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Revised phylogeny of African sand lizards (*Pedioplanis*), with the description of two new species from south-western Angola

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Abstract.—Although reptile diversity in Africa is high, it is poorly represented in Angola, with just 257 species known. Despite its greater surface area and habitat diversity Angola has significantly lower lacertid lizard diversity than adjacent Namibia. This is particularly notable in African sand lizards (*Pedioplanis*), where 10 species (two endemic) are known from Namibia but only two are recorded from adjacent Angola. *Pedioplanis benguellensis* was described from Angola, but its taxonomic status is problematic and it was previously synonymised with *P. namaquensis*. All other Angolan *Pedioplanis* were referred to Namibian *P. undata*, although this taxon is now known to comprise a complex of at least five different species and the relationship of Angolan material to this complex has not been assessed. In this study, we investigated the phylogenetic placement of Angolan *Pedioplanis* using two mitochondrial (ND2 and 16S) and one nuclear (RAG-1) markers. A Bayesian analysis was conducted on 21 samples from Angola, combined with existing data for 45 individuals from GenBank and three additional samples from central Namibia. The phylogeny demonstrates that *P. benguellensis* is a valid species and that it is not the sister taxon to *P. namaquensis* with which it has been morphologically confused. In addition, Angolan lacertids previously referred to *P. undata* are not conspecific with any of the Namibian or South African species in that complex. Rather, there is strong support for the presence in Angola of additional species of *Pedioplanis*, which form a well-supported sister clade to the *P. undata* complex (*sensu stricto*) of Namibia and two of which are described herein. These discoveries highlight the need for further biodiversity surveys in Angola, as similar increases in species diversity in other Angolan taxa might be found given sufficient investment in biodiversity surveys.

Key words.—Taxonomy, Lacertidae, phylogeny, southern Africa, species richness, cryptic species

Introduction

Recent decades have witnessed extensive taxonomic activity on reptiles in both Namibia and South Africa, with numerous new species described from both countries

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(1979–2011, Namibia 19 new species, South Africa 47 new species; W.R.B. pers. obs.). However, for much of this same period Angola was torn by civil unrest (1975–2002) and biodiversity research advanced little. Only three species of reptiles (all amphisbaenians) were described from the country during this period and these were all collected before the onset of civil war (Gans 1976). More recently, Haacke (2008) described a new species of gecko, *Afrogecko plumicaudus*, from south-western Angola that was first found in 1971, but whose description was delayed for 37 years due to restricted access to Angola and the lack of fresh material. These unfortunate circumstances have left the region's biodiversity poorly understood. This is especially relevant when viewed against the recent revolution in taxonomy, where the use of molecular methods has profoundly assisted in uncovering cryptic species and formerly unknown lineages (Beheregaray & Caccone 2007; Bickford *et al.* 2007).

Southern Africa, the geographic region south of the Cunene (in the west) and the Zambezi (in the east) rivers, has the highest reptile diversity in Africa, both in terms of species and family richness (Branch 2006). Within this region, South Africa has exceptional reptile diversity (381 species, 44.6% endemicity; W.R.B. pers. obs.). Although alpha diversity for Namibia is lower (228 species, 21.2% endemicity; W.R.B. pers. obs.), this could be due to its smaller geographic area (Namibia 0.82 million km^2, South Africa 1.22 million km^2) and reduced habitat diversity. Angola, however, is approximately the same size as South Africa (1.25 million km^2) with diverse habitats ranging from desert in the south to lowland rain forest in the north, with a complex topography and numerous isolated highlands. Despite this, Angolan reptile diversity (257 species; Blanc & Fretey 2002) is only slightly richer than that of adjacent Namibia and much lower than that of South Africa. Therefore, it is likely that Angolan biodiversity remains poorly known and, as the country rebuilds its infrastructure after years of civil war, it is imperative that modern biodiversity surveys and checklists are developed to inform conservation planning.

