea level rise	Pickford, 1998, 2002; Pickford & Senut, 1997, 1999; Senut et al., 1994, 2009; Ward et al., 1993
Onset of desertification in the south, conditions become temperate and winter rainfall regime begins	Northern Namib	Early Miocene 17-16 Ma	discovery of fossil mammals and bird eggshells in Namib aeolianites.	Pickford 2000
Onset of aridification in the north	Northern Namib	Late Oligocene 22 Ma	Tracing stable isotopes in eggshells and mammalian enamel	Pickford 2011

Northern Namib reigon had permanent water; southern Namib region had temporary water and dry	North and South	Mid Eocene	Northern region dominated by anuran fauna in the Eocene (Pipids, Ranoids) — indicates permanent water and aquatic systems. In the south, fresh water mollusc and ostacod fossils indicate temporary water sources. Presence of amphisbaenid fossils lends support to warm–mediterannian climate in southern region.	Pickford et al 2008a, 2008b; Pickford et al., 2011; Rage et al., 2013
Early evidence of semi-arid conditions	Southern Namibia, Klinghardt Mountains	Mid Eocene, Bartonian, 38-41 Ma	fossiliferous limestone deposits – (small mammals) found in western foothills	Pickford et al 2013, Padayachee & Proches 2016
Tropical condistions persist. Region relatively well vegetated, and under a summer rainfall regime	Southern Namibia, Sperrgebiet region	Early-Mid Eocene, Lutetian, 48-41 Ma	fossiliferous deposits	Pickford et al 2008

ii. Time calibrated species trees

Presently, some agreement exists in the literature for the age of origins for The Namib Desert sometime in the Early Miocene, with substantial periods of glaciation and subsequent aridification that are less well known (Ward et al.1993, Pickford 2002, Pickford & Senut 1999, Dupont et al. 2005, Senut et al., 2009). Temporally, the earliest indication of aridified climatic shifts from vegetated, tropical conditions with a summer rainfall regime (conditions confirmed from fossiliferous findings in the Sperrgebiet region of the Southern Namib dated to the Lutetian, 48-41 Ma, Pickford et al. 2008) was derived from fossiliferous limestone deposits of small mammals in the western foothills of the Klinghardt Mountains in southern Namibia from the Bartonian period of the Mid-Eocene (38-41 Ma). Collectively, the fossiliferous finds from Silica North, Silica South, Eocliff and Black Crow have been important to present day understanding of divergent progression of Mid-Eocene conditions in the north and south of the Namib. The fauna in the northern portion of present-day Namib was predominantly anuran fauna with confirmed presence of fresh water mollusks and ostracods implying some permanent water sources and aquatic systems, whereas in the south, some composition of grazing mammals and terrestrial molluscs was present, indicating grasslands, temporary water reserves and subhumid to semi-arid conditions were warm but dry (Pickford et al. 2013, Padayachee & Proches 2016). Collectively, the fossiliferous finds from Silica North, Silica South, Eocliff and Black Crow have been important to present day understanding of progression of Mid-Eocene conditions. The fauna in the northern portion of present-day Namib was predomnantly anuran fauna with confirmed presence of fresh water mollusks, ostracods and amphisbaenids, implying some permanent water sources and aquatic

systems, whereas in the south, some composition of grazing mammals and terrestrial molluscs was present, indicating grasslands, temporary water reserves and subhumid to semi-arid conditions were warm but dry (Pickford et al. 2008a, 2008b, Pickford et al. 2011, Rage et al. 2013). Although this has been the earliest evidence of climatic shifts towards the desert conditions observed today, the progression is estimation to have intensified in the Early Miocene 17–16 Ma. Fossil mammals and bird eggshells recovered from Namib aeolianites found south of Walvis Bay indicate a shift from subtropical conditions to temperate conditions and a shift from a summer rainfall regime to a winter rainfall regime, similar to this region's present-day climatic conditions (Pickford 2000). After ths time, global oceanic cooling and the expansion of the Antarctic Ice cap likely influenced the onset of hyper arid conditions in the north (Pickford 1998, 2002, Pickford & Senut 1997, 1999, Senut et al. 1994, 2009, Ward et al. 1993). In the Middle-Late Miocene, 16–7 Ma pollen data, tracing stable isotopes in eggshells and mammalian enamel as well as terrestrial flora diversification data suggest hyper-aridifcation begins in the Southwest, proceeds northwards and eastwards. At the time, the Benguell Upwelling System causes summer drought in southern Namibia, start of southern desertification in the Namib, Benguella Current was forced northward along the southwest Africa (Senut et al. 2009. Dupont et al. 2011). This period, approximately 16–17 Ma, marks the potential onset of hyper arid conditions in the Namib. In the late Miocene, isotopic studies revealed atmospheric CO_2 decrease as a result of the conversion of woodland to grassland in sub-saharran Africa (Cerling et al. 1997). At this time, other portions of the African sub continent were becoming dreir, however this onset was much later than that estimated for the Namib (Figure 5). Uplift of the West African Escarpment caused decreased rainfall

and humidity along the Namib coast in the Mid-Miocene as well. While the eastern branch began uplift as early as Eocene–Oligocene times, the western branch began to develop much later (Sepulchre et al. 2006, Cerling et al. 1997). In the Pliocene/Pleistocene, the Cooling of the Indian Ocean surface temperature and glacial/interglacial cycles happening globally at this time lead to the continuedspreading of grassland in previous forested areas in sub-Saharran Africa (Cane and Molnar 2001, deMenocal 2004). Regardless of the assumption that aridification was naturally progressive, periods of fluctuation in the Late Pleistocene have been identified. A decrease in sediment runoff indicating increasingly aridified conditions was found in the Sperrgebeit Region, which contemporarily receives more rainfall now than it did during the Little Ice Age (Eitel 2005, Eitel et al. 2002). This period was followed by a genera decrease in humidity post-fluctuation during the Holocene in northwestern Namibia according to stable nitrogen isotope data fossilized rock *Procavia capensis* dung middens (Chase et al. 2010, Figure 32).

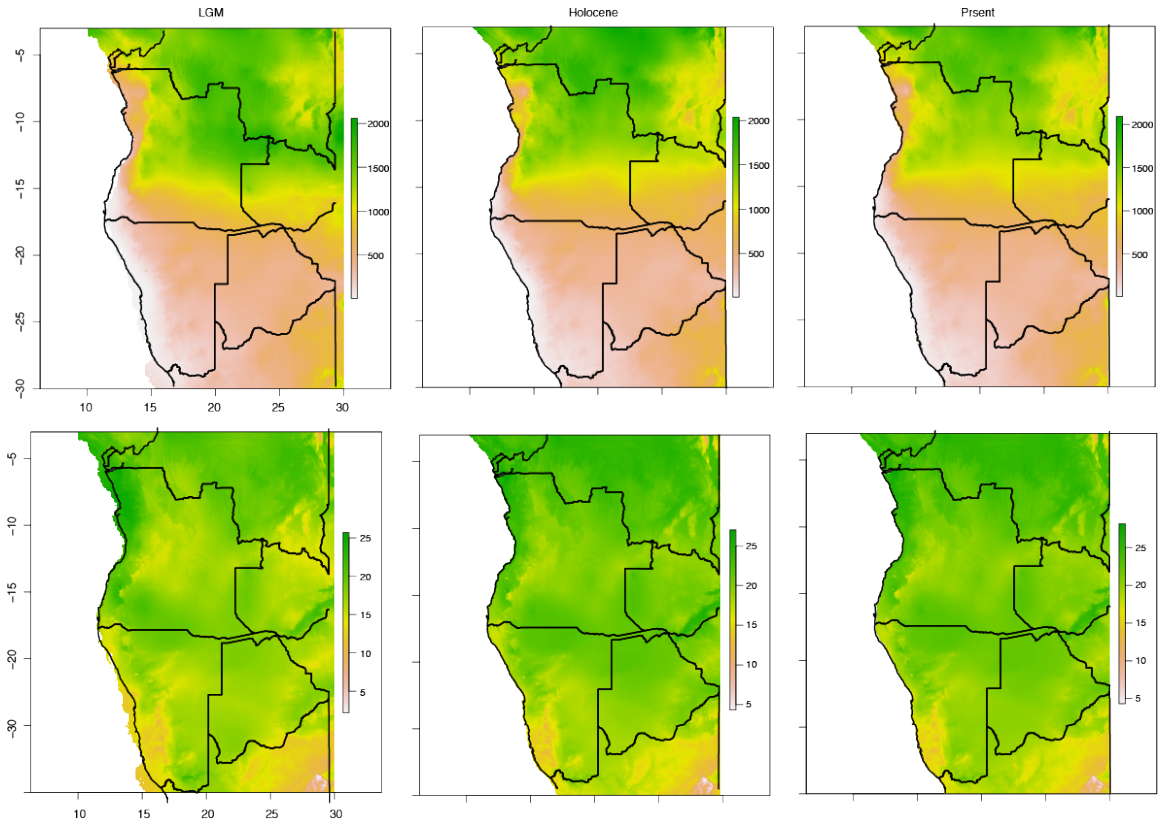


Figure 32. Progressive shifts in annual rainfall (top) and annual mean temperature for southwestern Africa. Downscaled and calibrated climate data from simulations with Global Climate Model CCSM4 were used for paleoclimatic projections for the Last Glacial Maximum (LGM, approx. 22 kyr) and Mid-Holocene (approx. 6 kyr) at 2.5 minute spatial resolution. Contemporary climate data were obtained from weather stations on a 30 arc-second resolution grid (Hijmans et al. 2005, WorldClim).

Because the age of the Namib Desert is largely controversial and *Rhoptropus* is autochthonous to the region, it is an ideal group for further investigation of this issue for several reasons. Whereas most vertebrate groups have autapomorphic species in non-arid groups that have adapted to this extreme habitat, this group is entirely contained within the Namib Desert, including the hyper-arid regions (Branch 1999a). This characteristic of *Rhoptropus* in addition to a small but well sampled number of species allows for investigation of *in situ* cladogenesis within the context of the Namib. Allozymic studies of

the genus *Rhoptropus* indicate an Early to Mid-Tertiary origin of the group, however, characteristics of allozyme-based studies render this information subject to a large degree of temporal error (Bauer and Good, 1996). The use of time calibrated phylogenetic analyses that implement a molecular clock and multilocus species-level approach, it is be possible to estimate not only the age of origin for the genus *Rhoptropus*, but also the comparable ages of all intrageneric divergences, and thus potential climatic shifts for the Namib at these critical times.

iii. Molecular clocks and species divergence estimates

Based on the observation that genetic mutations occur at a relatively constant rate, molecular clocks measure the number of changes that accumulate in the gene sequences of different species over time. The molecular clock assumes that differences in DNA sequence between two species are proportional to the time elapsed since divergence from the Most Recent Common Ancestor (MRCA). For these ultrametric tree estimations, branch lengths will be proportional to time (Zuckerkandl and Pauling 1965). Another assumption of the molecular clock theory is that the number of differences between any two-gene sequences increases over time, therefore the number of mutations in a given sequence of DNA can be used to measure evolutionary time. This information can be used to determine the fixed date of species divergences from a common ancestor (Runnegar 1982). Such clocks must be calibrated with known dates to determine this rate of mutation. Because information from fossil taxa is fairly scarce with respect to squamates as a whole, the molecular clock is useful because it allows the rate of genetic change from dated fossil divergences to be applied to speciation events for which no fossil data is

available (Benton & Ayala 2003, Benton & Donoghue 2007). The fossil record itself is by no means perfect (Hedges & Kumar 2004, Van Tuinen & Hadly 2004, Reisz & Muller 2004). It is evident from empirical data that not all lineages evolve at similar rates for most organisms. Using a relaxed molecular clock allows you to incorporate independent rate heterogeneity per branch into a dating analysis when there is prior evidence that mutation is accumulating at different rates throughout the trees. To test for clock-like evolution of DNA sequences, a Relative Rates Test or Likelihood Ratio Test can be used. Relative Rates Test (RRT) compares the distance between the ancestor and one descendant relative to the distance between the same ancestor and another descendant. If mutations are constant, the difference between these two distances should effectively be zero, but this can be problematic to calculate when the tree topology is uncertain. A Likelihood Ratio Test (LRT) estimates two models and compares the fit of one model to the fit of the other with penalization for model parameterization, as overly complex models will always have a better fit, but with less predictive power. To calibrate rates of evolution on a phylogenetic tree in the absence of a molecular clock, a variety of calibration sources can provide information with varying degrees of certainty. The best source of relative rates to be used for absolute age estimation is the fossil record. A species' first record of appearance in the fossil record likely represents peak abundance rather than first emergence. The ages of these fossils are typically used as minimum constraints as the lineage cannot be younger than this age, but could certainly have been prevalent prior to the date of the only discovered specimen or series of specimens. Geological calibrations can be assigned to internal nodes. The assumption behind this class of calibrations is that divergence at the calibrated node was the result of a new

geological barrier (such as a mountain or river), either via continental vicariance or dispersal to oceanic islands. Geological calibrations must be used conservatively when examining biogeographical patterns to avoid circular inference, particularly so because they rely solely on the accuracy of dated geological structures and knowledge of historical distribution. Volcanic islands can be used as maximum age constraints, given the lesser certaining regarding the time of ancestral island colonization for endemic lineages, and the greater certainty that the ancestor of the endemic island species did not arrive before the island was formed. When geological or fossil calibrations are not available, secondary or indirect calibrations can be applied. These classes of calibrations use estimates of divergence and rates of molecular evolution from independent molecular dating studies and apply them to nodes in a tree with agreeing topology and taxa and using a linear regression across all nodes, dates can be estimated for the secondary tree. This method must be used with caution as error or bias in the primary dataset from which the secondary estimates will be propagated or even magnified in the new dating analysis. Finally, studies using paleoclimatic data for calibration data have been seen in the literature, where the origin of climatic conditions presumed to be essential for the survival of a particularly adapted group can be taken as a soft maximum age (Baldwin and Sanderson, 1998). This method is limited and relies too heavily on assumptions of unknown historic range, adaptation and thermal limits of species and dates inferred using such calibrations for terrestrial vertebrates should be interpreted with caution.

The availability of molecular sequence data may also constrain the ability to accurately interpret evolutionary events (Rodrı´guez-Trelles et al. 2003, Reisz & Muller 2004).

Although it has been observed that absolute age estimations can vary considerably depending on (1) calibration point selection, (2) completeness of sequence data and (3) analytical methods used relative ages tend to be approximately consistent across method and calibration types (Porter et al. 2005). By incorporating multiple, well-informed calibration points and overall complete sequence data, robust time tree calibrations are able to uncover the temporal, ecological and environmental context of evolutionary events (Kumar 2005).

II. Materials & methods

1. Taxon sampling

Sequence data for the following gekkotan families were included in the analysis in order to capture all relevant fossil and geological calibrations: gekkotans (Diplodactylidae (40 individuals), Eublepharidae (9 individuals), Gekkonidae (158 individuals), Phyllodactilidae (26 individuals), Sphaerodactylidae (42 individuals), and Pygopodidae (10 individuals). The following taxa were used as a squamate outgroup to Gekkota: *Amphisbaena alba, Anolis carolinensis*, *Aspidoscelis tigris*, *Dibamus bouretti*, *Elgaria kingie*, *Gallus gallus*, *Heloderma suspectum*, *Plestiodon inexpectatus*, *Podarcis sicula*, *Ramphotyphlops braminus*, *Rhineura floridana*, *Sphenodon punctatus*, *Tiliqua rugosa*, *Xantusia vigilis*, *Trioceros jacksonii* and *Python molurus* (see Gamble et al. 2015, Supplemental 2).

2. Sequence alignment and partitioning

The majority of non-*Rhoptropus* samples included in this analyses were previously sequenced and aligned for use in other studies (Gamble 2008, Gamble et al. 2015, Heinicke et al. 2016). Alignments for Gamble et al. 2015 were obtained from DataDryad, checked to ensure no stop codons were incorporated into the alignment, and reduced to match the concatenated loci dataset (ND2, mitochondrial, RAG1) available for *Rhoptropus*.

