



Singing on key: An integrative taxonomic revision of barking geckos (Gekkonidae: *Ptenopus*) with six additional species and keys for morphology and advertisement calls

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Abstract

Barking geckos, *Ptenopus* Gray, 1866 are burrowing geckos that occur across the xeric regions of southern Africa. They possess unique vocal abilities, with males producing loud advertisement calls to attract females. The taxonomy of the genus has remained stable for six decades, with three recognised species: *Ptenopus garrulus* (Smith, 1849), *P. kochi* Haacke, 1964, and *P. carpi* Brain, 1962. Within *P. garrulus*, two subspecies have been recognised since 1935: the nominotypical form (*P. g. garrulus*) and *P. g. maculatus* Gray, 1866. A recent phylogenetic analysis of the genus found that it contains eight to ten putative species. We used an integrated taxonomic approach to delimit a total of nine species, including evidence from phylogenetics, ecology, calls, and morphology. *Ptenopus g. maculatus* is elevated to full species, thereby restricting the geographic range of *P. garrulus* sensu stricto to the greater Kalahari. Additionally, four new species are named which were previously included in '*P. g. maculatus*': *Ptenopus adamanteus* **sp. nov.** from the southern Namib Desert, *P. circumsyrcticus* **sp. nov.** from the central Namib Desert, *P. kenkenses* **sp. nov.** from the northern Nama Karoo, and *P. australis* **sp. nov.** from southern Nama Karoo. As a result, the range of *P. maculatus* sensu stricto is restricted to the central northern Namib Desert. Furthermore, one new species previously included in *P. carpi* is named *P. sceletus* **sp. nov.** from the Skeleton Coast (northern coastal Namib Desert), thereby restricting the range of *P. carpi* sensu stricto to a small strip of coastal Namib Desert between the Swakop and Kuiseb rivers. The Namib Desert is the centre of diversity for the genus *Ptenopus*, containing seven of the nine species including the oldest divergent lineages. Two species-level keys are provided: a morphological key and a unique bioacoustic key to the advertisement calls.

Keywords

Bioacoustics, mate selection, phylogeography, substrate specificity, systematics

Introduction

The barking geckos, genus *Ptenopus*, are endemic to the xeric parts of southern Africa (Branch 1998). They have been termed one of the “most vociferous” of lizards, with males producing loud advertisement calls at the entrance of their burrows to attract females and maintain territories (Haacke 1969, 1975; Hibbitts 2006). These calls can be heard from hundreds of metres distant, and substantial choruses consisting of thousands of calling males have been recorded. As Smith (1849) remarked in the species description of *P. garrulus*: “and the number thus occupied is at times so great, and the noise so disagreeable, as to cause the traveller to change his quarters”. Barking geckos dig complex burrows within which most of their lives are spent, and in which mating and egg-laying takes place (Haacke 1975; Polakow 1997; Hibbitts 2006).

There are currently three described species of *Ptenopus*: *Ptenopus carpi* Brain, 1962, *P. kochi* Haacke, 1964, and *P. garrulus* (Smith, 1849), the latter containing two subspecies: *Ptenopus garrulus garrulus* and *P. g. maculatus* Gray, 1866. The species *P. garrulus* was initially described under the genus *Stenodactylus*, while ‘*P. maculatus*’ is the type species of the genus *Ptenopus* erected by Gray (1866). Boulenger (1885) synonymised ‘*P. maculatus*’ with *P. garrulus*, probably due to morphological similarity of the respective types. FitzSimons (1935) later erected subspecies for the forms *P. g. garrulus* and *P. g. maculatus*. Despite several taxonomic revisions including specimens from a wide geographic area (Loveridge 1947; Haacke 1964, 1975), this taxonomy of *P. garrulus* has been accepted for nearly 90 years, save the re-assignment of some specimens or geographic ranges to one subspecies or the other. The only diagnostic morphological variation between the subspecies that were identified by these authors were the colour pattern, number of scales around the midbody, and across the dorsal or ventral surfaces of the head. These characters were also found to vary within *P. g. maculatus*, to a lesser degree, among specimens from geographically disparate locations (Haacke 1975).

In a recent study, Becker et al. (2024) presented molecular and ecological evidence for the existence of eight to ten candidate species within *Ptenopus*. *Ptenopus garrulus* was found to be paraphyletic, containing potentially seven cryptic species, with different substrate and bioclimatic specialisations (Becker et al. 2024): Two putative species within the monophyletic subspecies *P. g. garrulus*, and five putative species within the paraphyletic subspecies *P. g. maculatus*. *Ptenopus kochi* and *P. carpi* were found to be valid species, although *P. carpi* may contain two species separated by a past vicariance event (Becker et al. 2024). These putative species represent deep evolutionary divergences with comparatively low morphological divergence being evident, and are therefore cryptic species (see Struck et al. 2018). Becker et al. (2024) proposed the need to investigate potential morphological differences among the newly proposed taxa. Furthermore, given the vocal nature of this genus, the differences in advertisement call characters among these

potentially new taxa need to be quantified and described (Becker et al. 2024).

Advertisement calls, like other courtship signals, tend to be under stabilising selection within a population, but diverge among genetically divergent populations or species (Paterson 1980; Lande 1981; Butlin and Ritchie 1989; Endler and Houde 1995). Mate-recognition as a stabilising force is mainly due to coevolution, which usually results from the necessary compatibility between the male signal and the female reception of that signal, within a population or species (Butlin and Ritchie 1989). The appreciation of vocal signals in geckos has received little attention compared to other vocal taxa such as birds, bats, and anurans. This is probably because most gecko species call softly, infrequently, and have simple calls. *Ptenopus* is a notable exception and some of the earliest research on species specificity of gecko advertisement calls were conducted on this genus (Brain 1962; Haacke 1964, 1969; Gramentz 2008). It is now more widely appreciated that gecko advertisement calls, like most vocal taxa, tend to be species-specific (Rohtla et al. 2019). The advertisement calls in *Ptenopus* provide an ideal model to apply the species properties of mate recognition to the species delimitation process.

Cryptic species are common across all branches of life (Jörger and Schrödl 2013). The lack of substantial morphological diversification despite deep evolutionary diversification is an evolutionary phenomenon with poorly understood mechanisms (Fišer et al. 2018; Struck et al. 2018). This is partly because the delimitation of cryptic species has been strongly biased towards genetic distance-based methods. There is a need to incorporate a more integrated, multicriteria approach to this problem (Fišer et al. 2018).

Here, we considered four operational criteria or lines of evidence to delimit species in the genus *Ptenopus* under the unified or general lineage species concept (GLC: de Queiroz 1998, 2007): Phylogenetic, ecological, morphological (either asphenetic cluster, or as diagnostic fixed difference) and recognition (advertisement calls and sexual dichromatism). We interpreted the phylogenetic and ecological evidence from Becker et al. (2024), in combination with new evidence from calls and morphology, to evaluate the validity of putative species based on cumulative evidence from at least three operative criteria. We named and described the newly identified species and provide descriptions of their calls and natural history.

Materials and Methods

Field sampling: Calls and morphology

Geckos were located using a T16 LED Lenser torch to spot eye-shine at night (this method may be aided with binoculars), and/or by their vocalisations at dusk. Male advertisement calls of each *Ptenopus* species were recorded with digital recorders including Olympus

Table 1. Putative species from Becker et al. (2024) and the names now assigned to these taxa, including new species and subspecies described below.

Putative taxa	Species name assigned
<i>Ptenopus garrulus garrulus</i> (North + South)	<i>Ptenopus garrulus</i> sensu stricto
<i>Ptenopus garrulus maculatus</i> Southeast	<i>Ptenopus australis</i> sp. nov.
<i>Ptenopus garrulus maculatus</i> South	<i>Ptenopus adamanteus</i> sp. nov.
<i>Ptenopus garrulus maculatus</i> Central	<i>Ptenopus circumsyrticus</i> sp. nov.
<i>Ptenopus garrulus maculatus</i> East	<i>Ptenopus kenkenses</i> sp. nov.
<i>Ptenopus garrulus maculatus</i> North	<i>Ptenopus maculatus</i> sensu stricto*
<i>Ptenopus kochi</i>	<i>Ptenopus kochi</i>
<i>Ptenopus carpi</i> sensu stricto	<i>Ptenopus carpi</i> sensu stricto
<i>Ptenopus carpi</i> North	<i>Ptenopus sceletus</i> sp. nov.
*raised from a subspecies	

WS–802, Bell DVR–6006, and N28 Professional HD Intelligent, at a resolution of 16 bit and sampling rate of 48 kHz, at a distance of ~60 cm from the calling males. The recorders were placed at the burrow entrance of a calling male with a small crescent of soil around as a wind shelter. DS1922L/T/E/S temperature logger iButtons were placed behind the burrow entrance to record the environmental temperature at which geckos are willing to call, with their head out of the burrow. Geckos were subsequently captured from the burrows or while foraging, and photographed using a Nikon D3100 camera with 18–55 zoom lens and 22 mm Meike digital zoom extension tubes. Photographs included various angles (usually dorsal, ventral, and lateral) of the entire gecko, the head, the hands and feet, the vent, and around the body, marking the gecko on the white belly with a marker pen (to keep count of scales), with a ruler for scale, for morphometric analyses (for geckos that were released). The snout-vent length (SVL) and total length (TL) were also measured before release. Some geckos were collected as voucher specimens: These were photographed also to capture colour variation. Geckos were euthanised by injecting MS-222, after which a liver sample was extracted from a small mid-ventral incision; specimens were then fixed in 10% formalin, rinsed, and stored in 75% ethanol. All new specimens collected as vouchers, were deposited at the National Museum of Namibia (NMNW).

Systematics and species concept

Species in the genus *Ptenopus* were delimited based the general lineage or unified species concept (GLC: de Queiroz 1998, 2007). Under this concept, four operational criteria or lines of evidence were used to assess whether a species is supported as a separately evolving metapopulation lineage: Phylogenetic, ecological, (mate) recognition, and morphological (phenetic cluster or diagnosable difference).

Evidence for the phylogenetic and ecological operational criteria were based on the results from Becker et al. (2024), which served as a starting point for species delimitation in the present paper. The relationship between the putative species names used in Becker et al. (2024)

and species names used here, are thus provided (Table 1). We present additional data for ecology, recognition, and morphology in this paper, to test the validity of nine out of these ten putative species. One additional putative species split between “*P. g. garrulus* North” and “South” (as in Becker et al. 2024), will require the collection of additional data to validate. As such, these two putative species are currently treated as a single taxon: *Ptenopus garrulus*.

Under the phylogenetic criterion, several steps or sub-criteria were employed to thoroughly test, carried over from Becker et al. (2024). 1. A phylogeny was fitted based on nuclear (c-mos) and mitochondrial (ND2 and 16S) genes and well-supported clades were identified. 2. Species delimitation analyses were conducted. 3. Multiple regression on distance matrices models (MRMs) were used to either validate a putative species clade as a discontinuous divergence, or invalidate a divergence as merely a genetic cline (isolation-by-distance). 4. If validated by subcriteria 1–3, co-occurrence patterns of these putative species were used to further test their validity: If the putative species occur sympatrically or parapatrically in close contact, this was considered strong evidence of evolutionary independence.

For the ecological criterion, clear, consistent, and relatively discontinuous differences between putative species in their substrate preference (Becker et al. 2024), bioclimatic region (Sayre et al. 2013) or biome/ecoregion (Dinerstein et al. 2017) were used as evidence for evolutionary independence.

For the mate recognition criterion, significant differences in any bioacoustic characters of the advertisement calls, or fixed differences in visual characteristics with signalling potential (sexual dichromatism and eye colour) were interpreted as evidence for evolutionary independence.

For the morphological criterion, phenetic clusters (quantitative, significant differences among morphological characters) or diagnosable, fixed differences (qualitative) were interpreted as evidence for evolutionary independence. Because the morphological differences between the recognised species are already defined (Haacke 1964), these were only additionally investigated within the cryptic species complexes or groups: The “*P. garrulus* group”, meaning all seven putative species

previously included in '*P. garrulus*'; the "*P. carpi* group", meaning the two putative species previously included in '*P. carpi*'.

A conservative stance was used in delineation of species with this integrative taxonomic framework (Padial et al. 2010), describing only species supported cumulatively by at least three operative criteria.

The original species descriptions, type specimens, and type localities were consulted to draw accurate nomenclatural conclusions. Chresonymies for previously recognised species can be found in Haacke (1975) and Uetz et al. (2025), but we only refer to synonymy of substantial taxonomic revisions and/or the first-use of a name in the taxonomic literature, in each species account. Museum abbreviations used for catalogue numbers were: The Natural History Museum London (formerly British Museum of Natural History, **BMNH**); National Museum of Namibia (**NMNW**); Ditsong National Museum of Natural History (formerly the Transvaal Museum, **TM**); Port Elizabeth Museum (**PEM**).

Phylogenetic analyses and co-occurrence

This section is a summary of the phylogenetic methods used for easy reference. For a more detailed methods section, refer to Becker et al. (2024).

The phylogeny included samples from 79 *Ptenopus* individuals (see Table S1) and one *Narudasia festiva* (out-group) sample. Two mitochondrial markers (ND2 and 16S) were used for all phylogenetic analyses, while one nuclear marker (c-mos) was sequenced for selected individuals only, to resolve the relationships of deeper phylogenetic divergences. Bayesian inference (BI) analyses were run in MrBayes 3.2.7 (Huelsenbeck and Ronquist 2001) and maximum likelihood (ML) analyses in RAXML-VI-HPC v7.0.4 (Stamatakis 2006), on the combined dataset of 2016 characters, partitioned into the three genes.

Two models were used for species delimitation: Automatic barcode gap detection (**ABGD**; Puillandre et al. 2012) and Bayesian general mixed Yule-coalescent model (**bGMYC**) v. 1.0 (Carstens and Reid 2012), using the mitochondrial markers.

Multiple regression on distance matrices models (**MRMs**) in R (v. 4.1.0, R Core Team 2021) were used to test for a positive relationship between mitochondrial sequence divergence (p distance) and various explanatory variables (as distance matrices – refer to Becker et al. 2024) including geographic distance, on pairs or groups of putative species (clades). If geographic distance explained the largest portion of the variability in p distance for a particular pair or set of putative species, this was interpreted as evidence for isolation-by-distance (**IBD**), and thus evidence against evolutionary independence of these putative species (clades).

Sequence divergence between the species was estimated in MEGA X (Kumar et al. 2016) using uncorrected net mean p distances for each of the genes separately.

Co-occurrence pattern as either allopatric, parapatric, or sympatric was deduced from field observations and occurrence data (see Distribution mapping, below). The co-occurrence states of all species pairs were compiled into a matrix.

Bioacoustic analyses of advertisement calls

A total of 890 calls from 105 individuals, sampled from the nine putative species and from various localities or populations, were analysed (Table S1). Only calls from genotyped populations were included in this study. No more than 10 calls per individual were included, usually the first ten. Call characters were averaged per individual for all analyses.

Individual calls were cut as separate WAV files and analysed with a customised code (File S1) using the program R (R Core Team 2016), including packages soundgen (Anikin 2019) and seewave (Sueur et al. 2008). Program Audacity (Audacity Team 2019) was used to analyse aspects of some calls which could not be properly estimated using the Rscript (usually because of other call interference, noise, or the volume being too low).

The call characters measured and terminology used were based on recommendations developed by Köhler et al. (2017) for frog taxonomy. Some of these characters are comparable to those previously used for *Ptenopus* (Haacke 1969; Gramentz 2008), but even these characters were slightly differently applied. Previous literature described the calls as a series of "clicks", "squeaks" (Haacke 1964, 1969), or "syllables" (Gramentz 2008). We use the standardised term "notes" (being generally longer in duration than "pulses" and not conjoined, as defined in Köhler et al. 2017), harmonious with broadly applied bioacoustic terminology, to describe this component.

Haacke (1969) noticed that calls sound different (lower and slower, sometimes fewer notes) late at night and/or at lower temperatures. We confirmed this observation by recording several individuals throughout the night, while measuring temperature. Calls from outside the main chorus period (late at night and/or in cold temperatures) were therefore excluded from analyses. We were able to conclude, through many calls recorded from the same individuals over time, that the note duration and inter-note interval increase or decrease proportionally, if the call becomes faster or slower due to varying temperatures. We therefore developed several additional call characters or metrics (described below) to distinguish the rhythmic components of the call in a consistent manner, which are not substantially influenced by varying temperatures.

Thirteen bioacoustic characters were measured, including newly proposed characters which are ratio-based: 1. Number of notes; 2. note repetition rate (s^{-1}); 3. median note duration (ms); 4. note 1 duration deviance (difference between the first note duration and the median note duration, in percentage of the median); 5. median inter-note interval (ms); 6. inter-note interval range (as a percentage of the median inter-note interval: a measure of variability).

ity); 7. median call density (median note duration divided by median inter-note interval, no units, with “denser” calls having longer notes and shorter intervals); 8. call duration (s); 9. dominant frequency or upper frequency peak (kHz)—most *Ptenopus* species have two frequency peaks of similar amplitude, but the upper peak is usually the dominant frequency; 10. lower peak frequency, where relevant (kHz)—this may be the dominant frequency at further recording distances; 11. basal frequency (Hz); 12. bandwidth, or upper and lower 90% (of peak amplitude) bandwidth frequencies (kHz); 13. call period (call duration plus following inter-call interval). Characters 11–13 could not be measured for many individuals, and were only used descriptively.

Characters 1–10 were further analysed to test for significant differences among species. Analysis of variance (ANOVA) tests were used for meristic or continuous characters, while non-parametric Kruskal-Wallis tests were used for the ratios. Where the ANOVA indicated significant difference, a post hoc pairwise Tukey’s Honest Significant Difference test was used; for Kruskal-Wallis tests, pairwise Wilcoxon rank sum tests were used for post hoc comparisons. All these characters were represented by box and whisker plots, compiled in R.

Morphology

Photographs of newly collected material (from genotyped populations – 258 individuals total) and physical specimens (total 48) of various putative species were examined to identify useful diagnosable morphological characters (Table S1). Some meristic characters were measured and statistically analysed, while other qualitative, observed traits are also described in the diagnoses. Snout-vent length (SVL) and tail length (TL) was measured with callipers for most specimens from all species; TL was only measured for specimens with full original tails. The TL as a percentage of SVL was calculated and qualitatively compared among species.

Thorough analyses of meristic and morphometric characters in the genus *Ptenopus* supported only three

clearly distinct species (Haacke 1975). Hence, the new species proposed here are cryptic species, with a lower level of morphological differentiation than was previously accepted as species-level, despite deep evolutionary divergence. This includes six species within the *P. garrulus* group (*P. garrulus* sensu stricto, *P. maculatus* sensu stricto, *P. adamanteus* **sp. nov.**, *P. circumsyrcticus* **sp. nov.**, *P. kenkenses* **sp. nov.**, and *P. australis* **sp. nov.**) and two species within the *P. carpi* group (*P. carpi* sensu stricto and *P. sceletus* **sp. nov.**). To maintain an integrated approach in the delimitation of cryptic species beyond genetic p distance (Fišer et al. 2018), smaller variations in morphological characters were identified within these two cryptic species groups (*P. garrulus* and *P. carpi* groups, respectively) that showed potential to consistently differentiate among these cryptic species. Within each group, we tested whether the variation within these characters is greater among than within these cryptic species.

Within the *P. garrulus* group, the number and shape of the scales on the snout, and the number of body or head scales were identified as potentially useful morphometric/meristic characters; see Becker (2023) for a more thorough explanation of other features excluded. No sexual dimorphism was found in any of the traits included here (Becker 2023). The following morphometric data were gathered for the *P. garrulus* group: The number of scales in contact in a straight line across the top of the head between the eyes, in line with the mid-pupil of the pupils–interorbital scales (IOS), the number of midbody scale rows (MBSR), and the inter-nasal scales (INS) were counted. Supplemental data of IOS and MBSR counts were extracted from Haacke (1975), including only data from the localities close to genotyped populations. The original specimen data were not available, so a dataset was generated from a normal distribution using the sample size, mean, standard deviation, and range supplied by Haacke (1975), in R package truncnorm (Mersmann et al. 2018). Furthermore, the following relative measurements (in pixels) were taken using ImageJ (Schneider et al. 2012), on a single full frontal photograph of the gecko’s snout (Fig. 1), for all *P. garrulus* group putative

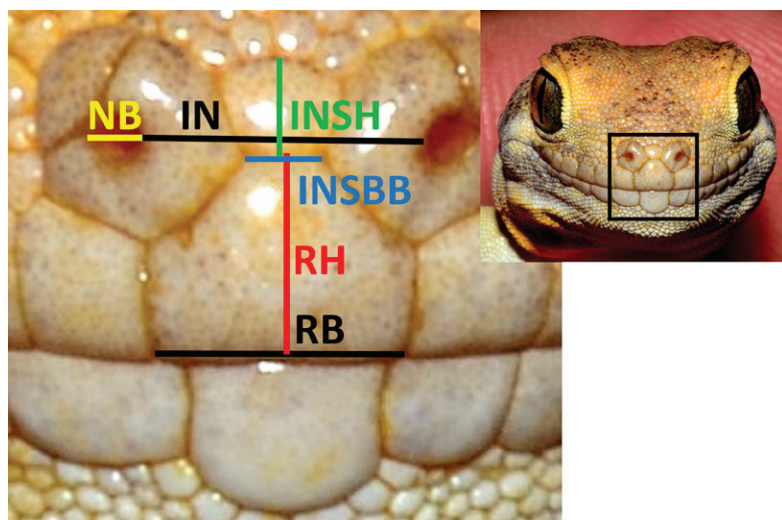


Figure 1. Relative measurements taken on full frontal photographs of the snout of *Ptenopus garrulus* group specimens for morphometric analyses. Refer to Methods: Morphology for the full name and explanation of each morphometric character displayed.

taxa: Nostril (horizontal diameter) breadth (NB); inter-narial distance, from the nearest edges of the nares (IN); rostral (horizontal) breadth at the lower edge of the lip (RB); rostral (vertical) height (RH); horizontal breadth of the base of the largest inter-nasal scale in contact with the rostral (INSBB); vertical height of the largest inter-nasal scale (INSH).

Significant differences among *P. garrulus* group putative species were tested for in seven morphological characters, including ratios (e.g., as quantification of shape and size of scales on the snout): 1. **IN/INSBB**, 2. **RB/RH**, 3. **INSH/NB**, 4. **MBSR**, 5. **IOS**, 6. **IOS/MBSR**, and 7. **INS**. Analysis of variance (ANOVA) tests were used for meristic characters, while non-parametric Kruskal-Wallis tests were used for the ratios. Where the ANOVA indicated significant difference, a post hoc, pairwise Tukey's Honest Significant Difference test was used; for Kruskal-Wallis tests, pairwise Wilcoxon rank sum tests were used for post hoc comparisons. All these variables were represented by box and whisker plots, compiled in R.

For the two *P. carpi* group putative species, iris colouration and sexual dichromatism of gular patches were inspected in 105 photographed individuals from various genotyped populations (Table S1). Iris colouration was qualitatively compared using photographs taken by the same camera, flash, and lenses (see Field Sampling, above), and the same colour balance settings. Colours were descriptively assigned. The presence or absence of a clear yellow gular patch was recorded for males and females (typically, all males have a yellow gular patch). In the potential contact zone close to the Swakop River, photographs from iNaturalist (<https://www.inaturalist.org>) records close to the Swakop River were also included for additional data on iris colouration and gular patches.

The following additional measurements in mm were reported, only for the type series of all newly described species: Head length (**HL**), measured ventrally from the tip of the snout to the anterior narrowest portion of the throat, usually between two subtle neck folds (jawline is usually obscured); head width (**HW**), at the widest point; head height (**HH**), at the jaw angle behind the eye; horizontal eye diameter (**EYE**); distance between the anterior corners of the eyes or eye-distance (**EED**); number of upper labials (**UL**); number of lower labials (**LL**); number of post-mental chin scales (**PM**).

Distribution mapping

Updated occurrence maps were produced for *Ptenopus* species based on published records and maps reviewed in Haacke (1975), new records and observations from this manuscript, and occurrence records downloaded from GBIF (GBIF.org 2021c, 2021a, 2021b). Positive occurrence of a species was confirmed or inferred based on genotyped records and call recordings, while the GBIF and previously published records were only used to infer the presence or absence of the genus in an area. Distributions were then inferred based on known habitat determinants of each species, considering ecoregion or bioclimate and soils. Soil maps from the Harmonised World Soil Database v2.0 (<https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v20/en>) and the Atlas of Namibia (Atlas of Namibia Team 2022b), and ecoregion or bioclimate maps (Sayre et al. 2013; Dinerstein et al. 2017) were used to for these distributional inferences.

Results

Phylogenetic operational criterion (including co-occurrence)

Species delimitation analyses indicated between six and 25 species (Fig. 2). Results from the MRMs (refer to Becker et al. 2024 for more detailed results and explanation of MRMs) suggested that some of these divergent clades likely represent a single population isolated by distance (IBD significant), while others represented truly separate lineages indicated by lines separating clades on Figure 2. The most significant predictor of genetic divergence between sister species, according to the MRMs, is also indicated in text boxes on Figure 2. Among the *P. garrulus* group species excluding the distantly related *P. maculatus* sensu stricto, with *P. kenkenses* **sp. nov.** and *P. circumsyrticus* **sp. nov.** as the earliest diverging taxon, substrate texture and substrate barriers were most strongly linked to genetic divergence (22% variation explained, M coefficient 0.040, $p < 0.001$). Winter vs. summer rainfall

Figure 2. Bayesian topology of *Ptenopus* (top right) based on mitochondrial genes 16S and ND2, and nuclear gene c-mos (top right), and map of confirmed species locations (top left) including type localities (high resolution image: can be zoomed for detail; modified from Becker et al. 2024). Nodes supported by both maximum likelihood ($\geq 70\%$ bootstrap) and Bayesian inference (≥ 0.95 posterior probability) analyses denoted by black circles; Bayesian inference only, with grey circles; maximum likelihood only, with white circles; one node with 0.94 posterior probability is indicated. The coloured bars to the right of the phylogeny indicate putative species based on three delimitation analyses; horizontal grey lines indicate divergences that were validated (i.e., not IBD) by MRM analyses, with grey text boxes on these lines indicating the explanatory variable most strongly associated with genetic divergence between sister species. Bar colours correspond to named species and confirmed species localities on the map, including type localities = white outlined stars. The grey bar indicates preferred substrate of each species, with shades corresponding to that on the map (dark grey = hard substrate, light grey = soft sand); various sandy patches were too fine to appear on the map, and *P. australis* **sp. nov.** occurs on sandy hummocks, although the wider soil-type in this area is not sand. Ecologically relevant geographic or climatic features are indicated by arrows and coloured text and shapes. Blocks A–D indicate contact zones of different species, shown enlarged in the bottom panels (satellite imagery), including labels indicating substrates, rivers, and scale bars (20 km).