Recent years have seen renewed interest in the African lacertid radiation (Arnold 1973, 1989a, 1989b, 1991), with increasing emphasis on phylogenetic relationships within the diverse African genera (Mayer & Benyr 1994; Harris *et al.* 1998; Fu 2000; Mayer & Pavlicev 2007; Salvi *et al.* 2011). Few studies, however, have addressed interspecific relationships within the larger African lacertid genera (e.g. *Nucras, Heliobolus, Latastia, Ichnotropis*). Despite the dearth of studies, cryptic species are often revealed whenever generic level studies are conducted. For example, Makokha *et al.* (2007) uncovered unexpected cryptic diversity within southern African *Pedioplanis*. Cryptic diversity, including a new genus and species, has also been discovered in disjunct populations of the tropical African lacertid *Adolfus* (Greenbaum *et al.* 2011).

The family Lacertidae is represented in Angola by 13 species within six genera. This diversity is comparable to other herpetologically rich areas in sub-Saharan Africa, e.g. Tanzania 13 species in seven genera and Kenya 11 species in seven genera (Spawls *et al*. 2002). It is, however, at least species-wise, significantly lower than that found in nearby Namibia (25 species in five genera) or South Africa (27 species in seven genera; Branch 1998). This is particularly so for the genus *Pedioplanis* (African sand lizards), the most speciose ($n = 15$) lacertid genus in sub-Saharan Africa. Despite high diversity in neighbouring Namibia ($n = 10$) and South Africa ($n = 6$), Angola has only two recorded species, *P. benguellensis* (Bocage) and *P. undata* (Smith) (Boulenger 1921; Laurent 1964; Mertens 1971; Branch 1998) and probably

provides an example of underappreciated Angolan biodiversity. In addition, *P. benguellensis* has been the subject of a long-standing taxonomic debate spanning some 115 years, in which it was frequently synonymised with *P. namaquensis* (see below). As DNA samples for this species were previously unavailable, this issue was not settled by the most recent molecular phylogeny (Makokha *et al*. 2007). Similarly, Makokha *et al*. (2007) could only speculate that *P. undata*, a species found in northern Namibia, also extends into southern Angola. In this study, we focus on the Angolan radiation of this genus of lacertid lizards and re-assess their phylogenetic placement, taxonomy and the apparent low species richness currently recorded for the country.

During the Angolan Biodiversity Assessment and Capacity Building Project in January 2009, we visited south-western Angola as part of a biodiversity inventory team. Material was collected that allowed investigation into the evolutionary relationships within *Pedioplanis* by increasing geographic sampling for the genus. Given the past speculation regarding *Pedioplanis* from Angola (see below), we tested several hypotheses: (1) *P. benguellensis* is specifically distinct from *P. namaquensis*; (2) *P. benguellensis* and *P. namaquensis* are sister species; (3) Angolan *Pedioplanis* previously referred to *Pedioplanis undata* are not conspecific with other members of the *Pedioplanis undata* complex *sensu stricto* and represent a separate lineage(s). We used mitochondrial and nuclear DNA markers to examine these hypotheses and to investigate the phylogenetic relationships within *Pedioplanis* from both Angola and southern Africa.

Taxonomic background

Eremias benguellensis was described by Bocage (1867) from three specimens collected from 'Benguella' (= Benguela, Angola), although Bauer & Günther (1995) note that a lost syntype bears the locality 'Maconjo' (unlocated). The species was later considered by its author (Bocage 1895) to be synonym of *Eremias namaquensis* Duméril & Bibron. Boulenger (1918, 1921) reinstated *P. benguellensis* as a full species, diagnosing it from *P. namaquensis* (which has a semi-transparent lower eyelid) by the presence of a clear window, formed by a single black-edged scale in the lower eyelid. This revival was subsequently followed by Parker (1936), Monard (1937) and FitzSimons (1943) and yet Laurent (1964) with little documented analysis again relegated *P. benguellensis* to the synonymy of *P. namaquensis,* an arrangement that Mertens (1971) queried because of the difference in the presence of a 'brille' (one or two black-edged transparent scales forming a disk in the lower eyelid). Finally, Arnold (1989a, 1991) revived *P. benguellensis* and referred material from the western Kaokoveld in Namibia to this taxon (E.N. Arnold, pers. comm. to W.R.B.). This arrangement was followed by Branch (1998) and Griffin (2003) and voucher material from Namibia conforming morphologically to *P. benguellensis* in colour pattern, scalation and the condition of the brille is available (Okjivakandu, TM 38789–95; Opuwo, TM 33292, 38903; and Otjiwise, TM 38868, 38870–71; W.R.B. pers. obs., March 2010). Bauer *et al*. (1993) noted that lacertids from the Hoanib River, Namibia, provisionally referred to *P. namaquensis,* required further study and that

they may signal the presence of an additional species of *Pedioplanis* in the region. The possible relationship of this material to *P. benguellensis* was not discussed.