The best models of sequence evolution for the mitochondrial and nuclear datasets were determined using PartitionFinder v1.1.1 with penalization imparted for the number of parameters used in each model (Lanfear et al. 2012). The 'BEAST' PartitionFinder model used was used, meaning that parameterization schemes specifically employed in the context of the assumptions allowed by the program BEAST were explored. Because certain tree estimation programs can apply only a limited number of sequence evolution models, partition finder was run an additional time under the 'BEAST' setting, which allows for only two possible models: GTR and HKY, with G and I variants. The Bayesian Information Criterion (BIC) was used for model selection and the comparison of different partition schemes, branch lengths were linked, and the greedy heuristic search algorithm was selected to search for the best partition scheme. Sets of sites were defined by the partition scheme or data blocks grouped by gene and by codon for the RAG1 and ND2 concatenated mitochondrial and nuclear datasets. PartitionFinder results suggest the data should be divided into six partitions employing three distinct models: The GTR+I+ Γ model for ND2 position 1, ND2 position 2, RAG1 positions 1 + 2, and RAG1 position 3; the GTR+ Γ model for ND2 position 3 (sites: 2024, scheme lnL: 239990.61, scheme BIC:

488005.1575, parameters: 1054, summary in Table 11). As mentioned in the previous section, the GTR model is more complex albeit generalized than the HKY model and employs a number of additional parameters. Trees with low initial likelihoods due to a high number of parameters and many samples may struggle to converge in a reasonable number of steps using this model. In such instances, the HKY model was used use HKY in substitution for GTR for runs that did not reach convergence.

Table 11. Characteristics of the four sequence data partitions estimated by PartitionFinder. Ambiguously aligned positions were removed from all analyses and are not included in these calculations. Calculations include sequences from outgroup taxa as well as reduced *Rhoptropus* sampling used in divergence dating analyses (BEAST).

Partition	Model	Genes (Codons)	Base Pairs
1	GTR+I+G	RAG pos1, RAG1 pos2	1-1069\3, 2-1069\3
2	GTR+I+G	RAG1 pos3	3-1069\3
3	GTR+I+G	ND2 pos1	1070-2024\3
4	GTR+I+G	ND2 pos2	1071-2024\3
5	GTR+G	ND2 pos3	1072-2024\3
		Scheme lnL:	-239990.6168
		Scheme BIC:	488005.1575
		Number of params:	1054
		Number of sites:	2024

3. Divergence dating

a. Fossil calibrations

A number of relevant fossil calibrations are available for use in dating gekkonid phylogenies, and the application of available data has been used differentially in various

studies of gekkonid biogeography and trait evolution (e.g. Heinicke et al. 2011, Gamble et al. 2008, Gamble et al. 2015, Gamble et al. 2011, Nielson et al. 2011, Skipwith et al. 2015, Heinicke et al. 2016, Brennan et al. 2016). Perhaps the most important fossil calibration is derived from the divergence of gekkotans from other squamates (Hugall et al. 2007, Jonniaux & Kumazawa 2008, Vidal & Hedges 2005). The cranial elements of an unambiguous fossil gekkotan (*Hoburogekko suchanov*i) from the Lower Cretaceous, Mongolia has been recently published. Although this fossil cannot be assigned to any extant gekkotan subclades, it may represent an early radiation of the Gekkota. Because this fossil may span the Aptian-Albian geological era, the date selected from this region should reflect a realtively median age within this time frame, although older dates have been incorporated in the past, which have a profound effect on the age of deeper diverges (Daza, Alifanov & Bauer, 2012; Daza, Bauer & Snively, 2014, Daza et al. 2016)

Another valid fossil calibration that has been used in previous studies is the divergence between *dactylus roosevelti* and *Sphaerodactylus torrei*, calibrated from an amber-preserved fossil Sphaerodactylus from Hispaniola dated to the early Miocene to early Middle Miocene (Iturralde-Vinent & MacPhee 1996). Identification of *Sphaerodactylus sp*. And *S. dommeli* preserved in amber-bearing deposits from the Dominican Republic dated to approximately 15-20 Mya provide a narrowly constrained, minimum age for the colonization of the DR and subsequent divergence of *S. ocoae* from sister clade containing *S. roosevelt*i and *S. torrei* (from Cuba and Puerto Rico, respectively).

Lastly, the divergence between *Pygopus* and *Lialis* has been used as a calibration in

molecular dating analyses based on a fossil *Pygopus* dated to 20–22 Ma (Hutchinson, 1998). A more appropriate use of this fossil calibration could be implemented as a minimum age constraint for the divergence between *Pygopus* and *Paradelma* based on a this Miocene lower jaw fossil of *Pygopus hortulanus*. The best calibration of this fossil is to address*P. hortulanus* to be a close relative of extant *Pygopus*, although this is not the only possible relationship, therefore greater uncertainty is associated with the use of this calibration (Lee 2009b).

b. Geologic calibrations

A number of reasonable geological calibration constraints relative to gekkota are available for use in dating analyses. The first calibration point used was obtained from the age of the rocks from Reunion Island under the assumption that the ancestor of *Phelsuma borbonica* colonized this region it soon after the island was formed 21 Ma (Austin et al. 2004), as well as the estimated age of volcanic origin of Grand Comoro, 0.5 Ma, assuming that *Phelsuma comorensis* colonized Grand Comoro soon after its emergence (Rocha et al. 2007). Maximum divergence time between clades of *Phelsuma* endemic to Madagascar's eastern offshore islands were used to incorporate this geological information. Specifically, *P. rosagularu*s+*P. guentheri*+*P. grogonza* (endemic to Mauritius, ~7-8 Ma), *P. comorensis* (endemic to Grand Comoro, ~1 Ma) and *P. inexpectata*+*Phelsuma borbonica* (endemic to Reunion Island, ~5 Ma) were used as monophyletic constraints for island geological calibrations (Heinicke et al. 2011; Duncan & Storey 1992; Gillot et al. 1994; Raxworthy et al. 2008). An additional geological calibration from the Early Miocene was also included. A lizard fossil from St. Bathans confirms that New Zealand was occupied

19–16 Myr by at least two *Hoplodactylus*-like gecko taxa, providing a minimum age constraint for the divergence of endemic New Zealand diplodactylan taxa from mainland sister diplodactylan species (Lee et al. 2009a). It should be noted that the use of island age as a maximum calibration point for endemic clades may be misleading in cases where an endemic clade may have evolved on an island that is now submerged (Thorpe et al. 2005, Head 2011), but given that molecular, geologic, and phylogenetic estimates are all subject to error, such calibrations may be theoretically sound in alternative situations (Rocha et al. 2007). Rather, it is most parsimonious to assume that the common ancestor of an endemic monophyletic terrestrial island clade originated on its associated island and not elsewhere (Hedges & Conn 2012). A biogeographic calibration point which has been used in the past is the vicariant divergence of taxa on either side of the Tein Shan-Pamir collision zone, as the rise of this range is dated to 10 million years before present (Macey et al. 1999, Tapponier et al. 1981, Abdrakhmatov et al. 1996). The implementation of this calibration specifically refers to the MRCA of *Teratoscincus roborowskii* and *Teratoscincus scincus* on either side of the divide. Although this calibration has been used in a number of studies (Bansal and Karanth 2013, Gamble et al. 2008, Gamble et al. 2015, Gamble et al. 2011, Nielson et al. 2011, Garcia-Porta & Ord 2013, Highem et al. 2016, Garcia-Porta et al. 2016), the validity of dates applied and taxa incorporated due to uncertainty of historical distributions are spurious.

c. Priors: calibrations & constraints

Using BEAST 1.8.2 (Drummond and Rambaut, 2007) a time scale analysis of

evolution for the genus *Rhoptropus* was estimated. The algorithm includes a large number of parameter estimates in comparison to basic BI branch length and topology parameterization of other phylogenetic programs, therefore the ability of this program to search available tree space is comparatively reduced. For this reason, constraints were enforced on the topology of *Rhoptropus* geckos to match that of the concatenated nuclear and mitochondrial analysis. BEAST will evaluate each prior in order, and zero probability for any prior will result in in a total tree likelihood that is approaching negative infinity, and the rest of the posterior will not be calculated. Enforcement of known constraints from previous analyses, such as family level groupings, will improve starting tree topologies and allow chains to more quickly obtain stationary distributions. For this reason, additional constraints were placed at the family level for all gekkotans (Diplodactylidae, Eublepharidae, Gekkonidae, Phyllodactilidae, Sphaerodactylidae, and Pygopodidae) to reduce run time and allow the algorthim more search optimal tree space. Because the monophyly of Diplodactyloidea was not recovered in initial runs resulting in low likelihood scores, this larger group was constrained as well. The root position of the tree and the proportion of trees with that particular internal or external root provide a posterior probability for this position. Therefore, while it is not necessary to designate an outgroup, strong priors for outgroups may require ingroup constraint. Given the importance of gekkotans as a focal ingroup with a root calibration, a constraint on the monophyly of Gekkota was also enforced. The root prior (MRCA Gekkota) was given an exponential distribution (mean = 10 Ma, offset = 100 Ma, initial = 100 Ma) encompassing the youngest applied estimate for this divergence (see Gamble et al. 2015, Brennan et al. 2016, Heinicke et al. 2016, offset = 110; Daza, Alifanov & Bauer 2012, Daza, Bauer &

Snively 2014, Daza et al. 2016). Four constraints were also applied to internal nodes. A geological calibration for the most recent common ancestor (MRCA) of *Phelsuma rosagularis*, *P. inexpectata* and *P. borbonica* (uniform prior; mean = 0–8 Ma; Heinicke et al. 2011). A fossil calibration for the MRCA of sampled *Sphaerodactylus* from the Dominican Republic (Hispaniola) and its sister clade from Cuba and Puerto Rico *S. torrei* + *S. nigropunctatus*; *S. elegans* + *S. leucaster* + *S. notatus* + *S. townsendii* + *S. nicholsi* + *S. argus* + *S. grandisquamis* + *S. roosevelti,* with a higher mean value than previous studies have applied due to informative estimates regarding the age of Sphaerodactylidae (previous studies: mean = 3 Ma, Gamble; this study: exponential prior; mean = 5 Ma, offset = 15 Ma, initial = 20 Ma; Gamble et al. 2016, Heinicke et al. 2016, Gamble et al. 2008, Kluge 1995, Iturralde-Vinent & MacPhee 1996). Another geological calibration for the MRCA of endemic New Zealand diplodactylids and the sister clade of mainland Australian diplodactylid geckos: NZ: *Woodworthia maculatus, Hoplodactylus duvaucelii, Tukutuku rakiurae, Dactylocnemis pacificus, Mokopirakau granulatus, Toropuku stephensi, Naultinus rudis, Naultinus grayii, Naultinus elegan* and *Naultinus gemmeuss*; AUS: *Crenadactylus ocellatus, Rhynchoedura ornata, Lucasium damaeum, Lucaseum stenodactylum, Diplodactylus tesselatus, Diplodactylus conspicillatus, Strophurus strophurus, Strophurus aberrans, Strophurus elderi, Hesperoedura reticula, Oedura marmorata, Nebulifera robusta* and *Amalosia rhombifer* (exponential prior; mean = 17 Ma, offset = 16 Ma, initial = 20 Ma; Lee et al. 2008). A final fossil calibration was used for the MRCA of Pygopus and Paradelma. Given the uncertainty for the placement of the *Pygopus hortulanus* fossil, the following pygopodids were included in this calibration set wit the exclusion of *Delma*: *Lialis burtonis*, *Ophidiocephalus taeniatus*, *Paradelma*

orientalis, *Pygopus lepidopodus*, *Pygopus nigriceps*, *Pletholax gracilis*, *Aprasia inaurita* and *Aprasia parapulchella* (exponential prior; mean = 10 Ma, offset = 20 Ma, initial = 30 Ma; Hutchinson 1997, Lee et al. 2009, Brennan et al. 2016). Although the MRCA of *Teratoscincus roborowskii* and *T. scincus* on either side of the Tein Shan-Pamir collision zone has been used a geological calibration in previous studies (Macey et al. 1999, Tapponier et al. 1981, Abdrakhmatov et al. 1996, Gamble et al. 2008, Gamble et al. 2016), this validity of this calibration is questionable relative to the use of known island emergence dates as maximum constraints, is relatively distant from the focal group and uninformative, and therefore excluded from all dating analyses in this study. A summary of all calibrations employed and justification for their use can be found in Table 12.

Table 12. Priors and justification summary for calibration of dated phylogeny. Fossil taxa used to calibrate the divergence time analysis (BEAST). Analytical parameters for hard-minimum and soft-maximum calibrations are provided.

Prior	Explanation	Class	Dist.	Mean	Offset	Reference
MRCA *Phelsuma*	Maximum divergence time between clades of phelsuma endemic to Madagascar's eastern offshore islands. Specifically, *P. rosagularus*+*P. guentheri*+*P. grogonza* (endemic to Mauritius, ~7-8 Ma) and *P. inexpectata*+*Phelsuma borbonica* (endemic to Reunion Islan, ~5 Ma)	Biogeo.	uniform	0–8 Ma	–	Heinicke et al. 2011; Duncan & Storey 1992; Gillot et al. 1994; Raxworthy et al. 2008

MRCA *Sphaerodactylus*	*Sphaerodactylus sp*. And *S. dommeli* preserved in early Miocene to early Middle Miocene (15-20 Mya) amber-bearing deposits from the Dominican Republic provide a narrowly constrained, minimum age for the colonization of the DR and subsequent divergence of *S. ocoae* from sister clade containing *S. roosevelt*i and *S. torrei* (Cuba, PR, respectively)	fossil	Exp.	5 Ma	15 Ma	Kluge 1995, Iturralde-Vinent & MacPhee 1996
MRCA NZ + AUS	Early Miocene St. Bathans lizard fossil recordx confirms that NZ was occupied 19–16 Myr by at least two *Hoplodactylus*-like gecko taxa, providing a minimum age constraint for the divergence of endemic NZ Diplodactylan taxa from mainland sister taxa	fossil	Exp.	17 Ma	16 Ma	Lee et al 2009a
MRCA *Pygopus*	Minimum age for the divergence between *Pygopus* and *Paradelma* based on a Miocene lower jaw fossil of *Pygopus hortulanus*. The best calibration of this fossil is *P. hortulanus* as a close relative of extant Pygopus, but this is not the only possible relationship, therefore greater uncertainty is associated with the use of this calibration.	fossil	Exp.	10 Ma	20 Ma	Hutchinson 1997, Lee et al. 2009b, Brennan et al 2016
MRCA *Teratoscincus*	Vicariant divergence of taxa on either side of the Tein Shan-Pamir collision zone, the rise of this range is well dated 10 million years before present.	Biogeo.	Exp.	3 Ma	10 Ma	Macey et al. 1999, Tapponier et al., 1981; Abdrakhmatov et al., 1996
MRCA Gekkota	Unambiguous fossil gekkotan (*Hoburogekko suchanov*i) from Lower Cretaceous, Aptian-Albian of Mongolia represented by cranial elements. Cannot be assigned to any extant gekkotan subclades, may represent an early radiation of the Gekkota.	fossil	Exp.	10 Ma	100 Ma	Daza, Alifanov & Bauer, 2012; Daza, Bauer& Snively, 2014, Daza et al 2016

d. Priors: tree models

Two models frequently employed in divergence dating analyses are the Yule Speciation model and the birth-death-sampling model. The Yule Speciation is a simple one-parameter model nested inside the general birth-death-sampling model (Yang and Rannala 1997) that assumes a pure birth process. In complicated datasets with a number of parameters to estimate, this model will introduce fewer parameters than the birth death model. On a dataset of large size (>300 terminals), a birth-death prior may be more appropriate as multiple samples of the same species will violate the birth-death model, but there has almost certainly been extinction in the tree (e.g. calibration points), therefore a Yule speciation prior is not entirely appropriate either (Stadler 2009). The birth-death sampling model essentially estimates a constant rate of speciation and extinction, but better than no extinction incorporated at all. The distribution of branch lengths assumed for each of these priors should be very similar. Dates should be equivalent on a shallow scale, but deeper divergences, especially near the root, could certainly vary. If sampling size does not include all species, the proportion of missing taxa cannot be incorporated into the model, which can be problematic for the Yule speciation model, however the birth-death model has the option to incorporate incomplete sampling. If multiple individuals per species are included, this violates the assumptions of both models, as this approach is more suitable for a coalescent prior which varies quadratically with the number of lineages spanning an internode which will produce very different results than the linear variance of the Yule model. For this reason, more than one tree prior was applied to determine likelihood variance and date estimates between both approaches. In order to meet the assumptions of both models, the conservative mean ND2 percent

nucleotide sequence divergence between *Rhoptropus diporus* and *Rhoptropus bradfieldi* (11.5%) was used as a minimal estimate between lineages to be incorporated into the analyses. A representative sample was included in the BEAST analysis from all monophyletic clusters with >11.5% mean ND2 nucleotide sequence divergence from their closest sister group (17 individuals total). Two alternative datasets, one incorporating only one individual per lineage (11 individuals total) and one incorporating multiple individuals per descried lineage and putative new lineages were also incorporated (44 individuals total). For each of these separate iterations, both the birth-death and Yule speciation tree prior were applied.

