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Original article

# The biogeographical influence of the Tankwa Karoo Basin on reptile distribution in south-western South Africa

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Abstract.—Point distribution data were used to evaluate the biogeographical influence of the arid Tankwa Karoo Basin on the distribution of reptiles in the south-western districts of South Africa. Under-representation of the Tankwa Karoo in the dataset required an additional field survey of this region. Prior to the survey, available records from the Tankwa Karoo Basin represented only 13 reptile species. A total of 36 species (24 lizards, nine snakes, three chelonians) was recorded during our survey of this area. Turnover across the Basin is high, species richness is lower than in surrounding mountainous areas and there are no species endemic to the area. The Tankwa Karoo Basin acts as a dispersal barrier for many reptile species occurring in the surrounding more mesic areas. At the same time, the ranges of a number of typical northern, arid-adapted species extend southward along the Tankwa plains. A number of species range extensions in the region are reported.

Key words.—Tankwa Karoo Basin, reptile distribution, species turnover, range extensions, dispersal corridor, dispersal barrier

The Tankwa Karoo Basin is an arid basin in south-western South Africa, between the Swartruggens and Cederberg Mountains in the west and the Roggeveld Escarpment in the east (Fig. 1). It forms part of the Rainshadow Valley Karoo Bioregion, one of the six bioregions defined by Mucina *et al.* (2006) as constituting the Succulent Karoo Biome. Mean annual precipitation in the basin is extremely low, ranging from 70–110 mm. With the absence of the influence of coastal fog, the basin is one of the driest areas in the Succulent Karoo Biome and for most of the year resembles a desert landscape (Mucina *et al.* 2006). The biogeographical significance of this apparently inhospitable stretch of land has not been determined for any faunal group. The potential capacity of the basin to act as a dispersal barrier or dispersal corridor, for example, is unknown. The aim of our study was to investigate the biogeographical influence of the Tankwa Karoo Basin on the distribution of reptiles in the south-western districts of South Africa. Such knowledge is important for effective conservation planning, particularly in the light of global climate change.

The Greater Cederberg Biodiversity Corridor (GCBC) is a large-scale conservation corridor that was recently demarcated in the Greater Cape Floristic Region (GCFR) of South Africa (Low *et al.* 2004; Barodien 2005; Fig. 1), also commonly

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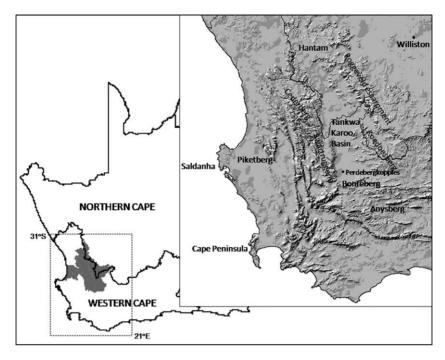


Figure 1. Map of South Africa indicating the study area, south of 31°S and west of 21°E, and the Greater Cederberg Biodiversity Corridor (shaded area). The insert shows the Tankwa Karoo Basin and surrounding mountains.

referred to as the Cape Floral Kingdom and encompassing the Fynbos Biome and the Succulent Karoo Biome. The west-to-east corridor section of the GCBC spans the Tankwa Karoo Basin (Fig. 1). The extreme paucity in reptile distribution data for the Tankwa Karoo Basin precluded any significant contribution of reptile data in the delineation of the boundaries of this regional planning unit (Anon 2005). An analysis of the biogeographical influence of the Tankwa Karoo Basin on reptile distribution therefore first required a detailed reptile survey of the basin. The results of our study would allow an evaluation of the relevance of the GCBC for reptile conservation, particularly the relevance of the eastern corridor section that spans the Tankwa Karoo Basin. We hypothesised that the Tankwa Karoo Basin would form a significant west-to-east dispersal barrier for reptiles, and that this would be demonstrated by a turnover of species across the Swartruggens and Cederberg Mountains, the Tankwa Karoo Basin and the Roggeveld Escarpment.