Lacerta undata was described by Andrew Smith (1838) and its subsequent history is confused and complex, complicated by loss of the types, confusion over the type locality and the subsequent description of numerous subspecies that collectively form the *P. undata* complex (Mertens 1954, 1955). Many of these issues were resolved by the designation of a neotype and restriction of the type locality to 'Windhoek' (see Mayer & Böhme 2000 for a full discussion). The presence of *Pedioplanis undata* in southern Angola was first noted by Boulenger (1921), who referred Angolan specimens from Maconjo, Benguella to the species. Laurent (1964) discussed additional Angolan material and the presence of the species in the country has been accepted by most subsequent authors (Mayer & Berger-Dell'Mour 1987; Berger-Dell'Mour & Mayer 1989; Bauer *et al.* 1993; Branch 1998; Makokha *et al*. 2007; Haacke 2008). However, since Laurent (1964), the status of *P. undata* has changed considerably. Mertens (1954, 1955) recognised three subspecies in the complex, whereas Mayer & Berger-Dell'Mour (1987), based on morphology and protein electromorphs, indicated that *undata, gaerdesi* and *rubens* should be treated as distinct species and retained *inornata* as a southern race of *P. undata*, although it was subsequently raised to a full species (Arnold 1991). Berger-Dell'Mour & Mayer (1989) described a new species, *P. husabensis*, which they considered to be also part of the *P. undata* complex. Within the *P. undata* complex the presence of a number of additional forms have also been signalled ('*undata*-N' and '*undata*-S', Mayer & Berger-Dell'Mour 1987; '*inornata*-central', Makokha *et al*. 2007), which remain of unresolved status. Mayer & Berger-Dell'Mour (1987: 275) noted that: 'In south-western Angola – northwest of the area of *undata*-N – a sharply striped form is living again, which is very similar to *undata*-S'. To date, the relationship between Angolan populations of *P. undata* to the suite of species in northern Namibia that comprise the *P. undata* complex (*P. undata*, *P. gaerdesi*, *P. rubens*, *P. inornata*) remains unstudied.

MATERIALS AND METHODS

Field Sampling Methods

We collected 49 *Pedioplanis* individuals from Cunene, Huila and Namibe Provinces (Fig 1). All specimens were collected by hand below the Leba escarpment in areas that comprised mainly sandy or gravel plains surrounding granite outcrops, with varying degrees of short grass cover and scattered thorn bush. Vegetation varied from semi-desert scrubland to woodland. Each specimen was collected as a voucher, fixed in 10% formalin and thereafter transferred to 50% iso-propanol for long-term storage. Vouchers were accessioned into the Port Elizabeth Museum (PEM), with representative material to be returned to Angola to form part of the revitalised faunal collections of the Lubango Museum (B. Huntley pers. comm.). Species were compared with morphological descriptions in the primary literature (Bocage 1867; Boulenger 1918, 1921; FitzSimons 1943; Mayer & Berger-Dell'Mour 1987; Berger-Dell'Mour & Mayer 1989) and with other *Pedioplanis* material housed in the herpetological collections of Bayworld, Port Elizabeth (formerly PEM) and