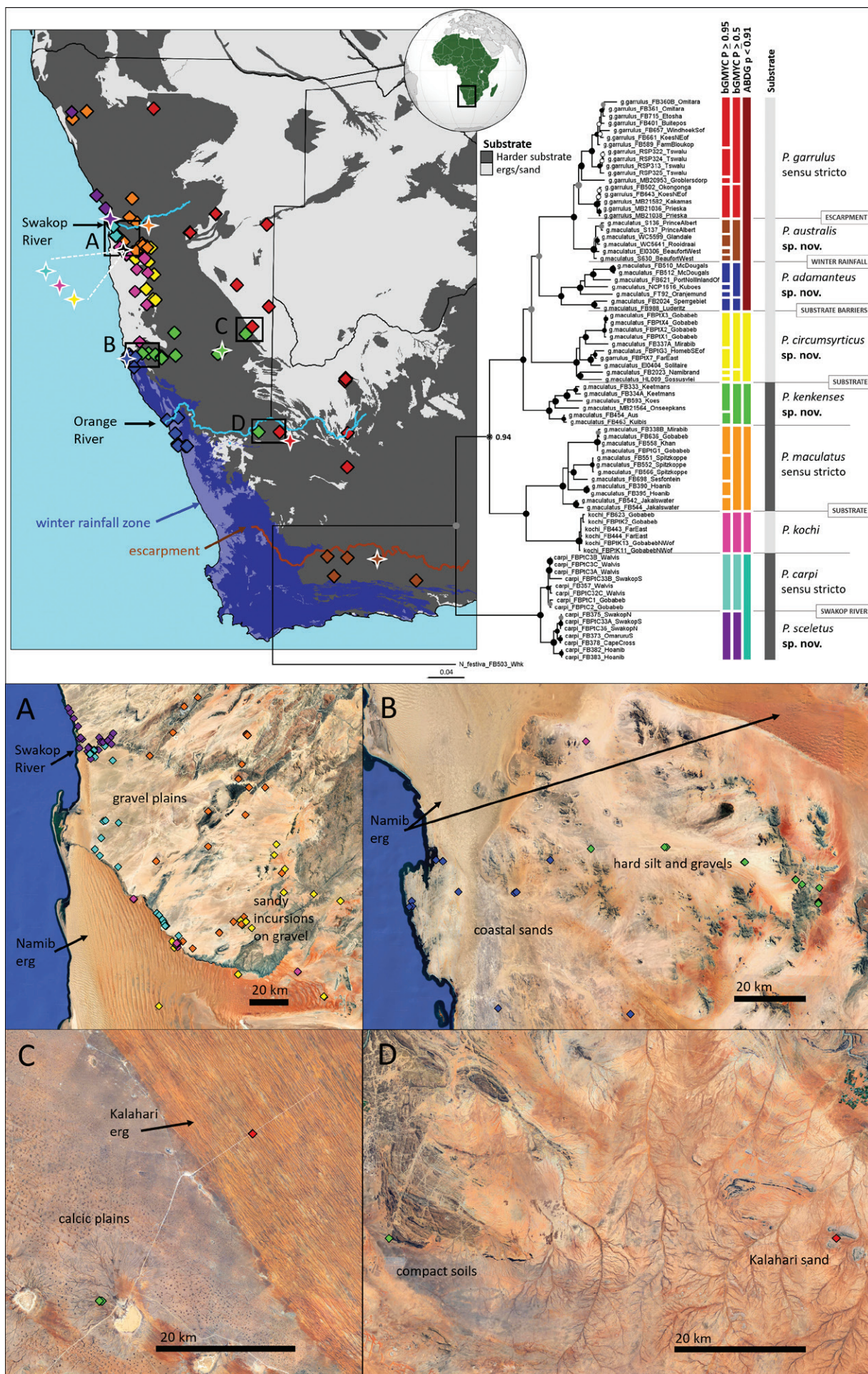


Table 2. Inter- and intraspecific pairwise uncorrected net sequence divergences (p distance, %) for the nine species of *Ptenopus*, based on the ND2 mitochondrial gene; intraspecific distances on the diagonal. Outlier values ($\leq 6\%$ interspecific or $> 6\%$ intraspecific p distance) are shown in boldface; more detailed p distances provided for closely related species pairs (*/*).

	Species	1	2	3	4	5	6	7	8	9
1	<i>P. carpi</i>	1.3								
2	<i>P. sceletus</i> sp. nov.	4.6*	1.6							
3	<i>P. australis</i> sp. nov.	22.6	22.4	1.3						
4	<i>P. circumsyrticus</i> sp. nov.	20.7	20.0	12.9	6.0					
5	<i>P. kenkenses</i> sp. nov.	19.7	19.6	11.8	9.1	6.4				
6	<i>P. garrulus</i>	21.0	20.4	5.7*	10.9	9.5	4.8			
7	<i>P. adamanteus</i> sp. nov.	19.1	18.7	10.1	8.5	8.0	9.0	8.8		
8	<i>P. maculatus</i>	18.2	17.6	18.0	14.9	14.2	16.5	13.9	6.0	
9	<i>P. kochi</i>	22.6	22.3	21.7	19.5	18.8	21.2	17.6	13.7	0.5

* At the contact zone of *P. carpi* sensu stricto and *P. sceletus* sp. nov. (samples 0 – 36 km apart), interspecific p distance range is 5.7–7.4% (simple mean 6.3%), compared to 0.0% (n = 3) mean intraspecific p distance for *P. sceletus* sp. nov. and 2.3% (n = 3) intraspecific p distance for *P. carpi* sensu stricto here.

+ Interspecific p distance range is 7.5–11.3% (simple mean 8.7%) including samples <300 km apart, compared to only 1.3% mean intraspecific p distance for *P. australis* sp. nov. including samples up to 320 km apart, and only 4.8% mean intraspecific p distance for *P. garrulus* sensu stricto including samples up to 1400 km apart.

Table 3. Inter- and intraspecific pairwise uncorrected net sequence divergences (p distance, %) for the nine species of *Ptenopus*, based on the 16S mitochondrial gene; intraspecific distances on the diagonal. Outlier values ($\leq 3.5\%$ interspecific or $> 3.5\%$ intraspecific p distance) are shown in boldface; more detailed p distances provided for closely related species pairs (*/*).

	Species	1	2	3	4	5	6	7	8	9
1	<i>P. carpi</i>	0.3								
2	<i>P. sceletus</i> sp. nov.	0.1*	0.6							
3	<i>P. australis</i> sp. nov.	11.2	10.9	0.8						
4	<i>P. circumsyrticus</i> sp. nov.	10.0	9.6	7.2	2.8					
5	<i>P. kenkenses</i> sp. nov.	9.5	9.1	6.2	5.9	2.9				
6	<i>P. garrulus</i>	10.3	9.8	1.4*	6.4	5.2	2.2			
7	<i>P. adamanteus</i> sp. nov.	8.4	7.9	6.3	4.8	3.5	4.9	4.3		
8	<i>P. maculatus</i>	10.2	9.9	10.7	8.8	7.4	9.6	7.2	3.5	
9	<i>P. kochi</i>	13.3	13.1	12.6	10.4	9.1	11.7	9.0	4.3	0.6

* At contact zone (samples 0–36 km apart), interspecific p distance range is 0.4–0.5% (simple mean 0.4%), compared to only 0.1% mean intraspecific p distance for *P. sceletus* sp. nov. and 0.3% for *P. carpi* sensu stricto here.

+ Interspecific p distance is 1.5–9.8% (simple mean 2.9%) including samples <300 km apart, compared to mean intraspecific p distance of only 0.8% for *P. australis* sp. nov. including samples up to 320 km apart, and 2.2% for *P. garrulus* sensu stricto including samples up to 1400 km apart.

zones were most strongly linked to genetic divergence of *P. adamanteus* sp. nov. from its sister species (51% variation explained, M coefficient 0.082, $p < 0.001$), whereas the great escarpment was most strongly linked to genetic divergence between *P. australis* sp. nov. and *P. garrulus* sensu stricto (26% variation explained, M coefficient 0.022, $p < 0.001$). Finally, the Swakop River as a linear geographic feature and potential barrier in the past or present, was most strongly linked to genetic divergence between *P. carpi* and *P. sceletus* sp. nov. (42% variation explained, M coefficient 0.021, $p < 0.001$).

The nine species supported by the phylogeny as clades, phylogenetic species delimitation, and MRMs, which were further tested by other species delimitation criteria (below), are indicated by different colours on the phylogeny (Fig. 2).

Genetic divergences between most of these species pairs (Tables 2, 3, 4) are substantial (net mean p distance: 8.0–22.6% ND2; 3.5–13.3% 16S; 0.16–1.29% c-mos). In

comparison, the genetic divergence between *P. australis* sp. nov. and *P. garrulus* sensu stricto is small (p distance: 5.7% ND2; 1.4% 16S; most samples differ by one or two bp in c-mos). In addition, *P. sceletus* sp. nov. is only slightly divergent from *P. carpi* (p distance: 4.6% ND2; 0.1% 16S; no c-mos divergence). However, interspecific p distance is much higher between all sampled *P. australis* sp. nov. and *P. garrulus* sensu stricto individuals than intraspecific p distances at comparable geographic distances (Tables 2, 3). Similarly, intraspecific p distances between *P. sceletus* sp. nov. and *P. carpi* sensu stricto at the contact zone, are substantially greater than the intraspecific p distances, especially at comparable geographic distances (Tables 2, 3). Intraspecific mitochondrial p distance is unusually high within *P. adamanteus* sp. nov. (Tables 2, 3), which may represent a steep clinal change (Becker et al. 2024), while some intraclade c-mos divergence is evident within *P. australis* sp. nov. and *P. circumsyrticus* sp. nov. (Table 4).

Table 4. Inter- and intraspecific pairwise uncorrected net sequence divergences (p distance, %) for the nine species of *Ptenopus*, based on the c-mos nuclear gene; intraspecific distances on the diagonal. Outlier values (0% interspecific, >0% intraspecific p distance, or unable to calculate = NA) are shown in boldface.

	Species	1	2	3	4	5	6	7	8	9
1	<i>P. carpi</i>	0.00								
2	<i>P. sceletus</i> sp. nov.	0.00	0.00							
3	<i>P. australis</i> sp. nov.	0.67	0.70	0.18						
4	<i>P. circumsyrticus</i> sp. nov.	0.68	0.78	0.16	0.09					
5	<i>P. kenkenses</i> sp. nov.	0.95	1.04	0.54	0.17	0.00				
6	<i>P. garrulus</i>	0.93	1.02	NA*	0.17	0.51	0.00			
7	<i>P. adamanteus</i> sp. nov.	0.70	0.79	0.27	NA	0.26	0.26	0.00		
8	<i>P. maculatus</i>	0.94	1.02	0.55	0.27	0.53	0.52	0.27	0.00	
9	<i>P. kochi</i>	1.20	1.29	0.62	0.52	0.78	0.77	0.53	0.26	0.00

* There is a one-to-two bp difference between *P. australis* sp. nov. and all *P. garrulus* sensu stricto samples, except for three individuals of *P. garrulus* which also have this (ancestral?) haplotype.

Table 5. Interspecific co-occurrence pattern for the nine species of *Ptenopus* as either allopatric (A), parapatric (P) or sympatric (S). Lower-case letters indicate co-occurrence to a limited geographic extent, i.e. not the primary zone of contact between the relevant species. Question marks indicate inferred, but uncertain co-occurrence based on expected distributions.

	Species	1	2	3	4	5	6	7	8
1	<i>P. carpi</i>								
2	<i>P. sceletus</i> sp. nov.	P/s							
3	<i>P. australis</i> sp. nov.	A	A						
4	<i>P. circumsyrticus</i> sp. nov.	P	A	A					
5	<i>P. kenkenses</i> sp. nov.	A	A	A	A/p				
6	<i>P. garrulus</i>	A	A	A	A	P			
7	<i>P. adamanteus</i> sp. nov.	A	A	A	A/p?	P	A		
8	<i>P. maculatus</i>	S	P/s	A	P/s	A	A	A	
9	<i>P. kochi</i>	P	A	A	P	P	A	P	P/s

Evolutionary independence of all sister species pairs and some of the more distantly related species was further validated by sympatric and/or parapatric occurrence of these lineages, except in the case of *P. australis* sp. nov. which does not occur in close contact with *P. garrulus* sensu stricto or other species (Table 5).

The closely related species *P. carpi* sensu stricto and *P. sceletus* sp. nov. occur parapatrically across the Swakop River near the coast, with a small zone of sympatric occurrence in the Rössmund area (~8 km inland), within 3 km south of the river. This river is not an impermeable barrier to dispersal: It is ephemeral and *Ptenopus* even occurs in the riverbed in some places. Despite this, *P. carpi* sensu stricto was exclusively recorded on the southern side of the river or contact zone, while *P. sceletus* sp. nov. generally occurs north of the river, in the river, and immediately to the south. In the small sympatric zone south of the river, 57% of photographed animals conformed to *P. sceletus* sp. nov. and 43% to *P. carpi* sensu stricto phenotypes according to gular and iris colouration (Table S1; see Recognition / morphology: Eye colour and sexual dichromatism below). These species clearly remain genetically separated in and around the contact zone. Of the 52 animals observed, sampled, and photographed within 6 km on either side of the Swakop River, only one individual was phenotypically intermediate between these spe-

cies. This female (NMNW R11775) was within the mitochondrial haplogroup of *P. sceletus* sp. nov. with typical *P. sceletus* sp. nov. iris colouration, but it had a yellow gular patch like *P. carpi* sensu stricto. This individual may therefore be a hybrid. However, this seems to be a rarity.

Ecological operational criterion

Nearly all the *Ptenopus* species presented here are ecologically divergent from their closest relatives and/or geographically closest neighbours (Fig. 2 shows most ecologically relevant features, but ecoregions and bioclimate could not be clearly indicated on Fig. 2). *Ptenopus kenkenses* sp. nov. occurs on different substrates (harder) and in a different ecoregion (Gariep Karoo) than its sister species. *Ptenopus circumsyrticus* sp. nov. occurs in a different ecoregion (Namib Desert) and bioclimate (Tropical Desert) than its closest sister species, although on the same substrate (sand). *Ptenopus adamanteus* sp. nov. occurs in a different ecoregion (Namaqualand-Richtersveld Steppe) and bioclimate (Mediterranean Desertic Hyperoceanic) from its closest sister species, although on the same substrate (sand). *Ptenopus australis* sp. nov. occurs in a different ecoregion (Nama Karoo Shrublands) and bioclimate (Mediterranean Xeric Semi-hyperoceanic)

than its closest sister species (*P. garrulus* sensu stricto), although on the same substrate (sand). *Ptenopus garrulus*, by contrast, occurs in the Kalahari Xeric Savanna and surrounding Kalahari ecoregions, and in Tropical Xeric and Tropical Desertic bioclimates. *Ptenopus garrulus* sensu stricto and *P. australis* **sp. nov.** are furthermore separated by a substantial geographic barrier, the Great Escarpment, and are unlikely to be able to converge in future.

Ptenopus maculatus sensu stricto and its sister species *P. kochi* clearly occur on different substrates, parapatrically (Fig. 2: block A) across the Kuiseb River (hard gravel and soft sand, respectively), although they overlap in terms of ecoregion and bioclimate. *Ptenopus carpi* sensu stricto and *P. circumscriptus* **sp. nov.** also occur parapatrically across the Kuiseb River (Fig. 2: block A), and sympatrically with *P. maculatus* sensu stricto and *P. kochi*, respectively. All four these species can be found occupying different patches of substrate, merely metres apart, around and in the ephemeral Kuiseb River. *Ptenopus adamanteus* **sp. nov.** and *P. kenkenses* **sp. nov.** can similarly be found occurring only hundreds of metres apart on different substrates (Fig. 2: block B), and the same can be said for *P. garrulus* sensu stricto and *P. kenkenses* **sp. nov.** (Fig. 2: block C and possibly D).

By exception, the closely related *P. carpi* and *P. sceletus* **sp. nov.** occur in very similar habitats and on identical substrates. They occur parapatrically across the Swakop River and sympatrically immediately to the south of the river (Fig. 2: block A).

Mate recognition operative criterion: Advertisement calls

ANOVA and Kruskal-Wallis test results revealed significant differences ($p \leq 0.001$) among species for all 10 bioacoustic characters analysed. Post hoc comparisons showed significant differences in some characters between all comparative species pairs, except between *P. garrulus* sensu stricto and its sister species, *P. australis* **sp. nov.** (Fig. 3). In this case, substantial but non-significant differences were found in note repetition rate, median call density, and lower peak frequency (Fig. 3). Sample size for *P. australis* **sp. nov.** was low ($n = 4$), hence few differences with other species were statistically significant.

Mate recognition / morphology operative criteria: Eye colour and sexual dichromatism in *P. carpi* group

The variation of sexual dichromatism from across the range of *P. carpi* (Table S1; Fig. S1) revealed that all females in the range of *P. carpi* sensu stricto had gular patches ($n = 23$ photographed, additional individuals observed), while no females with gular patches were found in the range of *P. sceletus* **sp. nov.**, north of the Swakop River ($n = 23$ photographed, additional individuals observed). However, one individual (NMNW R11775) from 2 km south of the river was genotyped and found to match the mitochondrial haplogroup for the species *P. sceletus* **sp. nov.** (these two species are identical in terms of nuclear c-mos) but had a yellow gular patch, as in *P. carpi* sensu stricto.

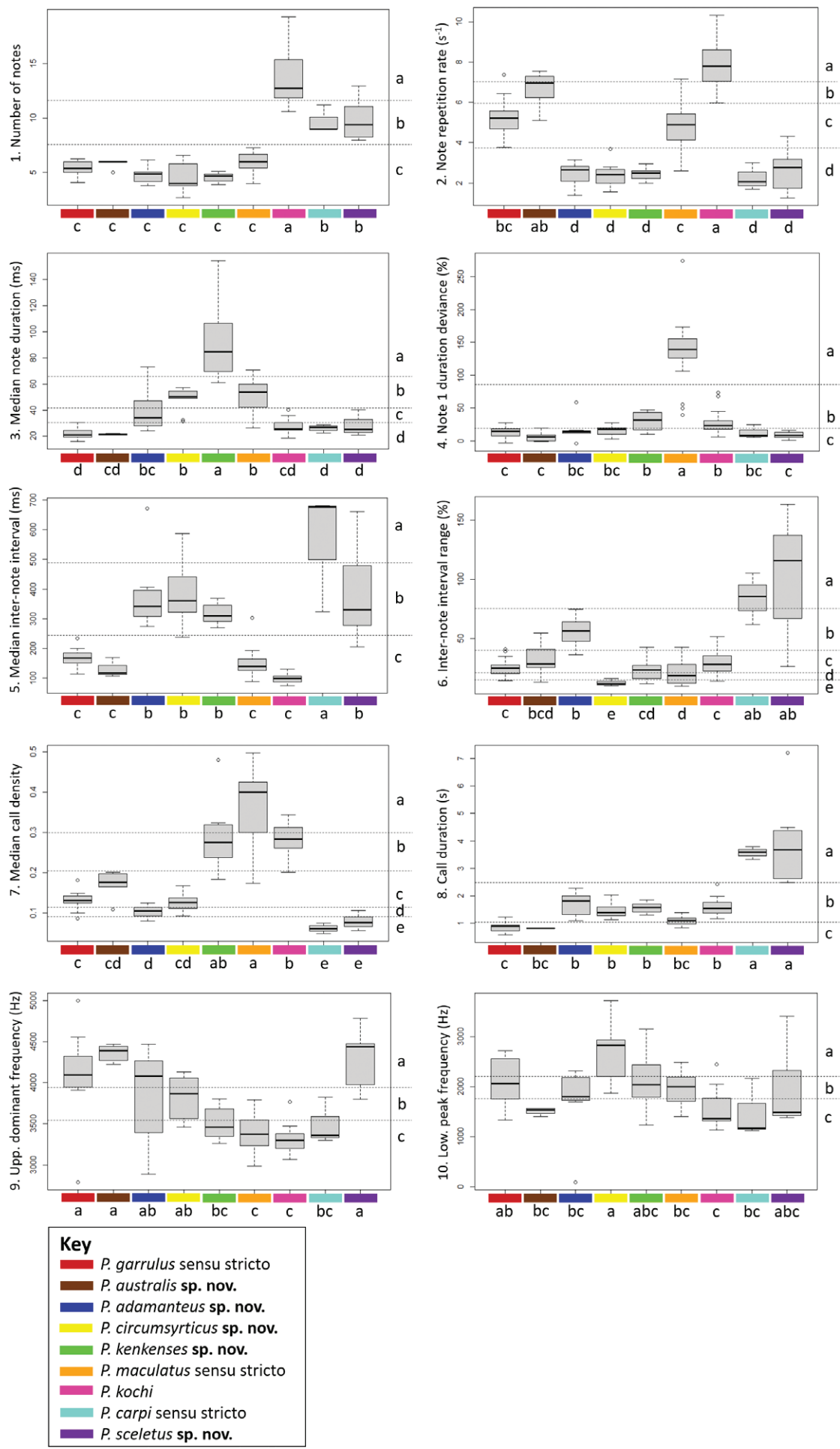
For iris colouration (Table S1; Fig. S2), all *P. carpi* sensu stricto individuals had red (light red to dark red) irises ($n = 43$ photographed, additional individuals observed), while all *P. sceletus* **sp. nov.** individuals had silver to brown irises ($n = 51$ photographed, additional individuals observed). Of these, six iNaturalist records from just south of the Swakop River (phylogenetics shows both clades occur here) with silver or brown eyes were tentatively assigned to *P. sceletus* **sp. nov.** Individual NMNW R11775 (mitochondrial species *P. sceletus* **sp. nov.**, but occurring south of the river) had red-brown eyes. Only one individual of *P. sceletus* **sp. nov.** had ochre (similar to “light red”) eyes, although this individual was found 400 km north of the Swakop River, far from the contact zone between the species.

Morphology operative criterion: Phenetic clusters and qualitative fixed differences in *P. garrulus* group

ANOVA and Kruskal-Wallis tests reveal significant differences ($p \leq 0.001$) among species for all seven morphological characters (including morphometric ratios and meristic characters) analysed. Post hoc comparisons showed significant differences in one or more characters between all species pairs, except between *P. garrulus* sensu stricto and *P. kenkenses* **sp. nov.** (Fig. 4).

All the specimens of *P. kenkenses* **sp. nov.** have some dark pigmented scales on the fore-and-hindfoot soles,

Figure 3. Box and whisker plots of the bioacoustic characters analysed using ANOVA / Kruskal-Wallis tests, for species of *Ptenopus*. Numbered characters (numbered as in Methods) and their units are indicated on y-axis labels. Species colours correspond to those on Figure 2 and indicated on the key. Significant differences (according to pairwise post hoc tests) are indicated through homogeneous groupings: Species not significantly different in the present character are one group, as indicated by lower-case letters. Species that share the same letters not differing significantly from each other; species with multiple letters are not significantly different from any other species sharing those letters. Approximate divisions between the groups are indicated by dotted lines perpendicular to the y-axis, and the group letters are indicated to the right of each graph.



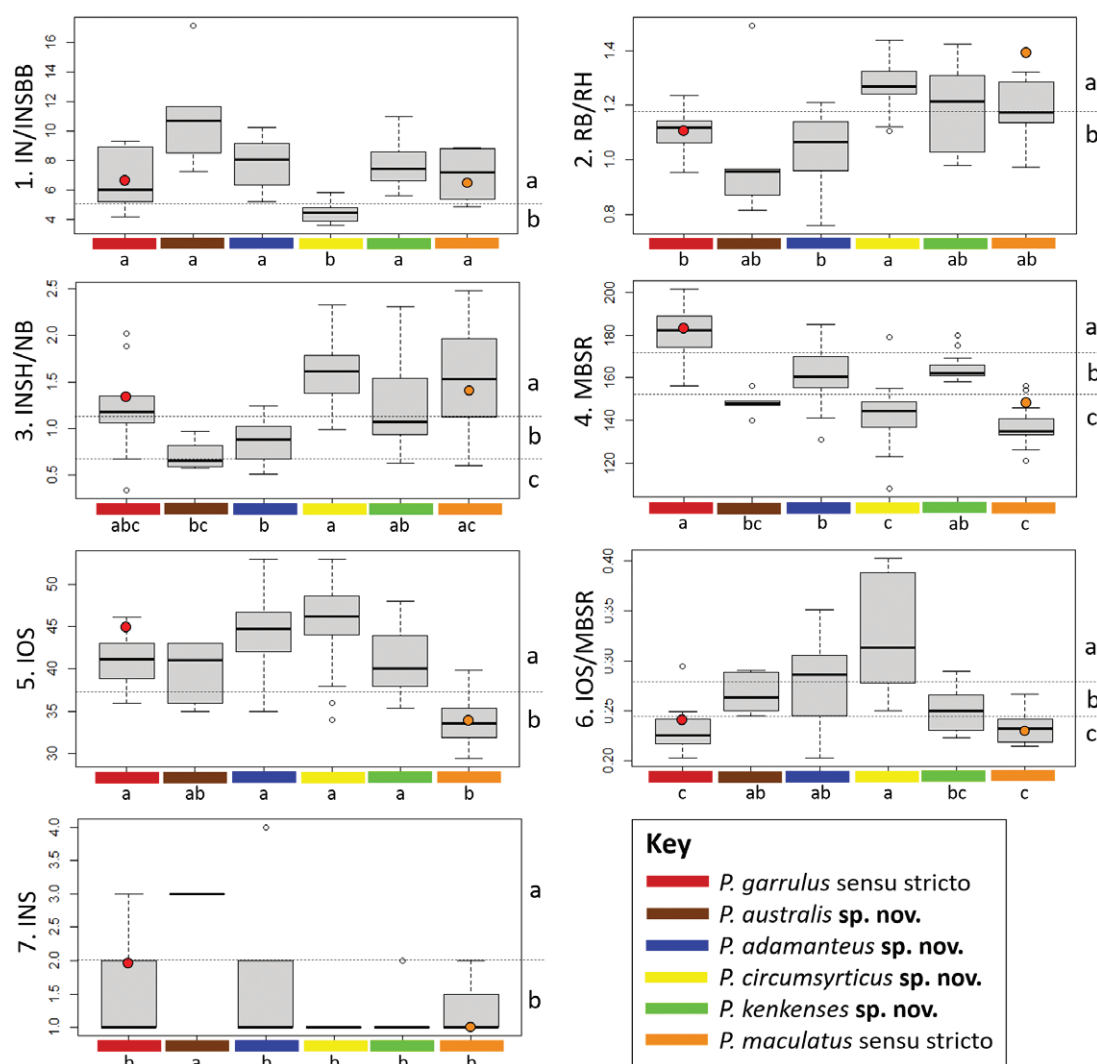


Figure 4. Box and whisker plots of the morphological characters analysed using ANOVAs or Kruskal-Wallis tests, for cryptic species of the *Ptenopus garrulus* group. Numbered characters (numbered as in Methods) are indicated on y-axis labels: 1. Internarial / internasal scale base breadth; 2. rostral breadth / height; 3. internasal scale height / nostril breadth; 4. mid-body scale rows; 5. inter-orbital scales; 6. interorbital / mid-body scales; 7. inter-nasal scales. Species colours correspond to those on Figure 2 and indicated on the key. Significant differences (according to pairwise post hoc tests) are indicated through homogenous groupings: Species not significantly different in the present character are one group, as indicated by lower-case letters. Species that share the same letters not differing significantly from each other; species with multiple letters are not significantly different from any other species sharing those letters. Approximate divisions between the groups are indicated by dotted lines perpendicular to the y-axis, and the group letters are indicated to the right of each graph.

while all *P. garrulus sensu stricto* specimens had some pinkish, unpigmented scales on the soles. This appears to be a fixed difference between these species, but may be difficult to see on old, preserved specimens. Furthermore, toe fringes tended to be clearly more extensive on *P. garrulus sensu stricto* than other *P. garrulus* group species including *P. kenkensis sp. nov.*, except for some *P. circumscriptus sp. nov.* individuals.