BEAUTi 1.8 was used to create initial BEAST input files, further modeification to the xml file was performed manually (Drummond et al. 2012). Uncorelated relaxed clock models assuming an underlying lognomal distribution (UCLD) of evolutionary rates were used to avoid the inaccurate estimates that have been obtained in the past using the exponential distribution of evolutionary rates (Baele et al. 2013). A uniform prior (0-10, initial = 0.1) was used for the mean growth rate for both the Yule and birth-death models. A uniform prior (0-1, initial = 0.5) was used for the birth-death model relative death rate. An exponential prior (mean = 0.3) was used for the standard deviation of the UCLD model and a uniform prior (0-1) was used on the mean of the UCLD model (Vanneste et al. 2013). All fossil calibrations outline previously were set with exponential or uniform distributions and bounded by the minimum and maximum ages outlined above. A starting tree with branch lengths and topology satisfying all the constraints was estimated in RAxML and converted into a chronogram with applied calibrations using the chronos

function in the R package ape (Paradis 2004). Other parameters were kept to their default prior distribution or were indirectly specified through other parameters.

The BI analysis was implemented in BEAST 1.8.2 (Drummond et al. 2012). All tree topologies between partitions were linked using both a Yule tree prior and uncorrelated lognormal relaxed clock for several runs and a Birth-Death tree prior and uncorrelated lognormal relaxed clock for alternative runs. Four replicate analyses were run for 100 million generations sampled every 10000 generations. The first 2500 generations trees were removed as burn-in resulting in 7500 total trees. Effective sample sizes were estimated in Tracer 1.5 (>300 for all parameters in each run) to confirm adequate chain length and mixing. Convergence was assessed using Gelman & Rubin's r statistic (Gelman et al. 1995). Independent runs were conducted to ensure parameters estimates were equivalent. The harmonic mean estimate (HME) has been used to compare models for Bayesian analyses (Newton and Raftery, 1994), however this estimator can overestimate the marginal likelihood which may result in the best fitting model not being selected. Alternatively, Bayesian models can be compared using a posterior simulation-based analogue of Akaike's information critereon (AICM, Raftery et al. 2007). Comparisons of different model evaluation techniques confirm that AICM is more reliable than HME and less subject to overestimation of the marginal likelihood (Baele et al. 2012). In this study, marginal likelihood estimates (MLEs) were used to compute log-Bayes factors (BFs) in order to compare the yule and birth-death priors for a given dataset strategy using the HME. BF differences above five were used as indication that one model

was significantly favored over the other. The AICM estimation was performed on the samples collected in the MCMC, but this approach is not performed on the MLEs. HME and AICM estimates and BFs were calculated using Tracer v1.6.0 in order to compare runs with different models (Baele et al. 2012, Baele et al. 2013).

III. Results

A. Estimation sensitivity to tree model and sampling

Convegence of the dating analysis was indicated by ESS scores greater than 200 for all parameters for the post burn-in trees (Likelihood ESS, Table 17). Tracer plots indicated convergence was reached for all BEAST runs prior to the burn-in threshold. The choice of branching process prior had little effect on age estimates for the focal taxon group (*Rhoptropus*), however estimates were slightly older under the Yule Speciation prior analyses. Bayes factor values, calculated with the Marginal Likelihood estimates of the AIMC analysis support the birth-death process as the better tree prior (Table 14) in two of the three datasets (min, species). Contrastingly, HME recovered conflicting model selection, with the Yule favored over the Birth-Death for two of the three datasets (species, max). These results agree with previous tests of model selection in the literature, showing that HME overestimates MLE and may not reliably select the best -upported model (Condamine et al. 2014). Focusing only on B-D analyses, the dataset wich used species-level sampling rather than the maximum or minimum number of species had overall higher model support as well.

Table 14. Comparisons of birth-death (BD) and Yule Speciation (Yule) tree priors. Values indicate HME, harmonic mean estimate, AICM (estimated from bootstrap replicates), ESS, effective sample size, BF: Bayes Factor (the difference between the AICM of the birth-death and the Yule prior). Positive values indicate support for the birth-death prior. Dataset comparisons indicate minimal sampling (min), maximum sampling (max), and species-level sampling (species).

sampling strategy	tree prior	AICM	HME	ESS (logL)	BF
min	BD	22758	-223387	850	-23.6
	Yule	22781	-223410	1900	
max	BD	22741	-226785	930	29.4
	Yule	22712	-226741	1150	
species	BD	22677	-218895	770	-28.5
	Yule	22705	-218863	1020	

B. Divergence dates

Divergence time estimates (and ranges) for selected nodes, based on ND2 and RAG1 sequence data produced estimates for the divergence of *Rhoptropus* and *Pachydactylus* to be around 60 Ma (55–67 Ma), which is in agreement with previous studies (Gamble et al. 20012, Heinicke et al. 2011, Gamble et al. 2016, Heinicke et al. 2016, Figure 33). The diversification of *Rhoptropus* began much later, 36.3 Ma (32–40 Ma), which may indicate significant extinction has occurred along this branch. At this time, early evidence for region decrease in humidity has been reported in the Namib region, and subsequent diversification events around this time may be correlated to shifts in vegetation and climate (Figure 24). The split for *R. afer* from all other *Rhoptropus* is 31.6 (26.7–36.8 Ma), which is closely clustered with the split for *R. montanus* from the clade containing *R. boultoni* + *R. taeniostictus* + *R. benguellensis* + *R. biporosus* + *R. barnardi* is 32.8 (28.8–37.1 Ma) whch roughly corresponds to the onset of uplift in the West African Rift system

that resulted in increased aridification in the lowlands (Figure 23, Table 13). *R. boultoni* split from the group containing *R. taeniostictus* + *R. benguellensis* + *R. biporosus* + *R. barnardi*) 29.9 Ma (26.1–33.8 Ma). *R. taeniostictus* from the clade comprised of R.benguellensis + R. biporosus + R. barnardi) 26 Ma (22.5–29.9 Ma). *R. benguellensis* divergered from the R. biporosus + R. barnardi group about 23.3 Ma (20.0–26.8 Ma), and the collective*R. biporosus*/*R. barnardi* group radiation occurred about18.9 Ma (16.1–21.8) with subsequently younger dates for the origin of the previously described and new lineages identified in Angola and Namibia (range, 15.1–5.3 Ma).

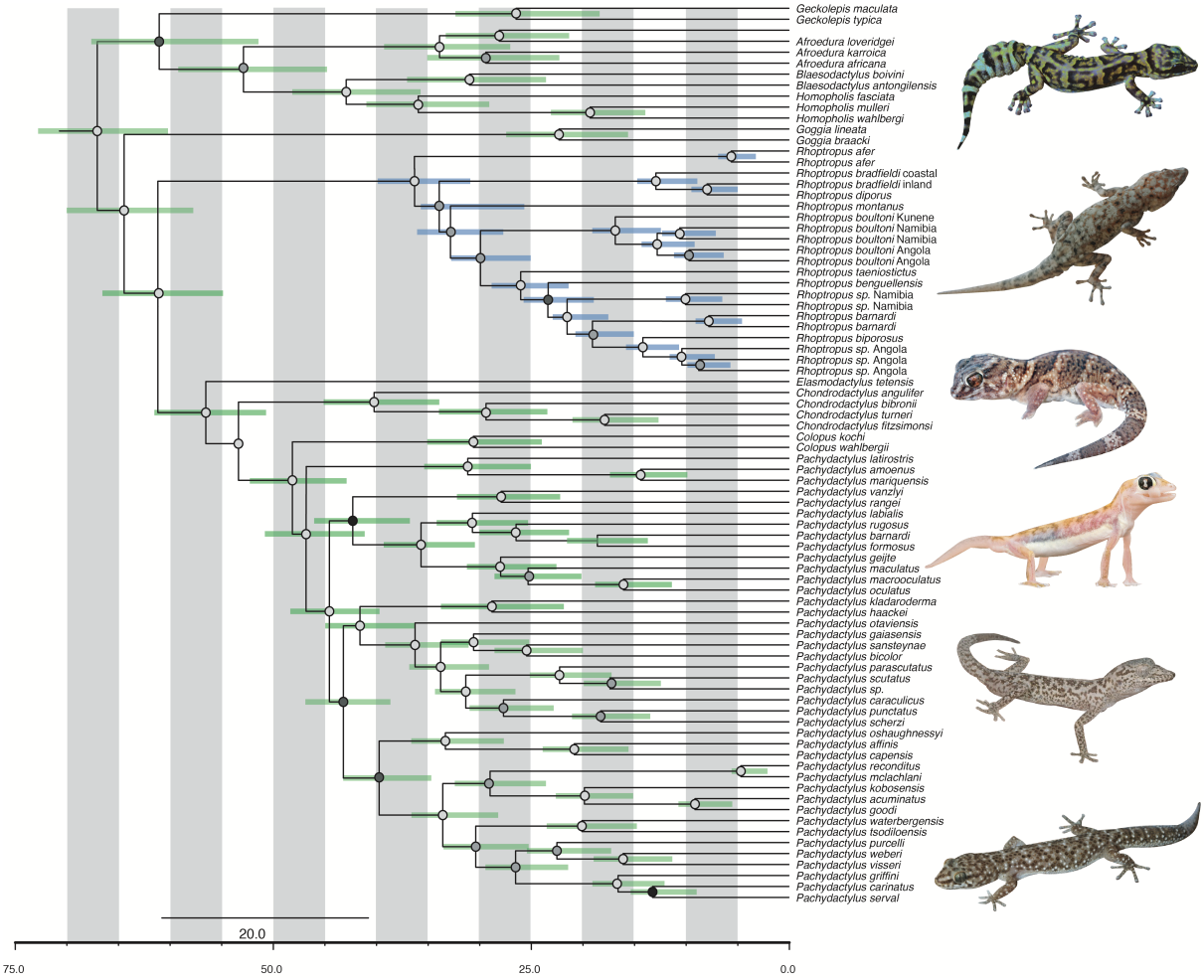


Figure 23. Time-calibrated phylogeny. The topology is the maximum clade credibility tree estimated in BEAST with distant outgroups cropped for clarity. Support values (Bayesian posterior probabilities, light grey indicates posterior probabilities of 1.0, medium grey indicates posterior probabilities of 0.95-0.99 and dark grey indicates 0.94-0.90 posterior probability) and 95% Highest Posterior Density (HPD) confidence intervals (blue bars represent *Rhoptropus,* green bars are representative of non-*Rhoptropus* gekkonids) are given at nodes.

The age of early *Rhoptropus in situ* speciation does not coincide with the extreme arid onset of Namib Desert xerification (17–18 Ma, Figure 34, Table 13) in association with the movement of Polar ice caps and ancient climate change in the north. Rather, this divergence from other Southern African gekkonids could have resulted as early as the Late Eocene-Early Oligocene when the first shifts in climate towards xeric conditions were

recorded in southwestern Namibia. Subsequent speciation events, however, collaborate with the shift in norther habitats to extreme aridity, in the overall tumultuous geologic and climatic history of the Namib.

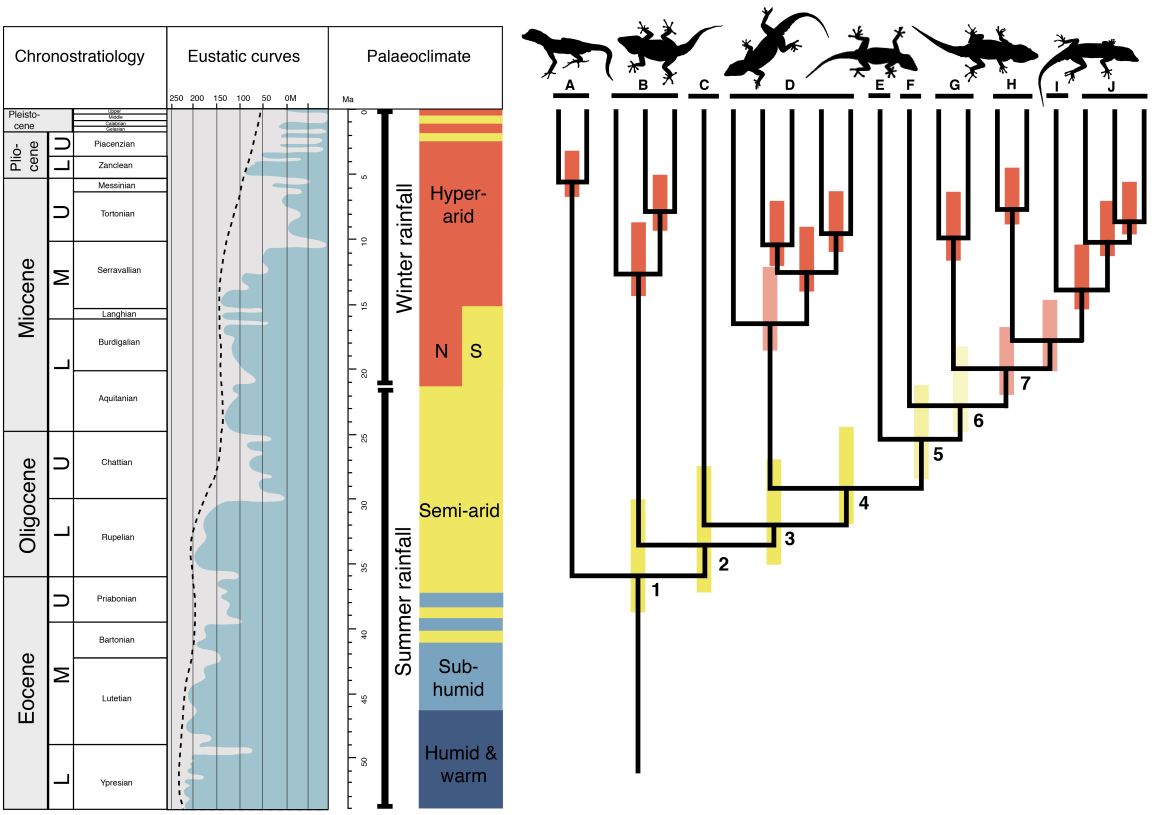


Figure 34. (A) Summarized dates for *Rhoptropus* diversification events beginning around the early Miocene as they coincide with key aridification events in the Namib, letters correspond with median node ages listed in Table 4. (B) Post-Cretaceous eustatic history (Haq et al. 1987, modified by Miller 2009) and a summary of palaeoclimate in the Namib region. Evidence suggests that region decrease in humidity began while hyper-arid conditions and winter rainfall, more typical of contemporary climate, began by the end of the Early Miocene.

Table 13. Mean ages (in Myr) and the corresponding 95% highest posterior density ranges (HPD) for major *Rhoptropus* lineages, obtained using nonparametric rate smoothing (node labels shown in Figure 23).