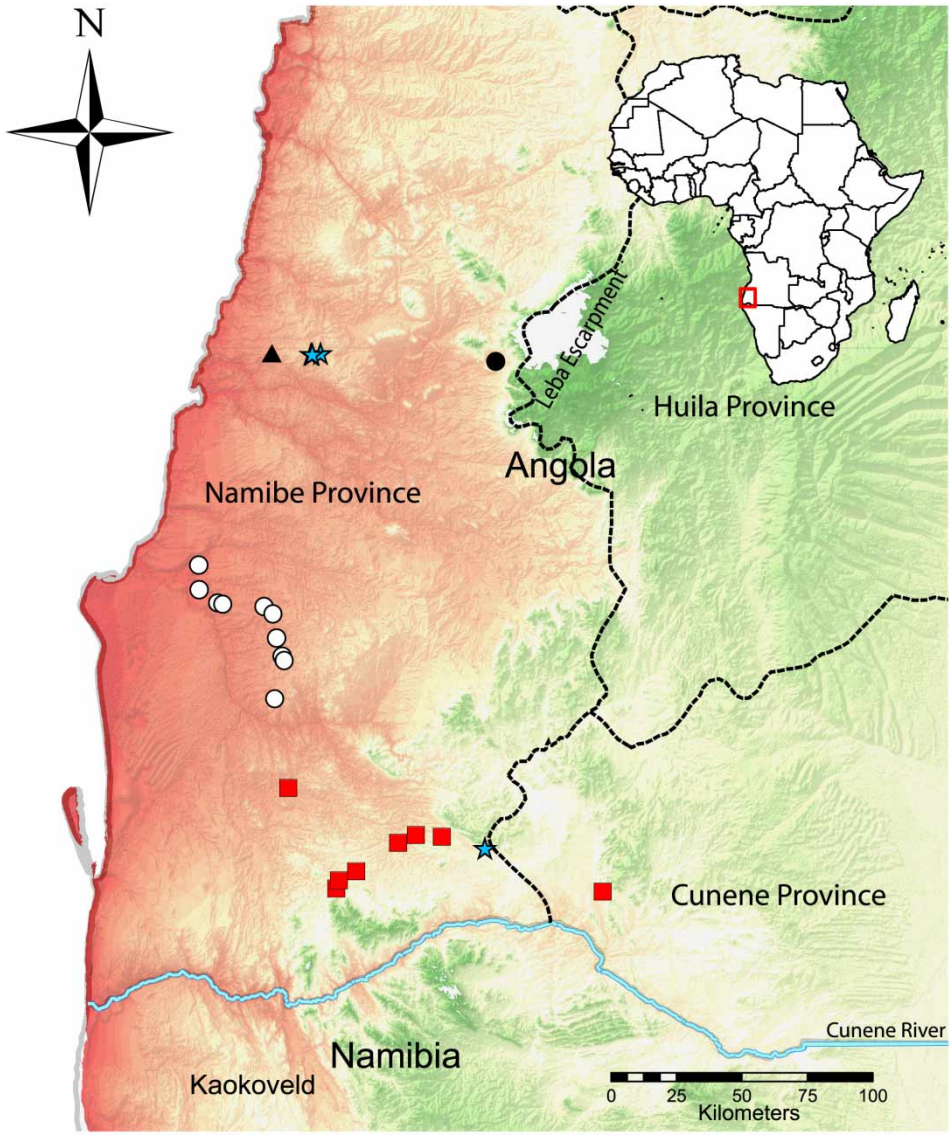

Figure 1. Collection sites of *Pedioplanis* from Angola, coded by the clade into which they fall (stars = *P. benguellensis*; white circles = *P. haackei* sp. nov.; squares = *P. huntleyi* sp. nov.; triangle = *P. sp* 1; black circle = *P. sp* 2).

the Ditsong: National Museum of Natural History Northern Flagship Institute, Pretoria (formerly Transvaal Museum; TM). No topotypic material of *P. benguellensis* was available for morphological or genetic comparison and the original type specimens of *Eremias benguellensis* Bocage were lost in the fire that destroyed the Lisbon Museum (Bauer & Günther 1995). Therefore, some material

was conservatively assigned to *P. benguellensis* based on diagnostic features (ventral scale counts and the presence of a single black-edged scale over the lower eyelid) that match the description for the species provided by Boulenger (1921).