Taxonomic accounts

All nine species described below were supported by at least three lines of evidence (Table 6), and can most easily be distinguished by advertisement call (Table 7).

Chresonymies (including all major taxonomic revisions with the given names) are provided for each species, along with a short taxonomic and nomenclatural discussion.

Updated distributions are provided in species accounts and on Figure 5. Most species are clustered around western Namibia, in and around the Namib Desert (Fig. 5). *Ptenopus garrulus sensu stricto* is the most widespread species by far (range = 923,000 km²), with a range 10 times the area of the second most widespread species (*P. kenkensis*), while *P. carpi sensu stricto* is the most range-restricted with a range of only 2700 km² (Fig. 5).

Table 6. Lines of evidence or operative criteria under the GLC, which support each species of *Ptenopus* (as ‘yes’ or ‘no’). The total number of criteria supporting each species as a separately evolving metapopulation lineage is indicated (see Methods). ‘Recognition’ = ‘Mate Recognition’.

Putative Species	Phylogenetic	Ecological	Recognition	Morphological	Total
<i>P. garrulus</i> sensu stricto	yes	yes	no	yes	3
<i>P. australis</i> sp. nov.	yes	yes	no	yes	3
<i>P. adamanteus</i> sp. nov.	yes	yes	yes	yes	4
<i>P. circumsyrcticus</i> sp. nov.	yes	yes	yes	yes	4
<i>P. kenkenses</i> sp. nov.	yes	yes	yes	yes	4
<i>P. maculatus</i> sensu stricto	yes	yes	yes	yes	4
<i>P. kochi</i>	yes	yes	yes	yes	4
<i>P. carpi</i> sensu stricto	yes	no	yes	yes	3
<i>P. sceletus</i> sp. nov.	yes	no	yes	yes	3

Table 7. Cheat-sheet to the key bioacoustic characters per species for quick identification. Only mean values are displayed. Bold-face values and descriptive remarks are the key features distinguishing a particular species from most other species and/or the most similar species’ calls. Refer to Figure 3 for full range of values per species; refer to bioacoustics key for step-by-step guide; refer to Figure 20 for call typical call forms; refer to File S2 for call audio files.

Species	1. number of notes	2. note repetition rate (s ⁻¹)	3. median note duration (ms)	4. note 1 duration deviation (%)	5. median inter-note interval (ms)	6. inter-note interval range (%)	7. median call density	8. call duration (s)	9. upper dominant frequency (kHz)	10. lower peak frequency (kHz)	Descriptive remark
<i>P. garrulus</i>	5	5.2	21	15	168	25	0.13	0.9	4.1	2.1	Fast, quite regular
<i>P. australis</i> sp. nov.	6	7.0	21	6	117	29	0.18	0.8	4.4	1.5	Very fast, high-pitched
<i>P. adamanteus</i> sp. nov.	5	2.6	34	14	341	56	0.10	1.8	4.1	1.8	Slow, last note delayed
<i>P. circumsyrcticus</i> sp. nov.	4	2.4	50	18	360	12	0.13	1.4	3.9	2.8	Slow, regular
<i>P. kenkenses</i> sp. nov.	5	2.5	84	31	309	23	0.27	1.6	3.5	2.0	Long notes, short intervals
<i>P. maculatus</i>	6	4.9	54	139	140	19	0.40	1.1	3.4	2.0	First note much longer
<i>P. kochi</i>	13	7.8	25	23	99	28	0.28	1.5	3.3	1.4	Fast, many notes
<i>P. carpi</i>	9	2.1	27	8	675	85	0.06	3.6	3.4	1.2	Starts slow, then faster
<i>P. sceletus</i> sp. nov.	9	2.8	25	8	329	116	0.08	3.7	4.4	1.5	Starts faster, then slows or consistent

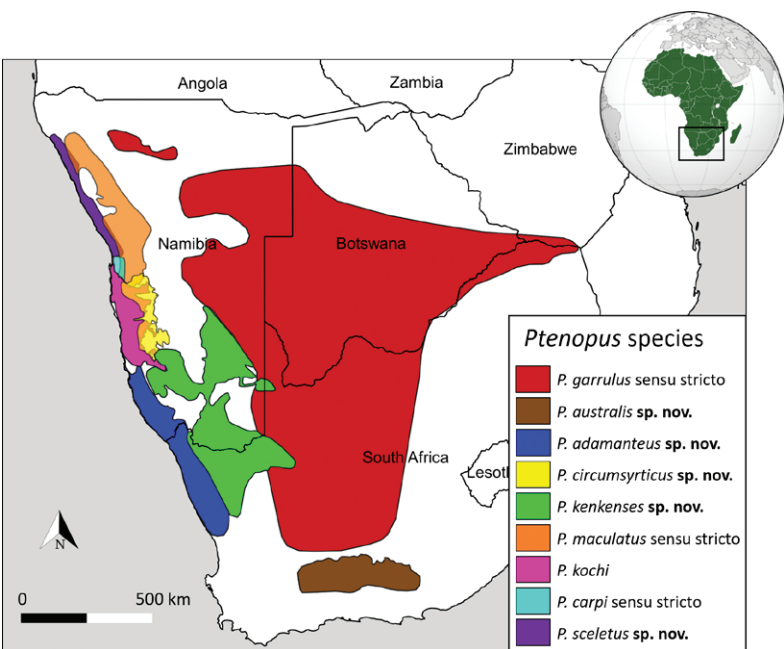


Figure 5. Revised, interpreted distributions of *Ptenopus* species in southern Africa (high resolution map, can be zoomed for detail). Some species’ ranges overlap, shown with translucent overlapping shapes on the map. Others likely occur parapatrically along extended contact zones, represented by opaque, touching shapes. For further clarity, co-occurrence patterns for all species pairs are shown on Table 5, and confirmed individual records on Figure 2.

Ptenopus kochi Haacke, 1964

Figures 6, 20I

Common names.

Koch's barking gecko

Afrikaans: Duin blafgeitjie

Chresonymy.

Ptenopus garrulus maculatus (in part) – FitzSimons (1943: 13)

Ptenopus garrulus (in part) – Brain (1962)

Ptenopus kochi Haacke, 1964: 1, pls. I–V, Haacke (1969: fig. 3a),
Haacke (1975: 227)

Comment. A description of the morphology of this species is not revised here. An updated diagnosis, some natural history observations, and a formalised bioacoustic call description, are provided.

Holotype. TM 28809, adult male, collected from “Gobabeb, South West Africa [Namibia], central Namib Desert (–23° 37' South, 15° 03' East, 408 m)”, by Wulf D. Haacke in October 1963.

Paratypes. TM 24993–4, collected by Charles Koch in October 1957; TM 25880–1, 25887, 25889–90, collected by Charles K. Brain in May 1959; TM 28442–6, 28448–55, 28625–7, collected by Wulf D. Haacke in October 1963. Locality: same as holotype.

Material examined. See Table S1 for vouchered (1) and unvouchered photographed (16) specimens, DNA samples (16 available, 7 sequenced), and call recordings (20) included (total $n = 34$).

Diagnosis. The largest *Ptenopus* (SVL max. 65.1, mean 61.1, $n = 23$) with the longest tail (TL 83% [range 63–96%] of SVL, $n = 23$), an overall plump appearance, extensive toe fringes and elongated fringed scales on the fingers compared to other species. It is distinguished from all other congeners by a combination of the following characters: Body and head scales finer than other species, with MBSR 187–210 (vs. generally <200 for *P. garrulus* and <180 for other species); dorsal colour pattern (Fig. 6) finely speckled with a few somewhat enlarged cream or yellow spots (somewhat similar to *P. garrulus*, vs. banded in *P. carpi* and *P. sceletus* **sp. nov.** and large paired, oval marking in *P. maculatus*, *P. circumscriptus* **sp. nov.**, *P. kenkenses* **sp. nov.**, and northern populations of *P. adamanteus* **sp. nov.**); the tail, fore- and hind-foot soles are completely or partially pink and unpigmented, whereas the rest of the ventrum is white (similar to *P. garrulus* except for the tail, vs. immaculate white in *P. maculatus*, *P. adamanteus* **sp. nov.**, *P. circumscriptus* **sp. nov.**, and black- or dark grey-speckled in *P. kenkenses* **sp. nov.**); the yellow pigment in males is not limited to the throat, but extends over the sides of the snout, head, neck, and body (also the case in some *P. garrulus*). For a more detailed morphological description, see Haacke (1964, 1975).

Colouration. In life (Fig. 6), colouration varies from bright to dull orange with yellow (especially in males) or whitish spots covering the dorsum, and differing degrees of dark brown spots or reticulations sometimes being present. The tail is spotted or lightly reticulated to somewhat barred dorsally, with a yellow or whitish tip.

Ventrally, animals are immaculate white with pinkish patches on the limbs, soles, and tail. Males have brilliant yellow throats, the colour extending across the entire ventral and dorso-ventral surface of the head and often along the lateral surfaces of the body and legs.

In preservative, the dorsal colours eventually fade to beige, brown, and grey. The brighter colours, especially yellow, eventually fade completely.

Advertisement call. (Figs 3, 20H) Consists of 13 notes (range 11–19) uttered in rapid succession with a note rate of 7.90 s⁻¹ (range 5.98–10.33). Note duration is short (27 ms [range 18–40]) and relatively regular, sometimes slightly shorter as the call progresses, with note 1 duration deviance low (20% [range 6–31]). The inter-note intervals are usually short (98 ms [range 75–130]) and regular with inter-note interval range low (30% [range 14–52]). Median call density is high (0.28 [range 0.20–0.34]) and call duration long (1.6 s [range 1.2–2.4]). The basal frequency is 382 Hz (range 301–492) but very soft and may be inestimable, with harmonic bands louder towards the upper dominant frequencies, the upper at 3.3 kHz (range 3.1–3.88) and a clear lower dominant frequency around 1.4 (range 1.1–1.9) kHz, about half the upper dominant frequency. Frequency appears to remain constant throughout the notes and call, as is the case with the (human) perceived pitch. Bandwidth (90%) is difficult to estimate consistently: approximately 0.7–4.9 kHz.

This species calls more intensively and for a shorter period of time than its sympatric or parapatric congeners (*P. carpi*, *P. maculatus* and *P. circumscriptus* **sp. nov.**). Calling also commences earlier in the day than these congeners. Call period (mean 74 s) varies greatly, but can be as low as 9 seconds during peak chorus activity. Calling activity is crepuscular, commencing shortly before or at sunset, and ending at nightfall. Sporadic calls may occasionally be heard later at night, in the morning, or on overcast days (Haacke 1969).

Distribution and habitat. Occurs throughout the Namib erg in the central Namib Desert, Namibia, except possibly in the southwestern extreme of this erg in the winter rainfall zone, near Lüderitz. The northern limit of its distribution is generally aligned with the northern extent of the sand sea.

The habitat of this species was initially described as the silts in Kuiseb River and the interdune plains by (Haacke 1964), and was even referred to afterwards as the “interdune barking gecko” (Branch 1998). In reality, this species rarely occurs on the interdunes and its occurrence in and around the Kuiseb River is more coincidental with sandy intrusions from the adjacent Namib erg. Its primary habitat is characterised by the dune plinth, being the base of the dune where the sand is loose, but before it slopes

more steeply. “Dune plinth barking gecko” would thus be a more suitable substitute common name. Its occurrence on the interdunes is only peripheral, except in instances where the interdunes sand is very loose, similar in composition to a typical dune plinth. True interdune plains in the Namib erg are occupied primarily, or solely, by *P. circumsyrticus* **sp. nov.**

Ptenopus kochi occurs parapatrically alongside *P. circumsyrticus* **sp. nov.** throughout the Namib erg, and in occasional sympatry or occasional syntopy. It also occurs parapatrically with *P. carpi* and *P. maculatus* along the Kuiseb River. Some *P. kochi* do occur on the northern banks of the Kuiseb River, occasionally in sympatry with *P. maculatus* and *P. circumsyrticus* **sp. nov.**, on

sandier patches of the gravel plains. These animals are genetically divergent from those on the southern side of the river.

Natural history. Breeding generally occurs from September to December (Polakow 1997), but this species may occasionally call throughout much of a year following above-average rainfall. Rainy weather may cause calling activity to cease for days to weeks.

It has previously been characterised as being nocturnal (Haacke 1969), but is more crepuscular. This species is more frequently observed on the surface during the day (e.g., Murray and Lease 2015) than congeners, except perhaps for *P. circumsyrticus* **sp. nov.**

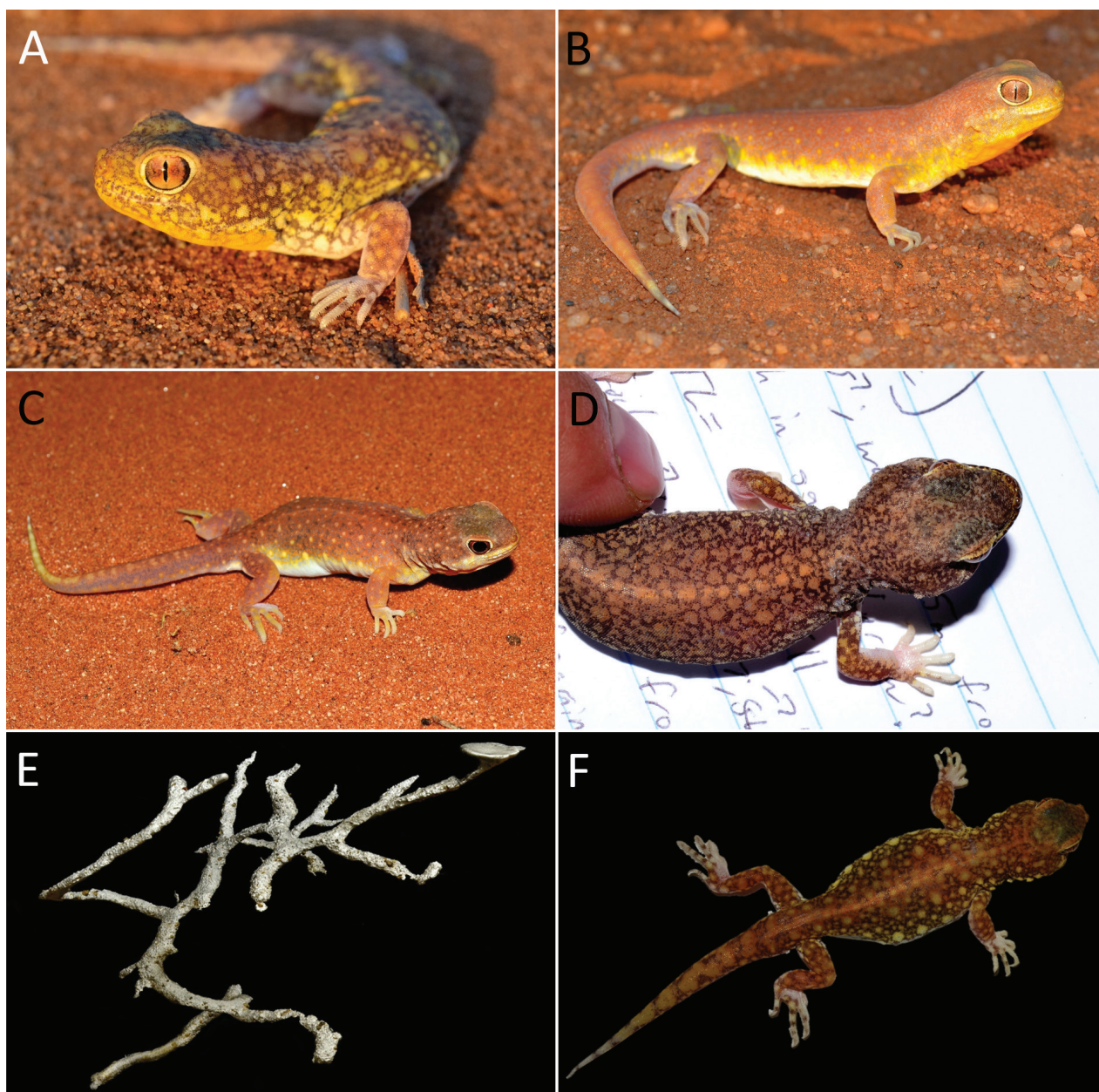


Figure 6. Life colour variation and burrow cast of *Ptenopus kochi*: **A** NMNW R11725 from Gobabeb, Erongo Region, Namibia (−23.5779, 15.0423); **B** FB2120 from NamibRand Nature Reserve, Hardap Region, Namibia (−24.9770, 15.9302); **C** NMNW R11751 from Far East Dunes, Hardap Region, Namibia (−23.7953, 15.7825); **D** FBPK13 from NW of Gobabeb (−23.3591, 14.8171); **E** aluminium burrow cast (uncatalogued) from Gobabeb (−23.5622, 15.0403); **F** individual A, showing typical yellow incursions on the body of males. Photos by Francois S. Becker.

Courtship appears to be more complex than in other species, and also more variable. Some courtship encounters witnessed by FB were similar to that of *P. maculatus*, with the female simply approaching the calling male and the male responding with a few calls. The female then scratches rapidly at the burrow entrance to indicate she wants to enter, after which the male retreats backwards and the female follows him inside. In other encounters, the males may exit the burrow and display their gular patch to the approaching female. Yet more variations, including mutual head bobbing and soft vocalisations, have been observed (Polakow 1997). In some cases, the female may inspect the burrow of a potential suitor, entering through one opening and leaving through another soon after, if she (presumably) finds the burrow unsuitable (Polakow 1997). Mating takes place within the burrow, with the male usually uttering something similar to the advertisement call from within the burrow, after a female has entered.

Fighting is common among closely-spaced males. In one observation (FB), a young male charged a much larger calling male at its burrow entrance, from several metres away. The two animals stood belly-to-belly on their back legs, rapidly clawing one-another with their hands for one or two seconds, before the younger male retreated. Scars from bite-marks on the body are commonly observed in both sexes, but more often in males.

The burrows of *P. kochi* tend to be more complex than other species, often with more than one entrance (Polakow 1997; FB observations). Males, females, and hatchlings share burrows for extended periods of time, and a male and female will generally use separate entrances to the same burrow system. See Polakow (1997) and Haacke (1964, 1978) for additional notes on *P. kochi* courtship and ecology.

Ptenopus garrulus (Smith, 1849) sensu stricto

Figures 7, 20A

Common names.

Kalahari barking gecko / Garrulous barking gecko

Afrikaans: Kalahari blafgeitjie / Grondgeitjie

Chresonymy.

Stenodactylus garrulus Smith, 1849: Append. 6

Ptenopus garrulus (part) – Boulenger (1885: 15), Brain (1962: 3), Haacke (1964: 3)

Ptenopus garrulus garrulus – FitzSimons (1935: 524), Loveridge (1947: 31), Haacke (1975: 214), Haacke (1969: 89)

Ptenopus garrulus maculatus (part) – Mertens (1955: 51), Mertens (1971: 44)

Comment. Sir Andrew Smith did not specify the type locality of *P. garrulus* beyond “sandy districts in the interior of southern Africa” (Smith 1849). Smith did not name specimens in his description, although FitzSimons (1937a) later noted which specimens were the types used

by Smith. Smith described type specimens as buff orange, having a spotted colour pattern and poorly or non-barred tail. Smith travelled and collected extensively in Namaqualand and briefly in southern Namibia, prior to his description of *P. garrulus* (Skelton 2018). These areas contain the three species as presently treated (Figs 2, 5): *Ptenopus adamanteus* **sp. nov.**, *P. kenkenses* **sp. nov.**, and *P. garrulus* sensu stricto. Of these, only the *P. garrulus* sensu stricto commonly occurs on orange, sandy substrate, with the body colour to match. The description “inland of South Africa” probably rules out the coastal and near-coastal regions occupied by *P. adamanteus* **sp. nov.** Hence, the southern Kalahari in the northern or central regions of the Northern Cape Province, South Africa, most likely contain the type locality, making *P. garrulus* sensu stricto as presently treated, the most likely candidate for this name (see Fig. 2). We therefore elevate the subspecies ‘*P. g. garrulus*’ to full species, and thereby exclude all species previously referred to as ‘*P. g. maculatus*’, from *P. garrulus* sensu stricto.

The morphological characters and colour pattern of the *P. garrulus* type specimens from the BMNH (1946.8.23.43–49) fall within the range of *P. garrulus* sensu stricto in this study (except slight deviations in IOS, typically ≤ 46 for *P. garrulus* sensu stricto, for two specimens: BMNH 1946.8.23.44 IOS = 48 and 1946.8.23.46 IOS = 47). Specimen BMNH 1946.8.23.47 conforms most unambiguously to these morphological characters (Fig. 4) and typical colour pattern. Hence, we designate BMNH 1946.8.23.47 (male) as the lectotype for *P. garrulus* sensu stricto.

Lectotype. BMNH 1946.8.23.47, collected from “sandy districts in the interior of southern Africa” (probably Northern Cape, South Africa), by Andrew Smith between 1834 and 1836.

Paralectotypes. BMNH 1946.8.23.43–46, 1946.8.48–49, same collection details as the lectotype.

Additional material examined. See Table S1 for vouchers (11) and unvouchered photographed (13) specimens, DNA samples (33 available, 20 sequenced), and call recordings (23) included (total $n = 44$ excluding types).

Diagnosis. A small *Ptenopus* (SVL max. 53.4 mm, mean 46.6 mm, $n = 22$) with a moderate tail (TL 69% [range 50–86%] of SVL, $n = 17$) and a generally slender appearance. This species is easily distinguished from *P. kochi*, *P. carpi* and *P. sceletus* **sp. nov.** by a combination of the following morphological characters: Toes extensively fringed laterally (similar to *P. kochi* vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.**), with fringe length roughly equal to the breadth of the toe between fringes (vs. fringe length generally less than half toe breadth in *P. carpi* and *P. sceletus* **sp. nov.**); having white pigmented ventral scales with some pink, unpigmented scales on the (hand/foot) soles (vs. pink, unpigmented patches also on the tail and limbs in *P. kochi*, and white entire in *P. car-*

pi and *P. sceletus* **sp. nov.**); having MBSR ~182 (range 156–202, $n = 31$) (vs. 187–210 in *P. kochi* and usually <135 in *P. carpi* and *P. sceletus* **sp. nov.**). It is further distinct from *P. carpi* and *P. sceletus* **sp. nov.** by the nasals being more swollen and the nostrils partially covered by internal projections of the upper labials, and by more-or less speckled dorsal colour pattern (vs. banded pattern in *P. carpi* and *P. sceletus* **sp. nov.**); from *P. kochi* by having fingers laterally fringed with pointed triangular scales (vs. elongated pointed scales in *P. kochi*).

From congeners previously included under '*P. garrulus*', *P. garrulus* sensu stricto is distinguished by: (when live) patches of pink, unpigmented scales on soles (vs. white pigmented in other species and white or slightly pinkish with dark brown speckles in *P. kenkenses* **sp.**

nov. and *P. australis* **sp. nov.**); having higher RB/RH (~1.12, range 0.95–1.24, $n = 10$) than *P. australis* **sp. nov.** (≤ 0.97); having higher MBSR (~182, range 156–202, $n = 31$) than *P. australis* **sp. nov.**, *P. circumsyrticus* **sp. nov.**, and *P. maculatus* sensu stricto (usually <149); dorsal colour pattern relatively speckled, consisting of >2 longitudinal rows of white spots (rows may join to form irregular bands), including 5–7 clear (but not large) dorsolateral pairs of light spots between pectoral and pelvic girdles, with indistinct dark patches not touching the white, or dark patches absent, and indistinct or no patterning on ventro-lateral sides of the face, vs. 4–5 large and distinctive paired, light, ovoid markings interspaced by distinct dark mottled patches usually touching the light markings, and ovoid patterning on ventro-lateral portions of the face



Figure 7. Life colour variation and substrate matching in *Ptenopus garrulus*: **A** NMNW R11351 from Etosha, Oshikoto Region, Namibia (–18.9979, 15.8657); **B** NMNW R10846, from farm Bloukop (–25.0953, 19.8497), Hardap Region, Namibia; **C** FB724 from locality A; **D** NMNW R11581 from farm Okongonga, Hardap Region, Namibia (–24.4529, 18.7631); **E**, **F** NMNW R11577 from south of Windhoek, Khomas Region, Namibia (–22.8691, 17.1561). Photos by Francois S. Becker.

being more distinctive in *P. kenkenses* **sp. nov.** (and some populations of *P. adamanteus* **sp. nov.** or *P. circumscriptus* **sp. nov.**); toe fringes being generally more extensive (with fringe length roughly equal to the breadth of the toe between fringes) than other species (fringe length usually about half toe breadth), but similar to *P. australis* **sp. nov.**

Colouration. In life (Fig. 7), colouration varies with substrate colour, as in other species. The colour pattern tends to be speckled or juxtaposed with light, dark, and coloured scales, the lighter (cream or white) speckles usually tending to larger dots or asymmetrical bars in some locations. On the tail, light-and-dark bars are usually evident dorsally. Background colour forms, matching various substrate colours, include brick red, cream or grey, and grey-brown. Ventrally, animals are immaculate white, with faded dark grey or brown patterning around the lateral margins, and pinkish patches on the (hand/foot) palms/soles. Males have bright yellow, heart-shaped gular patches which may extend onto the lateral margins of the head and body, and anterior surfaces of the legs.

In preservative, the lighter colours fade to off-white or beige, and all the darker colours appear various shades of dark brown or grey. The brighter colours, especially yellow, fade completely.

Advertisement call. The advertisement call (Figs 3, 20A) consists of 5.4 notes (4–6) uttered in rapid succession, with a note rate of 5.28 s^{-1} (range 3.76–7.37). Note duration is short, 22 ms (range 16–31), and highly regular, with note 1 deviance 15% (range 3–27%). Inter-note intervals are short (168 ms [range 114–234]) and regular, although latter intervals can be slightly longer; inter-note interval range 14–34%. Call density relatively low (0.13 [range 0.09–0.18]). Call duration is very short, only 0.86 s (range 0.6–1.2). The basal frequency is ~450 Hz (range 373–508) but very soft and may be inestimable, with harmonic bands louder towards the dominant frequency at 4.2 kHz (range 3.9–5.1); a very slight lower peak frequency band is evident at around or just below half the dominant frequency (roughly 1.3–2.6 kHz, cannot always be reliably estimated). Frequency appears to modulate briefly up, then down by ~100 Hz with each note, or remain constant. The (human) perceived pitch tends to be higher than that of most other species. Bandwidth (90%) is difficult to estimate consistently: approximately 0.6–8.2 kHz, usually wider than other species.