Clade	Node	Mean Age (Myr)	95% CI (Myr)
Rhoptropus sensu lato	1	36.3	32.0-40.9
R. afer(all other Rhoptropus)	2	31.6	26.7-36.8
R. montanus(R. boultoni+R. taeniostictus+ R.benguellensis+R.biporosus+R.barnardi)	3	32.8	28.8-37.1
R. boultoni(R. taeniostictus+ R.benguellensis+R.biporosus+R.barnardi)	4	29.9	26.1-33.8
R. taeniostictus(R.benguellensis+R.biporosus+R.barnardi)	5	26	22.5-29.9
R. benguellensis(R. biporosus+R. barnardi)	6	23.3	20.0-26.8
R. biporosus+R. barnardi radiation	7	18.9	16.1-21.8

IV. Discussion & broader impacts

A. The Namib Desert

1. Radiations & speciation

The evolutionary "response" of some organisms to the extinction of a previously dominant group can be indicative of an adaptive radiation. Adaptive radiations are characterized by the rapid exploitation by a clade of the sudden availability of new environmental resources, or increased ability to compete for those resources. Such radiations can also occur through the development of a key innovation in which a gain of function allows

exploitation of new ecological resources previously unavailable to other groups and/or dispersal to new, uninhabited regions and adaptation to the wide array of niches available in such locations (Givinsch & Systema 2000). The common factor in each adaptive radiation is the availability of novel resources that become accessible to a group, either through the elimination of previous ecological competition, the exploitation of resources that were previously unaccessed or unavailable, and the interplay of rapid evolution with both that results in myriad new forms (Glor 2010). For *Rhoptropus*, it is possible that the onset of intensified aridity resulted in local extinction of non-adapted groups, where as *Rhoptropus* could have been operating in pockets of slightly higher aridity due to affinity for Rocky coastal and inland habitat, allowing them to exploit newly available niche space. Although no obvious innovations have been conclusively assoiated with the diversification of this group, Rhoptropus have elongate limbs, toes, variant locomotive mechanisms and speeds, and metabolic activity in comparison to other closesly related gekkonids, and their dial pattern is also distinctively different (Nagy 1993, Collins et al. 2014, Fuller et al. 2011, higham 2015, Higham et al. 2010, Higham et al. 215). Explosive Diversity over a short period of time does not necessarily need to be accompanied by key innovation, however, but this phenomena and the phenomena of an adaptive radiation are frequently misinterpreted in the literature (Glor 2010). A significant number of studies have linked extreme diversification to climatic shifts such as the Cape Floristic fauna of South Africa (7–8Ma), Begonia plants in sub Saharan Africa during the Pro-Pleistocene, Plebotomus sandflies in the Mediterraninan subregion throughout the Pleistocene Nothobranchius fishes from the cyclic humidification during the uplft of the East African Uplift, and Darkling Beetles in the Namib Desert (Richardson et al. 2001, Pala et al. 2014,

Esseghir et al. 2000, Dorn et al. 2014, Steckel et al. 2010). By driving refugia isolation or providing novel habitat for population shifts/expansion events and adaptive evolution, aridification events can have a profound effect on species diversity and the spatial structuring of these lineages. Previous ecological investiongations presented in this study have indicated that precipitation and substrate are important predictors of suitable habitat for *Rhoptropus,* however, the historical niche of these animals is not well known. Climatic projections are unable to establish past climatic niche, however, evidence from isotope and fossil record studies has lent insight to the historical environment of the Namib Desert region. While other closely relatied groups such as P*achydactylus* and *Chondrodactylus* have few desert-adapted constituents, these lineages are much younger than Rhoptropus as a whole, and the diversity of other gecko groups in this region is much lower in comparison.

The genus *Rhoptropus* is of interest beyond the biological realm with regards to habitat and historical distributions. Whereas most desert species are extreme outliers of mostly non-arid groups (see Figure 6), *Rhoptropus* is one of the few vertebrate genera to have had its origins entirely within the Namib Desert (Figure 4). The age of such desert-adapted groups is of particular interest to geologists studying the unresolved age of the Namib Desert and its historical climatic shifts (Ward & Seely 1983). This study provides a biological perspective to the historical climate of the Namib, where Rhoptropus lineages accumulated after the onset of aridification is proposed to have begun, and the majority of speciation events coincide with the progressive hyper-arid climatic period of the world's oldest desert.

B. Climate change

Although southern Africa is not considered a high impact area for future climate change, the fauna of this desert region rely heavily on the advective fog belt of the western coast for moisture in this arid to hyper-arid climate (Lancaster 2002, Henschel & Seely 2008,). Should the advent of future climate change disrupt the Benguella and this associated cold advective fog, it is likely significant downstream effects on the endemic fauna would be observed (Olivier, 1995). The Namib Desert has had a significant influence on the biotic history of southern Africa, as many taxa originated in and became highly adapted to this old, hyper-arid region sometime in the before dispersing to and replacing the local fauna of more recent arid habitats (Senut et al. 2009). The history of desertification in southern Africa is also intimately linked with the history of polar ice caps and climate change in the Miocene. Locality information associated with different species of *Rhoptropus* can be used to test different hypotheses about the evolution of endemic desert taxa. This will improved knowledge of the processes that lead to endemism can help to identify priorities in conservation planning This project will thus provide valuable information to future climate change projections and conservation decisions by increasing understanding of the climatic history of the Namib and the impact of this history on endemic desert species (Thullier et al. 2006, Foden et al. 2007, Pearson & Raxworthy 2009, Haensler et al. 2011).

APPENDIX

Supplemental 1. Genetic samples, distributional information and GenBank accession numbers of specimens used in this study. Samples indicated in bold were included in the divergence time analyses (BEAST). The following field series and institutional abbreviations were used: AMB, Aaron M. Bauer; CAS, California Academy of Sciences; KTH, Krystal H. Tolley; MCZ, Museum of Comparative Zoology, Harvard University; JB, Jon Boone; JVV, Jens V. Vindum; WC, Werner Conradie. Columns marked with an X represent GenBank placeholders.

Species	Gene			ID		Locality	
Original Species	**ND2**	**RAG1**	**MAP1A**	**Field ID**	**Locality**	**Latitude**	**Longitude**
Rhoptropus afer	X	X		AMB 6531	Namibia, N bank Huab River, Huab River Bridge	-20.901111	13.525
Rhoptropus afer	X	X		AMB 7138	Namibia, SE flank of Rossing Mountain	-22.533611	14.8375
Rhoptropus afer	X	X		AMB 7141	Namibia, SE flank of Rossing Mountain	-22.533611	14.8375
Rhoptropus afer	X	X		AMB 7142	Namibia, SE flank of Rossing Mountain	-22.533611	14.8375
Rhoptropus afer	X	X		AMB 7162	Namibia, 2 km S Wlotzkasbaken	-22.430278	14.462222
Rhoptropus afer	X	X	X	AMB 7163	Namibia, 2 km S Wlotzkasbaken	-22.430278	14.462222
Rhoptropus afer	X	X		AMB 7532	Namibia, Hertesbaii, Cape Cross Road	-21.835833	14.071944
Rhoptropus afer	X	X		MCZ 23016	Namibia, 12 km E Walvis Bay	-22.916623	14.58424
Rhoptropus afer	X	X		MCZA 38238	Namibia, 31 km N Swakopmund	-22.428333	14.461944
Rhoptropus afer	X	X	X	MCZA 38239	Namibia, 31 km N Swakopmund	-22.428333	14.461944
Rhoptropus afer	X	X		MCZA 38241	Namibia, 31 km N Swakopmund	-22.428333	14.461944
Rhoptropus afer	X	X		MCZZ 23028	Namibia, 19.4 km E Coast Road to Brandberg	-21.13323	14.771072
Rhoptropus afer	X	X		KTH 09158	Angola, Namibe District, road to Tambor	-16.066667	12.433333
Rhoptropus afer	X	X		KTH 09175	Angola, Namibe District, road to Omauha Lodge	-15.237192	12.135056
Rhoptropus afer	X	X		KTH 09182	Angola, Namibe District, 10 km S Red Canyon Camp, near Omauha Lodge	-15.372962	12.237366

Rhoptropus afer	X			AMB 7161	Namibia, 2 km S Wlotzkasbaken	-22.417803	14.462222
Rhoptropus barnardi		X		CAS 254759	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475194	12.463194
Rhoptropus barnardi		X	X	CAS 254761	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475194	12.463194
Rhoptropus barnardi		X		CAS 254837	Angola, Namibe District, Iona National Park, Omauha Lodge	-16.200333	12.400028
Rhoptropus barnardi		X		CAS 254954	Angola, Namibe District, Reserva de Namibe	-15.773167	12.333028
Rhoptropus barnardi		X	X	CAS 254844	Angola, Namibe District, Iona National Park, Rio Curoca crossing, N side	-16.301889	12.420278
Rhoptropus barnardi 4	X	X		MCZ 28739	Namibia, Farm Bambatsi	-20.193889	15.455111
Rhoptropus barnardi 4	X	X		MCZ 28771	Namibia, Farm Ohange	-19.509444	17.560444
Rhoptropus barnardi 4	X	X	X	MCZ 28781	Namibia, Farm Ohange	-19.516361	17.572222
Rhoptropus barnardi 4	X	X		MCZ 28783	Namibia, Farm Ohange	-19.495917	17.558556
Rhoptropus barnardi 4	X			AMB 6420	Namibia, 59 km W Kamanjab, Torabasi Road	-19.653889	14.350833
Rhoptropus barnardi 4	X	X		AMB 8046	Namibia, Kunene River, 17 km E Swartbooisdrift	-17.434056	13.993889
Rhoptropus barnardi 4	X	X	X	AMB 8050	Namibia, Swartbooisdrift, towards Epembe	-17.381361	13.829556
Rhoptropus barnardi 4	X	X		CAS 254846	Angola, Namibe District, Iona National Park, Rio Curoca crossing, S side	-16.304083	12.416667
Rhoptropus barnardi 4	X	X	X	CAS 254847	Angola, Namibe District, Iona National Park, Rio Curoca crossing, S side	-16.304083	12.416667
Rhoptropus barnardi 4	X	X		CAS 254856	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, N side of river	-16.287306	12.559972

Rhoptropus barnardi 4	X	X		CAS 254863	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, S side of river	-16.290003	12.562194
Rhoptropus barnardi 4	X	X	X	MCZA 27668	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X		MCZA 27669	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X		MCZA 27670	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X		MCZA 27672	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X		MCZA 27674	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X	X	MCZA 27678	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X	X	MCZA 27681	Namibia, Epupa Falls Camp	-17	13.23
Rhoptropus barnardi 4	X	X		MCZA 38955	Namibia, 35 km S Epupa Falls	-17.316066	13.233333
Rhoptropus barnardi 4	X	X		MCZF 38578	Namibia, Grootberg pass, W side	-19.84	13.233333
Rhoptropus barnardi 4	X			MCZZ 23068	Namibia, Gai-As Spring	-20.766944	14.02
Rhoptropus barnardi 4	X	X		MCZZ 37982	Namibia, near Kunene River	-17.263611	12.442778
Rhoptropus barnardi 4	X	X		MCZA 38222	Namibia, 10 km N Red Drum	-17.770556	13.551389
Rhoptropus barnardi 4	X	X		MCZA 38973	Namibia, 28 km E Orumpembe, near Sanitatas	-18.187222	12.7375
Rhoptropus barnardi 4	X	X		MCZF 38520	Namibia, Farm Uisib	-19.551667	17.236389
Rhoptropus barnardi 4	X	X		MCZF 38525	Namibia, Farm Uisib	-19.551667	17.236389
Rhoptropus barnardi 4	X			MCZF 38531	Namibia, Farm Uisib	-19.551667	17.236389
Rhoptropus barnardi 4	X			MCZZ 37987	Namibia, Kaokolandm, near Kunene River, mouth of Marienfluss	-17.263611	12.442778
Rhoptropus barnardi 4	X	X		MCZA 38989	Namibia, 23 km E Orupembe	-18.18321	12.735258
Rhoptropus benguelensis	X	X		ANG 174 WC 1814	Angola, Cuanza Sol Province, 3.5 km W Conde	-10.853583	14.638806
Rhoptropus benguelensis	X	X		ANG 201 WC 1834	Angola, Cuanza Sol Province, 3.5 km W Conde	-10.853583	14.638806
Rhoptropus benguelensis	X	X		ANG 249 WC 1833	Angola, Cuanza Sol Province, 3.5 km W Conde	-10.853583	14.638806

Rhoptropus benguellensis		X		ANG 247	7km E on road to Cubal, Benguela District, Angola	-12.9994	13.79861
Rhoptropus biporosus		X		CAS 254786	Angola, Namibe District, Iona National Park, 20 km SSW Espenhierra	-16.931694	12.245
Rhoptropus biporosus		X		CAS 254825	Angola, Namibe District, Iona National Park, Espenhierra	-16.795917	12.354417
Rhoptropus biporosus				CAS 254957	Angola, Namibe District, Reserva de Namibe	-15.774278	12.333111
Rhoptropus biporosus		X		CAS 254959	Angola, Namibe District, Iona National Park, 9.65 km WSW Espenhierra	-16.811997	12.271264
Rhoptropus biporosus 2	X	X		MCZA 38988	Namibia, 22 km E Orupembe	-18.244722	12.650833
Rhoptropus biporosus 2	X		X	AMB 6943	Namibia, 18.3 km W Orupembe, road to Munotun River	-18.148611	12.39
Rhoptropus biporosus 2	X	X	X	CAS 254779	Angola, Namibe District, Iona National Park	-16.533467	12.4456
Rhoptropus biporosus 2	X	X		CAS 254787	Angola, Namibe District, Iona National Park, 20 km SSW Espenhierra	-16.931694	12.245
Rhoptropus biporosus 2	X	X		CAS 254788	Angola, Namibe District, Iona National Park, 20 km SSW Espenhierra	-16.931694	12.245
Rhoptropus biporosus 2	X	X		CAS 254794	Angola, Namibe District, Iona National Park, Espenhierra	-16.788861	12.357611
Rhoptropus biporosus 2	X	X	X	CAS 254802	Angola, Namibe District, Iona National Park, Espenhierra	-16.7853	12.35445
Rhoptropus biporosus 2	X	X		CAS 254803	Angola, Namibe District, Iona National Park, Espenhierra	-16.7853	12.35445
Rhoptropus biporosus 2	X	X		CAS 254805	Angola, Namibe District, Iona National Park, Espenhierra	-16.785283	12.354683

Rhoptropus biporosus 2	X			CAS 254813	Angola, Namibe District, Iona National Park, Espenhierra	-16.786864	12.357964
Rhoptropus biporosus 2	X		X	CAS 254820	Angola, Namibe District, Iona National Park, Espenhierra	-16.787306	12.358167
Rhoptropus biporosus 2	X	X		CAS 254821	Angola, Namibe District, Iona National Park, Espenhierra	-16.78575	12.358417
Rhoptropus biporosus 2	X	X	X	CAS 254822	Angola, Namibe District, Iona National Park, Espenhierra	-16.788361	12.357278
Rhoptropus biporosus 2	X	X		CAS 254823	Angola, Namibe District, Iona National Park, Espenhierra	-16.792667	12.355278
Rhoptropus biporosus 2	X	X		CAS 254824	Angola, Namibe District, Iona National Park, Espenhierra	-16.794861	12.354806
Rhoptropus biporosus 2	X		X	MCZA 38977	Namibia, 15 km E Orupembe	-18.183281	12.659226
Rhoptropus biporosus 2	X	X	X	MCZA 38978	Namibia, 16 km E Orupembe	-18.183273	12.66873
Rhoptropus biporosus 2	X			MCZA 38985	Namibia, 19 km E Orupembe	-18.183249	12.697242
Rhoptropus biporosus 2	X	X		MCZA 38991	Namibia, 25 km E Orupembe	-18.183187	12.754266
Rhoptropus biporosus 2	X			MCZZ 23002	Namibia, 7 km N Palmwag	-22.666667	14.566667
Rhoptropus biporosus 2	X		X	CAS 254958	Angola, Namibe District, Iona National Park, Espenhierra	-16.788944	12.35775
Rhoptropus boultoni	X	X		AMB 8048	Namibia, Kunene River, 17 km E Swartbooisdrift	-17.434056	13.993889
Rhoptropus boultoni Angola	X	X		CAS 254752	Angola, Namibe District, Iona National Park, 3.4 km SW Espenhierra, Lion Cave	-16.812083	12.339778
Rhoptropus boultoni Angola	X	X		CAS 254757	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475889	12.462694
Rhoptropus boultoni Angola	X	X		CAS 254758	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475889	12.462694