Morphological Analysis

The following measurements were recorded from each individual, which were later used for species diagnoses: snout–vent length (SVL) – tip of the snout to the anterior edge of the cloaca; tail length (Tail) – tip of tail to posterior edge of the cloaca; total length (TL) – combined SVL and Tail; head length (HL) – from the anterior edge of the occipital/parietal scale to the tip of the snout; head width (HW) – maximum HW (just behind eye); lower jaw length – anterior edge of jaw bone to tip of lower jaw; inter-limb length – distance between axillary and inguinal regions; body length – anterior edge of enlarged collar to anterior edge of cloaca; collar to snout – tip of snout to anterior edge of enlarged collar scale; forelimb length – from elbow to wrist; hindlimb length – from knee to heel; longest finger and toe.

The following scalation details were recorded: supralabials – in front of subocular; infralabials; longitudinal ventral scale rows; transverse rows of ventrals; chinshields; supraciliars (SC); femoral pores; midbody scales; collar plates; gular scales; lamellae on fourth toe; number of smaller scales in front of supraoculars (SO) touching frontal and prefrontal; number of granules in front of SO and rows of granules between SC and SO. The presence of tympanic shield and scalation of the lower eyelids were investigated.

DNA Extraction, Amplification and Sequencing

Liver tissue or tail tips were collected from all individuals before fixation and stored in 99% ethanol. Total genomic DNA was extracted with a proteinase-K digestion followed by a standard salt extraction protocol (Bruford *et al*. 1992). Choice of mitochondrial and nuclear markers was based on creating a matching dataset to that of Makokha *et al*. (2007). Portions of two mitochondrial (16S and ND2) and one nuclear (RAG-1) markers were amplified using standard polymerase chain reaction (PCR) conditions: 2 μl genomic DNA (ca. 25 ng/μl) was added to a reaction containing 10 × thermophilic buffer (50 mM KCl, 10 Mm Tris-HCl, pH 9.0), 2.5 mM $MgCl_2$, 0.2 μM of each primer, 0.2 mM dNTPs and 0.025 U/μl Taq polymerase. The PCR profile included an initial denaturing step at 95°C for 1 min, followed by 35 cycles of 95°C for 1 min, 55°C for 30 seconds and 72°C for 60 seconds, with a final extension at 72°C for 5 min. Primers and annealing temperatures used were as follows: 16S primers (54–57°C) 16Sa and 16Sb (Palumbi 1996), ND2 primers (54°C) vMet and vTrp (Cunningham & Cherry 2004) and RAG-1 primers (57°C) F211 and R1392 (Makokha *et al.* 2007). PCR products were sent to Macrogen, Inc. (Korea) for sequencing, using the forward primer for each fragment. Sequences were checked and aligned using Geneious Pro v.4.5.6 (Drummond 1996), saved as nexus files and heterozygous positions in the nuclear gene were coded as ambiguous. Twenty-four bases within the 16S marker were excluded from all analyses due to ambiguous alignment. All new sequences have been added to EMBL (see Online Supplementary Material).

Phylogenetic Analysis

Sequences from 21 Angolan individuals were supplemented with three additional samples from central Namib (two *P. husabensis* and one *P. inornata*) and combined with homologous sequences for 48 individuals of *Pedioplanis* available in GenBank (Makokha *et al.* 2007; DQ871037-DQ871208), resulting in a dataset of 72 individuals (see Online Supplementary Material). Two outgroup taxa (*Heliobolus lugubris* and *Nucras tessellata*) used by Makokha *et al.* (2007) were also included to make these datasets comparable. A partition homogeneity test was carried out using PAUP v4.0b10 (Swofford 2002) with 100 repartitions. This test indicated no conflict ($p > 0.05$) between the two mitochondrial markers. However, there was conflict between the two genomes and this conflict was already present for the original dataset (Makokha *et al*. 2007), which we re-analysed using the partition homogeneity test. To ensure that differences in topology would not affect our interpretation, two analyses were carried out: (1) mitochondrial only; (2) all markers analysed together to produce a single phylogeny. A Bayesian analysis was conducted on both datasets with 1087 base pairs (bp) for the mitochondrial and 1817 bp for the combined dataset (16S 487 bp, ND2 600bp, RAG-1 730 bp) using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003) via the remote-upload CBSU cluster (cbsuapps.tc.cornell.edu). Separate partitions were set up for each marker (i.e. three partitions), but the analysis was also run with the two coding genes partitioned by codon (totalling seven partitions). Using Modeltest (Posada & Crandall 1998), the best-fit model of sequence evolution was determined for each marker using both the Log likelihood ratio test (LRT) and the Akaike information criterion tests. In each case, the model with the fewest parameters was chosen and the rate categories for MrBayes set accordingly (16S: GTR + I + G, nst = 6; ND2: TrN + I + G, nst = 6; RAG: GTR + I + G, nst = 6), including invariable sites, and the alpha shape parameter for the gamma distribution to account for among-site rate heterogeneity (Yang 1997). The Markov Chain Monte Carlo (MCMC) was run for 10 million generations with trees sampled every 1 000 generations. Log-likelihood scores became stationary at 20 thousand generations, although the average standard deviation of split frequencies did not stabilise until 2–3 million generations for both datasets. Therefore, 3 000 trees were removed as burn-in. Tracer v1.4.1 (Rambaut & Drummond 2007) was used to check that the effective sample size of all parameters was greater than 200 after burn-in. The MCMC was run twice for each partitioning option with random starting trees, to ensure the results converged on the same topology and posterior probabilities, and that local sampling optima had been avoided. We considered nodes with ≥ 0.95 posterior probabilities as well supported.