#### MATERIALS AND METHODS

#### **Study Area and Species Data**

To investigate the significance of the Tankwa Karoo Basin for reptile distribution, the region south of 31° latitude and west of 21° longitude in South Africa was selected as study area. The western part of the Western Cape Province as well as the adjacent southern sections of the Northern Cape Province (Roggeveld and northern Tanqua Karoo) are included in the defined study area (Fig. 1).

The dataset of species distribution records used in this study was obtained from the CapeNature database. A large portion of the records in this database was contributed by various museums as well as scientific and academic institutes across the country. A large amount of data was also contributed by the SCARCE project (Survey of Cederberg Amphibians and Reptiles for Conservation and Tourism) of which the current study formed a part. An inherent feature of the data is therefore that records originate from sightings and specimen collections compiled over a number of years with no standard sampling strategy. On closer inspection of the dataset, it was noted that the Tankwa Karoo region was grossly under-represented (Fig. 2). It was therefore deemed necessary to conduct a systematic survey of this under-sampled region to supplement the dataset.

The distribution records are all geo-referenced and were translated from point data to a regular grid with the GIS software package ArcView 3.2 (ESRI), following the methods of Guisan & Hofer (2003). The distribution data were aggregated in this way at two grid resolutions namely, quarter degree squares (QDS) and eighth degree squares (EDS), based on the South African National Grid System. This method basically generated two presence/absence datasets from the presence-only data which could be used in subsequent analyses.

#### Selection of Sampling Localities

The Tankwa survey was implemented with the intent that sampled areas should be representative of the whole region and also that a maximum number of species be detected. Selection of particular sampling localities was largely governed by the ability to identify and contact landowners, and subsequent granting of permission to conduct a survey on their property. However, the overall selection was directed by the condition that sampling localities should be spaced out throughout the length and breadth of the region, with the additional requirement that the sampling effort within each vegetation unit [as defined in Mucina & Rutherford (2006)] should be roughly proportional to the size of each of these units within the total area.

#### Survey Method

Surveys were conducted by actively searching for reptiles sheltering underneath vegetation and rocks or within crevices. This method allowed us to cover a large area and a variety of different retreat sites. Active searches were also conducted during night-time to ensure maximum detection of species. Animals were caught by hand or small noose where necessary for accurate identification. The GPS coordinates of the point where each animal was encountered, were recorded.

A maximum of two voucher specimens of each species encountered were collected from each location. Voucher specimens were preserved using standard preservation methods: sacrificed individuals were fixed in 10% formaldehyde and preserved in 70% alcohol. All specimens were catalogued and entered in the Ellerman Collection of the University of Stellenbosch. Sight records were also entered into the database.

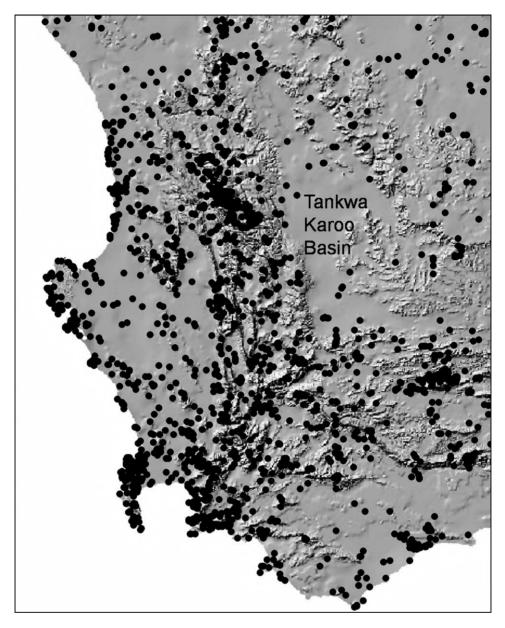


Figure 2. Reptile distribution records in the CapeNature database for the area south of  $31^{\circ}$ S and west of  $21^{\circ}$ E, showing the paucity in data for the Tankwa Karoo Basin.