Rhoptropus boultoni Angola	X	X	X	CAS 254795	Angola, Namibe District, Iona National Park, Espenhierra	-16.7915	12.351683
Rhoptropus boultoni Angola		X		CAS 254828	Angola, Namibe District, Iona National Park, Omauha Lodge	-16.197917	12.399806
Rhoptropus boultoni Angola	X	X		CAS 254834	Angola, Namibe District, Iona National Park, Omauha Lodge	-16.200333	12.400028
Rhoptropus boultoni Angola	X	X		CAS 254849	Angola, Namibe District, Iona National Park, Rio Curoca crossing, S side	-16.304083	12.416667
Rhoptropus boultoni Angola		X	X	CAS 254850	Angola, Namibe District, Iona National Park, Rio Curoca crossing, S side	-16.304083	12.416667
Rhoptropus boultoni Angola	X	X		CAS 254857	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, S side of river	-16.288806	12.561111
Rhoptropus boultoni Angola	X	X	X	CAS 254858	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, S side of river	-16.288806	12.561111
Rhoptropus boultoni Angola	X	X		CAS 254861	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, S side of river	-16.288806	12.561111
Rhoptropus boultoni Angola		X		CAS 254862	Angola, Namibe District, Iona National Park, Rio Curoca, Pediva Hot Springs, S side of river	-16.288806	12.561111
Rhoptropus boultoni Angola	X	X		CAS 254865	Angola, Namibe District, Iona National Park, S bank Rio Curoca	-16.304333	12.4171

Rhoptropus boultoni Angola	X	X		CAS 254892	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044667	13.159056
Rhoptropus boultoni Angola	X	X		CAS 254921	Angola, Namibe District, Pico Azevedo	-15.534	12.491972
Rhoptropus boultoni Angola		X		CAS 254922	Angola, Namibe District, Pico Azevedo	-15.534	12.491972
Rhoptropus boultoni Angola		X	X	CAS 254923	Angola, Namibe District, Pico Azevedo	-15.534	12.491972
Rhoptropus boultoni Angola		X		CAS 254925	Angola, Namibe District, Pico Azevedo	-15.534	12.491972
Rhoptropus boultoni Angola	X	X	X	CAS 254946	Angola, Namibe District, Pico Azevedo	-15.534944	12.491528
Rhoptropus boultoni Angola	X	X		CAS 254947	Angola, Namibe District, Pico Azevedo	-15.534944	12.491528
Rhoptropus boultoni Angola	X	X		CAS 254949	Angola, Namibe District, Pico Azevedo	-15.534944	12.491528
Rhoptropus boultoni Angola	X	X		CAS 254950	Angola, Namibe District, Pico Azevedo	-15.534944	12.491528
Rhoptropus boultoni Angola	X	X	X	MCZA 27677	Namibia, Epupa Falls Camp	-17	13.233333
Rhoptropus boultoni Kunene	X	X	X	ANG 293	Angola, Namibe District, 50km E Namibe, road to Leba Pass	-15.015583	12.555028
Rhoptropus boultoni Kunene	X	X	X	CAS 254902	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.015306	12.642444
Rhoptropus boultoni Kunene	X			MCZA 38221	Namibia, 10 km N Red Drum	-17.770556	13.551389
Rhoptropus boultoni Kunene	X	X		MCZZ 37984	Namibia, Kunene River	-17.263611	12.442778
Rhoptropus boultoni Kunene	X	X		MCZZ 37986	Namibia, Kunene River	-17.263611	12.442778
Rhoptropus boultoni Kunene	X	X		ANG 243 WC 1840	Angola, Huila District, 13km N Quilengues, road to Benguela	-13.972472	14.047167
Rhoptropus boultoni Kunene	X			CAS 254894	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044639	13.158611
Rhoptropus boultoni Namibia		X	X	MCZ 28753	Namibia, Farm Ombaru Ost	-20.421736	15.461444

Rhoptropus boultoni Namibia	X			MCZ 28755	Namibia, Farm Ombaru Ost	-20.421736	15.461444
Rhoptropus boultoni Namibia	X	X		MCZ 28756	Namibia, Farm Ombaru Ost	-20.421736	15.461444
Rhoptropus boultoni Namibia	X	X		MCZ 28757	Namibia, Farm Ombaru Ost	-20.421736	15.461444
Rhoptropus boultoni Namibia	X			AMB 4027	Namibia, Kamanjab/Etosha Region, Farm Lobshorn	-19.765467	14.844
Rhoptropus boultoni Namibia	X	X		AMB 6485	Namibia ,Kunene Region, Twyfelfontein	-20.590556	14.372222
Rhoptropus boultoni Namibia	X	X		AMB 8044	Namibia, Kunene River, 17 km E Swartbooisdrift	-17.434056	13.993889
Rhoptropus boultoni Namibia	X	X		MCZA 27688	Namibia, Epupa Falls Camp	-17	13.233333
Rhoptropus boultoni Namibia	X	X		MCZA 27689	Namibia, Epupa Falls Camp	-17	13.233333
Rhoptropus boultoni Namibia	X	X		MCZA 38211	Namibia, 10 km N Red Drum	-17.770556	13.551389
Rhoptropus boultoni Namibia	X	X	X	MCZA 38901	Namibia, 62 km E Kamanjab, Farm Amolinda	-19.808056	15.379444
Rhoptropus boultoni Namibia	X	X		MCZA 38902	Namibia, 62 km E Kamanjab, Farm Amolinda	-19.808056	15.379444
Rhoptropus boultoni Namibia	X			MCZA 38905	Namibia, 62 km E Kamanjab, Farm Amolinda	-19.808056	15.379444
Rhoptropus boultoni Namibia	X	X		MCZZ 23122	Namibia, Farm Otjitambi	-19.859167	15.195833
Rhoptropus boultoni Namibia	X	X		MCZZ 23123	Namibia, Farm Otjitambi	-19.859167	15.195833
Rhoptropus boultoni Namibia	X	X	X	MCZZ 23124	Namibia, Farm Otjitambi	-19.859167	15.195833
Rhoptropus boultoni Namibia	X	X		MCZZ 37901	Namibia, 27.8 km E Groetberg Pass	-19.717222	14.311667
Rhoptropus bradfieldi	X	X		AMB 6367	Namibia, Gai-As	-20.788333	14.112222
Rhoptropus bradfieldi		X		AMB 7049	Namibia, 29 km N Swakopmund, Hentiesbaai Road	-22.427222	14.464722
Rhoptropus bradfieldi coastal	X			AMB 7152	Namibia, 2 km S Wlotzkasbaken	-22.430278	14.462222
Rhoptropus bradfieldi coastal	X			AMB 7156	Namibia, 2 km S Wlotzkasbaken	-22.430278	14.462222
Rhoptropus bradfieldi coastal	X		X	AMB 7157	Namibia, 2 km S Wlotzkasbaken	-22.430278	14.462222
Rhoptropus bradfieldi coastal	X		X	AMB 7535	Namibia, 4.1 km N of Mile 72 on Hertesbaii, Cape Cross Road	-21.835833	14.071944

Rhoptropus bradfieldi coastal	X			JV1829B	Namibia, Hertesbaii Road, 30 km N Swakopmund	-22.412592	14.533333
Rhoptropus bradfieldi inland	X			MCZA 28049	Namibia, near Swakop River, D1901 Jct	-22.637222	14.7275
Rhoptropus bradfieldi coastal	X			MCZA 38225	Namibia, 31.1 km N Swakopmund, Hentiesbaai Road	-22.428333	14.461944
Rhoptropus bradfieldi coastal	X	X		MCZA 38226	Namibia, 31.1 km N Swakopmund, Hentiesbaai Road	-22.428333	14.461944
Rhoptropus bradfieldi inland	X	X		MCZA 38249	Namibia, N bank Swakop River, D1901 Jct	-22.639167	14.632222
Rhoptropus bradfieldi inland		X		MCZF 38605	Namibia, near Swakop River, D1901 Jct	-22.638333	14.728333
Rhoptropus bradfieldi inland	X	X		MCZZ 23005	Namibia, near Swakop River, D1901 Jct	-22.6375	14.728333
Rhoptropus bradfieldi inland	X			AMB 7136	Namibia, SE flank Rossing Mountain	-22.533611	14.8375
Rhoptropus cf. barnardi 3	X	X	X	MCZZ 37805	Namibia, Gai-As	-20.779167	14.075
Rhoptropus cf. barnardi 3	X	X		MCZ 28327	Namibia, Farm Omandumba	-21.497528	15.629972
Rhoptropus cf. barnardi 3	X	X	X	MCZ 28671	Namibia, Farm Omandumba	-21.497528	15.629972
Rhoptropus cf. barnardi 3	X	X		MCZ 28696	Namibia, Farm Omandumba	-21.497861	15.626306
Rhoptropus cf. barnardi 3	X			JB 210	Namibia		
Rhoptropus cf. barnardi 3	X	X		MCZ 37915	Namibia, Sesfontein, Para Camp	-19.131944	13.588889
Rhoptropus cf. barnardi 3	X			MCZF 38590	Namibia, Khumib River	-18.654722	12.6575
Rhoptropus cf. barnardi 3	X			MCZF 38591	Namibia, Khumib River	-18.654722	12.6575
Rhoptropus cf. barnardi 3	X			MCZF 38592	Namibia, Khumib River	-18.654722	12.6575
Rhoptropus cf. barnardi 3	X	X	X	MCZF 38968	Namibia, near Sanitatas, road to Orupembe	-18.1875	12.737778
Rhoptropus cf. barnardi 3	X	X		MCZF 39000	Namibia, Sesfontein, Para Camp	-19.131944	13.588889
Rhoptropus cf. barnardi 3	X	X		MCZZ 23018	Namibia, 14 km E Orupembe	-18.183287	12.649722
Rhoptropus cf. barnardi 3	X	X	X	EMBRYO	Namibia, collected with 9/06 specimens		

Rhoptropus cf. barnardi 3	X	X		KTH 09076	Angola, Huila District, Tchiviuguiro	-15.066667	13.55
Rhoptropus cf. biporosus		X		CAS 254780	Angola, Namibe District, Iona National Park	-16.657233	12.437083
Rhoptropus cf. biporosus		X		MCZA 38994	Namibia, 27 km E Orupembe	-18.183163	12.773274
Rhoptropus cf. biporosus 1	X	X		CAS 254955	Angola, Namibe District, Reserva de Namibe	-15.773167	12.333028
Rhoptropus cf. biporosus 1	X	X		CAS 254890	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044667	13.159056
Rhoptropus cf. biporosus 1	X			ANG 179 WC 1861	Angola, Namibe District, N Namibe	-14.924083	12.371917
Rhoptropus cf. biporosus 1	X	X	X	ANG 196 WC 1795	Angola, Namibe/Huila District, 15km W base of Leba Pass	-15.055028	13.07425
Rhoptropus cf. biporosus 1	X	X		ANG 213 WC 1860	Angola, Namibe District, N Namibe	-14.924083	12.371917
Rhoptropus cf. biporosus 1	X			ANG 231 WC1812	Angola, Huila District, 13km N Quilengues, road to Benguela	-13.972472	14.047167
Rhoptropus cf. biporosus 1	X			ANG 232 WC 1858	Angola, Namibe District, N Namibe	-14.924083	12.371917
Rhoptropus cf. biporosus 1	X	X		ANG 317	Angola	-14.762845	12.492052
Rhoptropus cf. biporosus 1	X			ANG 318	Angola	-14.762845	12.492052
Rhoptropus cf. biporosus 1	X	X	X	CAS 254760	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475194	12.463194
Rhoptropus cf. biporosus 1	X	X	X	CAS 254762	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475194	12.463194
Rhoptropus cf. biporosus 1	X	X	X	CAS 254765	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475278	12.462194
Rhoptropus cf. biporosus 1	X	X		CAS 254766	Angola, Namibe District, 7.35 km NW Pico Azevedo	-15.475278	12.462194
Rhoptropus cf. biporosus 1	X	X	X	CAS 254842	Angola, Namibe District, Iona National Park, N Tambor	-15.996361	12.406667

Rhoptropus cf. biporosus 1	X	X		CAS 254836	Angola, Namibe District, Iona National Park,Omauha Lodge	-16.200333	12.400028
Rhoptropus cf. biporosus 1	X	X		CAS 254873	Angola, Huila District, Leba Pass, between river and highway	-15.070028	13.243472
Rhoptropus cf. biporosus 1	X	X		CAS 254881	Angola, Huila District, Leba Pass, between river and highway	-15.070333	13.243806
Rhoptropus cf. biporosus 1	X	X		KTH 09129	Angola, Namibe District, 50 km W Humpata	-15.016189	12.91576
Rhoptropus diporus	X	X		AMB 8833	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-21.073972	14.169889
Rhoptropus diporus	X	X		AMB 7550	Namibia, Bradberg Wes Myn	-21.074722	14.165833
Rhoptropus diporus	X	X	X	AMB 7555	Namibia, Bradberg Wes Myn	-21.074722	14.165833
Rhoptropus diporus		X	X	AMB 7588	Namibia, 22.4 km N Ugab River Crossing, Gai-As Road	-20.783056	14.108611
Rhoptropus diporus	X	X		AMB 7594	Namibia, 22.4 km N Ugab River Crossing, Gai-As Road	-20.783056	14.108611
Rhoptropus diporus		X	X	AMB 8465	Namibia, 50 km S Ugab River	-20.966944	14.110278
Rhoptropus diporus	X	X	X	AMB 8466	Namibia, 50 km S Ugab River	-20.966944	14.110278
Rhoptropus diporus	X	X		AMB 8467	Namibia, 50 km S Ugab River	-20.966944	14.110278
Rhoptropus diporus		X		AMB 8474	Namibia, False Gai-As	-20.788056	14.111389
Rhoptropus diporus	X			AMB 8475	Namibia, False Gai-As	-20.788056	14.111389
Rhoptropus diporus	X	X		AMB 8815	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus	X	X		AMB 8816	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X		AMB 8817	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X		AMB 8818	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X	X	AMB 8819	Namibia, False Gai-As	-20.788056	14.111556

Rhoptropus diporus		X		AMB 8820	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X	X	AMB 8821	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X		AMB 8822	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X	X	AMB 8823	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X		AMB 8824	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X	X	AMB 8825	Namibia, False Gai-As	-20.788056	14.111556
Rhoptropus diporus		X		AMB 8833	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-22.073972	15.169889
Rhoptropus diporus	X	X	X	AMB 8834	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-22.073972	15.169889
Rhoptropus diporus	X	X		AMB 8835	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-23.073972	16.169889
Rhoptropus diporus	X	X		AMB 8836	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-24.073972	17.169889
Rhoptropus diporus	X			AMB 8837	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-25.073972	18.169889
Rhoptropus diporus	X	X		AMB 8838	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-26.073972	19.169889
Rhoptropus diporus	X	X	X	AMB 8839	Namibia, cricket pitch (D2303), 10 km SW Brandberg West Mine Dump	-27.073972	20.169889
Rhoptropus diporus	X			AMB7554	Namibia, Brandberg West Mine Dump	-21.074722	14.165833
Rhoptropus diporus		X		MCZR 183736	Namibia, Klein Gai-As	-20.787778	14.110833
Rhoptropus diporus		X		MCZ Z 23080	Namibia, Klein Gai-As	-20.787778	14.110833
Rhoptropus diporus	X	X		MCZZ 23081	Namibia, Klein Gai-As	-20.787778	14.110833
Rhoptropus diporus	X	X		MCZZ 23083	Namibia, Klein Gai-As	-20.787778	14.110833