In addition, a maximum likelihood (ML) search was run using RAxML HPC 7.2.8 (Stamatakis 2006) on the CIPRES Science Gateway (www.phylo.org/sub_sections/portal/) for both the mitochondrial and the full dataset. The datasets were partitioned as in the Bayesian analysis, with a GTR + I + G model for all markers and rapid bootstrapping halted automatically (Stamatakis *et al*. 2008). This analysis was run three times to ensure that independent ML searches produced the same topologies. We considered nodes with a bootstrap value of $\geq 75\%$ as well supported in this analysis.

To investigate the hypothesis that *P. namaquensis* and *P. benguellensis* are monophyletic sister species, a backbone-constrained topology of the Bayesian tree

was created using MacClade 4.0 (monophyly enforced for *P. namaquensis* and *P. benguellensis* with all other species collapsed to form a polytomy). The set of trees (post burn-in from the Bayesian analysis) were then filtered in PAUP v4.0b10 (Swofford 2002) according to the constraint. The percentage of trees agreeing with that backbone were then used as an estimate of support associated with that particular node. In addition, the Shimodaira–Hasegawa (S-H) test was used to examine if there was a significant difference between the enforced topology (i.e. monophyly of *P. namaquensis* and *P. benguellensis*) and the Bayesian consensus topology.

RESULTS

Molecular Analysis

The Bayesian search (Fig 2) produced the same basic topology and node support as the likelihood search (tree not shown) and the various partitioning options in the Bayesian analysis had no effect on node support or tree topology. The mitochondrial tree (see Online Supplementary Material) differed from the nuclear tree for the placement of *P. breviceps* but this placement lacked support, except in the likelihood analysis of the full dataset. Overall, the phylogenetic analyses revealed the presence of several very well supported clades (posterior probabilities ≥ 0.95, likelihood bootstrap $\geq 75\%$), similar to those found by Makokha *et al.* (2007), with some notable exceptions. There is a previously unknown Angolan clade with a number of new lineages, none of which corresponds to any of the known species within *Pedioplanis*. None of these Angolan lineages can be assigned to *P. undata* or any of the related species within the *P. undata* complex. Two of the lineages are represented by single individuals (KTH09–104 and KTH09–120). The uncorrected *p*-distances between these new Angolan lineages (1.8% for 16S, 7.2% for ND2, 0.5% for RAG) are similar to those found between other species of *Pedioplanis* (typically 2–4% for 16S, 7–16% for ND2, 1–2% for RAG; Makokha *et al.* 2007) and between species within other lacertid genera (Mayer & Pavlicev 2007; Greenbaum *et al*. 2011). Second, there is a monophyletic clade that corresponds morphologically to *P. benguellensis* (see below: confirmed by comparison of voucher specimens with the description provided by Boulenger (1921)), which appears to be sister to both the *P. undata* complex and the new Angolan clade, although that relationship is not supported by a high posterior probability or ML bootstrap.