### **Species Turnover**

Species turnover between the Tankwa Karoo Basin and the surrounding areas was simply expressed as the proportion of species lost and gained from one area to the other [see Koleff *et al.* (2003) for a list of beta diversity measures]. The proportion was calculated by dividing the number of species unique to both the focal (c) and the neighbouring (b) area with the sum of (c), (b), and (a), – the number of species shared

by the two areas. The resultant turnover value ranges between zero (no turnover) and one (complete turnover, no shared species). For the comparison of the Tankwa Karoo Basin with the greater Cederberg area and Roggeveld escarpment, respectively, the aggregated species occurrence data for blocks of five adjacent quarter degree square (QDS) cells in each region were compared (Fig. 3A). In the case of the Roggeveld escarpment data from a sixth grid cell containing the well-sampled Williston area were added to overcome the problem of undersampling in the general escarpment area. In addition, two blocks of four adjoining QDS cells were selected just south and just north of the Tankwa Basin and compared with a transect of four QDS cells within the Basin for the investigation of species compositional turnover along the north-south axis of the region (Fig. 3B).

The method of comparing species composition, and subsequently determining species turnover across the Tankwa Karoo Basin, by means of transects/blocks composed from adjacent QDS grid cells, was chosen in order to avoid (1) the problem of arbitrarily defining the limits of the regions, and (2) comparing areas of unequal size with each other. As mentioned, an exception was made in the case of the Roggeveld escarpment and plateau because the inclusion of the additional grid cell was considered to improve the result rather than affect it negatively.

#### RESULTS

### **Species Distributions**

Prior to our survey, the CapeNature database included records from the Tankwa Karoo Basin for 13 reptile species only. The survey extended this number to a total of

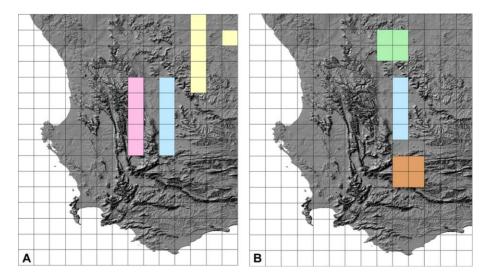


Figure 3. Quarter degree grid cells of which the aggregated species occurrence data were used to calculate the species compositional turnover (beta diversity) between (A) the larger Cederberg area (west), Tankwa Karoo Basin (east) and the Roggeveld escarpment and plateau (northern), and between (B) the Tankwa Karoo Basin (west) and the areas north (Hantam area) and south (Bonteberg area) thereof.

36 species (24 lizards, nine snakes, three chelonians; see Online Supplementary Material). The survey generated distribution data for five quarter degree squares which previously had no reptile distribution records, for one quarter degree square which previously had only a single record and for another quarter degree square which previously only had three records. At the finer resolution (eighth degree square), data were generated for 16 cells for which no data were recorded previously only had two records.

New records which extend their existing distribution ranges were recorded for the Giant Ground Gecko (*Chondrodactylus angulifer*; see Online Supplementary Material; distribution record A), the Armadillo Girdled Lizard (*Cordylus cata-phractus*; see Online Supplementary Material; distribution record B), the Striped Leaf-toed Gecko (*Goggia lineata*), the Thin-skinned Thick-toed Gecko (*Pachydacty-lus kladeroderma*), the Western Three-striped Skink (*Trachylepis occidentalis*; see Online Supplementary Material; distribution record C), the Horned Adder (*Bitis caudalis*; see Online Supplementary Material; distribution record D) and the Black Spitting Cobra (*Naja nigricollis woodi*).