Rhoptropus diporus	X	X		MCZZ23082	Namibia, Klein Gai-As	-20.787778	14.110833
Rhoptropus montanus		X	X	CAS 254880	Angola, Huila District, Leba Pass, between river and highway	-15.070333	13.243806
Rhoptropus montanus	X	X		CAS 254866	Angola, Huila District, Leba Pass overlook	-15.077	13.232917
Rhoptropus montanus	X	X		CAS 254867	Angola, Huila District, Leba Pass overlook	-15.077	13.232917
Rhoptropus montanus	X	X		CAS 254868	Angola, Huila District, Leba Pass overlook	-15.077306	13.2325
Rhoptropus montanus	X	X		CAS 254869	Angola, Huila District, Leba Pass overlook	-15.076667	13.233778
Rhoptropus montanus	X	X	X	CAS 254870	Angola, Huila District, Leba Pass overlook	-15.076667	13.233778
Rhoptropus montanus	X	X		CAS 254871	Angola, Huila District, Leba Pass overlook	-15.076667	13.233778
Rhoptropus montanus	X	X		CAS 254872	Angola, Huila District, Leba Pass overlook	-15.076667	13.233778
Rhoptropus montanus	X			CAS 254882	Angola, Huila District, Leba Pass, between river and highway	-15.070333	13.243806
Rhoptropus sp.		X		CAS 254801	Angola, Namibe District, Iona National Park, Espenhierra	-16.792417	12.354833
Rhoptropus sp.		X		CAS 254879	Angola, Huila District, Leba Pass, between river and highway	-15.070333	13.243806
Rhoptropus sp.		X		CAS 254883	Angola, Huila District, Leba Pass, between river and highway	-15.070333	13.243806
Rhoptropus sp.		X		CAS 254893	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044639	13.158611
Rhoptropus sp.				CAS 254948	Angola, Namibe District, Pico Azevedo	-15.534944	12.491528
Rhoptropus sp.		X		KTH 09116	Angola, Namibe District, 31.5 km E Namibe	-15.195919	12.447038

Rhoptropus sp.		X	X	KTH 09204	Angola, Namibe District, 40 km S Omauha Lodge, road to Espinheirra	-15.737336	12.211676
Rhoptropus sp.		X		CAS 254891	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044667	13.159056
Rhoptropus taeniostictus	X	X		ANG 291	Angola, Namibe District, 50km E Namibe, road to Leba Pass	-15.015583	12.555028
Rhoptropus taeniostictus	X			ANG 292	Angola, Namibe District, 50km E Namibe, road to Leba Pass	-15.015583	12.555028
Rhoptropus taeniostictus	X		X	ANG 260	Angola, Namibe District, 52 km N road to Lucira	-14.658056	12.527167
Rhoptropus taeniostictus	X			ANG 160 WC 1863	Angola, Namibe Province, N Namibe	-14.924083	12.371917
Rhoptropus taeniostictus	X		X	ANG 172 WC 1864	Angola, Namibe Province, N Namibe	-14.924083	12.371917
Rhoptropus taeniostictus	X		X	ANG 200 WC 1805	Angola, Namibe Province, N Namibe	-14.924083	14.372139
Rhoptropus taeniostictus	X			ANG 205 WC 1806	Angola, Namibe Province, N Namibe	-14.924083	12.371917
Rhoptropus taeniostictus	X		X	ANG 220 WC 1866	Angola, Namibe Province, N Namibe	-14.924083	12.371917
Rhoptropus taeniostictus	X			ANG 246 WC 1859	Angola, Namibe Province, N Namibe	-14.924083	12.371917
Rhoptropus taeniostictus	X	X		CAS 254898	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016083	12.645083
Rhoptropus taeniostictus	X	X	X	CAS 254901	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016	12.643556
Rhoptropus taeniostictus	X			ANG 319	Angola	-14.762845	12.492052
Rhoptropus taeniostictus	X			ANG 329	Angola	-14.762845	12.492052
Rhoptropus taeniostictus		X		CAS 254889	Angola, Namibe District, 2.0 km E Mangueiras, Namibe-Lubango road	-15.044667	13.159056

Rhoptropus taeniostictus	X			CAS 254895	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016111	12.643694
Rhoptropus taeniostictus	X	X	X	CAS 254904	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016861	12.642194
Rhoptropus taeniostictus		X		CAS 254905	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016861	12.642194
Rhoptropus taeniostictus	X	X		CAS 254908	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016111	12.642722
Rhoptropus taeniostictus		X		CAS 254911	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016361	12.642333
Rhoptropus taeniostictus		X		CAS 254916	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.015917	12.642389
Rhoptropus taeniostictus	X	X		CAS 254917	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016694	12.642194
Rhoptropus taeniostictus	X	X		CAS 254918	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016694	12.642194
Rhoptropus taeniostictus		X		CAS 254919	Angola, Namibe District, Namibe-Lubango Road, 1.8 km W Caraculo	-15.016917	12.641778

Supplemental 2. Details of outgroup taxa included for BEAST analyses (modified from Gamble et al. 2014 suppl. materials and Heinicke et al. 2016). The following field series and institutional abbreviations were used: ABTC, Australian Biological Tissue Collection; AMB, Aaron M. Bauer; AMCC, Ambrose Monell Cryo Collection, American Museum of Natural History; AMS, Australian Museum, Sydney; BPBM, Bernice P. Bishop Museum; BPN, Brice P. Noonan; CAS, California Academy of Sciences; CD, Charles Daugherty; CHUNB, Coleção Herpetológica da Universidade de Brasília; DB, Don Buden; ENS, Eric N. Smith; FG/MV, Frank Glaw and Miguel Vences; FGZC, Frank Glaw; FK, Fred Kraus; FLMNH, Florida Museum of Natural History; FMNH, Field Museum of Natural History; Glor, Rich E. Glor; GVH, Gerald V Haagner; ID, Indraneil Das; JAC, Jonathan Campbell; JB, Jon Boone; JFBM, James Ford Bell Museum of Natural History, University of Minnesota; DJH, D. James Harris; JEM, John E. Measey; JS, Jay Sommers; JVV, Jens V. Vindum; KU, University of Kansas Museum of Natural History; LJAMM, Luciano J. Avila and Mariana Morando; LSHC, La Sierra University Herpetological Collection, L. Lee Grismer; LSUMZ, Louisiana State University Museum of Zoology; MCZ, Museum of Comparative Zoology, Harvard University; MF, Mike Forstner; MHNSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos; MTR, Miguel T. Rodrigues; MTSN, Trento Museum of Natural Sciences; MV, Museum of Victoria; MVZ, Museum of Vertebrate Zoology, Berkeley; MZUSP, Universidade de São Paulo, Museu de Zoologia; NMZ, National Museum of Zimbabwe; QM, Queensland Museum; PMNH, Pakistan Museum of Natural History,; PEM, Port Elizabeth Museum; RAH, Rod A. Hitchmough; RMB, Rafe M. Brown; ROM, Royal Ontario Museum; SAM, South Australian Museum; SC, Salvador Carranza; TG, Tony Gamble; WBJ, W. Bryan Jennings; WDH, Wulf D. Haacke; USNM, National Museum of Natural History, Smithsonian Institution; YPM, Yale Peabody Museum; ZCMV, Miguel Vences; ZFMK, Zoologisches Forschunginstitut und Museum Alexander Koenig; ZSM, Zoologische Staatssammlung München.

Family	Species	ID	Locality	RAG1	ND2
Diplodactylidae	*Carphodactylus laevis*	AMS 143258	Lamb Range, Queensland, Australia	EF534781	GU459943
Diplodactylidae	*Nephrurus levis*	QM 140561	Western Australia, Australia	GU459544	AY369018
Diplodactylidae	*Orraya occultus*	QM A002513	Queensland, Australia	JQ945320	JX041389
Diplodactylidae	*Phyllurus platurus*	AMB 42	Sydney, NSW, Australia	HQ426314	JX024357
Diplodactylidae	*Saltuarius swaini*	AMS 143262	Lamb Range, Queensland,	JQ945338	JX024356
Diplodactylidae	*Underwoodisaurus milii*	AMB 499	Denham, Western Australia, Australia	EF534780	JX041460
Diplodactylidae	*Uvidicolus sphyrurus*	AMS R152351	Mt. Yulladunida, Kaputar Natl. Park, New South Wales, Australia	GU459543	GU459944
Diplodactylidae	*Amalosia rhombifer*	AMS 136216	Queensland, Australia	JQ945319	JX024363
Diplodactylidae	*Bavayia cyclura*	AMB 7683	nr. Voh, New Caledonia	HQ426264	JX041315
Diplodactylidae	*Bavayia geitaina*	AMB 7229	Mt. Ouin, New Caledonia	JQ945285	JX041316

Diplodactylidae	*Correlophus ciliatus*	AMS 146595	Rivière Bleue, New Caledonia	EF534778	JX024438
Diplodactylidae	*Crenadactylus ocellatus*	AMS R162089	Trephina Gorge, Northern Territory, Australia	AY662627	JX024364
Diplodactylidae	*Dactylocnemis pacificus*	CD 859	Pupuha, New Zealand	GU459385	GU459788
Diplodactylidae	*Dierogekko insularis*	AMS R161069	Ile Art, Belep Ids., New Caledonia	JQ945306	JF972458
Diplodactylidae	*Diplodactylus conspicillatus*	AMS 158426	Sturt Natl. Park, NSW, Australia	HQ426278	JQ173628
Diplodactylidae	*Diplodactylus tesselatus*	AMS 143855	Stonehenge area, Queensland, Australia	JQ173725	JQ173631
Diplodactylidae	*Eurydactylodes agricolae*	AMS R149366	Mt. Panié, New Caledonia	GU459547	DQ533758
Diplodactylidae	*Hesperoedura reticulata*	SAMA R23035	73k E Norseman, Western Australia, Australia	FJ855450	EF681803
Diplodactylidae	*Hoplodactylus duvaucelii*	FT277	Brothers Island, New Zealand	GU459441	GU459844
Diplodactylidae	*Lucasium damaeum*	AMB 54	58 km S Alice Springs, NT, Australia	HQ426279	GU459953
Diplodactylidae	*Lucasium stenodactylum*	AMS 139897	El Questro Station, Western Australia, Australia	JQ173724	JQ173630
Diplodactylidae	*Mniarogekko jalu*	AMS R161238	11 km NW Koumac, Dome de Tiebaghi, New Caledonia	JQ173759	JX024435
Diplodactylidae	*Mokopirirakau granulatus*	RAH340	Maud Island, New Zealand	GU459408	GU459811
Diplodactylidae	*Naultinus elegans*	No ID	Whangarei, New Zealand	GU459354	GU459757
Diplodactylidae	*Naultinus gemmeus*	RAH 464	Hakataramea, New Zealand	GU459361	GU459764
Diplodactylidae	*Naultinus rudis*	RAH388	Hamner are, New Zealand	GU459369	GU459772
Diplodactylidae	*Nebulifera robusta*	ABTC3938	near Rathdowney, Queensland, Australia	JQ173756	JQ173662
Diplodactylidae	*Oedodera marmorata*	CAS 230936	Paagoumène, New Caledonia	JQ945318	GU459947
Diplodactylidae	*Oedura marmorata*	AMS 143861	Stonehenge area, Queensland, Australia	EF534779	GU459951
Diplodactylidae	*Paniegekko madjo*	AMS R149329	Mt. Panié, New Caledonia	JQ945286	GU459950

Diplodactylidae	*Paradelma orientalis*	QM J56089	20 km N Capella, Queensland, Australia	HQ426304	AY134605
Diplodactylidae	*Pseudothecadactylus lindneri*	MVZ 99544	Kakadu Natl. Park, NT, Australia	HQ426318	GU459946
Diplodactylidae	*Rhacodactylus leachianus*	AMB 7189	Ilot Moro, New Caledonia	GU459548	GU459949
Diplodactylidae	*Rhynchoedura ornata*	AMS 155371	Sturt National Park, New South Wales, Australia	GU459553	GU459954
Diplodactylidae	*Strophurus aberrans*	AMS 136023	Tanami Road, Western Australia, Australia	JQ173761	JQ173667
Diplodactylidae	*Strophurus elderi*	AMS 130987	Silver City Hwy, New South Wales, Australia	JQ173763	JQ173669
Diplodactylidae	*Stropurus strophurus*	AMS 140536	Denham, Western Australia, Australia	JQ173766	JQ173672
Diplodactylidae	*Toropuku stephensi*	RAH554	Coromandel Peninsula, New Zealand	GU459381	GU459784
Diplodactylidae	*Tukutuku rakiurae*	RAH238	Stewart Island, New Zealand	GU459382	GU459785
Diplodactylidae	*Woodworthia maculata*	RAH 292	Titahi Bay, New Zealand	GU459449	GU459852
Eublepharidae	*Aeluroscalabotes felinus*	JB 16	Cameron Highlands, Malaysia	HQ426259	JX041301
Eublepharidae	*Coleonyx brevis*	TG 00194	Hudspeth County, Texas, USA	HQ426271	JX041333
Eublepharidae	*Coleonyx mitratus*	TG 00075	unknown	HQ426272	JX041334
Eublepharidae	*Coleonyx variegatus*	CAS 205334	Imperial Co.,California, USA	EF534777	JX041335
Eublepharidae	*Eublepharis macularius*	JS 2	Pakistan	EF534776	JX041350
Eublepharidae	*Goniurosaurus araneus*	JFBM 15830	Vietnam	HQ426286	JX041364
Eublepharidae	*Goniurosaurus luii*	TG 00795	China	HQ426287	JX041365
Eublepharidae	*Hemitheconyx taylori*	JB 12	Somalia	HQ426295	JX041371
Eublepharidae	*Holodactylus africanus*	CAS 198845	Kajiado District, Kenya	HQ426296	JX041372
Gekkonidae	*Afroedura karroica*	PEM FN1112	Eastern Cape Province, South Africa	JQ945277	JX041302
Gekkonidae	*Afroedura loveridgei*	GVH 3969	Mozambique	JQ945278	JX041303

Gekkonidae	*Afrogecko porphyreus*	CAS 206995	Cape Hangklip, Western Cape Prov., South Africa	EF490723	EF490776
Gekkonidae	*Agamura persica*	FMNH 247474	Makran Dist., Baluchistan, Pakistan	JQ945281	JX041306
Gekkonidae	*Ailuronyx tachyscopaeus*	MCZ F38717	Silhouette Island, Seychelles	JQ945282	JX041307
Gekkonidae	*Ailuronyx trachygaster*	AMB 8160	Silhouette Island, Seychelles	JQ945283	JX041308
Gekkonidae	*Alsophylax pipiens*	CAS 238805	Bulgan, Khovd, Mongolia	JQ945284	JX041309
Gekkonidae	*Altiphylax stoliczkai*	PMNH2323	Pakistan, Gilgit-Baltistan, Skardu, Satpara Dam	KC152018	KC151971
Gekkonidae	*Asiocolotes levitoni*	PMNH2431	Afghanistan, Logar Province, Aynak Village	KC152022	KC151974
Gekkonidae	*Blaesodactylus antongilensis*	ZSM 410/2005	Nosy Mangabe, Toamasina Prov., Madagascar	EU054229	EU054253
Gekkonidae	*Bunopus tuberculatus*	CAS 228737	Sharjah, United Arab Emirates	JQ945287	JX041317
Gekkonidae	*Calodactylodes illingworthorum*	AMB7415	Serawa, Pitakumbura, Sri Lanka	JQ945288	JX041318
Gekkonidae	*Chondrodactylus angulifer*	MCZ R184984	Klein Aus Vista, Namibia	JQ945289	–
Gekkonidae	*Chondrodactylus fitzsimonsi*	AMB 4669	30 km N Swakopmund, Namibia	EU293645	JX041321
Gekkonidae	*Christinus marmoratus*	CAS 193884	Wirralie, Ladysmith, New South Wales, Australia	JQ945290	JX041322
Gekkonidae	*Cnemaspis africana*	CAS 168872	Amani, Tanga, Tanzania	JQ945291	JX041323
Gekkonidae	*Cnemaspis dickersonae*	MTSN 8604	Uzungwa Scarp, Tanzania	JQ945292	JX041324
Gekkonidae	*Cnemaspis kandiana*	AMB 7508	Masimbula, Godakawela, Sri Lanka	JQ945293	JX041325
Gekkonidae	*Cnemaspis kendalii*	LSHC 6562	Kepong, Selangor, Malaysia	JQ945294	JX041326
Gekkonidae	*Cnemaspis limi*	LSHC 6267	Pulau Tioman, Malaysia	EF534809	JX041327
Gekkonidae	*Cnemaspis podihuna*	AMB 7449	Mihintale, Sri Lanka	JQ945295	JX041328
Gekkonidae	*Cnemaspis uzungwe*	MTSN 5603	Chita, Uzungwe Scarp,	JQ945296	JX041329