The phylogeny obtained does not support the hypothesis that *P. benguellensis* and *P. namaquensis* are sister species, as previously hypothesised (Bocage 1867; Laurent 1964; Makokha *et al.* 2007). None of the 7 000 Bayesian trees was compatible with these two species forming a monophyletic lineage. In addition, the S-H test indicated that enforced monophyly resulted in a significantly worse likelihood score than the observed topology of the Bayesian consensus topology (Δ –LnL $= 29.28$, $p < 0.05$).

DISCUSSION

Several new lineages of *Pedioplanis* were revealed during this study, two of which are described here as new species (see below). Our geographic sampling suggests

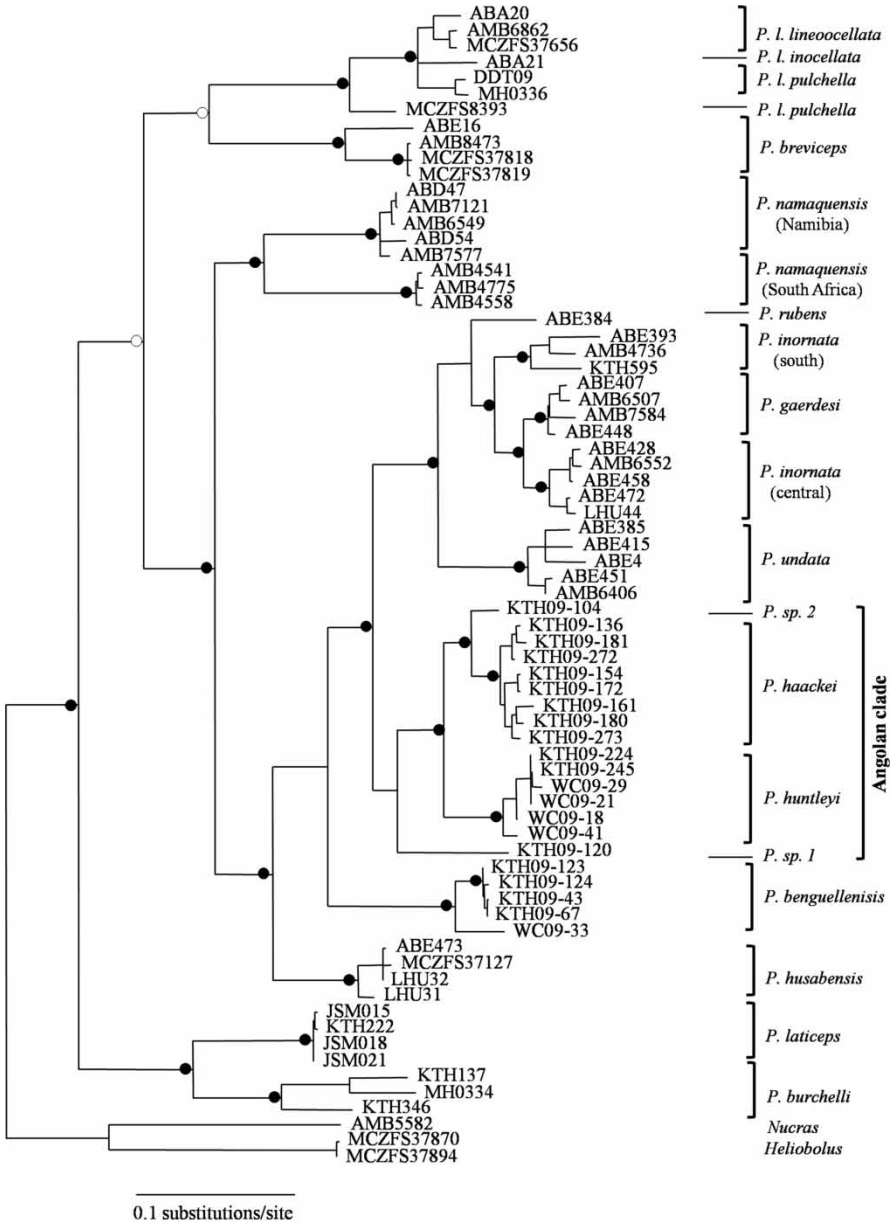

Figure 2. Bayesian consensus phylogram for *Pedioplanis*. Node support with posterior probabilities ≥ 0.95 and maximum likelihood bootstrap $\geq 75\%$ are indicated with a black circle. Nodes supported only by likelihood analysis are indicated with a white circle.