During peak chorus activity, this species calls much more frequently than most other species, the call period being very short: mean 25 s, and as low as 4 s. However, calling activity is short in most localities visited by the author, usually commencing around 20 min after sunset, and lasting only 20–40 mins. Calling may continue later if the moon is above the horizon and conditions are warm, but at an extremely decreased rate. More extensive and intensive choruses, lasting throughout the night, have been recorded shortly after rain (Haacke 1969).

Habitat and distribution. This is the most widespread member of the genus, occurring on sandy soils across

much of arid or semi-arid (generally above 150 mm but less than 550 mm annual rainfall) southern Africa, but not in the Namib Desert or the pro-Namib (Fig. 5). It occurs on sandy flats, interdunes, and on vegetated dunes or hummocks, but usually not on steep dunes. In one location (south of Windhoek) it was found occurring on consolidated, silty soils, but this is unusual. Calling is seasonal, taking place in the austral spring, from June in the northernmost extreme, and from September or October in the southernmost extreme of its distribution.

Natural history. The main calling period coincides with the breeding season (Hibbitts et al. 2012). In the northern limits of its distribution, the main breeding season appears to be between June and early September, but moves later southward (author observations). Most observations on this species were made in the southern Kalahari. Here, they breed between September and November (see Hibbitts et al. 2005, although this includes data from several *Ptenopus* species in addition to *P. garrulus*; Hibbitts et al. 2012) and possibly until late January, as hatchlings (<32 mm SVL) have been recorded between October and May (Haacke 1975), and yolked eggs were recorded within females between late August and late January (Pianka and Huey 1978). Clutch size appears to be one egg, although a second clutch may develop shortly after the first (Hibbitts et al. 2005). One nest was found to contain three eggs, although one or two of these may have been *Pachydactylus wahlbergi* (Haacke 1975). Minimum recorded hatchling SVL was 23.7 mm (Haacke 1975).

Haacke (1969) observed *P. garrulus* calling during March at the Nosob Camp, Kgalagadi-Gemsbok National Park, South Africa, after a rainfall event, suggesting that rainfall may cause bouts of calling outside the normal breeding season. During the observed event, the geckos called throughout the night, rather than the normal calling period around sunset. A similar observation was made at the Aha Hills, Namibia (northern portion of the distribution), during early February (Predinger pers. com.). For further notes on natural history and behavioural ecology of *P. garrulus*, see Hibbitts and Whiting (2005), Hibbitts (2006), Hibbitts et al. (2007, 2012).

Ptenopus maculatus Gray, 1866 *sensu stricto*

Figures 8, 20G–H

Common names.

Damaraland barking gecko / Spotted barking gecko

Afrikaans: Damaraland blafgeitjie

Chresonymy.

Ptenopus maculatus Gray, 1866: 640, pl. 38: 1

Ptenopus garrulus (part) – Boulenger (1885: 15), Brain (1962: 314), Haacke (1964: 3)

Ptenopus garrulus maculatus (part) – Mertens (1955: 51), Haacke (1969: fig. 3d), Brain (1962: 3, 14), Haacke (1975: 221), Bauer et al. (1993: 127)

Comment. *Ptenopus maculatus* was described from “Damaraland”, collected by Karl (= Charles) J. Andersson. This species was synonymised under the name ‘*P. garrulus*’ (Boulenger 1885). Subsequently, ‘*P. g. maculatus*’ was resurrected at subspecies level (FitzSimons 1935), which has been regarded as valid ever since. Most of the earliest references to this subspecies, including the initial synonymisation with ‘*P. garrulus*’ (e.g., FitzSimons 1935, 1937b; Loveridge 1947), referred to specimens included in our treatment of *P. adamanteus* **sp. nov.** and *P. kenkenses* **sp. nov.**, but exclude those from the type locality of ‘*P. maculatus*’. Mertens (1955), Haacke (1975), and several subsequent authors also referred to specimens from a broad geographic range, encompassing that of several species (current manuscript), as ‘*P. g. maculatus*’.

According to Andersson’s notes and the location names used at the time (see map in Andersson 1855 and 1872), “Damaraland” referred to the Erongo Region in Namibia. Notably, Andersson stayed at “Otjimbingue” [Otjimbingwe] briefly in 1851 and again in the 1860’s for several years, where this species occurs, and where it may have been collected. While staying here, a battle occurred on his property between the Damaras under chief Kama-herero, who had taken shelter at his house after fleeing their enslavement under the “Namaqua” (Nama) tribe Afrikaner, then under leadership of Christian Afrikaner (son of Jonker Afrikaner), leading to a victory by the Damara (Andersson 1875).

From the *P. garrulus* group species, “Damaraland” contains only *P. maculatus* sensu stricto (as presently treated). Additionally, the type specimens (BMNH 1946.8.23.53, 54) and a detailed drawing from the type description match the colour pattern and appearance of *P. maculatus* sensu stricto. Finally, the morphometric measurements of the BMNH types generally support this classification, and most unambiguously so for BMNH 1946.8.23.54 (Fig. 4). Hence, this specimen is assigned as the lectotype.

We elevate the subspecies ‘*P. g. maculatus*’ to full species, thereby restricting the range of *P. maculatus* sensu stricto to the central and northern Namib Desert, north of the Kuiseb River (Fig. 5), and excluding *P. adamanteus* **sp. nov.**, *P. kenkenses* **sp. nov.**, *P. circumsyrcticus* **sp. nov.**, and *P. australis* **sp. nov.**, from *P. maculatus* sensu stricto.

Haacke (1969) described the calls of *P. maculatus* sensu stricto and of *P. circumsyrcticus* **sp. nov.**, from areas near Gobabeb (Central Namib Desert, Namibia), but was unable to link individual specimens with their calls. Haacke (1969) also described calls of *P. adamanteus* **sp. nov.** as ‘*P. g. maculatus*’. The call of *P. maculatus* sensu stricto is described and distinguished in a standard taxonomic framework below.

Lectotype. BMNH 1946.8.23.54, collected from “South Africa, Damaraland” (Erongo Region – possibly Otjimbingwe, Namibia.), by Karl (=Charles) J. Andersson prior to 1864 (probably in 1851 or between 1855 and 1858,

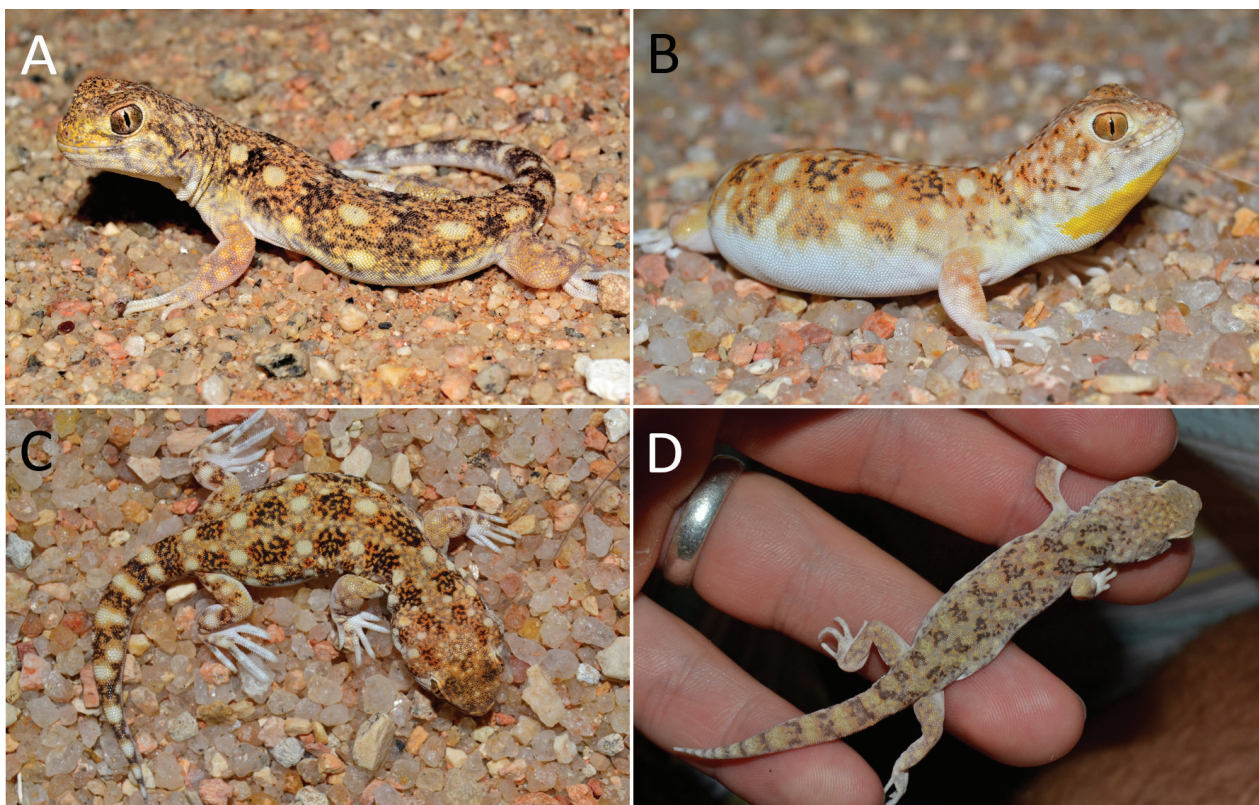


Figure 8. Life colour variation and substrate matching in *Ptenopus maculatus*: **A** Unvouchered individual from Gobabeb, Erongo Region, Namibia (–23.5668, 15.0379); **B** NMNW R11693 from Spitzkoppe, Erongo Region, Namibia (–21.8393, 15.1946); **C** NMNW R11668 from the same locality as B; **D** NMNW R11688 from Hoanib River, Kunene Region, Namibia (–19.3630, 13.1502). Photos by Francois S. Becker.

while travelling through and working in this area), as the lectotype for *Ptenopus maculatus*.

Paralectotype. BMNH 1946.8.23.53, same collection details as the lectotype.

Additional material examined. See Table S1 for unvouchered photographed (35) specimens, DNA samples (37 available, 12 sequenced), and call recordings (28) included (total $n = 69$ excluding types).

Diagnosis. A moderately large *Ptenopus* (SVL max. 60 mm, mean 51.7 mm, $n = 34$) with a moderate tail (TL 69% [range 58–78%] of SVL, $n = 21$) and stout appearance. It is easily distinguished from *P. kochi*, *P. carpi*, and *P. sceletus* **sp. nov.** by the following characters: Toes being intermediately fringed laterally (vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.**, and extensively fringed in *P. kochi*), with fringe length being at least half the breadth of the toe between fringes; having MBSR ~ 135 (range 126–146, $n = 35$; vs. >180 in *P. kochi* and usually <135 in *P. carpi* and *P. sceletus* **sp. nov.**); by dorsal colour pattern with four to five large, paired, ovoid markings on a darker background, interspaced by dark brown wavy or broken blotches (vs. more finely spotted in *P. kochi* and banded in *P. carpi* and *P. sceletus* **sp. nov.**).

From congeners previously included in '*P. garrulus*' it is distinguished by: Higher IN/INSBB ~ 7.2 (range 4.9–8.8, $n = 8$) than *P. circumsyrcticus* **sp. nov.** (median 4.5, range 3.6–5.8, $n = 13$); higher RB/RH ~ 1.17 (range 0.97–1.32, $n = 8$) than *P. australis* **sp. nov.** (<0.97) and *P. adamanteus* **sp. nov.** (usually <1.1); higher INSH/NB ~ 1.53 (range 0.60–2.49, $n = 8$) than *P. australis* **sp. nov.** (usually <0.80) and *P. adamanteus* **sp. nov.** (usually <1.00); lower MBSR (~ 135 , range 126–146, $n = 35$) than *P. kenkenses* **sp. nov.** (≥ 158) and *P. garrulus* (≥ 156 , usually >170), and somewhat lower than *P. adamanteus* **sp. nov.** (median 160, range 141–185, $n = 30$); lower IOS ~ 34 (range 29–40, $n = 35$) than other species (usually >37); lower IOS/MBSR ~ 0.23 (range 0.21–0.27, $n = 8$) than *P. circumsyrcticus* **sp. nov.** (usually >0.27), *P. adamanteus* **sp. nov.**, and *P. australis* **sp. nov.** (usually >0.25); having 1–2 internasal scales in contact with the rostral, vs. three in *P. australis* **sp. nov.**; having a different colour pattern than *P. garrulus* (usually more finely speckled, ovoid markings being much smaller).

Colouration. In life (Fig. 8), the dorsal colour pattern consists of 4–6 large, cream/yellow/white paired ovoid markings from the neck to tail base with various light, coloured and dark brown juxtaposed speckles, darker colours coalescing into ill-defined paired patches between the oval markings; white ovoid markings laterally. Background dorsal colour is usually light brown or camel with occasional bright orange, pink, or purple speckling. The ventrum is immaculate white. Males have bright yellow gular patches. In some specimens, the yellow pigment extends onto the nose or patchily onto lateral margins of the head and neck.

In preservative, the lighter colours fade to off-white or beige, and all the darker colours appear various shades of dark brown or grey. The yellow fades completely after some days or weeks in ethanol.

Advertisement call. The advertisement call of *P. maculatus* (Figs 3, 20F typical call, 20H Hoanib River population) consists of 6 notes (range 4–7, sometimes 8 in Hoanib River population) uttered in rapid succession, with a note rate of 4.99 s^{-1} (range 2.58–7.17). Note duration is long, 50 ms (range 26–71), with the first note being notably longer than the rest, note 1 duration deviance 138% (range 39–274); the Hoanib River population has a relatively shorter first note than the typical call. The inter-note intervals are usually short (145 ms [range 88–303]) and regular with inter-note interval range 20% (range 10–42), although the first interval may be slightly longer. Call density is higher than all other species, mean 0.36 (range 0.17–0.50). Call duration is short (1.1 s [range 0.8–1.4]). The basal frequency is 380 Hz (range 301–517) but very soft and may be inestimable, with harmonic bands louder towards the (upper) dominant frequency at 3.4 kHz (range 3.0–3.8), while a clear but softer lower frequency peak is evident at around 1.7 kHz (range 1.4–2.0), just below half the (upper) dominant frequency. Frequency appears to modulate briefly up (~ 0.2 kHz), then drastically down by ~ 0.5 kHz with the first note, and less severely down in the notes following. The first note tends to be louder, have a slightly higher dominant frequency, and a slightly higher (human) perceived pitch than the following notes. Bandwidth (90%) is difficult to estimate consistently: approximately 0.9–4.8 kHz.

Call period (mean 110 s) varies greatly, but can be as low as 10 seconds during peak chorus activity. Calling commences shortly before or at sunset and may continue throughout the night after moonrise and before moonset. Calling activity is more pronounced around the austral spring and/or summer. Rainy weather usually causes calling activity to cease for days to weeks. This species rarely calls during the day.

Habitat and distribution. *Ptenopus maculatus* occurs on hard substrates, not on soft sand. In the southern and central portions of its range it occurs on granite-weathered gravel. The central Namib gravel plains are almost entirely granite-based gravel (Atlas of Namibia Team 2022a) and the species is widespread and common in this area. In the northern reaches of its distribution, *P. maculatus* occurs on silts, in patchy floodplains, riverbeds, or pans. It has not been found closer than 25–50 km, nor further than 200 km, from the coast.

In the west it occurs syntopically with *P. carpi* and probably with *P. sceletus* **sp. nov.** which prefer the same soils. However, these species occur closer to the coast within the fog zone and the range of overlap is minimal. It occurs parapatrically with *P. sceletus* **sp. nov.** in the northern portions of its range, where *P. maculatus* prefers silts while *P. sceletus* **sp. nov.** occurs on gravels. Along the edges of the Namib erg, *P. maculatus* occurs parapatrically alongside *P. circumsyrcticus* **sp. nov.** and *P. kochi*

(which occur on sand or sandier patches of gravel plains), or occasionally in sympatry or syntopy with these species where the substrates mix.

Natural history. Like the other species, *P. maculatus* males call from their burrow entrance and antagonistic behaviours between males are common if two burrow entrances are within ~2 m. Aggressors will sometimes utter the advertisement call as they look for the transgressing male, possibly to elicit a response. Males will increase calling frequency if a female approaches the burrow. Males may exit the burrow and approach the female, and after a brief encounter will follow the females into the burrow. Alternatively, the male will remain in place until the female scratches at the burrow entrance; the male then reverses into the burrow and the female follows. The male will utter a muffled version of the advertisement call inside the burrow, where copulation likely commences. After about an hour, the female will emerge partially from the burrow entrance, surveying the surrounding area with her head erect for a long time. This behaviour is repeated throughout the first night after a female moves into a new burrow, and its purpose may be to memorise the location of the new burrow entrance. Males presumably move out of the burrow after the female has moved in, as males and females have not been observed living in the same burrow.

Ptenopus australis sp. nov.

<https://zoobank.org/34D35556-BE86-4D2D-BC87-E018D-E7D822F>

Figures 9, 10, 20B

Common names.

Southern barking gecko

Afrikaans: Suiderlike blafgeitjie

Chresonymy. *Ptenopus garrulus maculatus* – Oelofsen and Vorster (1976), Rebelo et al. (2018)

Comment. Specimens of this species have not yet been included in any taxonomic revision of this genus, only in two publications on range extensions of '*P. g. maculatus*'. These records were further notably included in the range maps of '*P. g. maculatus*' by Branch (1998), and of '*P. garrulus*' by Bates et al. (2014), Telford et al. (2022), and Tolley et al. (2023).

Holotype. PEM R23122, adult male, collected from farm Rooidraai, Eastern Cape Province, South Africa (−32.4645, 23.6330, 860 m a.s.l.) by Werner Conradie, Alexander Rebelo, and Philip Jordaan, on 2 November 2017.

Paratypes. PEM R23118–23121, adult males except for PEM R23120 (allotype), collected from farm Doringkraal, Eastern Cape, South Africa (−33.0479, 24.9611,

305 m a.s.l.), by Werner Conradie, Alexander Rebelo, and Philip Jordaan, on 31 October 2017.

Additional material examined. See Table S1 for additional unvouchered photographed specimen (1), and call recordings (4) examined (total n = 5 excluding types).

Etymology. This is the most southern *Ptenopus* species, occurring near the southernmost tip of Africa. Therefore, we use the specific epithet "*australis*", the Latin (masculine) adjective meaning "southern".

Diagnosis. The smallest *Ptenopus* (SVL max. 44.6 mm, mean 42.7 mm, n = 5) with the shortest tail of any *Ptenopus* species (TL 61% of SVL, only one specimen had full original tail, but other paratypes/holotype lost a very small portion of the tail tip and they still appear to be similarly short) and a moderately stout appearance. It is distinguished from *P. kochi*, *P. carpi*, and *P. sceletus* **sp. nov.** by: Being substantially smaller; toes being intermediately fringed laterally (vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.** and extensively fringed in *P. kochi*), with fringe length being at least half the breadth of the toe between fringes (vs. generally less than half in *P. carpi* and *P. sceletus* **sp. nov.**, and generally equal to in *P. kochi*); ventral surface being generally white or cream with some unpigmented and/or dark brown-speckled scales on the (hand/foot) soles (vs. substantial pink, unpigmented patches on the tail and limbs in *P. kochi*, and immaculate white in *P. carpi* and *P. sceletus* **sp. nov.**); having MBSR 140–156, mean 148 (n = 5) (vs. ≥187–222 in *P. kochi* and usually <135 in *P. carpi* and *P. sceletus* **sp. nov.**); a generally brown-and-cream spotted appearance with some paired light and dark markings dorsally (vs. pinkish or orange, more evenly spotted pattern in *P. kochi* and banded pattern in *P. carpi* and *P. sceletus* **sp. nov.**). It is further distinct from *P. carpi* and *P. sceletus* **sp. nov.** by the nasals being more swollen and the nostrils partially covered by internal projections of the upper labials; from *P. kochi* by having fingers laterally fringed with pointed triangular scales (vs. elongated pointed scales in *P. kochi*).

From congeners previously included in '*P. garrulus*' it is distinguished by: A smaller internasal scale, with higher IN/INSBB (~10.6, range 7.3–11.6, n = 5) and lower INSH/NB (~0.65, range 0.57–0.97, n = 5) than *P. circumscriptus* **sp. nov.** (IN/INSBB <6, INSH/NB usually >0.97); having lower RB/RH (<1) than these congeners (usually >1, except for some *P. adamanteus* **sp. nov.** individuals); having lower MBSR (~148, range 147–149, n = 5) than *P. garrulus* and *P. kenkenses* **sp. nov.** (≥158); IOS/MBSR (~0.26, range 0.24–0.29) usually higher than *P. garrulus* (~0.23, range 0.20–0.25, n = 10); having 3 internasal scales in contact with the rostral (vs. usually <3 for *P. garrulus* and *P. adamanteus* **sp. nov.**, ≤2 for *P. kenkenses* **sp. nov.** and *P. maculatus*, and only 1 in *P. circumscriptus* **sp. nov.**).

Holotype description. (Fig. 11). Adult male, SVL 44.63 mm with original tail short with blunt tip, 21.99 mm (49.3% of SVL). Body and head covered with minute

hexagonal to round scales of a similar size, dorsally and ventrally, with scales on limbs slightly larger. Mid-ventral incision, T-shaped, for removal of liver sample. Body stout, MBSR 149, IOS 43, HL 13.48 mm, HW 8.33 mm, HH 5.68 mm, EED 3.87 mm. Upper labials 7, lower enlarged labials 7; nine granules bordering the mental. Clear but not prominent superciliary ridges tapering above mid-eye level; right eyelid partially depressed by the fixing process with skin folds on the forehead. Prenasal scales slightly swollen, separated by three small, asymmetrical internasal scales in contact with the rostral, with IN/INSBB 17.14, INSH/NB 0.65; nostrils almost entirely covered by projection from the upper nasal. Rostral is large, with RB/RH 0.96; mental deep and slightly pointed ventrally. EYE 2.58 mm, pupil vertical; ear opening is oblique ($\sim 40^\circ$), and narrow with small, slightly projecting scales at the anterior margin. Toes elongate, slightly flattened, with elongate fringed scales; small, pointed, barely projecting triangular fringes on the fingers; strong, recurved and pointed nails on fingers and toes.

Colouration. In life, the paratype PEM R23121 (Fig. 10A–B) has a dorsal background colour light brown with cream and dark brown asymmetrical blotches and a few orange spots or blotches (holotype appears to have been

similar, but darker with finer patterning); light and dark dorsal markings merge into poorly defined ‘bands’ on the tail that become more defined distally; dark brown blotches extend onto lateral surfaces with slight, dark grey markings below the lateral line on the white (similar to holotype); ventrum is immaculate white except for the slight dark grey mottling laterally, which is more visible on the head and tail; slight dark speckling and some unpigmented or pinkish scales on hand palm, while foot sole is densely pigmented with dark speckles. Clear, bright yellow gular patch; the bright yellow does not extend onto the lateral surfaces of the head, body, or onto the limbs. Iris is light silver.

In preservative (Fig. 9), the lighter colours have faded to off-white or beige, the darker colours remain various shades of dark brown or grey, while the orange and yellow have faded completely (on paratype PEM R23121 and presumably on the holotype and others). The eyes turned a milky blue-grey.

Variation. See Table S1 for paratype and additional material measurements and scale counts, which does not vary substantially among the types. Colour pattern varies relatively little among specimens, with darker or lighter, finer or coarser colour patterns being visible. Males have



Figure 9. Holotype (PEM R23122) of *Ptenopus australis* sp. nov. from Rooidraai, Eastern Cape Province, South Africa (-32.4645 , 23.6330). Scale bar = 1 cm. Photos by Werner Conradie.

bright yellow gular patches, and may have slight yellow infusions on the legs and face (Fig. 10C).

Advertisement call. The advertisement call (Figs 3, 20B) consists of 5.8 notes (range 5–6) uttered in rapid succession, with a note rate of 6.68 s^{-1} (range 5.10–7.54). Note duration is short, 21 ms (range 21–22), and highly regular, with note 1 duration deviance 6% (range -1–19%). Inter-note intervals are short (117 ms, range 107–169 ms) and regular, although the last interval can be slightly longer; inter-note interval range 29% (range 13–55%). Call density moderately low (0.18, range 0.17–0.20). Call duration shortest of all species, only 0.82 s. The basal frequency was inestimable within our sample set, with the dominant frequency at 4.4 kHz (range 4.2–4.5 kHz); a very slight lower peak frequency band may present around 1.3 kHz. Frequency appears to remain constant throughout the short note. The (human) perceived pitch tends to be higher than that of most other species. Band-

width (90%) is difficult to estimate consistently with the recordings available.

During peak chorus activity, this species appears to call much more frequently than most other species (although sample size is small), the call period being a very short 9 seconds. The typical period of calling activity in a day is not known, but the analysed calls (during full chorus) were recorded 20–40 minutes after sunset.

Habitat and distribution. This species occurs on open Karoo scrub plains with sandy or gravelly substrate (Rebello et al. 2018), usually near small dune hummocks, south of the Great Escarpment in the Western Cape of South Africa (essentially the southern Nama Karoo). It has not been recorded in sympatry with any other species.