			Tanzania		
Gekkonidae	*Colopus kochi*	CAS 214308	59 km N Swakopmund, Namibia	JQ945297	JX041336
Gekkonidae	*Colopus wahlbergii*	NMZ 16974	Kalamba Station, Kazungula Dist., Zambia	JQ945298	JX041337
Gekkonidae	*Crossobamon orientalis*	ID 7618	vic. Sam, Rajasthan, India	JQ945299	JX041338
Gekkonidae	*Cryptactites peringueyi*	CAS 186374	Krom River Estuary, Eastern Cape Prov., South Africa	JQ945300	JX041339
Gekkonidae	*Cyrtodactylus angularis*	FMNH 265815	Muang Sa Kaeo, Sa Kaeo, Thailand	JQ945301	JX041340
Gekkonidae	*Cyrtodactylus ayeyarwadyensis*	CAS 216446	Rakhine, Myanmar	EU268287	EU268348
Gekkonidae	*Cyrtodactylus novaeguineae*	FK 11689	West Sepik, Papua New Guinea	HQ426274	JX041343
Gekkonidae	*Cyrtodactylus philippinicus*	FMNH 236073	Mt. Guitinguitin, Sibuyan Island, Philippines	JQ945304	JX041344
Gekkonidae	*Cyrtodactylus triedrus*	35A	Sri Lanka	JQ945308	JX041352
Gekkonidae	*Cyrtopodion kohsulaimanai*	PMH2388	Pakistan, Dera Ghazi Khan, Khar Garden	KP640629	KC151965
Gekkonidae	*Cyrtopodion scabrum*	TG 00109	Egypt	HQ426275	JX041345
Gekkonidae	*Dixonius siamensis*	LSHC 7328	Phnom Aural, Pursat Prov., Cambodia	EU054283	EU054299
Gekkonidae	*Dixonius vietnamensis*	FMNH 263003	Keo Seima Dist., Mondolkiri Prov., Cambodia	EU054281	EU054297
Gekkonidae	*Ebenavia inunguis*	ZCMV 2099	Marojejy, Madagascar	HQ426280	JX041348
Gekkonidae	*Elasmodactylus tetensis*	PEM 5551	Niassa Game Reserve, Mozambique	JQ945307	JX041349
Gekkonidae	*Geckolepis maculata*	FGZC 463	Montagne d'Ambre, Madagascar	EU054211	EU054235
Gekkonidae	*Gehyra australis*	AMS 139934	El Questro Station, Western Australia, Australia	JN019145	JN019081
Gekkonidae	*Gehyra cf. oceanica*	BPBM 23349	Parkop, Toricelli Mts., West Sepik Prov., Papua	JQ945309	JN393922

			New Guinea		
Gekkonidae	*Gehyra dubia*	AMS 152245	Daydawn, New South Wales, Australia	JN393956	JN393911
Gekkonidae	*Gehyra mutilata*	AMB 6582	Penang, Malaysia	JN393962	JN393917
Gekkonidae	*Gehyra nana*	AMS 140070	McGowens Beach, Kalumburu area, Western Australia, Australia	JN393963	JN393918
Gekkonidae	*Gehyra variegata*	AMS 140478	Millstream, Western Australia, Australia	JN393973	JN393929
Gekkonidae	*Gekko badenii*	JB 13	Vietnam	JN019130	JN019065
Gekkonidae	*Gekko cf. grossmanni*	No ID	unknown	JN019129	JN019064
Gekkonidae	*Gekko chinensis*	LSHC 4209	Wuzhi Shan, Hainan Id., China	JN019123	JN019058
Gekkonidae	*Gekko gecko*	No ID	unknown	EF534813	EU054288
Gekkonidae	*Gekko mindorensis*	KU 303912	Barangay Formon, Sitio Balogbob, Cueba Simbahan, Mindoro Oriental Prov., Philippines	JN019140	JN019076
Gekkonidae	*Gekko monarchus*	PEM R5412	Port Elizabeth, Eastern Cape, South Africa	JN019141	JN019077
Gekkonidae	*Gekko subpalmatus*	AMB 6567	Chengdu, Sichuan, China	JN019128	JN019063
Gekkonidae	*Gekko vittatus*	BPBM 19780	Rossel Id., Louisiade Ids., Milne Bay Prov., Papua New Guinea	JN019134	JN019069
Gekkonidae	*Goggia lineata*	AMB4762	Richtersveld National Park, Northern Cape Prov., South Africa	JQ945310	JX041353
Gekkonidae	*Hemidactylus brasilianus*	MZUSP 92493	Parque Nacional da Serra das Confusões, Piauí, Brazil	EU268290	EU268351
Gekkonidae	*Hemidactylus fasciatus*	ROM 19891	Sapo Nat'l Park, Sinoe, Liberia	JQ945311	EU268371
Gekkonidae	*Hemidactylus flavivirdis*	FMNH 245515	Punjab Province, Pakistan	EU268294	EU268355

Gekkonidae	*Hemidactylus frenatus*	AMB 7411	Pidenipitiya, Sri Lanka	EF534814	EU268357
Gekkonidae	*Hemidactylus greeffi*	CAS 219044	Praia da Mutamba, Sao Tomé	EU268308	EU268369
Gekkonidae	*Hemidactylus imbricatus*	TG 00568	Pakistan	HM559703 HQ426506	EU268354
Gekkonidae	*Hemidactylus mabouia*	JEM 1864	Wundanyi, Kenya	HQ426291	JX041368
Gekkonidae	*Hemidactylus macropholis*	CAS 227520	Bari Region, Puntland State, Somalia	HQ426292	JX041369
Gekkonidae	*Hemidactylus palaichthus*	LSUMZ H–12421	Roraima, Brazil	EU268307	EU268368
Gekkonidae	*Hemidactylus platyurus*	FMNH 245519	Makran District, Baluchistan Province, Pakistan	EU054271	EU054287
Gekkonidae	*Hemiphyllodactylus titiwangsaensis*	LSHC 7208	Cameron Highlands, Pahang, Malaysia	JN393978	JN393934
Gekkonidae	*Hemiphyllodactylus yunnanensis*	FMNH 258695	Makran District, Baluchistan Province, Pakistan	JN393979	JN393935
Gekkonidae	*Hemitheconyx caudicinctus*	TG 00180	Pakxong Dist., Champasak Prov., Lao PDR	HQ426294	JX041370
Gekkonidae	*Heteronotia binoei*	AMS 151170	unknown	EU054285	EU054301
Gekkonidae	*Heteronotia planiceps*	AMS 140331	Sturt Natl. Park, New South Wales, Australia	EU054284	EU054300
Gekkonidae	*Homopholis fasciatus*	TG 00191	23.3 km NNW jct. Tunnel Creek RD. with Great Northern Hwy., Western Australia, Australia	EU054226	EU054250
Gekkonidae	*Indogekko rohtasfortai*	PMNH2391	unknown	KC152027	KC151979
Gekkonidae	*Kolekanos plumicaudus*	WDH 1	Pakistan, Dera Ghazi Khan, Khar Garden	JQ945279	JX041304
Gekkonidae	*Lepidodactylus lugubris*	AMB 4111	Parque Nacional do Iona, Cunene Prov., Angola	EF534812	JX041377
Gekkonidae	*Lepidodactylus novaeguineae*	BPBM 15842	Kirimati, Kiribati Boiaboiawaga Id., Milne Bay Prov., Papua New Guinea	JQ945312	JX041378

Gekkonidae	*Lepidodactylus orientalis*	BPBM 19794	Sudest Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea	JN019144	JN019080
Gekkonidae	*Luperosaurus cumingii*	RMB 3546	Cumiagi, Philippines	JQ945313	JX041379
Gekkonidae	*Lygodactylus bivittis*	FG/MV 2001.A21	Andasibe, Madagascar	JQ945314	JX041380
Gekkonidae	*Lygodactylus bradfieldi*	AMB 7628	63.5 km W Kamanjab, Kunene Region, Namibia	HQ426301	JX041381
Gekkonidae	*Lygodactylus mirabilis*	FG/MV 2000.B3	Madagascar	HQ426300	JX041382
Gekkonidae	*Lygodactylus tolampyae*	FG/MV 2001.C14	Ankarafantsika, Madagascar	HQ426302	JX041383
Gekkonidae	*Matoatoa brevipes*	FG/MV 2002.2237	Tulear area, Madagascar	EF490724	EF490777
Gekkonidae	*Mediodactylus brachykolon*	PMNH2165	Pakistan, NWFP, Battagram City, Chaphar Gram Bridge	KC152029	KC151981
Gekkonidae	*Mediodactylus russowii*	AMB 8701	unknown	JQ945315	JX041384
Gekkonidae	*Mediodactylus spinicauda*	CAS 228709	Birjand, Khorasan Prov., Iran	JQ945316	JX041385
Gekkonidae	*Microgecko helenae*	JB 27	unknown	JQ945317	JX041386
Gekkonidae	*Nactus pelagicus*	CAS 229289	Mt. Gouémba, New Caledonia	EU054275	EU054291
Gekkonidae	*Nactus vankampeni*	FK11384	Wewak, East Sepik Prov., Papua New Guinea	EU054279	EU054295
Gekkonidae	*Narudasia festiva*	AMB 3243	Narudas, Namibia	EF534808	JX041387
Gekkonidae	*Pachydactylus gaiasensis*	AMB 7596	Gai-As, Namibia	JQ945322	JX041391
Gekkonidae	*Pachydactylus kladaroderma*	PEM FN1253	Molteno Pass, Western Cape Prov., South Africa	JQ945323	JX041392
Gekkonidae	*Pachydactylus punctatus*	MCZ R184457	Farm Celine, Limpopo Prov., South Africa	EU293646	JX041393
Gekkonidae	*Pachydactylus acuminatus*	MCZF23188		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus affinis*	MB5		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus amoenus*	JM1095		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus barnardi*	JB76		XXXXXX	XXXXXX

Gekkonidae	*Pachydactylus bicolor*	JV1857	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus capensis*	AMB8361	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus caraculicus*	MCZA38952	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus carinatus*	AMB4534	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus formosus*	AMB5574	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus geijte*	MCZA28203	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus goodi*	MCZF38445	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus griffini*	MCZZ23196	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus haackei*	AMB4506	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus kobosensis*	AMB6869	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus labialis*	MCZF38412	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus latirostris*	JB104	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus macrooculatus*	JB246	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus maculatus*	AMB3880	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus mariquensis*	MB21009	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus mclachlani*	MCZF38678	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus oculatus*	PEM1284	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus oshaughnessyi*	DGB611	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus otaviensis*	MCZF38512	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus parascutatus*	AMB7633	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus purcelli*	PEM1270	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus rangei*	AMB7167	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus reconditus*	MCZZ23128	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus sansteynae*	AMB6350	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus scherzi*	MCZF38577	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus scutatus*	AMB4041	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus serval*	MCZZ23149	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus sp*	MBarts002	XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus tsodiloensis*	Good	XXXXXX	XXXXXX

Gekkonidae	*Pachydactylus visseri*	JB59		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus waterbergensis*	MCZF38508		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus weberi*	AMB4802		XXXXXX	XXXXXX
Gekkonidae	*Pachydactylus rugosus*	CAS 201905	Sendelingsdrif, Richtersveld National Park, Northern Cape Prov., South Africa	JQ945325	JX041395
Gekkonidae	*Pachydactylus vanzlyi*	JVV 1761	Munutum River, Namibia	JQ945326	JX041396
Gekkonidae	*Paragehyra gabriellae*	FGZC 2366	Grotte Ampasy, Madagascar	JQ945328	JX041399
Gekkonidae	*Paroedura masobe*	JBFM 15832	Madagascar	EF536145	EF536193
Gekkonidae	*Paroedura picta*	FG/MV 2002.B1	Berenty, Madagascar	EF536149	EF536197
Gekkonidae	*Perochirus ateles*	DB Dmale	Dehpelhi Id., Pohnpei, Federated States of Micronesia	JN393984	JN393938
Gekkonidae	*Phelsuma borbonica*	JB 95	Réunion	HQ426305	JX041400
Gekkonidae	*Phelsuma laticauda*	FGZC 2705	Antalaha Airport, Madagascar	JQ945329	JX041401
Gekkonidae	*Phelsuma madagascariensis*	FG/MV 2002.797	Manongarivo, Madagascar	EF534811	JX041402
Gekkonidae	*Phelsuma modesta*	ZSM 35/2004	Ambovombe, Madagascar	HQ426307	JX041403
Gekkonidae	*Phelsuma ocellata*	CAS 186351	22 km E Sendelingsdrif, Richtersveld National Park, Northern Cape, South Africa	HQ426308	JX041429
Gekkonidae	*Phelsuma rosagularis*	JB 109	Mauritius	HQ426306	JX041404
Gekkonidae	*Pseudogekko smaragdina*	KU 303995	Quezon, Philippines	JQ945332	JX041420
Gekkonidae	*Ptenopus carpi*	CAS 214534	20 km N Swakopmund, Namibia	JQ945333	JX041422
Gekkonidae	*Ptychozoon kuhli*	RMB 1134	Malaysia	JQ945334	JX041423
Gekkonidae	*Ptychozoon lionatum*	CAS 221168	Bago Div., Myanmar	JQ945335	JX041424
Gekkonidae	*Ramigekko swartbergensis*	JB 47	Swartberg Mts., Western Cape Prov., South Africa	JQ945280	JX041305
Gekkonidae	*Rhoptropus afer*	MCZ R183711	Rössing Mt., Namibia	JQ945336	JX041430
Gekkonidae	*Rhoptropus boultoni*	CAS 214713	Twyfelfontein, Namibia	EF534810	JX041431

Gekkonidae	*Rhoptropus diporus*	MCZ R183737	Brandberg Wes Myn, Namibia	JQ945337	JX041432
Gekkonidae	*Siwaligekko battalensis*	PMNH2301	Pakistan, NWFP, Battagram City, Chaphar Gram Bridge	KC152035	KC151983
Gekkonidae	*Stenodactylus doriae*	JB2	captive	KC152037	KC151985
Gekkonidae	*Stenodactylus sthenodactylus*	MVZ 235804	Dakhlet Nouâdhibou Region, Mauritania	JQ945339	JX041441
Gekkonidae	*Tenuidactylus caspius*	CAS 228602	Touran Protected Area, Semnan Prov., Iran	JQ945340	JX041448
Gekkonidae	*Tenuidactylus elongatus*	JB127	Gobi, China	JX440677	JX440516
Gekkonidae	*Tenuidactylus fedtschenkoi*	JEM346	Uzbekistan, 5km from Nurata, Aktau Mtns	KC152040	KC151989
Gekkonidae	*Tenuidactylus longipes*	CAS 228830	Tabas, Yazd Prov., Iran	JQ945341	JX041449
Gekkonidae	*Tropiocolotes tripolitanus*	MVZ 238922	Tafokin, Agadez, Niger	JQ945343	JX041459
Gekkonidae	*Urocotyledon inexpectatus*	MCZF 38723	Silhouette Island, Seychelles	JQ945344	JX041461
Gekkonidae	*Uroplatus giganteus*	ZSM 55/2005	Marojejy, Madagascar	EF490737	EF490790
Gekkonidae	*Uroplatus guentheri*	ZSM 476/2001	Ankarafantsika, Madagascar	EF490725	EF490778
Gekkonidae	*Uroplatus henkeli*	FG/MV 2000.C1	Nosy Be, Madagascar	EF490743	EF490796
Gekkonidae	*Uroplatus phantasticus*	FG/MV 2002.640	Ranomafana, Madagascar	EF490746	EF490799
Phyllodactylidae	*Asaccus platyrhynchus*	CAS 227605	Wilayat Nazwa, Oman	EU293625	JX041313
Phyllodactylidae	*Asaccus sp.*	JB 15	Mirbat, Oman	EU293626	JX041314
Phyllodactylidae	*Garthia gaudichaudii*	SC 1	Chile	HQ426281	JX041351
Phyllodactylidae	*Gymnodactylus amarali*	CHUNB 38646	Cocalzinho, Goiás, Brazil	HQ426288	JX041366
Phyllodactylidae	*Haemodracon riebeckii*	JB 11	Socotra Island, Yemen	EU293627	JX041367
Phyllodactylidae	*Homonota darwinii*	LJAMM 4601	Puerto Deseado, Santa Cruz, Argentina	EU293628	JX041373
Phyllodactylidae	*Homonota fasciata*	TG 00085	Paraguay	EU293629	JX041374
Phyllodactylidae	*Phyllodactylus reissii*	JB 39	Peru	EU293632	JX041410
Phyllodactylidae	*Phyllodactylus tuberculosus*	KU 289758	PN El Imposible, Ahuachapán, El Salvador	EU293630	JX041411