#### **Species Turnover**

High  $\beta$ -values indicated species losses and gains between the Tankwa Basin and the larger Cederberg area to the west (0.64) and between the Tankwa Basin and the Roggeveld escarpment and plateau to the east (0.68; Table 1). Species turnover between the Cederberg and Roggeveld areas was found to be especially high (0.91). Forty five species were recorded in the Cederberg transect, 30 in the Tankwa transect and 24 for the Roggeveld escarpment and plateau (Table 2). Twenty one species were unique to the Cederberg transect, three to the Tankwa transect, and seven to the Roggeveld transect. The Cederberg and Tankwa transects shared 14 species, the Tankwa and Roggeveld transects six species, and the Cederberg and Roggeveld transects four species (Table 2).

Similar to the west-east axis, turnover along the north-south axis was also found to be high (Tables 3, 4). Twenty two species were unique to the Southern transect, 10 to the Tankwa transect, and eight to the Northern transect. The Southern and Tankwa transects shared five species, the Tankwa and Northern transects four species, and the Southern and Northern transects four species (Table 4). Six species were recorded in all three transects.

Table 1. Species turnover ( $\beta$ ) between the Tankwa Karoo Basin, the greater Cederberg area in the west, and the Roggeveld escarpment and plateau in the east, was calculated by dividing the number of species unique to both the focal (c) and the neighbouring (b) area with the sum of (c), (b) and (a) – the number of species shared by the two regions.  $\beta$ -values range between a minimum of zero (no turnover) and a maximum of one (complete turnover).

	а	b	С	β
Tankwa vs. Roggeveld	13	11	17	0.68
Tankwa vs. Cederberg	20	25	10	0.64
Roggeveld vs. Cederberg	5	40	12	0.91

С	Т	R	C & T	T & R	C, T & R	C & R
A. australis	B. caudalis	A. aculeata	B. arietans	A. hispida	C. polyzonus	A. atra
A. porphyreus	N. nivea	C. namaquensis	C. angulata	C. angulifer	N. tessellata	A. lubricus
B. atropos	T. occidentalis	D. scabra	C. bibronii	D. multimaculata	P. lineoocellata	L. capensis
B. gutturale		M. suborbitalis	C. cataphractus	H. boulengeri	P. mariquensis	P. purcelli
B. rubida		P. garrulus	C. subtessellatus	L. gracilior	P. notostictus	
C. mclachlani		P. namaquensis	G. lineata	P. laticeps	T. sulcata	
D. typus		R. schinzi	M. knoxii	P. tentorius		
G. hexapora			P. capensis			
G. microlepidota			P. formosus			
H. signatus			P. geitje			
L. guttatus			P. rhombeatus			
L. rufulus			P. weberi			
M. lineatus			T. capensis			
N. woodi			T. variegata			
P. burchelli			Ū			
P. microlepidotus						
Ps. capensis						
R. lalandei						
T. beetzii						
T. homalocephala						
T. montana						

Table 2. Summary of the reptile species unique to or shared between three transects in the larger Cederberg area (C), the Tankwa Basin (T) and the Roggeveld escarpment and plateau (R) (see Online Supplementary Electronic Material for full species names).

Table 3. Species turnover ( $\beta$ ) between the Tankwa Karoo Basin, the Hantam area in the north, and the Bontberg area in the south, was calculated by dividing the number of species unique to both the focal (c) and the neighbouring (b) area with the sum of (c), (b) and (a) – the number of species shared by the two regions.  $\beta$ -values range between a minimum of zero (no turnover) and a maximum of one (complete turnover).

	a	b	С	β
Tankwa vs. south	11	26	14	0.78
Tankwa vs. north	10	12	15	0.73
South vs. north	10	12	27	0.80