Natural history. Very little is known about the natural history of this species, although it is assumed to be simi-

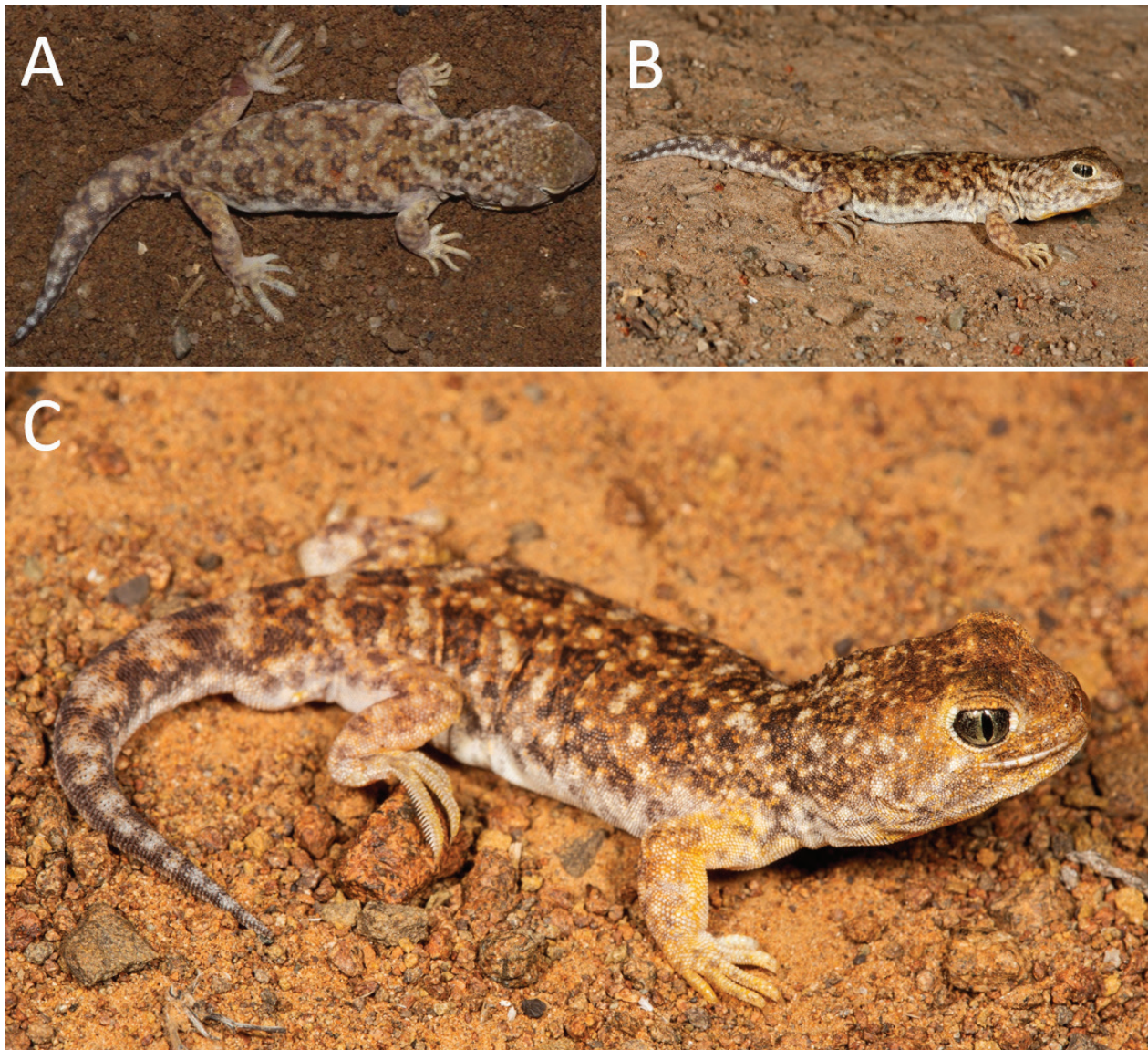


Figure 10. Life colour variation in *Ptenopus australis* sp. nov.: A, B PEM R23121 from farm Doringkraal, Western Cape Province, South Africa (−32.3355, 22.2053), photos by Alexander Rebello; C iNaturalist record 58938339 from NE of Beaufort West, Western Cape Province, South Africa (−32.2087, 22.7614), photo by Courtney Hundermark.

lar in many aspects to congeners, particularly to the sister species, *P. garrulus*, which also occurs in a similar climatic setting. So far, calls have only been recorded during late October, during the austral spring (recordings in this manuscript; Rebelo et al. 2018). The breeding period is expected to last for at least 2–3 months, as in the closely related *P. garrulus* and *P. adamanteus* **sp. nov.** As in several other species, they call from their burrow entrances in exposed or partially concealed locations (Rebelo et al. 2018).

Ptenopus adamanteus **sp. nov.**

<https://zoobank.org/D4643381-921D-4D6F-8C6E-97C179302FC9>

Figures 11, 12, 20C–D

Common names.

Diamond coast barking gecko

Afrikaans: Diamantkus blafgeitjie

Chresonymy.

Ptenopus garrulus maculatus (in part) – FitzSimons (1935: 525; Haalenberg, Luderitzbuch, Soebartsfontein); FitzSimons (1937b:160; Port Nolloth, Kamaggas), Haacke (1969: 92; Annisfontein, Daberas, Sendelingsdrif, Swartpoort), Mertens (1971: 44; southwestern localities), Haacke (1975; southwestern localities)

Ptenopus garrulus (in part) – Brain (1962: fig. 3; southwestern localities)

Comment. All coastal and near-coastal specimens in the southern Namib Desert (Namibia) and Richtersveld (South Africa) previously referred to as ‘*P. g. maculatus*’, are presently assignable to this species. It appears to not occur sympatrically with any other species, except potentially with *P. kenkenses* **sp. nov.** on the eastern margins of its range. Northern and southern populations of this species display several notable differences, including body-size. However, phylogenetic evidence presently suggests that these populations may form a gradual cline, rather than being two distinct species.

Holotype. NMNW R11390, adult male, collected from Grosse Bucht, south of Lüderitz, ||Karas Region, Namibia (–26.73379, 15.10412, 29 m a.s.l.), by Francois S. Becker and Bertha Buiswalelo on 27 September 2022.

Paratypes. NMNW R11391–3 (two adult males and one adult female NMNW R11391 = allotype), same collection details as the holotype; NMNW R11350, subadult female, collected from the pump house along main road, Sperrgebiet, ||Karas Region, Namibia (–26.9932, 15.3584), by Dayne Braine on 10 September 2021.

Additional material examined. See Table S1 for unvouchered photographed specimens (21), DNA samples (17 available, 7 sequenced), and call recordings (8) included (total n = 28 excluding types).

Etymology. This species is named in reference to the diamond-scattered coastline that forms its habitat, including the Sperrgebiet in Namibia and the Richtersveld in South Africa, where extensive diamond mining occurred historically and continues to this day. We use the specific epithet “*adamanteus*”, the Latin adjective meaning “of diamond”, framed in the male genitive to match the gender of *Ptenopus*.

Diagnosis. Southern populations of this member of the genus have a small body size (SVL max. 45.1 mm, mean 39.4 mm, n = 19) with long tails (TL 77%, range 60–99%, n = 19) while that of the northern populations is moderate (up to 50.8 mm, mean 49.7 mm, n = 6), with a moderately long tail (TL 71%, range 67–76%, of SVL) and an overall lean appearance. It is distinguished from *P. kochi*, *P. carpi*, and *P. sceletus* **sp. nov.** by: Toes being intermediately fringed laterally (vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.** and extensively fringed in *P. kochi*), with fringe length being at least half the breadth of the toe between fringes (vs. generally less than half in *P. carpi* and *P. sceletus* **sp. nov.**, generally equal to in *P. kochi*); having MBSR 141–185 (vs. ≤131 in *P. carpi* and *P. sceletus* **sp. nov.** and >185 in *P. kochi*); by having on the dorsum 4–5 paired, more-or-less symmetrical, light-coloured, ovoid markings on the body, about half the diameter of the eye or larger, interspaced by dark brown blotches (vs. more finely patterned dots in *P. kochi* and banded pattern in *P. carpi* and *P. sceletus* **sp. nov.**). It is further distinct from *P. carpi* and *P. sceletus* **sp. nov.** by the nasals being more swollen and the nostrils partially covered by internal projections of the upper labials; from *P. kochi* by having fingers laterally fringed with pointed triangular scales (vs. elongated pointed scales in *P. kochi*), and having white pigmented ventral scales on entire ventral surface (vs. pink, unpigmented patches on the tail and limbs in *P. kochi*).

From congeners previously included in ‘*P. garrulus*’ it is distinguished by: Having immaculate white pigmented scales on soles, vs. some pink, unpigmented scales on soles of *P. garrulus* and *P. australis* **sp. nov.**, and dark speckling on the soles of *P. kenkenses* **sp. nov.** and *P. australis* **sp. nov.**; having a usually smaller internasal scale than *P. circumscriptus* **sp. nov.**, with IN/INSBB ~8 (usually >6.0, vs. usually <6.0 in *P. circumscriptus* **sp. nov.**); higher RB/RH (~1.1, usually ≥1 and <1.2) than *P. australis* **sp. nov.** (usually ≤1.0), but lower than *P. circumscriptus* **sp. nov.** (usually >1.1); usually lower INSH/NB (usually <1.1) than *P. circumscriptus* **sp. nov.** (usually >1.1); having a generally higher IOS (mean 45, range 35–53, n = 30) and IOS/MBSR (mean 0.29, usually >0.24) than *P. maculatus* (IOS usually <37, IOS/MBSR usually <0.24); having one or two inernal scales in contact with the rostral vs. three in *P. australis* **sp. nov.**

Holotype description. (Fig. 11). Adult male, SVL 49.94 mm with original tail 35.20 mm (70.5% of SVL). Body and head covered with minute hexagonal to round scales of a similar size, dorsally and ventrally, with scales on limbs notably larger. Small mid-ventral incision for re-

moval of liver sample. Body slender, MBSR 170, IOS 53, HL 15.87 mm, HW 11.19 mm, HH 6.68 mm, EED 5.89 mm. Upper labials 8, lower enlarged labials 8 with an additional small, elongate scale on the inflection of the jaw; eight granules bordering the mental. Clear but not prominent superciliary ridges tapering above mid-eye level; a single row of elongated scales around the anterior and upper margins of the eye with curved tips posteriorly, the scales being smaller and rounder along the posterior and dorsal edges. Prenasal scales swollen, separated by one small, asymmetrical hexagonal internasal scale in contact with the rostral, with IN/INSBB 6.90, INSH/NB 0.50; nostrils partially covered by projection from the upper nasal. Rostral is narrow and tall, with RB/RH 0.76, MB/RB 0.89. Eyes intermediate, EYE 3.46 mm, pupil vertical; ear opening is oblique ($\sim 45^\circ$), and narrow with small, slightly projecting scales at the anterior margin.

Toes elongate, flattened, with elongate fringed scales, small, pointed, triangular fringes on the fingers; strong nails on fingers and toes, being larger and thicker on the fingers.

Colouration. In life, the holotype (Fig. 12A) has a dorsal background colour of dull orange or light brown with light grey-purple, cream, and grey spots; four pairs of large, cream/white, ovoid markings on the back interspaced by diffuse, mottled, dark brown-purple patches; these markings coalesce into alternating cream and light purple/brownish bars on the tail (9 dark bars, the last two very faint). Laterally the colours and markings fade, with immaculate white ventrum. Laterally, the body has five white circular markings, dorsally outlined with light brown/purple. Yellow gular patch extensive, with additional yellow spots on the snout, laterally on the head,

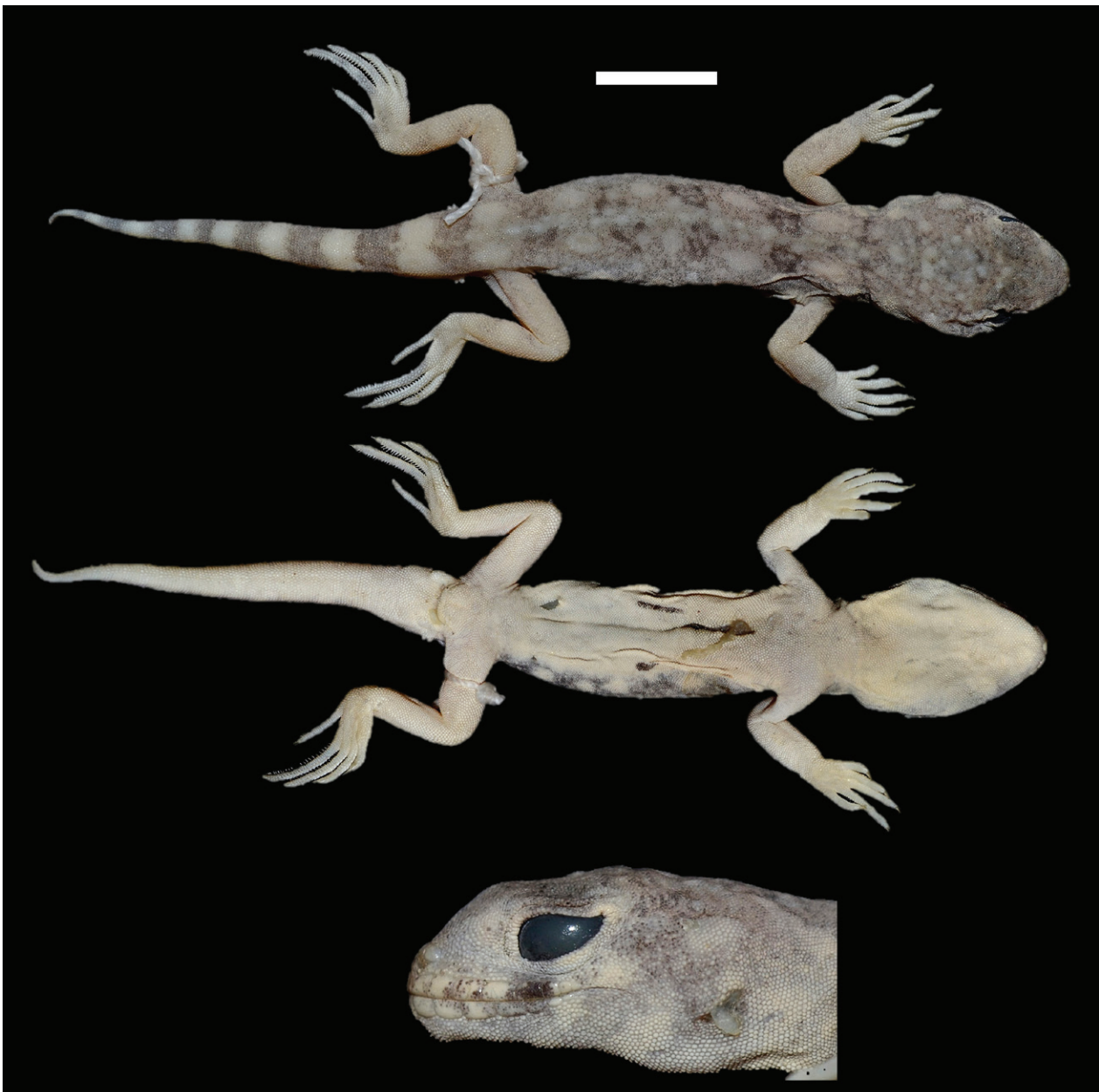


Figure 11. Holotype (NMNW R11390) of *Ptenopus adamanteus* sp. nov. from Grosse Bucht Bay, ||Karas Region, Namibia ($-26.7338, 15.1041$). Scale bar = 1 cm relative to full ventral and dorsal views. Photos by Francois S. Becker.

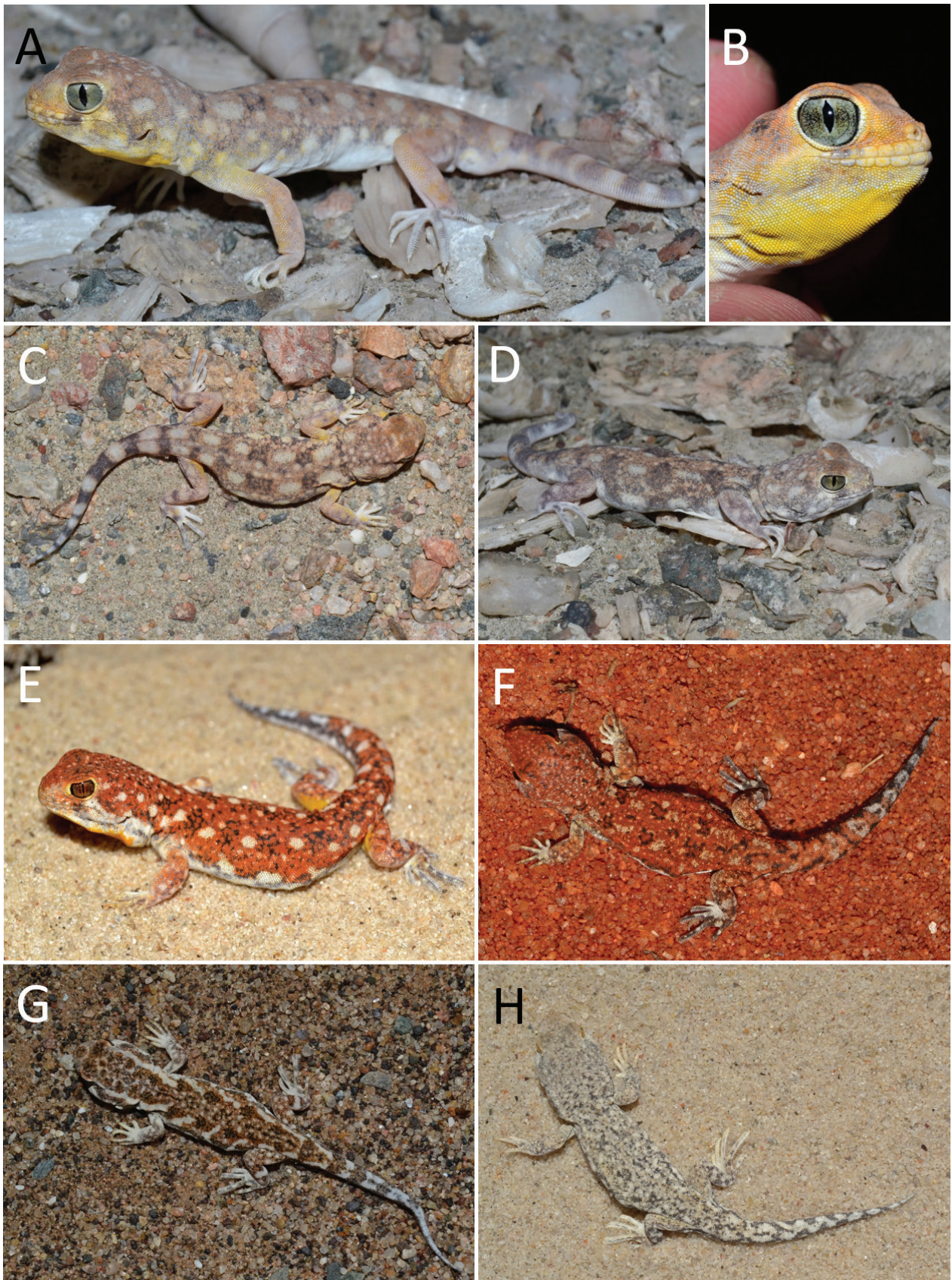


Figure 12. Life colour variation and substrate matching in *Ptenopus adamanteus* sp. nov. (A–D: northern populations; E–H: southern populations): **A** NMNW R11390 (holotype), from Grosse Bucht, ||Karas Region, Namibia (–26.7338, 15.1041); **B**, **C** NMNW R11393 (paratype) from near locality A (–26.7208, 15.1026); **D** NMNW R11391 (allotype), from locality A; **E** NMNW R11610 from 30 km E of Port Nolloth, Northern Cape Province, South Africa (–29.3049, 17.1836), not on native substrate; **F** NMNW R11611 from the same locality as E on native substrate; **G** NMNW R11598 from Oranjemund, ||Karas Region, Namibia (–28.5541, 16.4982); **H** unvouchered specimen from Port Nolloth (–29.2403, 16.8631), only 30 km W of locality of E/F. Photos by Francois S. Becker.

body and neck, and on anterior surfaces of the back legs. The iris is a light green-grey or greenish camel.

In preservative (Fig. 12), the lighter colours faded to off-white or beige and the darker colours to shades of dark brown or grey, while the immaculate white areas appear more cream. The yellow has faded completely and the iris is milky blue-grey.

Variation. Refer to Table S1 and Figure 4 for range of morphometric characters, including the paratypes. Internasal scale is typically small and asymmetrical; rostral typically narrow and tall; toe fringes relatively extensive. Dorsal colouration highly variable, matching the wide variation of substrate colours and surface textures across its range. Northern populations (Fig. 12A–D) have a similar colour pattern to the holotype, whereas the southern populations (Fig. 12E–H) have a more finely speckled or dotted appearance somewhat similar to *P. garrulus*. The northern populations occur more often on deflation plains with pebbles or coarse sand on the surface (despite finer sand beneath the surface), whereas the southern populations tend to occur in fine sandy substrates—which may account for the colour pattern difference (this appears to be the pattern across the genus). Observed colour variations include overall cream, greyish, ochre, or even brick red background colouration with speckling colour variations including brown, white, olive, purple, orange, and black. Ventrally, animals are immaculate white, although some southern populations possess black or dark grey speckling on the throat and lateral edges of the body, occasionally intruding onto the belly. Males have bright yellow gular patches which often extend onto the lateral head and body, and yellow on anterior surfaces of the hind leg.

Advertisement call. The advertisement call (Figs 3, 20C) consists of 5 notes (range 4–6), uttered slowly at a rate of 2.81 s^{-1} (range 2.64–3.15). Note duration is short (29 ms [range 24–34]) and highly consistent; note 1 duration deviance 9.2% (range 4–16). Inter-note intervals 313 ms (range 274–341), with a notably longer final interval; inter-note interval range high, 52.2% (range 36–66). Median call density is low, 0.09 (range 0.08–0.11); call duration 1.4 s (range 1.1–1.8). The basal frequency is ~415 Hz (range 370–516, but very soft and may be inestimable, with harmonic bands louder towards the (upper) dominant frequency at 4.4 kHz (range 4.1–5); usually no notable lower peak frequency peak is evident. Frequency appears to remain more or less constant throughout the note, and (human) perceived pitch is notably lower in northern than southern populations, and also coastal compared to inland populations. Bandwidth (90%) is difficult to estimate consistently: approximately 0.5–7.3 kHz.

In coastal populations this species does not call often (longer call periods and fewer evenings of calling), but inland populations are more vocal. This is probably due to higher incidence of cold, foggy, windy weather closer to the coast, in which calling activity is reduced. Call period (5–20 s, mean 14 s) is short compared to most other species during peak chorus activity. It mainly calls from

about 30 minutes before sunset until nightfall, with occasional calling later at night. This species may call sporadically throughout the day, particularly under foggy or cloudy conditions.

Habitat and distribution. (Fig. 5). This species occurs on small coastal dunes, sandy plains, and on deflation plains in the southern Namib Desert, or the Namaqualand-Richtersveld steppe ecoregion (see Dinerstein et al. 2017). It occurs from the edge of the intertidal zone, inland to about 50–80 km from the coast. The habitat falls within the coastal fog zone and receives rain predominantly in the austral winter.

Natural history. While its breeding phenology is not well known, our sampling suggests that calling/breeding peak activity occurs from September to November, like several other species. This species often wanders on the surface throughout the night, far from its burrow, and may be active despite cold, foggy weather, similar to *P. carpi* and *P. sceletus* **sp. nov.** The burrows are relatively complex with multiple side-tunnels, and a few egg clutches, usually two eggs but occasionally one, have been found inside burrows occupied by a female. This species occasionally closes the burrow entrance from the inside before daybreak, but may also be active diurnally, especially after or during foggy weather. Hatchlings have been observed digging their own burrows a day after hatching, and it is therefore expected that they do not remain in the parent burrows for any length of time. Males and females have not been observed sharing a burrow. This species has been observed feeding on spiders and termites, and it likely eats various arthropods.

Ptenopus circumsyrticus **sp. nov.**

<https://zoobank.org/925BDD3B-A2EB-4933-A6AA-B0F85D98D3BD>

Figures 13, 14, 20E

Common names.

Interdune barking gecko

Afrikaans: Duinstraat blafgeitjie

Chresonymy.

Ptenopus garrulus (in part) – Brain (1962: fig. 3; central Namib)

Ptenopus garrulus maculatus (in part) – Haacke (1969: fig. 3b–c),
Haacke (1975: 225; central Namib Desert, notably Gobabeb)

Comment. Specimens of *P. circumsyrticus* **sp. nov.** were not included in the earliest mentions of the name *P. g. maculatus* (e.g., FitzSimons 1935), but were included in several later works, including notably those of Haacke (1964, 1969, 1975). Haacke (1969) described the calls of both *P. maculatus* sensu stricto and *P. circumsyrticus* **sp. nov.** from the area surrounding Gobabeb, under the name '*P. g. maculatus*', noting the clear differences. However, Haacke did not manage to match the two distinct calls

with particular specimens in the area where they are sympatric (on the gravel plains of the central Namib Desert), and hence was uncertain about whether the different calls reflected intraspecific or interspecific variation. It is also worth noting that, in this sympatric zone, the two species can be readily distinguished by the internasal scale in *P. circumsyrticus* **sp. nov.** being large and in broad contact with the rostral, separating the nasal scales clearly, whereas *P. maculatus* has one or more small and rounded granules, barely separating the nasal scales. This morphological distinction is less clear in allopatric populations.

Holotype. NMNW R11394, adult male, collected from the interdunes plains south of the Kuiseb River from Gobabeb Research Station, ||Karas Region, Namibia (−23.57053, 15.03618, 415 m a.s.l.), by Francois S. Becker on 6 September 2022.

Paratypes. NMNW R11395 (allotype, adult female), R11396 and R11622 (adult males), with the same collection details as the holotype; R11346 (adult male) and R11371 (adult female), collected near the type locality (−23.5697, 15.0388), by Francois S. Becker on 17 September 2021.

Additional material examined. See Table S1 for vouchers (3) and unvouchered photographed specimens (13), DNA samples (16 available, 11 sequenced), and call recordings (11) included (total $n = 25$ excluding types).

Etymology. This species is named in reference to its habitat: It occurs in and around the sand sea, on interdune plains or dune streets, and on sandy plains at the edge of the sand sea. They do not occur on the dunes themselves. Thus, we use the specific epithet “*circumsyrticus*”, the Latin adjective meaning “around the dune”, framed in the male genitive to match the gender of *Ptenopus*.

Diagnosis. A moderately small *Ptenopus* (SVL max. 54.9 mm, mean 48.6 mm, $n = 16$) with a short tail (TL 62% [range 48–73] of SVL, $n = 8$) and a lean appearance. It is distinguished from *P. kochi*, *P. carpi*, and *P. sceletus* **sp. nov.** by being substantially smaller; toes being intermediately fringed laterally (vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.** and extensively fringed in *P. kochi*), with fringe length being at least half the breadth of the toe between fringes (vs. generally less than half in *P. carpi* and *P. sceletus* **sp. nov.**, generally equal to in *P. kochi*), although fringing can be more extensive in specimens found in looser sand, such as close to Walvis Bay or Far East Dunes; by dorsal colour pattern, characterised by paired, large, subsymmetrical, light ovoid markings interspaced by dark blotches (vs. spotted pattern in *P. kochi* and banded pattern in *P. carpi* and *P. sceletus* **sp. nov.**). It is further distinct from *P. carpi* and *P. sceletus* **sp. nov.** by the nasals being more swollen and the nostrils partially covered by internal projections of the upper labials; from *P. kochi* by having fingers laterally fringed with pointed triangular scales (vs. elongated pointed scales in *P. kochi*), having white pigmented scales on entire ven-

tral surface (vs. pink, unpigmented patches on the tail and limbs in *P. kochi*), and having MBSR 108–179 (vs. >180 in *P. kochi*), with finer lepidosis presenting in specimens found in looser sand.