Phyllodactylidae	*Phyllodactylus unctus*	ROM 39002	La Paz, Baja California Sur, Mexico	HQ426312	JX041412
Phyllodactylidae	*Phyllodactylus wirshingi*	TG 00722	Guanica, Puerto Rico	JQ945331	JX041413
Phyllodactylidae	*Phyllodactylus xanti*	ROM 38490	Baja California Sur, Mexico	EF534807	JX041414
Phyllodactylidae	*Phyllopezus lutzae*	CHUNB 50462	Mata de São João, Bahia, Brazil	HQ426265	JX041415
Phyllodactylidae	*Phyllopezus maranjonensis*	ZFMK 84995	Balsas, Amazonas, Peru	EU293633	JX041416
Phyllodactylidae	*Phyllopezus pollicaris*	CHUNB 43850	São Domingos, Goiás, Brazil	HQ426313	JQ825317
Phyllodactylidae	*Phyllopezus pollicaris*	MZUSP 92491	Parque Nacional da Serra das Confusões, Piauí, Brazil	EU293635	JX041417
Phyllodactylidae	*Phyllopezus przewalskii*	TG00105	Paraguay	JN935445	JQ825594
Phyllodactylidae	*Ptyodactylus guttatus*	TG 00072	Egypt	EU293636	JX041425
Phyllodactylidae	*Tarentola americana*	MVZ 241223	13 km E of Pilon, Granma Province, Cuba	HQ426332	JX041442
Phyllodactylidae	*Tarentola chazaliae*	TG 00130	Morocco	EU293638	JX041443
Phyllodactylidae	*Tarentola delalandii*	JB 43	Canary Islands	EU293639	JX041444
Phyllodactylidae	*Tarentola deserti*	JB 44	unknown	HQ426333	JX041445
Phyllodactylidae	*Tarentola fascicularus*	JB 29	unknown	HQ426334	JX041446
Phyllodactylidae	*Tarentola mauritanica*	TG 00129	Egypt	EU293641	JX041447
Phyllodactylidae	*Thecadactylus rapicauda*	USNM 561446	St. Croix, U.S. Virgin Islands	EU293643	JX041456
Phyllodactylidae	*Thecadactylus rapicauda*	ENS 7108	Izabal, Guatemala	EU293642	JX041455
Phyllodactylidae	*Thecadactylus solimoensis*	KU 214929	Cuzco Amazonico, Madre de Dios, Peru	EU293644	JX041457
Pygopodidae	*Aprasia inaurita*	SAMA R40729	2 km E of Burra, South Australia	FJ571632	AY134574
Pygopodidae	*Aprasia parapulchella*	MV D66569	Bendigo Whipstick, Victoria, Australia	HQ426260	GU459941
Pygopodidae	*Delma butleri*	SAMA R36144	Coonbah, New South Wales, Australia	HQ426276	AY134584
Pygopodidae	*Delma tincta*	AMS 151607	Sturt Natl. Pk., NSW, Australia	HQ426277	JX041347
Pygopodidae	*Lialis burtonis*	TG 00078	Provinsi Papua, Indonesia	EF534782	JX024354

Pygopodidae	*Ophidiocephalus taeniatus*	SAM R44653	Todmorden Station, South Australia, Australia	HQ426303	AY134601
Pygopodidae	*Pletholax gracilis*	WBJ 2483	Lesueur National Park, Western Australia, Australia	HQ426315	AY134602
Pygopodidae	*Pygopus lepidopodus*	WBJ 1206	Lesueur National Park, Western Australia, Australia	HQ426319	AY134603
Pygopodidae	*Pygopus nigriceps*	MVZ 197233	81 km S Alice Springs, Northern Territory, Australia	EF534783	JX024355
Sphaerodactylidae	*Aristelliger georgeensis*	JB 101	unknown	HQ426261	JX041310
Sphaerodactylidae	*Aristelliger lar*	JB 01	Dominican Republic	EF534805	JX041311
Sphaerodactylidae	*Aristelliger praesignis*	USNM 337563	Kingston, St. Andrew Parish, Jamaica	HQ426262	JX041312
Sphaerodactylidae	*Chatogekko amazonicus*	LSUMZ H–16400	Manaus, Amazonas, Brazil	HQ426268	JX041319
Sphaerodactylidae	*Coleodactylus brachystoma*	MZUSP 92569	Piauí, Brazil	EF534792	JX041330
Sphaerodactylidae	*Coleodactylus cf. brachystoma*	CHUNB 43901	São Domingos, Goiás, Brazil	HQ426270	JX041331
Sphaerodactylidae	*Coleodactylus septentrionalis*	LSUMZ H–12351	Roraima, Brazil	EF534791	JX041332
Sphaerodactylidae	*Euleptes europaea*	No ID	Liguria, Italy	EF534806	JN393941
Sphaerodactylidae	*Gonatodes albogularis*	MVZ 204073	Limon, Costa Rica	EF534797	JX041354
Sphaerodactylidae	*Gonatodes alexandermendesi*	BPN 1303	Imbaimadai, Guyana	EF534798	JX041355
Sphaerodactylidae	*Gonatodes annularis*	no ID	French Guiana	EF534794	JX041356
Sphaerodactylidae	*Gonatodes antillensis*	YPM17583	Westpunt Bay Beach, Curaçao	KP640630	KP640636
Sphaerodactylidae	*Gonatodes caudiscutatus*	KU 218359	Limon, Ecuador	EF534795	JX041357
Sphaerodactylidae	*Gonatodes concinnatus*	LSUMZ H–12688	Sucumbios, Ecuador	HQ426282	JX041359
Sphaerodactylidae	*Gonatodes daudini*	JB 38	Union Id., St. Vincent and Grenadines	EF534793	JX041360
Sphaerodactylidae	*Gonatodes humeralis*	MF 19492	Ecuador	EF534796	JX041361
Sphaerodactylidae	*Gonatodes ocellatus*	TG 00038	Tobago	HQ426284	JX041362
Sphaerodactylidae	*Gonatodes vittatus*	TG 00040	Trinidad	HQ426285	JX041363
Sphaerodactylidae	*Lepidoblepharis sp.*	KU 218367	Manabi, Ecuador	EF534789	JX041375

Sphaerodactylidae	*Lepidoblepharis xanthostigma*	MVZ 171438	Limon, Costa Rica	EF534790	JX041376
Sphaerodactylidae	*Pristurus carteri*	TG 00083	Yemen	EF534803	JX041419
Sphaerodactylidae	*Pristurus sp.*	TRJ-2009a	Sharjah, UAE	KP640631	GU271151
Sphaerodactylidae	*Pseudogonatodes guianensis*	KU 222142	Loreto, Peru	EF534784	JX041421
Sphaerodactylidae	*Quedenfeldtia moerens*	JB 77	Moroccco	HQ426320	JX041427
Sphaerodactylidae	*Quedenfeldtia trachyblepharus*	MVZ 178121	Oukaimeden, Morocco	EF534804	JX041428
Sphaerodactylidae	*Saurodactylus brosseti*	TG 00082	Morocco	EF534802	JX041433
Sphaerodactylidae	*Saurodactylus fasciatus*	DJH M616	Zumi, Morocco	HQ426322	JX041434
Sphaerodactylidae	*Saurodactylus mauritainicus*	DJH Sm61	NW of Ain Benimather, Morocco	HQ426323	JX041435
Sphaerodactylidae	*Sphaerodactylus argus*	TG 00125	Key West, Florida, USA	HQ426324	JX041436
Sphaerodactylidae	*Sphaerodactylus elegans*	YPM 14795	Monroe County, Florida, USA	EF534787	JN393942
Sphaerodactylidae	*Sphaerodactylus glaucus*	JAC 24229	Oaxaca, Mexico	HQ426325	JX041437
Sphaerodactylidae	*Sphaerodactylus leucaster*	Glor5269	Dominican Republic	KP640632	KP640638
Sphaerodactylidae	*Sphaerodactylus grandisquamis*	TG0099	Puerto Rico	HQ426326	KP640637
Sphaerodactylidae	*Sphaerodactylus nicholsi*	TG 00211	Bahia de la Ballena, Puerto Rico	HQ426328	JX041438
Sphaerodactylidae	*Sphaerodactylus nigropunctatus*	FLMNH 144010	Long Island, Bahamas	HQ426329	JX041439
Sphaerodactylidae	*Sphaerodactylus notatus*	FLMNH 132440	Miami–Dade County, Florida, USA	HQ426330	–
Sphaerodactylidae	*Sphaerodactylus torrei*	JB 34	Cuba	EF534788	JX041440
Sphaerodactylidae	*Sphaerodactylus townsendi*	TG00210	1 km W. Salinas, Puerto Rico	HQ426331	–
Sphaerodactylidae	*Teratoscincus keyserlingii*	CAS 228808	Yazd Province, Iran	EF534801	JX041450
Sphaerodactylidae	*Teratoscincus microlepis*	TG 00074	Pakistan	EF534800	JX041451
Sphaerodactylidae	*Teratoscincus przewalskii*	JBFM 15828	China	HQ426335	JX041452
Sphaerodactylidae	*Teratoscincus roborowskii*	TG 00070	China	EF534799	JX041453
Sphaerodactylidae	*Teratoscincus scincus*	JBFM 14252	Turkmenistan	HQ426336	JX041454
Outgroup	*Amphisbaena alba*	CHUNB 38770	Distrito Federal, Brasil	AY662619	AY662541
Outgroup	*Anolis carolinensis*	n/a	n/a	ENSACAT00000005087	AF294279
Outgroup	*Aspidoscelis tigris*	TG 00069	Maricopa County,	AY662620	U71332

			Arizona, USA		
Outgroup	*Dibamus bouretti*	ROM 36056	Quang Thanh, Cao Bang, Vietnam	AY662645	AY662562
Outgroup	*Elgaria kingii*	TG 00065	Navajo County, Arizona, USA	AY662603	AF085618
Outgroup	*Gallus gallus*	n/a	n/a	NM001031188	X52392
Outgroup	*Heloderma suspectum*	TG 00068	Arizona, USA	AY662606	AB167711
Outgroup	*Plestiodon inexpectatus*	TG 00792	Florida, USA	AY662632	AY607297
Outgroup	*Podarcis sicula*	TG 00124	Topeka, Kansas, USA	EF632239	NC011609
Outgroup	*Ramphotyphlops braminus*	No ID	Minneapolis, Minnesota, USA	AY662612	AY662539
Outgroup	*Rhineura floridana*	FLMNH 141814	Alachua County, Florida, USA	AY662618	AY605473
Outgroup	*Sphenodon punctatus*	No ID	n/a	AY662576	AF534390
Outgroup	*Tiliqua rugosa*	JFBM 13685	New South Wales, Australia	EF534815	JX041462
Outgroup	*Xantusia vigilis*	TG 00121	Los Angeles County, California, USA	AY662642	U71328
Outgroup	*Trioceros jacksonii*	n/a	n/a	FJ984187	AF448753
Outgroup	*Python molurus*	Python genome	captive	XM007441 886	HM581978

Supplemental 3. All unique georeferenced *Rhoptropus* localities obtained from global museum records for Namibia and Angola (117 total) plotted in Figure 4.

	Latitude (DD)	Longitude (DD)
1	-15.5	13.5
2	-21.1	14.66667
3	-19.61667	14.85
4	-22.58333	15
5	-19.38333	13.21667
6	-17.26667	12.45
7	-18.15	12.55
8	-15.13333	12.13333
9	-14.86667	13.1
10	-13.86667	12.51667
11	-15.48333	13.36667
12	-17.26667	11.76667
13	-16.9	12.58333
14	-18.25	13.25
15	-16.98333	13.28333
16	-21.11667	14.65
17	-20.43333	14.58333
18	-18.06667	13.81667
19	-17.45	13.05
20	-20.86667	15.35
21	-19.6	13.86667
22	-20.93333	14.53333
23	-17.91667	12.55
24	-17.9	12.11667
25	-12.23333	17.41667
26	-22.21667	15.31667
27	-19.6	13.4
28	-15.46	12.4
29	-21.839	14.07367
30	-16.997	13.24733
31	-22.55	14.82
32	-18.16917	12.24278
33	-18.24472	12.65083
34	-20.76694	14.02
35	-21.07397	14.16989
36	-22.53361	14.8375
37	-22.43028	14.46222
38	-22.42833	14.46194

39	-23.16667	14.63333
40	-23.58333	15.06667
41	-19.31667	14.1
42	-22.83333	15.38333
43	-15.01667	12.66667
44	-18.28333	13.66667
45	-14.26667	12.38333
46	-20.75	14.33333
47	-21.3	14.71667
48	-19.18333	13.38333
49	-17.78333	12.51667
50	-12.21667	17.36667
51	-19.2	13.01667
52	-22.115	15.0175
53	-18.15883	12.21117
54	-18.194	12.389
55	-22.56704	14.66607
56	-21.75933	15.10713
57	-21.36667	13.94833
58	-20.78806	14.11156
59	-17	13.23333
61	-20.88333	16.18333
62	-18.88333	12.81667
63	-17.75	11.91667
64	-19.36667	12.7
65	-15.31667	13.53333
66	-16.75	12.36667
67	-23.33333	14.83333
68	-18.78333	12.93333
69	-21.31667	14.58333
70	-20.58333	14.36667
71	-19.05	13.45
72	-20.23333	13.93333
73	-19.75	13.41667
74	-17.27972	12.22278
75	-22.62647	14.66107
76	-20.77917	14.075
77	-19.55167	17.23639
78	-17.38136	13.82956
79	-21.91589	15.57342
80	-19.50944	17.56044
81	-21.76667	13.95
82	-23.3	14.81667

83	-21.81667	15.63333
84	-22.73333	15.35
85	-22.8	15.33333
86	-15.55	12.51667
87	-15.73333	12.95
88	-14.91667	13.5
89	-20.86667	14.31667
90	-17.61667	12.76667
91	-17.5	13.31667
92	-23.2	14.98333
93	-22.93333	15.28333
94	-19.73333	13.8
95	-20.59267	14.35733
96	-23.18333	14.65
97	-19.84	14.11361
98	-19.66833	14.33278
99	-22.63722	14.7275
100	-22.66667	14.53333
101	-22.06667	15.26667
102	-22.68333	14.88333
103	-23.11667	15.18333
104	-17.76667	13.65
105	-17.23333	12.83333
106	-14.8	12.5
107	-19.60517	14.76317
108	-21.51067	13.87033
109	-17.2925	12.4325
110	-17.77056	12.55139
111	-22.6375	14.72694
112	-20.42174	15.46144
113	-19.4	15.11667
114	-21	14.15
115	-22.83333	15.46667
116	-23.08333	14.91667
117	-22.83333	15.36667

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