#### DISCUSSION

#### **Distribution Records**

The reptilian fauna of the Tankwa Karoo Basin does not include any endemic species and can best be described as transitional as it has elements from all surrounding areas. With the general paucity of rocky habitats in the Tankwa Basin it is to be expected that rock-dwelling reptiles will be less well represented. Yet, wherever the plain is interrupted by isolated dolerite buffs or slightly elevated ridges, a complement of rock-dwelling forms typical of the surrounding mountainous areas, are present, typically the Karoo Girdled Lizard (Cordylus polyzonus), the Karoo Skink (Trachylepis sulcata), the Variegated Skink (Trachylepis variegata) and Bibron's Gecko (Chondrodactylus bibronii). The Southern Rock Agama (Agama *atra*), on the other hand, is notably absent in the Tankwa Basin and is restricted to the surrounding mountains (see Online Supplementary Material; distribution record E). Branch (1998) gives the range of A. atra as occurring throughout the Western Cape and most of the Northern and Eastern Cape. This is a gross over-estimation of its true range as it is clearly absent from the western coastal lowlands and from the Tankwa Karoo Basin. Its absence from the south-western coastal areas north of the Cape Peninsula has also been noted by Oelofsen et al. (1987).

The presence of *C. bibronii* in man-made structures throughout the basin, in many cases surrounded by vast stretches of rock-less habitat, highlights the exceptional dispersal ability of this rock-dwelling lizard. Rock-dwelling species in general have poor dispersal ability since morphological adaptations to a rock-dwelling lifestyle may constrain dispersal over extensive rock-less habitats. The presence of the Armadillo Lizard (*Cordylus cataphractus*) on the Perdebergkoppies, two small tillite outcrops surrounded by vast stretches of unsuitable habitat (Fig. 1), was also unexpected. This heavily armoured lizard is sluggish in nature (Mouton *et al.* 1999; Losos *et al.* 2002) and one would expect that predation pressure (Hayward 2007) would not allow dispersal over vast stretches of barren land.

The Cape Sand Lizard (*Pedioplanis laticeps*) is the most abundant species on the Tankwa plains (see Online Supplementary Material; distribution record F). Branch (1998) gives the range of this species as central Karoo, that is, the region to the north of the Tankwa Karoo Basin, the latter providing a north-south dispersal corridor for this species. It co-occurs with the Spotted Sand Lizard (*P. lineoocellata pulchella*) on the plains, but there is distinct habitat partitioning between the two (Du Plessis 2010). *Pedioplanis l. pulchella* prefers rocky habitat, while *P. laticeps* prefers the gravel plains with minimal vegetation cover. In the west, Knox's Desert Lizard (*Meroles*)

S	Т	Ν	S & T	N & T	N & S	N, S & T
A. meleagris	C. bibronii	B. cornuta	P. mariquensis	A. hispida	A. lubricus	B. arietans
A. atra	C. subtessellatus	D. multimaculata	P. notostictus	B. caudalis	L. capensis	C. angulata
A. australis	C. cataphractus	H. boulengeri	T. capensis	C. angulifer	P. tentorius	C. polyzonus
B. rubida	G. lineata	H. signatus	T. sulcata	P. weberi	R. lalandei	N. nivea
B. gutturale	L. gracilior	H. lacteus	T. variegata			P. geitje
C. cordylus	N. tessellata	L. nigricans	_			P. lineoocellata
G. typicus	P. capensis	P. cana				
H. areolatus	P. formosus	S. sexlineatus				
L. aurora	P. laticeps					
L. fiskii	T. occidentalis					
L. guttatus						
L. rufulus						
M. knoxii						
P. maculata						
P. oculatus						
P. burchelli						
P. subrufa						
P. rhombeatus						
P. microlepidotus						
T. homalocephala						
T. gularis						
T. montana						

Table 4. Summary of the reptile species unique to or shared between three transects in the Tankwa Basin (T) and the regions just to the south (S) and north (N) of the basin (see Online Supplementary Electronic Material for full species names).

*knoxii*) marginally enters the Tankwa Basin where it co-occurs with the two Sand Lizard species, but is restricted to sand habitat (Du Plessis 2010). The Southern Spiny Agama (*Agama hispida*) is also abundant in the central parts of the Tankwa Karoo Basin.