From congeners previously included in ‘*P. garrulus*’ it is distinguished by: The internasal scale usually being larger and broader than other species, with IN/INSBB being generally lower (median 4.5, range 3.6–5.8, but usually <4.7) than other species (usually >5.0); having higher RB/RH (median 1.27, usually >1.17) than *P. adamanteus* **sp. nov.**, *P. australis* **sp. nov.**, and *P. garrulus* (usually <1.17); having higher INS/NB (~1.61, usually >1.10) than *P. adamanteus* **sp. nov.**, *P. australis* **sp. nov.**, and *P. garrulus* (usually <1.20); having lower MBSR (median 144, usually <160) than *P. kenkenses* **sp. nov.** and *P. garrulus* (usually >160); higher IOS/MBSR (median 0.31, usually >0.25) than *P. maculatus* and *P. garrulus* (usually ≤0.25); having only one internasal scale in contact with the rostral, while *P. australis* **sp. nov.** has three; having no pink, unpigmented scales on the soles (vs. some unpigmented scales in *P. garrulus* and *P. australis* **sp. nov.**).

Holotype description. (Fig. 13). Adult male, SVL 48.75 mm with original tail 35.79 mm (73.42% SVL). Body and head covered with minute hexagonal to round scales of a similar size, dorsally and ventrally, with scales on limbs notably larger. Small mid-ventral incision for removal of liver sample. Body and head slender, MBSR 129, IOS 53, HL 14.62 mm, HW 10.99 mm, HH 5.57 mm, EED 5.81 mm. Upper and lower labials 8, six granules bordering the mental. Clear but not prominent superciliary ridges tapering above mid-eye level; a single row of elongated scales around the anterior and upper margins of the eye with curved tips posteriorly, the scales being smaller and rounder along the posterior and dorsal edges; nasal scales swollen, the prenasals separated by one large, hexagonal internasal scale in broad contact with the rostral, with IN/INSBB 4.69, INSH/NB 1.09; nostrils partially covered by projection from the upper nasal. Rostral broad, with RB/RH 1.44, MB/RB 0.81. Eyes intermediate, EYE 3.15 mm, pupil vertical. Ear opening is oblique (~45°) and narrow, with small, slightly projecting scales at the anterior margin. Toes elongate, flattened, with elongate fringed scales, small, pointed, triangular fringes on the fingers; strong nails on fingers and toes, being larger and thicker on the fingers.

Colouration. In life, the holotype (Fig. 14A) has a dorsal background colour of ochre with deep orange, cream, and dark brown spots, the darker spots aggregated in clusters; three pairs of larger, cream/light yellow, ovoid markings from the neck to the back, with one unpaired marking on the left lower back and another asymmetrical pair onto the tail base; light markings interspaced by diffuse, asymmetrical, mottled or spotted, dark brown patches; the tail has 11 dark bands, unevenly spaced and somewhat diffuse, with the last being very faint; the dorsal colours and markings fade to grey on the lateral edges with clear alternating light-and-dark markings; immaculate white ventrum. Yellow gular patch with faded edges.

In preservative (Fig. 13), the lighter colours have faded to off-white or beige, and all the darker colours appear various shades of dark brown or grey with some orange being evident. The yellow has faded completely.

Variation. Refer to Table S1 and Figure 4 for range of morphometric characters, including the paratypes. Internasal scale typically large and symmetrical; rostral typically broad; toe fringes relatively extensive, notably more so in areas with looser sand. As with other species, the colour of the animals usually matches that of the local substrate, although the patterning is similar to the holotype (Fig. 14). Background colour variations include ochre to brick red. Ventrally animals are immaculate white. Males have faded to bright yellow gular patches (typically less extensive than most other species), occasionally with slight yellow on hidden dorsal surfaces of the hind leg.

Advertisement call. The advertisement call (Figs 3, 20D) consists of 4.6 notes (range 3–7), uttered slowly

at a rate of 2.44 s^{-1} (range $1.57\text{--}3.68$). Note duration is long (48 ms [range 31–57]) and regular (note 1 duration deviance 16% [range 3–28]), with long, highly regular intervals (inter-note interval range 13% [range 10–20]) inter-note intervals of 385 ms (range 237–587). Median call density is low (0.129 [range 0.09–0.17]) and call duration is 1.49 s (range 1.1–2). The basal frequency is $\sim 383 \text{ Hz}$ (range 308–474), but very soft and may be inestimable, with harmonic bands louder towards the (upper) dominant frequency at 3.8 kHz (range 3.5–4.1); no clear lower peak frequency is evident. Frequency appears to modulate up by $\sim 0.5 \text{ kHz}$ in the course of the note, but (human) perceived pitch is usually monotonous throughout the notes and call. Bandwidth (90%) is difficult to estimate consistently: approximately 1–4.7 kHz.

The call strongly resembles the sound of bouncing marbles and on a warm evening on the interdunes thousands can be heard calling in chorus. Call period (mean 133 s) varies greatly, but can be as brief as 16 seconds during peak chorus activity. This species tends to occur



Figure 13. Holotype (NMNW R11394) of *Ptenopus circumsyrticus* sp. nov. from Gobabeb, Erongo Region, Namibia (-23.5705 , 15.0362). Scale bar = 1 cm relative to full ventral and dorsal views. Photos by Francois S. Becker.

(and call) at higher densities than the sympatric congeners *P. maculatus* and *P. kochi*. It calls from shortly before sunset and calling activity may continue throughout the night as long as the moon is above the horizon, particularly on warm evenings. This species occasionally calls during the day, especially during foggy or cloudy conditions, but generally not during rainy conditions.

Habitat and distribution. This species occurs on sandy soils including interdune plains within, and sandy plains around the northern and eastern edges of the Namib erg, Namibia (Fig. 5). It generally does not occur on the gravel plains north of the Kuiseb River except in a few sandier patches east of 15° longitude. This population is genetically divergent from other nearby popula-

tions in the Namib erg. It does not appear to occur along the south-eastern corner of the Namib erg, where slightly harder Arenosols are occupied by *P. kenkenses* **sp. nov.**, or along the southern or south-western edges of this erg, where the same soils are occupied by *P. adamanteus* **sp. nov.**

It has not been found in sympatry with *P. kenkenses* **sp. nov.**, but overlap is likely in the southern portion of its range. It occurs parapatrically alongside *P. kochi*, *P. maculatus*, and possibly *P. carpi* sensu stricto (near the northern border of the Kuiseb River), as these species occupy different substrates in close geographic proximity. Occasionally, it has been found in sympatry and even syntopy with *P. maculatus* on the sandier patches of the gravel plains north of the Kuiseb River, and with *P. kochi*

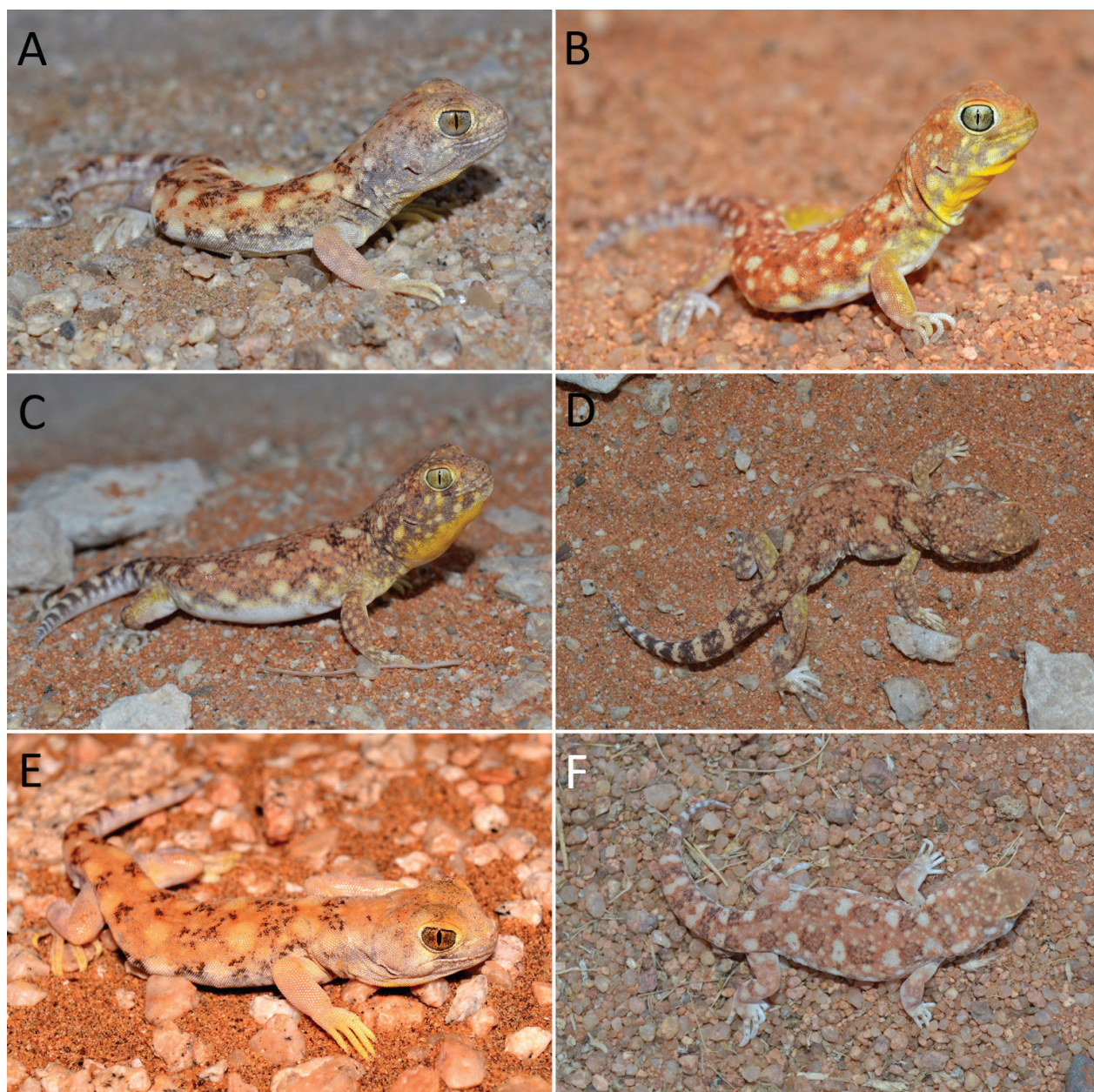


Figure 14. Life colour variation in *Ptenopus circumsyrticus* **sp. nov.**: **A** NMNW R11394 (holotype) from Gobabeb, Erongo Region, Namibia (−23.5732, 15.0368); **B** FB2003 (unvouchered) from Keerwerder, NamibRand, Hardap Region, Namibia (−24.9818, 15.9338); **C**, **D** FB2080 from NE of Gobabeb (−23.3175, 15.5700); **E** unvouchered specimen from near locality of C; **F** NMNW R11355 (paratype) from near locality of B (−24.9495, 16.0397). Photos by Francois S. Becker.

in the Namib erg, near the edges of the interdunes where the two species' preferred substrates overlap. On broad interdunes, *P. circumsyrticus* **sp. nov.** occurs in allopatry.

Natural history. The peak calling and breeding season is in the austral spring to summer (August to November), although some calling may take place outside this period. Two eggs (dried out) have been recovered from an abandoned burrow, so clutch size can be up to two. The burrows are generally less complex than the parapatric *P. kochi* and *P. maculatus*, and appear to be inhabited solitarily. Very small juveniles have been observed in burrows of their own. While multiple natural predators for *Ptenopus* spp. have been observed and hypothesised (Haacke 1975), one observation of a *P. circumsyrticus* **sp. nov.** being carried off by a large solifuge (le Roux pers. com. 2022) certainly constitutes a novel observation.

Ptenopus kenkenses **sp. nov.**

<https://zoobank.org/05DD5A0B-82F4-4D43-9015-124C21320DE2>

Figures 15, 16, 20F

Common names.

Nama barking gecko

Nama: ||en||ense / ||en||enses (“||” = lateral click)

Afrikaans: Nama blafgeitjie

Chresonymy.

Ptenopus garrulus maculatus (in part) – FitzSimons (1935: 525; Kanus), FitzSimons (1937b:160; Great Fish River), Mertens (1971; southern-central Namibia localities), Haacke (1975: 225; Great Karas Mountains, Keetmanshoop)

Ptenopus garrulus (in part) – Brain (1962a: fig. 3; southeastern localities)

Comment. All *Ptenopus* specimens that occur on compact substrates in the northern Nama Karoo, i.e., inland in the south of Namibia and from the Northern Cape (Great Karoo), are likely to be assignable to this species.

Holotype. NMNW R11389, adult male, collected from farm Goris near Giants' Playground, ||Karas Region, Namibia (−26.4538, 18.3097, 1106 m a.s.l.), by Francois S. Becker and Bertha Buiswalelo on 27 September 2022.

Paratypes. NMNW R10839 (adult female, allotype) and NMNW R10841 (adult male) collected from Koës, ||Karas Region, Namibia (−25.9364, 19.0869, 1000 m a.s.l.), by Francois S. Becker, Hileni Shivolo and Sisamu Baepi on 6 October 2020; NMNW R11388, adult male, with the same collection details as the holotype.

Additional material examined. See Table S1 for unvouchered photographed specimens (13), DNA samples (11 available, 7 sequenced), and call recordings (9) included (total n = 20 excluding types).

Etymology. This species is named after the Nama name for the gecko, “||en||enses”, pronounced with two lateral clicks (produced by clicking with one's tongue on the posterior-lateral roof of one's mouth, similar to the typical command given for a horse to speed up), in reference to the clicking sound that it makes. The name is usually formed in the Nama female genitive, indicated by the suffix “s”, because the animal is small. This gecko occurs throughout the Nama Karoo and various places that were historically, and are currently, occupied by the Nama people. The Nama are highly familiar with its call, and believe the bite of this gecko to be extremely venomous. Nama children are taught to treat it with caution. However, the authors have been bitten by this species, and have survived.

We use the specific epithet “*kenkenses*”, a noun in apposition. Since the Nama symbols cannot be included in a scientific name, the phonetically similar letter “k” is used instead. However, the use of Nama lateral clicks is recommended in the pronunciation of this name.

Diagnosis. A medium-sized *Ptenopus* (SVL max. 58 mm, mean 51.3 mm, n = 10) with a short tail (TL 65% [range 60–72] of SVL, n = 7) and a stout appearance. It is distinguished from *P. kochi*, *P. carpi*, and *P. sceletus* **sp. nov.** by the following characters: Toes being intermediately fringed laterally (vs. weakly fringed in *P. carpi* and *P. sceletus* **sp. nov.** and extensively fringed in *P. kochi*); having MBSR ~162, range 158–169 (vs. >180 in *P. kochi* and <135 in *P. carpi* and *P. sceletus* **sp. nov.**); by dorsal colour pattern being characterised by large, paired, light, subsymmetrical ovoid markings interspaced with or dominated by dense, dark brown mottled patches (vs. more finely spotted pattern in *P. kochi* and banded pattern in *P. carpi* and *P. sceletus* **sp. nov.**). It is further distinct from *P. carpi* and *P. sceletus* **sp. nov.** by the nasals being more swollen and the nostrils partially covered by internal projections of the upper labials; from *P. kochi* by having fingers laterally fringed with pointed triangular scales (vs. elongated pointed scales in *P. kochi*) and having entire ventrum covered in white/cream ventral scales with some dark brown/grey specking (vs. pink, unpigmented patches on the limbs and tail of *P. kochi*).

From congeners previously included in ‘*P. garrulus*’ it is distinguished by: Having a generally smaller internasal scale with higher IN/INSBB (median 7.4, range 5.6–11.0, n = 12), than *P. circumsyrticus* **sp. nov.** (usually <5.6); having a broader rostral with higher RB/RH (median 1.21, range 0.98–1.42, n = 12) than *P. australis* **sp. nov.** (<0.98); having generally higher MBSR (≥147) than *P. australis* **sp. nov.**, *P. circumsyrticus* **sp. nov.**, and *P. maculatus* (usually <147 except some *P. circumsyrticus* **sp. nov.**); having 2 or fewer internasal scales in contact with the rostral, while *P. australis* **sp. nov.** has three; colour pattern distinct from *P. garrulus* in having 4–5 large and distinctive paired, light, ovoid markings interspaced by distinct dark mottled patches usually touching the light markings (vs. more rows of and smaller white spots and overall more speckled pattern in *P. garrulus*), and ovoid patterning on ventro-lateral portions of the face

being more distinctive (vs. indistinct or absent in *P. garulus*).

Holotype description. (Fig. 15). Adult male, SVL 51.41 mm with original tail 30.61 mm (59.54% SVL). Body and head covered with minute hexagonal to round scales of a similar size, dorsally and ventrally, with scales on limbs notably larger. Small mid-ventral incision for removal of liver sample. Body slender, MBSR 166, IOS 48, HL 15.97 mm, HW 11.15 mm, HH 6.85 mm, EED 5.93 mm. Upper labials 6 enlarged, with 4–5 small granules up to the angle of the jaw, lower labials 8, the posterior scale elongate and thin, and six granules bordering the mental. Clear but not prominent superciliary ridges tapering from above mid-eye level. Around the eye is a single row of elongated scales around the anterior, dorsal, and posterior margins, but more rounded and smaller along the ventral margin. Nasal scales slight-

ly swollen, the prenasals barely separated by one small, rounded internasal scale in meagre contact with the rostral, with IN/INSBB 8.71, INSH/NB 1.03. Nostrils partially covered by projection from the upper nasal. Rostral broad, with RB/RH 1.42, MB/RB 0.75. Pupil vertical, EYE 3.46 mm. Ear opening is oblique ($\sim 45^\circ$) and narrow with small projecting scales at the anterior margin. The neck region behind the cheeks is slightly swollen with internal calcium deposits. Arms, legs, and tail stout in appearance. Toes elongate, flattened, with moderately elongate fringed scales, small, pointed, triangular fringes on the fingers; strong nails on fingers and toes, being larger and thicker on the fingers.

Colouration. In life, the holotype and similar paratype NMNW R11388 (Fig. 16A and C) has a dorsal background colour of light brown with orange, cream, and beige spots, with five intermediate paired, circular, markings on the



Figure 15. Holotype (NMNW R11389) of *Ptenopus kenkenses* sp. nov. from Giants' Playground, ||Karas Region, Namibia (-26.4538 , 18.3097). Scale bar = 1 cm relative to full ventral and dorsal views. Photos by Francois S. Becker.

neck and back interspaced by larger dark brown, irregular markings and some smaller cream dots and dark blotches that are more-or-less symmetrically scattered across the dorsal surface; the paired cream markings merge into bands on the tail (somewhat asymmetrical in the mid-tail) interspaced by 10–11 dark bars, which are barely noticeable on the nearly white tail tip; prominent dark brown to black dorsolateral markings; ventrum is immaculate white except for some dark grey mottling laterally, on ventral leg surfaces, and substantial dark mottling on (hand/foot) palms/soles. Extensive, bright yellow gular patch with faded anterior edges and a clear but speckled posterior edge, with a large white area on the throat; the bright yellow does not extend onto the lateral surfaces of the head, body, or onto the limbs. The iris is dark beige/light yellow-brown.

In preservative (Fig. 15), the lighter colours have faded to off-white or beige, while the darker colours remain shades of dark brown or grey, and the orange and yellow have faded completely. The iris is a milky blue-grey.

Variation. Refer to Table S1 and Figure 4 for range of morphometric characters, including the paratypes. While morphometric characters are relatively similar across all specimens, the colour patterns vary substantially, usually matching the local substrate (Fig. 16). Background dorsal colouration variations include brown, light orange, beige, or red-brown; some amount of orange speckling is usually present, particularly in the western populations. Ventrally, animals are immaculate white with grey or brownish speckling clearly visible on (hand/foot) palms/soles.

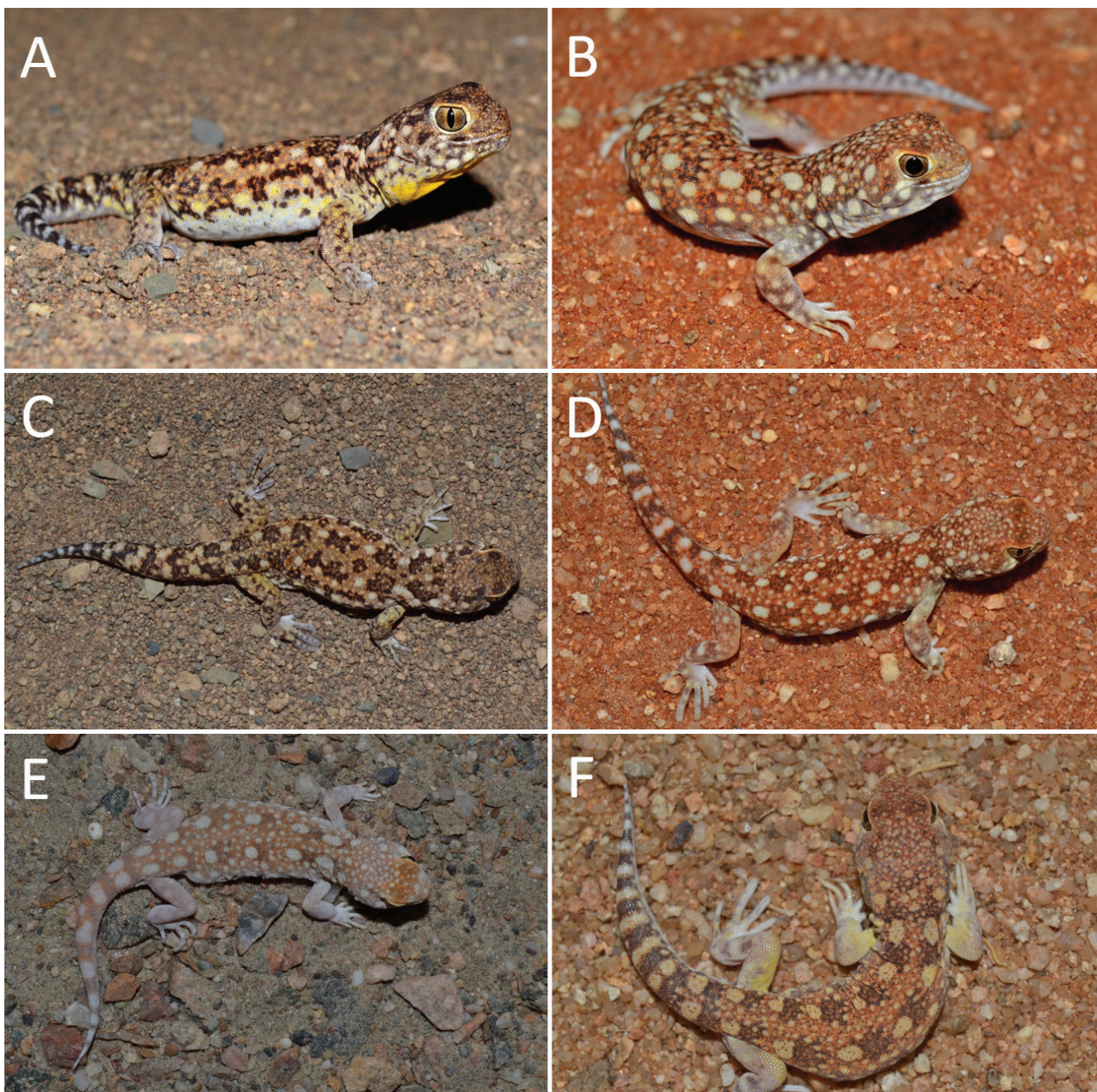


Figure 16. Life colour variation and substrate matching in *Ptenopus kenkenses* sp. nov.: **A, C** NMNW R11388 (paratype) from Giant's Playground, ||Karas Region, Namibia (−26.4538, 18.3097); **B** NMNW R11655 from S of Aus, ||Karas Region, Namibia (−26.7073, 16.2829); **D** NMNW R11648 from locality B; **E** FB454 from W of Aus (−26.5700, 15.8389); **F** FB456 from W of Aus (−26.6478, 16.2147). Photos by Francois S. Becker.

Males have bright yellow gular patches, while some male specimens also have yellow on the anterior or dorsal surfaces of the hind leg.

Advertisement call. The advertisement call (Figs 3, 20E) consists of 4.6 notes (range 4–5), uttered slowly at a rate of 2.45 s^{-1} (range $1.99\text{--}2.96$). Note duration is the longest of all species (92 ms [range 61–154]), the first usually notably longer than those following, with note 1 duration deviance 30% [range 10–47]. Inter-note intervals are 316 ms (range 269–368) and quite regular, inter-note interval range 23.3% (range 12–42). Median call density is high, 0.29 (range 0.18–0.48). Call duration is 1.57 s (range 1.3–1.9). The basal frequency is $\sim 399\text{ Hz}$ (range 366–474), but very soft may be inestimable, with harmonic bands louder towards the dominant frequency at 3.506 kHz (range 3.3–3.8); sometimes a very slight lower frequency peak is evident at around or just below half the dominant frequency (roughly 1.2–1.9 kHz, cannot always be reliably estimated). Frequency appears to modulate down by $\sim 0.4\text{ kHz}$ during the course of the note, and (human) perceived pitch also seems to modulate within each note, slightly reminiscent of dripping water. Bandwidth (90%) is difficult to estimate consistently: approximately 0.5–6.9 kHz.

Calling activity for this species commences $\sim 30\text{ min}$ before sunset and may continue late into the night if the moon is up. Call period (mean 84 s) varies considerably, but can be as low as 18 seconds during peak chorus activity. Peak calling activity occurs from September to November.

Habitat and distribution. This species occurs on consolidated soils such as gravel, alluvial silt, or compacted sandy soils throughout the northern Nama Karoo: southern Namibia and probably the Northern Cape, South Africa (Fig. 5). The exposed rocky surfaces of the Nama group sedimentary formation in central-southern Namibia appears to bisect its distribution. The northeastern edge of its range is the western edge of the Kalahari Sand Sea, as it does not occur on loose sand. There is only one confirmed record from South Africa near Onseepkans, Northern Cape, but similar soils occur more broadly throughout large parts of the Northern Cape Province.

It has not been recorded in sympatry with any other species but occurs parapatrically to *P. garrulus* near Koës, Namibia (with *P. garrulus* occurring in the Kalahari Sand Sea), and in the Northern Cape, South Africa (where patches of Kalahari sand occur on more consolidated soils). It has been recorded $\sim 40\text{ km}$ from the nearest confirmed *P. adamanteus* **sp. nov.** record in the west, and no closer than $\sim 60\text{ km}$ from the nearest confirmed *P. circumscriptus* **sp. nov.** record in the northwest of its range.

Natural history. Calling (and therefore breeding) activity appears to be seasonal, probably peaking in the austral spring and early summer. This species is seldom found on the surface, except early in the evening during peak chorus activity. Burrow entrances are nearly always sealed after calling ceases, or during the day; the entrance is

sealed from the inside, and it is so neatly disguised as to be almost entirely indistinguishable from the surrounding soil surface. The burrow is then re-opened before calling commences. It has been observed consuming large numbers of harvester termites (*Hodotermes mossambicus*), even up to 61% of its own body-weight, during sporadic events when these termites emerge en masse to forage (Bauer et al. 1989). All adult females collected by Bauer et al. (1989) in early October contained ovarian or unshelled oviductal eggs, suggesting an egg-laying period possibly later than November. One individual of *P. kenkenses* **sp. nov.** has been found to be infected by a tapeworm of the genus *Mesocostoides* (McAllister et al. 1995).

Aggregations of this species are sometimes observed on tarred roads late at night, numbering in the hundreds on a few kilometres of road. The reason for this behaviour is unknown.

Ptenopus carpi Brain, 1962 sensu stricto

Figures 17, 20J

Common names.

Carp's barking gecko

Afrikaans: Carp se blafgeitjie

Chresonymy. *Ptenopus carpi* Brain, 1962: plates 1b, c, e, fig. 1b, Haacke (1964: 3), Mertens (1971: 44), Haacke (1975: 230; in part)

Comment. The type locality of *P. carpi* is “gravel plain approximately 1 mile north of the Kuisib R. [Kuisib River] at Gobabeb, Central Namib Desert [Erongo Region], S.W.A. [Namibia]” ($-23.5456, 15.0400$). Currently, no *P. carpi* can be found at this location. The closest location of current occurrence from Gobabeb, is 9 km to the northwest. Charles Brain's son, Conrad Brain, who had attended the field trip, claims that they were a little lost that evening and likely the real type locality was more to the northwest, where the species currently occurs (Brain pers. comm. 2023).

Here, we split “*P. carpi*” into two species. The topotypical population south of the Swakop River is assigned the name *P. carpi* sensu stricto, while *P. sceletus* **sp. nov.** is described from north of the Swakop River, below. We hereby restrict the range of *P. carpi* sensu stricto to between the Kuisib and Swakop rivers. In light of this revision, the advertisement call of *P. carpi* sensu stricto has not been recorded or described before; Gramentz (2008) briefly described the call of *P. sceletus* **sp. nov.** (based on a single specimen collected north of the Swakop River) under the name “*P. carpi*”.

Ptenopus carpi sensu stricto is the only member of this genus that lacks sexual dichromatism, with both sexes displaying a yellow gular patch (Fig. 20E). The observations of FB contradict the original description of *P. carpi* (Brain 1962) in which females, collected in the month of May, apparently had no gular patch. Haacke (1975), who

collected *P. carpi* extensively from around the type locality, made observations corresponding with our own: That all *P. carpi* females possess a yellow gular patch. Haacke surmised that the presence of these patches on females may be seasonal. However, we have collected, photographed and observed multiple *P. carpi* sensu stricto females from across their range including the type locality and throughout the year (see Table S1; many additional observed individuals not tabled) and have not observed any female *P. carpi* sensu stricto without a gular patch; nor have we observed a gular patch in any *P. sceletus* sp. nov. females. Since the gular patches fade shortly after specimen preservation (not mentioned by previous authors), we argue that Brain (1962) may have assumed that sexual dichromatism was present while describing the species based on the preserved specimens, and failed to notice the gular patches on the live females. Alternatively, the gular patch may be missing under rare circumstances, although under what circumstances we shall not surmise.

Holotype. TM 25973, adult male, collected “on gravel plain approximately 1 mile north of the Kuisib R. [Kuisib River] at Gobabeb, Central Namib Desert [in the Eron-go Region], S.W.A. [Namibia]” (probably –23.5456, 15.0400), by Charles K. Brain in May 1959.

Paratypes. TM 25966–70, 25972, 25974–25979, 25981–86, 25990–93, 25995, 25997–8, 26207 (10 adults, 10 sub-adults and 6 juveniles), all from the same locality as the holotype.

Material examined. See Table S1 for unvouchered photographed specimens (49), DNA samples (32 available, 9 sequenced), and call recordings (3) included ($n = 51$).

Diagnosis. A large *Ptenopus* (SVL max. 64.7 mm, mean 53.7 mm, $n = 33$) with a moderate tail (TL 66.7% [range 61–72] of SVL) and lean appearance, with slender limbs and reduced toe fringes compared to other species. Preserved specimens are morphologically indistinguishable from *P. sceletus* sp. nov., but usually have a longer snout or narrower head (than *P. sceletus* sp. nov.), clearly visible from below (compare Figs 17E and 19E); live specimens can be distinguished by lack of sexual dichromatism, with females having a yellow gular patch as in males (Fig. 17E, vs. no female gular patch or very faint yellow in *P. sceletus* sp. nov.), and by red or ochre iris colouration (Fig. 17F, vs. silver to brown in *P. sceletus* sp. nov.). This species and *P. sceletus* sp. nov. are the only members of the genus with a clearly banded dorsal colour pattern on the body and tail. For a more detailed morphological diagnosis and description, see Haacke (1975).

Advertisement call. The advertisement call (Figs 3, 20I) consists of 10 (9–12) notes uttered in slow succession, with a note rate of 2.25 s⁻¹ (range 1.68–3.01). Note duration is short (26 ms [range 22–29]) and regular with note 1 duration deviance 12.8% (range 5.5–24.8). The in-

ter-note intervals are the longest of any species (560 ms [range 323–682]) and usually irregular, the inter-note interval range being the highest of any species (84% [range 62–105]); intervals are longer at the start and sometimes end of the call, but notably shorter in the middle: The call starts slow, speeds up, and then sometimes slows again. Median call density is the lowest of all species (0.06 [range 0.05–0.08]) and call duration is very long (3.6 s [range 3.3–3.8]). The basal frequency is 392 Hz (range 310–517) but very soft and usually inestimable, with harmonic bands louder towards the dominant frequencies, with the upper dominant frequency at 3.5 kHz (3.3–3.8) and a clear lower dominant frequency (sometimes more emphasised than the upper) around 1.4 kHz (1.1–1.9), less than half the upper dominant or frequency. Frequency appears to remain constant throughout the notes and call, as with the (human) perceived pitch, which is low and monotonous compared to most other species. The call is also notably softer than most other species. Bandwidth (90%) is difficult to estimate consistently, but is broad: approximately 2–5 kHz.

The call seems to vary more than other species, with calls sometimes having as few as one to three notes, especially late at night. Call period (mean 349 s) varies greatly, but is usually much lower than other species, and has not been recorded any faster than 2 min during peak chorus activity. This species does not chorus as notably as other species.

Calling activity is crepuscular to nocturnal, calls starting well after sunset and often continuing throughout the night to some degree. One instance of a notable chorus was recorded near Walvis Bay airport on 19 April 2018. Chorusing started abruptly at ~25 min after sunset, and lasted for about 20 minutes, with very reduced calling activity continuing later into the night. Calling appears to be somewhat seasonal with a peak around April to August, coinciding with lower fog incidence. Calling activity is more pronounced on warmer evenings but may continue despite cold, foggy conditions.

As with other species, *P. carpi* calls from the burrow entrance, although it may also call (advertisement call) occasionally while roaming. This could not be observed directly, but a wandering gecko was often spotted in the area where a call was just heard. Having said that, wandering geckos are easier to spot than geckos in a burrow.

Distribution and habitat. *Ptenopus carpi* occurs on hard gravel plains in the central Namib Desert, Namibia, from the northern banks of the Kuisib River to the southern banks of the Swakop River, central Namib Desert (Fig. 5). It does not tolerate soft, sandy substrates. *Ptenopus carpi* occurs in the Atlantic fog band, from the high water mark to approximately 50 km inland. It is one of the most common vertebrates on these coastal desert plains, but becomes increasingly rare to the east of its range. Here, it occurs syntopically with *P. maculatus*, and parapatrically with *P. kochi* and *P. circumscriptus* sp. nov. along the Kuisib River (the latter species occurring in or south of the river, while *P. carpi* occurs north of it). *Ptenopus carpi* and *P. kochi* can occasionally be found

only metres from each other, on two different substrates. *Ptenopus carpi* occurs parapatrically with *P. sceletus* **sp. nov.** across much of the Swakop River, and sympatrically in the Rössmund area just south of the river.

In light of this revision, *P. carpi* has a restricted range, estimated at ~1400 km². While most of its range is presently encapsulated by statutory protected areas (Namib-Naukluft National Park and Dorob Park), on the ground management of the habitat in these areas is poor. In particular, mining and industrial activities and the degradation of the gravel plains by motorists occurs within this the protected areas. The result is that more than 80% of

the species range is currently within zones encompassing active mining licenses, exclusive prospecting licenses, and reconnaissance licenses (Spatial Dimension 2024), and/or occupied by urban and industrial developments, an airport, and a military base. Considering the extensive geographic scope of these claims and properties, there are likely between four and ten threat locations according to IUCN guidelines (IUCN 2022). Given the continued decline in the extent and quality of its habitat, and the range of threats noted here, a full IUCN assessment could result in the species qualifying for a range of threat categories falling between NT and EN (B1ab).

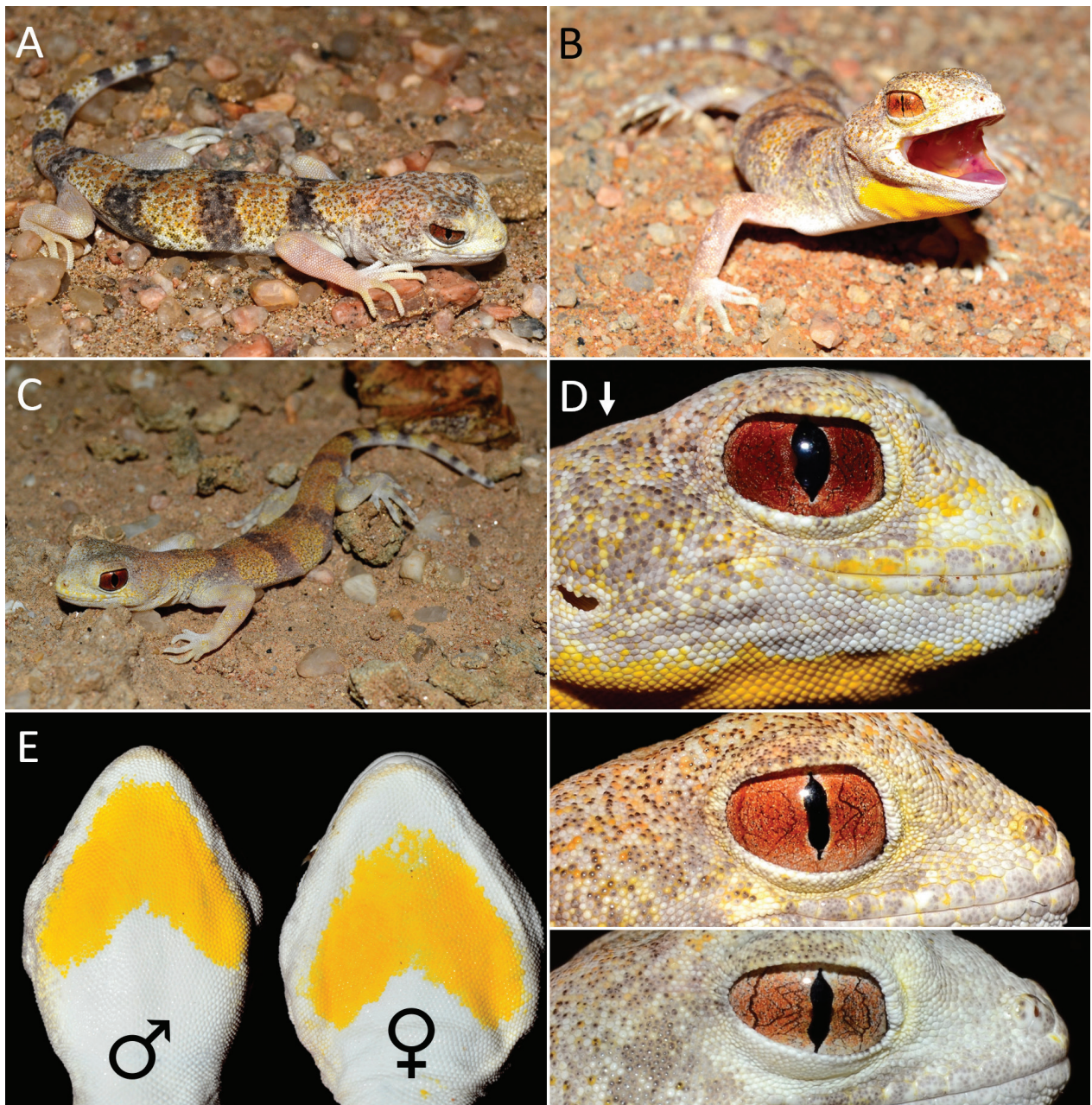


Figure 17. Life colour variation in *Ptenopus carpi*: **A** NMNW R11822 from Walvis Bay Airport, Erongo Region, Namibia (−23.0003, 14.6695); **B** NMNW R11809 from NW of Gobabeb, Erongo Region, Namibia (−23.4530, 14.9637); **C** NMNW R11815 from locality A; **D** NMNW R11798 from locality A, NMNW R11810, and NMNW R11808 from NW of Gobabeb (−23.4533, 14.9642), showing iris colouration variation from deep red to light ochre; **E** NMNW R11808 (male) and NMNW R11819 (female) from NW of Gobabeb (−23.4235, 14.9353), showing clear gular patches on both sexes (patch size and shape varies in both sexes, but tends to be more extensive in males). Photos by Francois S. Becker.

Natural history. The breeding season for *P. carpi* appears to be between April (earliest recorded calls) and August, with some juveniles having been found between November and February.

Ptenopus carpi does not call nearly as often as congeners (similar to *P. sceletus* **sp. nov.**) but appears to spend more time wandering on the surface, even far from its burrow. It is active much later into the night than congeners, often only emerging well after dark, and its activity is not dampened by cold or foggy conditions (as in most other species, except *P. sceletus* **sp. nov.** and, occasionally, *P. adamanteus* **sp. nov.**).

The burrow is usually shallower and simpler than those of other species but may have two to three side-branches and typically has an escape exit (as in other species). Gravid females observed (FB) generally contain two eggs, which are presumably laid in the burrow, as in other species.

Ptenopus carpi utters two different calls: The advertisement call and the single-pulse call, also previously noticed for the closely related *P. sceletus* **sp. nov.** (Gramentz 2008). Gramentz (2008), based on observations in captivity, suggested the single-pulse call may be a threat call, but FB's observations suggest this is not the function. This call is not notably uttered in response to disturbance or the close presence of a threat, and the first individuals to utter this call were often far from the observer. This call is uttered frequently in the wild by both *P. carpi* and *P. sceletus* **sp. nov.**, usually late at night after chorusing has ceased. Individuals clearly respond to each other, with several answering the first call uttered within a second or two. It is possible that this is a spacing mechanism, or a way for individuals to keep track of the population's general location as they wander on the surface. A squeak may be uttered if the animal is molested (as with other species) but this is not similar to the single-pulse, which is identical to a single note in the advertisement call. For more details on the natural history of *P. carpi*, see previous works (Brain 1962; Haacke 1975).

Ptenopus sceletus **sp. nov.**

<https://zoobank.org/940AB8E8-ED1C-4270-B5D0-B2F-4BA4BD400>

Figures 18, 19, 20K

Common names.

Skeleton Coast barking gecko
Afrikaans: Skedelkus blafgeitjie

Chresonymy.

Ptenopus carpi – Gramentz (2008)

Ptenopus carpi (in part) – Haacke (1975: 230)

Comment. *Ptenopus sceletus* **sp. nov.** is closely related to *P. carpi* but occurs predominantly north of the Swakop River, while *P. carpi* only occurs to the south. A single call from one individual in captivity was previously de-

scribed by Gramentz (2008) as '*P. carpi*', although the call and its variation is herein re-assessed and fully described in a standardised taxonomic framework.

Holotype. NMNW R12100, adult male, collected from NE of Swakopmund (Skeleton Coast), Erongo Region, Namibia (−22.6259, 14.5457), by Francois S. Becker on 21 April 2023.

Paratypes. NMNW R12101–3, adult males except for NMNW R12101 (adult female, allotype), same collection details as the holotype.

Additional material examined. See Table S1 for vouchered (2) and unvouchered photographed (50) specimens, DNA samples (34 available, 8 sequenced), and call recordings (7) included (total n = 62 excluding types).

Etymology. This species is named in reference to the Skeleton Coast, which generally refers to the coastal Namib Desert between the Swakop River and the Kunene River, encapsulating the species' entire distribution and type locality. In addition, the white or grey dorsal surfaces of the head and feet give the gecko a ghostly or skeletal appearance (Fig. 19B). We therefore use the specific epithet "*sceletus*", the Latin noun in apposition meaning "skeleton".

Diagnosis. A moderately large *Ptenopus* (SVL max. 57.1 mm, mean 52.7 mm, n = 18) with a moderate tail (TL 70% [range 62–80] of SVL, n = 12), an overall lean appearance, and comparatively slender limbs. In preserve state it is morphologically indistinguishable from *P. carpi* except by having a generally broader or shorter head/snout, when viewed from beneath (Fig. 19E). Live specimens are more easily distinguished, with only males possessing a bright yellow gular patch, as is typical for the genus (Fig. 19E, vs. gular patch in both sexes in *P. carpi* *sensu stricto*); by silver to brown iris colouration (Fig. 19F, vs. red or ochre in *P. carpi*). It is distinguished from all other congeners except for *P. carpi*, by a combination of the following characters: Banded dorsal colour pattern on the body and tail (vs. spotted or speckled pattern in *P. garrulus* and *P. kochi*, and large, paired, ovoid light markings interspaced by darker mottled patches in other species); weakly fringed toes, with fringe length being generally less than half the breadth of the toe between fringes (vs. more than half for other species); nostrils not covered internally by a projection from the upper nasal scale (vs. is covered partially or completely in other species); being larger than most congeners (except *P. kochi*), and having longer, leaner limbs.

Holotype description. (Fig. 18). Adult male, SVL 52.4 mm with original tail 37.2 mm (70.0% SVL). Body and head covered with minute hexagonal to round scales of a similar size, dorsally and ventrally, with scales on limbs notably larger. Body slender, MBSR 123, IOS 44, HL 16.9 mm, HW 12.3 mm, HH 7.5 mm, EED 6.6 mm. Upper labials 9 enlarged, the last being smaller at the an-

gle of the jaw; lower labials 9 enlarged and one smaller scale posteriorly; four granules bordering the mental. Clear, but not prominent, superciliary ridges tapering from above mid-eye level. Around the eye is a single row of elongated scales around the anterior, dorsal, and posterior margins, but more rounded and smaller along the ventral margin. Nasal scales very slightly swollen, the prenasals barely separated by one tall, thin, triangular internasal scale in narrow contact with the somewhat round, septagonal rostral. Eyes large, EYE 3.9 mm. Ear opening oblique ($\sim 45^\circ$), short and relatively broad, set on the far posterior corner of the head, with small, rounded, projecting scales at the anterior margin. The neck region

behind the cheeks is barely swollen with internal calcium deposits. Arms, legs, and tail lean. Toes elongate, moderately flattened and weakly fringed; small, pointed fringed scales on finger margins; strong nails on fingers and toes, being larger and thicker on the fingers.

Colouration. In life, the holotype (very similar to paratype NMNW R12103; Fig. 19A) has a dorsal background colour of light yellow to cream, with light orange speckles along the spine and dark purple-brown speckles or mottles all over, which coalesce to form a clearly banded dorsal colour pattern, with three dark bands on the body (the posterior being nearly split into two bars), eight bars on the

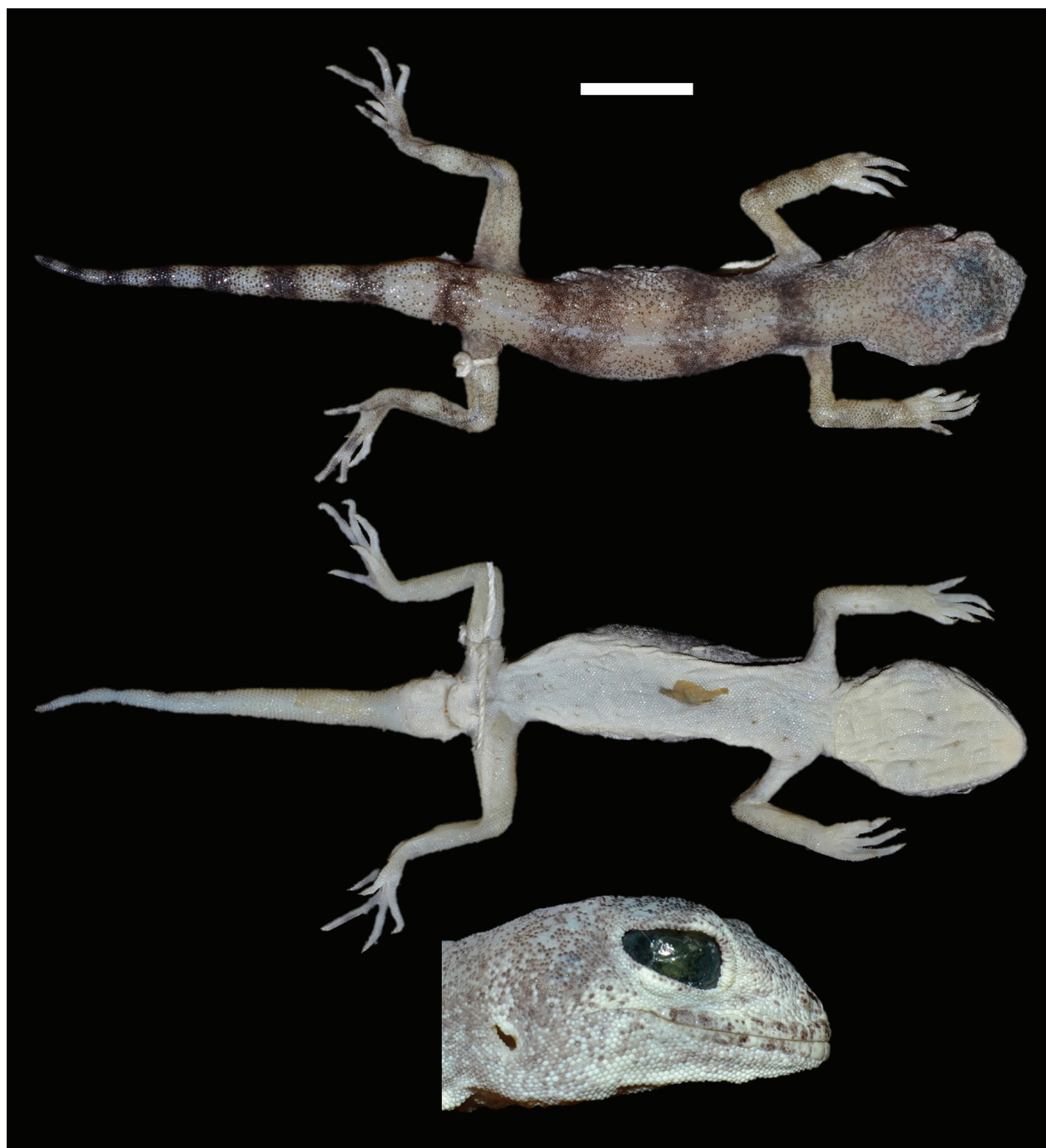


Figure 18. Holotype (NMNW R12100) of *Ptenopus sceletus* sp. nov. from NE of Swakopmund, Skeleton Coast, Erongo Region, Namibia (-22.6259 , 14.5457). Scale bar = 1 cm relative to full ventral and dorsal views. Photos by Francois S. Becker.

tail, and a faintly defined bar on the head between the eyes. The ventrum is immaculate white with a bright yellow gular patch that is nearly divided in the middle; some of this yellow colouration is also faintly visible on the dorsal surfaces of the limbs and snout. The iris is silver.

In preservative (Fig. 18), the lighter colours have faded to cream or off-white and the darker colours faded to various shades of grey-brown. The yellow and orange colours have completely faded. The iris is a milky blue-white.

Variation. Refer to Table S1 for range of morphometric characters, including the paratypes. Morphometric characters vary relatively little among specimens, although the colours vary somewhat (Fig. 19). The dorsal colour pattern consists of 3–4 dark brown or purplish bands on a beige, yellowish, or light orange background, densely speckled with dark brown, grey, purple and/or sometimes green; sometimes the speckling is very dense, giving the appearance that the gecko is not or barely banded; an ad-

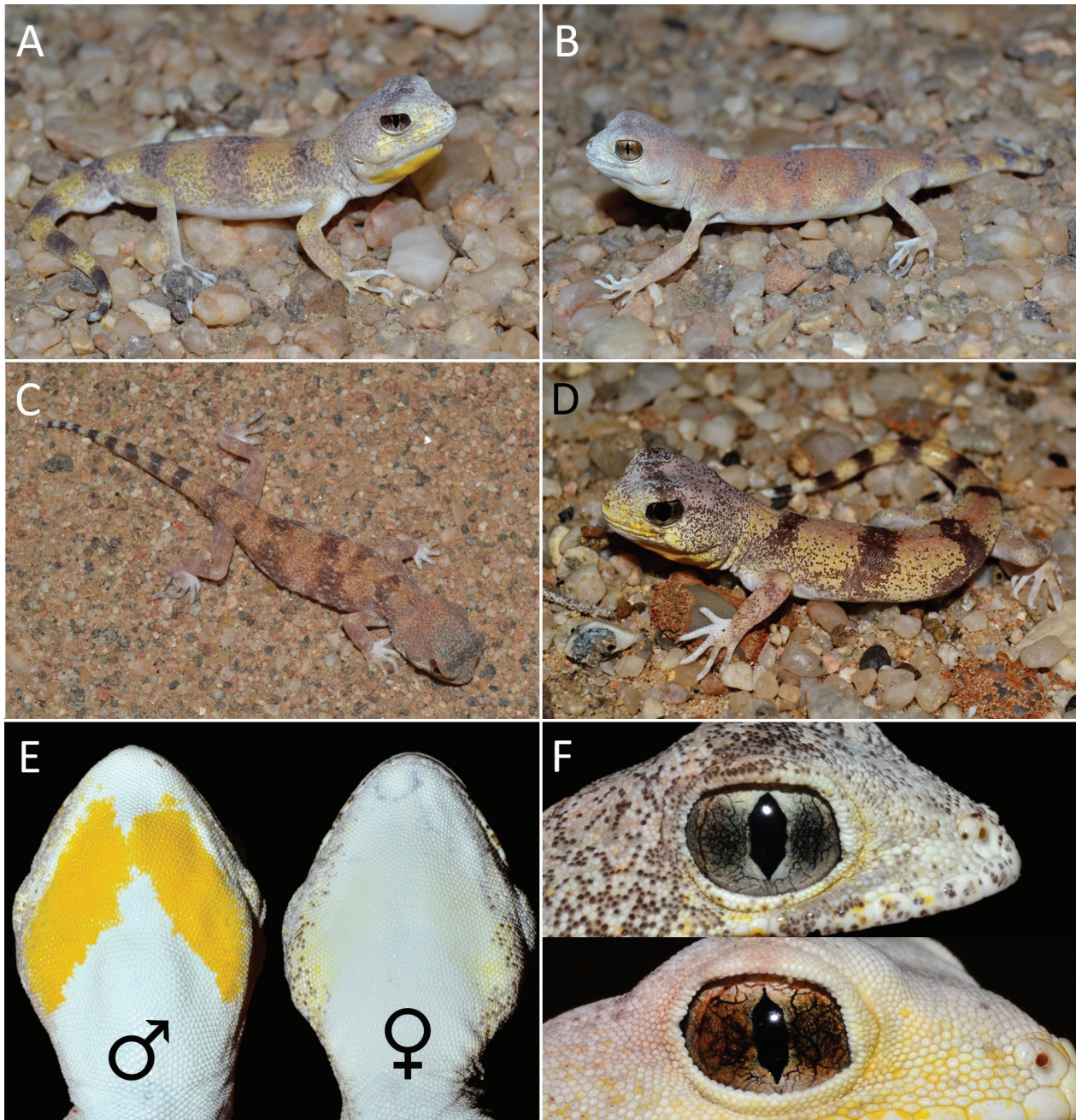


Figure 19. Life colour variation in *Ptenopus sceletus* sp. nov.: **A** NMNW R12103 (**paratype**) from N of Swakopmund, Erongo Region, Namibia (–22.6259, 14.5457); **B** NMNW R12101 (**allotype**) from locality A; **C** NMNW R11763 from Hoanib River, Kunene Region, Namibia (–19.3539, 13.1453); **D** NMNW R11754 from Henties Bay, Erongo Region, Namibia (–22.1584, 14.3086); **E** NMNW R12100 (**holotype**) and NMNW R011771 from the same locality as A, showing sexual dichromatism in gular patches of this species (male gular patch may be divided or undivided, while female only has slight shades of yellow on lateral edges); **F** NMNW R11771 from N of Swakop River near Swakopmund (–22.6652, 14.57619) and NMNW R11755 from N of the Omaruru River near Henties Bay (–21.7703, 14.5520), showing iris colour variation from silver (most common in the southern extreme of the range) to brown (more common further north). Photos by Francois S. Becker.

ditional six to eight dark bands occur on the tail. Banding tends to be clearer and colouration brighter in younger individuals (Fig. 19D). Males have bright yellow gular patches, sometimes partially or entirely split in the middle, while females do not, or have very faint yellow on the sides of the throat (Fig. 19E). Males also have light yellow infusions on the head, limbs, and body, while females tend to be paler overall (Fig. 19A–B); in populations further north, dorsal colouration tends to be duller (Fig. 19C). Iris colouration varies from silver to brown (Fig. 19F), with individuals in the southern populations tending to have silver eyes.