The range of the Giant Ground Gecko (*Chondrodactylus angulifer*) is depicted by Branch (1998) as reaching as far south as an imaginary east-west line through Saldanha and Piketberg. The CapeNature database, on which the range estimate was based, however, contains no records for this species south of  $32^{\circ}$  S within the study area. The range given by Branch (1998) therefore appears to be an overestimate. The four distribution records for *C. angulifer* are the first records for the Tankwa region and are also the most southerly records for this species in the study area. Like in the case of *P. laticeps*, the arid Tankwa Karoo Basin serves as a southward dispersal corridor for this species (see Online Supplementary Material; distribution record A). The ranges of terrestrial geckos, notably the Striped Dwarf Leaf-toed Gecko (Goggia lineata), Marico Thick-toed Gecko (Pachydactylus mariquensis) and Cape Thick-toed Gecko (Pachydactylus capensis) do not appear to be affected by the arid Tankwa Karoo Basin, these species also occur in the Basin. One exception is the Ocellated Thick-toed Gecko (P. geitje) which appears to be absent from the Tankwa plains. As far as rock-dwelling geckos are concerned, the basin acts as a dispersal barrier for the Rough Thick-toed Gecko (P. formosus), the Thin-skinned Thick-toed Gecko (P. kladeroderma) and the Cederberg Dwarf Leaf-toed Gecko (Goggia hexapora).

In contrast to the Giant Ground Gecko (*C. angulifer*), of which the range extends southwards along the whole breadth (west to east) of the basin, the Horned Adder (*Bitis caudalis*; see Online Supplementary Material; distribution record D) and the Bushmanland Tent Tortoise (*Psanmobates tentorius verroxii*), also two essentially northern forms in the study area, appear to have southern range extensions only along the western side of the basin. *Psanmobates t. tentorius* appears to be restricted to a narrow east-to-west zone in the southern part of the basin. One would expect a contact zone (or a zone of intergradation) between these two subspecies in the southwestern area of the basin.

There were only four previous records for the Western Three-striped Skink (*Trachylepis occidentalis*) within the study area, namely in the Anysberg region to the southeast of the Tankwa Karoo Basin. Although this species has a widespread distribution stretching from northern Namibia through the central karroid regions of the Northern Cape Province down to the Anysberg (Branch 1998), it has never been recorded in the Tankwa Karoo Basin. The new records reported here therefore extend this species' recorded range to the west (see Online Supplementary Material; distribution record C).

The Tankwa distribution records reported here for the Armadillo Girdled Lizard (*Cordylus cataphractus*), Striped Dwarf Leaf-toed Gecko (*Goggia lineata*) and Black Spitting Cobra (*Naja nigricollis woodi*) extend the known distribution ranges of these three species in an eastern direction. The new *N. n. woodi* record is located more than 75 km east from existing records in the database. The record for the Thin-skinned Thick-toed Gecko (*Pachydactylus kladeroderma*) on the slopes of the Pienaarsfontein mountain range, immediately to the west of the Koedoesberg Mountains (Fig. 1), extends the recorded distribution range of this gecko species to the west. This is a rock-dwelling species with a relatively restricted distribution from the inland Cape escarp to the southern Cape Fold Mountains (Branch 1998). The new record is more

than 60 km SW and 70 km NW from the two CapeNature database records nearest to it and extends the range in a western direction by approximately 45 km.

#### **Species Turnover**

Species turnover along both the west-east and north-south axes across the Tankwa Basin is high, a clear indication of the biogeographical influence of the Tankwa Karoo Basin on reptile distribution. We suggest that the arid basin forms a dispersal barrier for many species occurring in the more mesic surrounding areas. In the west and the south, the Cederberg/Swartruggens-Tankwa Karoo Basin and Bonteberg area-Tankwa Karoo Basin transitions also mark the transition between the Fynbos Biome and the Succulent Karoo Biome. The major transition in vegetation coincides with a major transition in reptile species composition. In the east and north the transition is less clearly demarcated, all areas falling within the Succulent Karoo Biome. The observation that the Tankwa Karoo Basin has higher species richness than the less arid Hantam area in the north (Fig. 1) is interesting and can probably be explained by the fact that several species (e.g. *C. cataphractus, P. kladeroderma, P. geitje, B. rubida*) from the Cederberg/Swartruggens and Roggeveld areas marginally enters the Tankwa Karoo Basin, but are absent in the Hantam area. It may also be that the Hantam area is still undersampled.