Advertisement call. The advertisement call (Figs 3, 20J) consists of 10 (8–13) notes uttered in slow succession, with a note rate of 2.60 s^{-1} (1.25–4.32). Note duration is short (28 ms [range 21–40]) and regular, note 1 duration deviance 8.7% (range 0.5–16.2). The inter-note intervals may be very long (387 ms [range 204–661]), but are shorter and more regular at the beginning, then tending to longer intervals as the call progresses: Call starts fast,

then slows down. Hence the inter-note interval range is usually high (102% [range 26–163]). Median call density very low (28.3 [range 20.9–40.3]) and call duration is both long and variable (3.9 s [range 2.5–7.2]). The basal frequency is 405 Hz (range 357–516) but very soft and usually inestimable, with harmonic bands louder towards the dominant frequency. The upper dominant frequency is at 4.3 kHz (3.8–4.8), and a clear (sometimes louder) lower dominant frequency is evident at around 2.0 kHz (1.4–1.9), usually less than half the upper dominant frequency. Frequency appears to remain constant throughout the notes and call, as is the case with the (human) perceived pitch, which is low and monotonous compared to most other species. Bandwidth (90%) is difficult to estimate consistently, but is broad: approximately 0.3–6.9 kHz.

The call appears to vary more than the calls of other species, except for *P. carpi*, with calls uttered late at night sometimes having only one to three notes. Call period (mean 365 s) varies greatly, but is usually lower than other species, and has not been recorded any shorter than 104 s during peak chorus activity. This species does

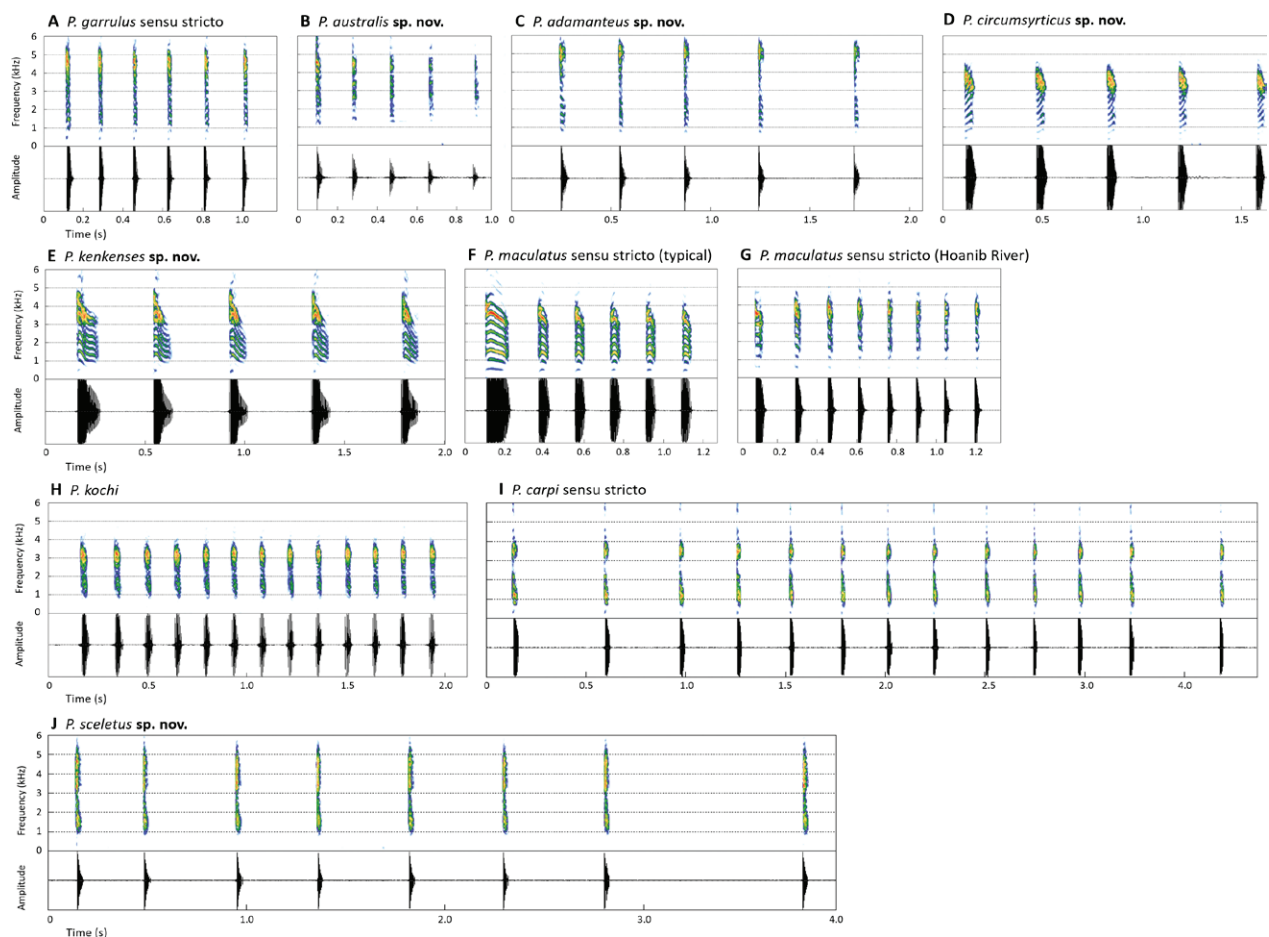


Figure 20. Sonograms (top graphs) and oscillograms (bottom graphs) of representative advertisement calls of *Ptenopus* species (A–J, species names indicated on graphs). Both x and y axes are directly comparable / equally scaled across species. Specimen numbers and localities: **A** NMNW R11585, NE of Koës, Hardap Region, Namibia; **B** iNaturalist 140169978 (Jacobus Retief), Merweville, Western Cape Province, South Africa; **C** NMNW R11622, E of Lüderitz, ||Karas Region, Namibia; **D** NMNW R11643, SW of Gobabeb, Erongo Region, Namibia; **E** NMNW R11657, NE of Keetmanshoop, ||Karas Region, Namibia; **F** NMNW R11704, Gobabeb; **G** NMNW R11716, Hoanib River, Kunene Region, Namibia; **H** NMNW R12114, Gobabeb; **I** NMNW R11843, NW of Gobabeb; **J** NMNW R11790, N of Swakopmund, Erongo Region, Namibia. The audio files on which this figure is based, are made available (File S2).

not chorus as notably as most other species. Calls can be heard from after sunset to late at night. Seasonal phenology of calling activity is not known, but calls have been recorded in May and October. Calling activity is more pronounced on warmer evenings, but may continue despite cold, foggy conditions.

As with other species, *P. sceletus* **sp. nov.** calls from the burrow entrance, although it may also call occasionally while roaming. This could not be observed directly, but a wandering gecko was often spotted in the area where a call was just heard—although wandering geckos are easier to detect than geckos in a burrow.

Distribution and habitat. This species occurs from the southern banks of the Swakop River, northwards in a narrow strip along the Skeleton Coast (northern Namib Desert), to the southern tip of the northern Namib erg, near the Kunene River (Namibia-Angola border; Fig. 5). Its habitat falls within the coastal fog zone and it occurs on compact, gravelly substrates.

This species occurs parapatrically with *P. carpi* across the Swakop River and sympatrically in the Rössmund area, just south of the river. *Ptenopus sceletus* **sp. nov.** occurs in sympatry or parapatry with *P. maculatus* in the

eastern portions of its range (*P. maculatus* occurs only on silts in the northern limits of its range, while *P. sceletus* **sp. nov.** remains on gravels in that area).

Natural history. The peak calling and breeding season of *Ptenopus sceletus* **sp. nov.** is probably between May and October (span of current call recordings), and juveniles have been found in November. This is slightly later than the apparent breeding season for *P. carpi*, but also coincides with months of somewhat lower fog incidence.

This species does not call nearly as often as most congeners, but appears to spend more time wandering on the surface, even far from the burrows (as in *P. carpi* and *P. adamanteus* **sp. nov.**). It is active much later into the night than most congeners, often only emerging well after dark, and its activity is not dampened by cold or foggy conditions (as in most other species).

The burrow is usually shallower and simpler than those of other species, but may have two to three side-branches and typically has an escape exit (as in other species). As in *P. carpi*, it utters two different calls: The advertisement call and the single-pulse call, the latter usually uttered late at night after the main calling activity has ceased, and especially during dense fog.

Morphological key to the species of *Ptenopus*

(see Fig. 1 for graphical reference to characters)

- 1 Toes weakly fringed; nasals not swollen, nostrils open; banded dorsal colour pattern.....2
 - Toes strongly fringed laterally; nasals more or less swollen; nostril partly closed by internal projection of upper nasal.....3
- 2 (Life): Iris red or ochre; bright yellow gular patch in both sexes, relatively narrow head..... *P. carpi*
 - (Life): Iris silver or brown; yellow gular patch absent in females, relatively broad head *P. sceletus* **sp. nov.**
- 3 Fingers flattened, fringed with elongated pointed scales; body scales minute (midbody scale rows 187–222); ventrum white with pink / unpigmented patches on the tail and limbs..... *P. kochi*
 - Fingers not depressed, edged with pointed triangular scales; body scales usually larger (midbody scale rows 110–202).....4
- 4 Extensive fringing on the toes, fringe length roughly equal to breadth of ventral scale attached to fringe; occurs on more-or-less sandy soils5
 - Intermediate fringing on the toes, fringe length usually less than breadth of ventral scale attached to fringe; occurs on consolidated soils8
- 5 Broad rostral (rostral breadth/rostral height usually >1.2); only one large internasal (internasal scale height/nasal breadth usually ≥1.3); midbody scale rows usually <160 and interorbital scales/midbody scale rows usually >0.27. *P. circumsyrticus* **sp. nov.**
 - Narrower rostral (rostral breadth/rostral height usually <1.2); 1–3 internasals, with internasal scale height/nasal breadth usually <1.4; midbody scale rows usually >140 and interorbital scales/midbody scale rows usually <0.3.....6
- 6 Midbody scale rows usually >170; interorbital scales/midbody scale rows usually <0.25; usually 1–2 internasal scales with internasal scale height/nasal breadth usually >1.0..... *P. garrulus*
 - Midbody scale rows usually <170; interorbital scales/midbody scale rows usually >0.25; internasal scale height/nasal breadth usually <1.07
- 7 Only 1–2 internasal scales in contact with rostral; midbody scale rows usually >155; rostral breadth/rostral height usually >0.95; interorbital scales usually >40..... *P. adamanteus* **sp. nov.**
 - Has 3 internasal scales in contact with rostral; midbody scale rows usually <155; rostral breadth/rostral height usually <0.95; interorbital scales usually <43..... *P. australis* **sp. nov.**
- 8 Midbody scale rows usually <150; interorbital scales usually <36; ventrum and soles immaculate white..... *P. maculatus*
 - Midbody scale rows >160, interorbital scales usually >36; palms/soles usually speckled or mottled with grey..... *P. kenkenses* **sp. nov.**

Advertisement calls key to the species of *Ptenopus*

- 1 Full call has >7 notes.....2
 - Full call has 7 or fewer notes.....4
- 2 Note rate >5 s⁻¹, inter-note interval range <55% (intervals regular), median call density >0.19, notes >9*P. kochi*
 - Note rate <5 s⁻¹, inter-note interval range usually >55%, median call density <0.12.....3
- 3 Upper dominant frequency <3.8 kHz, inter-note intervals long (median ≥500 ms) and decreasing (shorter) towards the middle of the call (note repetition gets faster), then sometimes increasing again..... *P. carpi*
 - Upper dominant frequency >3.8 kHz, inter-note intervals usually <500 ms and increasing towards the end of the call (note repetition slows down) or sometimes remaining consistent *P. sceletus* sp. nov.
- 4 Note 1 deviance >100%, median call density >0.17 *P. maculatus*
 - Note 1 deviance <50.....5
- 5 Note repetition rate >3.7 s⁻¹ *P. garrulus* / *P. australis* sp. nov.
 - Note repetition rate <3.7 s⁻¹6
- 6 Median call density >0.18, note duration >60 ms, first note usually notably longer *P. kenkenses* sp. nov.
 - Note duration regular, call density <0.187
- 7 Last inter-note interval notably longer than others, inter-note interval range >30% *P. adamanteus* sp. nov.
 - Inter-note intervals regular, range <30% *P. circumsyrticus* sp. nov.

Note: This key is most effective when applied to calls recorded during peak chorus time; this key is best used in combination with geographic location, as calls are usually more different where species occur adjacent or in sympatry. See Table 7 for a quick guide to features.

Number of notes in *P. carpi* can be lower than indicated in the key, sometimes uttering a single note (this type of call appears to have a different function than the advertisement call). In *P. maculatus* populations in the Hoanib River, north-western Namibia, the note 1 duration deviance is unusually low (~30%).

Discussion

An updated taxonomic treatment for *Ptenopus* shows there are at least nine species in the genus. Five are newly described, while one subspecies was raised to full species. These species are all supported by at least three lines of evidence under the GLC (de Queiroz 1998, 2007). The previously described species '*Ptenopus garrulus*' which had two subspecies has been split into six species. *Ptenopus garrulus* sensu stricto (previously the subspecies '*P. g. garrulus*') is a widespread species with comparatively little variation in genetics or advertisement call across its range. By contrast, the previous subspecies '*P. g. maculatus*' was split into five species (including *P. maculatus* sensu stricto) based on deeply divergent evolutionary lineages, different habitats (Fig. 2), calls (Fig. 3), and morphology (Fig. 4). The four newly described species previously under the name '*maculatus*' (*P. australis* sp. nov., *P. adamanteus* sp. nov., *P. circumsyrticus* sp. nov., and *P. kenkenses* sp. nov.) are in a single clade (Fig. 2), while *P. maculatus* sensu stricto is a sister taxon to *P. kochi* (which herein receives the taxonomic treatment as before), forming a separate clade to these new species. '*Ptenopus carpi*' was split geographically across the ephemeral Swakop River, with the northern species

described as *P. sceletus* sp. nov. and *P. carpi* sensu stricto (south of the river) being differentiated by lack of sexual dichromatism, red iris colouration, narrower head shape, and by the advertisement call having a different form, a lower dominant frequency, and longer inter-note intervals than *P. sceletus* sp. nov.

There are several instances where two or three species (including newly described species) are sympatric or syntopic with no indication of clinal changes from one species to the next. This shows that they behave as different species when in close proximity, with no evidence yet of interbreeding. One possible exception is a phenotypically intermediate individual between *P. carpi* and *P. sceletus* sp. nov., which was observed in the sympatric zone between these species. Even if this individual is a hybrid, one individual out of 52 observed at the contact zone is probably a rare event. The genetic divergence between *P. carpi* and *P. sceletus* sp. nov. is low, but entirely discontinuous: There is no genetic cline evident at the contact zone, including within the sympatric zone. More importantly, clear mechanisms for mate recognition have already emerged: Different advertisement calls, dramatically different iris colouration, and different sexual dichromatism seen nowhere else in the genus. This indicates that the two species are already in the third stage of the speciation process (Streelman and Danley 2003). This speciation event is comparatively younger than others in the genus, and not enough time has passed for more substantial genetic differences to emerge. These species are supported by three lines of evidence, which clearly supports their status as species under the GLC.

There is also moderately low genetic divergence between the sister species *P. australis* sp. nov. and *P. garrulus*, indicating another relatively young speciation event (Tables 2, 3, 4). These species do not occur sympatrically or parapatrically, hence their potential for interbreeding has not been tested. However, the Great Escarpment, the geographic barrier separating these species, is highly likely to remain a substantial barrier into the future at evolutionary timescales, ensuring that these species are

on separate evolutionary trajectories. Moreover, compared to other species in the genus, *P. garrulus* has low intraspecific genetic divergence (ND2 mean 4.8%, range 0.2–10.5%; 16S mean 2.2%, range 0.2–10.0%) considering its geographic spread is an order of magnitude greater than any other *Ptenopus* species, with some samples up to 1400 km apart. Similarly, all individuals of *P. australis* **sp. nov.** are genetically highly similar (ND2 mean 1.3%, range 0.5–1.7%; 16S mean 0.8%, range 0.2–1.4%) despite being separated by up to 320 km. The intraspecific divergence is substantially higher (ND2 range 7.5–11.3%, 16S range 1.5–9.8%), especially at comparable geographic distances. This discontinuous pattern of genetic divergence supports the conclusion that interbreeding between these species has been, and will remain highly unlikely, while gene-flow is present within these species. Moreover, the ecological conditions of the habitats (bioclimate, ecoregion, and vegetation types) are highly divergent between these species, and significant morphological differences have already arisen. This indicates that the second stage in the speciation process is complete (Streelman and Danley 2003). Indeed, these two species are morphologically more divergent than several other, genetically more divergent species within *Ptenopus*. The lack of significant advertisement call divergence is probably due to a lack of geographic contact, hence there is no selective pressure for divergent signals to arise. Nonetheless, three species delimitation criteria are satisfied, so these species are well-supported as separately evolving lineages under the GLC.

Despite the two recent speciation events formalised in this paper, we do not recommend further splitting *Ptenopus* or other gecko species based on comparatively low phylogenetic divergence alone. In this paper, several substantially deeper genetic divergences were not considered species-level, due to a lack of rigorous evidence that genetic divergence is discontinuous, and in the absence of several additional operational criteria being satisfied. Rather, rigorous sampling in the geographic contact zones between hypothesised species is needed, and an integrated approach must be used to draw any further taxonomic conclusions.

There is strong evidence of a mate recognition system in *Ptenopus* based on call divergence, similar to that recorded for other vocal groups such as anurans (Blair 1974; Köhler et al. 2017). All analysed call characters were significantly different among species. One or more characters were significantly different among all species pairs except between *P. garrulus* and *P. australis* **sp. nov.** – sister species which appear not to occur in close geographic contact. In contrast to many other vocal taxa (e.g., Loftus-Hills and Littlejohn 1992; Hobel and Gerhardt 2003), dominant frequency appears not to be the most important character for distinguishing species. Rather, the number of notes and rhythmic components of the calls were more common diagnostic characters. In the case of *P. carpi* and *P. sceletus* **sp. nov.**, the difference in sexual dichromatism and possibly iris colouration, appears to add visual mate recognition cues to the audial one. Divergence in calls and possibly other mate recognition cues, likely played

an important role in speciation events as a driver or a maintainer of separation between species.

Calls are a reliable species-identification character in *Ptenopus*. In keeping with the tradition of previous descriptions and taxonomic revisions of *Ptenopus*, this revision includes a major descriptive component of the advertisement calls and, for the first time, a key. A quick reference guide or “cheat-sheet” to the call features per species (Table 7) and audio files of the calls (File S2) are also provided. The advertisement call key is a useful tool for field identification of *Ptenopus*, as the calls are more easily detected and identified than the animals themselves. The bioacoustics description component in this manuscript is probably the most comprehensive of its kind for any non-avian reptile group.

Morphological characters were less reliable than calls for distinguishing *Ptenopus* species, indicating morphological conservatism in the genus. Although species *P. kochi* and *P. carpi* / *P. sceletus* **sp. nov.** are clearly distinct from the rest (Haacke 1975), the group of species previously lumped under the name ‘*P. garrulus*’, are not. There are significant differences among species for several morphological features such as the proportions of scales on the nose, IOS, and MBSR, but nearly all of these characters overlap among most species-pairs, and there are no significant differences between *P. garrulus* and *P. kenkenses* **sp. nov.** (Fig. 4). An assessment of all these characters in combination with adult size, colour pattern, and area of occurrence, is needed to distinguish species on a morphological basis. In addition, live specimens with their colour intact are more readily diagnosable than preserved specimens, because not all the diagnostic characters preserve well.

The updated distributions of *Ptenopus* species (Fig. 5) were based on the combination of new occurrence records (DNA samples, photographs, calls, and specimens) and different substrates and/or climatic regions. However, geographic gaps remain, and additional areas of sympatry or parapatry between some species are expected. The centre of diversity of *Ptenopus* is in the Namib Desert, which contains six of the nine species including the most divergent lineages, while a seventh (*P. kenkenses* **sp. nov.**) also occurs partially in the central-southern Namib Desert. Moreover, *Narudasia festiva*, the closest living relative to *Ptenopus*, also occurs in the Namib Desert. It is therefore possible that the genus originated in the central Namib Desert and thereafter diversified.

In the species descriptions, we summarise the knowledge on the ecology and life-history traits of all *Ptenopus* species, including new insights. There are several over-arching similarities throughout the genus, while other life-history traits appear to differ substantially. Termites are a major food source for most *Ptenopus* species, which do not need to forage more than a few metres from the safety of their burrows to feed on emerging termites. *Ptenopus* are usually patchily distributed, and higher abundances often correspond to higher abundances of termite nests or nest entrances. By exception, the coastal fog-band species (*P. carpi*, *P. sceletus* **sp. nov.** and *P. adamanteus* **sp. nov.**) tend to forage further and more

frequently than other species, and, from observations, their diet consists of a wider range of arthropods other than termites. One to two eggs (clutch size varies among species) are laid inside the burrow in all species, and mating appears to take place, invariably, within the burrow. Pre-mating rituals differ, but all species make use of both vocal (advertisement calls) and visual (gular patches) signals. The male provides the initial signals from his burrow entrance. In some species, the attracted female responds with soft vocal and/or visual signals, including scratching and head-bobbing, when approaching the calling male. Most species are solo occupants of their burrows, except for short periods of time post-copulation, after which females take over the male burrow. By contrast, *P. kochi* mating pairs and young share burrow systems for extended periods. Most species call and breed between spring and summer with differences in the length, variability, and starting time of the breeding season. The species *P. carpi* and *P. sceletus* **sp. nov.** appear to breed from winter to spring, contrary to the overall generic pattern. *Ptenopus* tend to be the most abundant lizard species in the arid areas where they occur. This relative success is likely owed to the security afforded by their burrow systems, which also have multiple side-branches and an escape exit. *Ptenopus* have excellent hearing compared to other lizards and are hyper-alert at their burrow entrances—a feature that makes capturing them extremely difficult, compared to co-occurring species. They are also shy, exceptionally well-camouflaged on the local substrate, and are able to efficiently attract mates from a distance and from the safety of their burrows. This genus has several interesting life-history traits which have the potential for many ecological and behavioural studies in the future.

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Supplementary Material 1

Table S1

Authors: Becker FS, Alexander GJ, Tolley KA (2025)

Data type: .xlsx

Explanation notes: Table of referred *Ptenopus* material including specimens, advertisement call recordings, DNA or tissue samples, and photos. GenBank accession numbers are indicated for all sequenced DNA samples for nuclear gene *c-mos*, or mitochondrial genes *ND2* and *16S*. Standard Darwin Core terms are used for metadata, while non-Darwin Core terms are capitalised. Morphological abbreviations: interorbital scales (IOS); number of midbody scale rows (MBSR); inter-nasal scales (INS); nostril (horizontal diameter) breadth (NB); internarial distance, from the nearest edges of the nares (IN); rostral (horizontal) breadth at the lower edge of the lip (RB); rostral (vertical) height (RH); horizontal breadth of the base of the largest inter-nasal scale in contact with the rostral (INSBB); vertical height of the largest inter-nasal scale (INSH); presence of a yellow gular patch and iris colouration is also indicated as described in the manuscript..

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Link: <https://doi.org/10.3897/vz.74.e153514.suppl1>

Supplementary Material 2

Figures S1, S2

Authors: Becker FS, Alexander GJ, Tolley KA (2025)

Data type: .pdf

Explanation notes: Bar charts of sexual dichromatism and iris colouration in the two putative species of '*Ptenopus carpi*'.

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Link: <https://doi.org/10.3897/vz.74.e153514.suppl2>

Supplementary Material 3

File S1

Authors: Becker FS, Alexander GJ, Tolley KA (2025)

Data type: .r

Explanation notes: R code for analysing batches of calls, cut into separate WAV files. Details of various functions, packages, and parameters to set, are included in the extensive comments. Please note the correct versions of the packages used in-text.

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Link: <https://doi.org/10.3897/vz.74.e153514.suppl3>

Supplementary Material 4

File S2

Authors: Becker FS, Alexander GJ, Tolley KA (2025)

Data type: .zip

Explanation notes: Zipped folder of .wav files: representative audio recordings of advertisement calls of the various *Ptenopus* species, including the recordings on which Fig. 20 was based.

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Link: <https://doi.org/10.3897/vz.74.e153514.suppl4>