The summary lists (Tables 2 and 4) of species unique to or shared between regions are a useful aid to inspect the compositional differences between the areas. It should be mentioned that these cannot be considered as complete lists and should only be regarded as a first step in the characterisation of the species assemblages concerned. Because of the nature of the dataset (point distribution) and the fact that only a limited number of cells from a particular region were included in the analyses, some species occurring in the relevant areas, but which have not yet been recorded in the specific grid cells used in the analysis, will be excluded from these lists.

In summary, the results of this study show that the Tankwa Karoo Basin acts as a dispersal barrier for many reptile species occurring in the surrounding more mesic areas. At the same time, it acts as a southward dispersal corridor for several species, notably *Chondrodactylus angulifer*, *Trachylepis occidentalis*, *Bitis caudalis*, *Dipsina multimaculata* and *Psammobates tentorius verroxii*. The significance of the Tankwa Karoo as a dispersal barrier in future climate change scenarios will be difficult to assess without knowledge of how rainfall patterns will change in the basin. Taking into account the greater number of shared species between the areas east and west of the basin than between areas north and south of the basin, west-east connectivity across the basin is, from a conservation point of view, probably more important than north-south connectivity. The Tankwa Karoo National Park, as part of the Greater Cederberg Biodiversity Corridor, already spans the basin along the west-east axis.

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#### **ONLINE SUPPLEMENTARY MATERIAL**

## Distribution Records for 38 Reptile Species Recorded in the Tankwa Karoo Basin. Those Records for Which No Accession Numbers are Provided, Represent Sight Records

*Agama atra*, H6101, 32.300, 19.513, S, Elandsvlei; 32.132, 20.126, O, Gannaga Pas – TKNP; H5936, 33.135, 19.652, S, Kareekloof; H6034, 32.955, 20.267, S, Klipbanks-fontein; H6074, 32.177, 20.156, S, Langkloof – TKNP; 32.175, 20.152, O, Langkloof – TKNP; 33.202, 19.732, O, R355 fork

*Agama hispida*, H6044, 32.655, 19.682, S, Blaauwboschkolk; H6045, 32.655, 19.682, S, Blaauwboschkolk; 32.585, 19.558, O, Elandsdrift; H6083, 32.722, 19.713, S, Gansfontein; 32.715, 19.708, O, Gansfontein; H6047, 32.611, 19.808, S, Groote Kapels Fontein; H6058, 32.582, 19.701, S, Tandschoonmaak

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H6137, 31.879, 19.643, S, Kleinhoek; 31.884, 19.631, O, Kleinhoek; 31.879, 19.655, O, Kleinhoek; H6052, 32.671, 19.648, S, Klipkraal; H5925, 32.924, 19.700, S, N'Wardouw H6067, 32.277, 20.104, S, Paulshoek – TKNP; 32.784, 20.035, O, Pienaarsfontein; 32.799, 20.066, O, Pienaarsfontein; H5975, 32.641, 20.091, S, Rooivlak; 32.778, 19.936, O, Spitskoppe; H6109, 32.550, 20.010, S, Vaalfontein; H6110, 32.550, 20.010, S, Vaalfontein; 32.180, 19.816, O, Varschfontein – TKNP; 32.046, 19.768, O, Witkloof; H6131, 32.070, 19.747, S, Witkloof

Distribution Records for (A) *Chondrodactylus angulifer*; (B) *Cordylus cataphractus*; (C) *Trachylepis occidentale*; (D) *Bitis caudalis*; (E) *Agama atra* and (F) *Pedioplanis laticeps* Within the Study Area. Records Obtained from the CapeNature Database are Depicted in Black While the Records From the Tankwa Survey are Depicted in White