that these new lineages are currently endemic to Angola. Two species of *Pedioplanis* were previously recorded to occur in Angola; *P. benguellensis* and *P. undata* (Boulenger 1921; Laurent 1964; Mertens 1971; Branch 1998; Makokha *et al.* 2007), but none of the new samples from Angola falls within clades representing those

species or agrees in colour pattern with *P. undata.* This new information suggests that *P. undata* is not present in Angola and, as currently understood, the species is endemic to Namibia.

Based on phylogenetic analysis, material referable to *P. benguellensis* does not fall within the same lineage as, nor is it sister to, *P. namaquensis* despite past speculation to the contrary (e.g. Bocage 1867; Laurent 1964; Makokha *et al.* 2007). Instead, *P. benguellensis* forms its own, well-supported clade that is basal to sister clades comprising the *P. undata* complex (south of the Cunene River) and to a new Angolan clade identified in this study. *Pedioplanis benguellensis* shares with *P. gaerdesi*, of the coastal Kaokoveld region, the characteristic single brille in the lower eyelid. However, it differs in habitus (e.g. longer tail) and colour pattern and in both our phylogeny and that of Makokha *et al.* (2007) *P. gaerdesi* falls within the *P. undata* complex. The relationship of Angolan *P. benguellensis* with northern Namibian specimens (Okjivakandu, Opuwo and Otjiwise), which on morphology can be assigned to the same taxon, remains unresolved and awaits the collection of fresh material for genetic analysis. Previous documentation of *P. namaquensis* from southern Angola (e.g. FitzSimons 1943, Mertens 1955, Makokha *et al.* 2007) results from previous confusion with *P. benguellensis,* and no specimens in the extensive holdings of the TM or PEM, or collected during our survey, support the presence of *P. namaquensis* in Angola.

The suggestion by Laurent (1964) that *P. undata* occurs in Angola was based on the shared characteristic feature of a double, dark-edged brille in the lower eyelid. However, this feature, although considered diagnostic for *P. undata* at the time, is not shared with all members of the *P. undata* complex (e.g. *P. gaerdesi*). All our Angolan material is genetically well defined and is not referable to any species of the Namibian *P. undata* complex. There remains the possibility that *P. undata* occurs elsewhere in southern Angola and that members of the Angolan clade identified here may also enter extreme northern Namibia. Further surveys are required to determine if the Cunene River forms a barrier between these sister clades.

With the addition of new data from Angola, it is clear that the *P. undata* clade plus the new Angolan species are sister to *P. benguellensis*, with *P. husabensis* falling outside this entire group. This is contrary to Arnold's (1991) suggestion, which placed *P. inornata* as a sister species to *P. namaquensis* and *P. husabensis.* Although Makokha *et al*. (2007) suggested that the *P. undata* complex is sister to *P. husabensis*, they lacked the Angolan material, which now reveals a much more inclusive clade that is sister to *P. husabensis.*

CONCLUSIONS

Our study shows that there is a formerly unknown radiation of *Pedioplanis* in Angola. The new genetic lineages noted here are also morphologically differentiated by body size, scalation and colouration (see below). We have sufficient material of two lineages to assess their specific status and describe them below. The significant genetic divergence and habitat differences of two other individuals (PEM R18540, 31.5km East of Namibe; PEM R18460, between Humpata and Namibe) suggest that they may also represent new taxa (see Online Supplementary Material). Assessment of their status awaits collection of additional material.

These findings revealed new endemic Angolan lacertids, and also increased the total number of species in the genus *Pedioplanis* to 17. The Appendix provides an a updated key to the genus *Pedioplanis*. This single survey has considerably advanced our knowledge of the central African lacertid fauna and highlights the need for additional biodiversity surveys in Angola and adjacent regions. Regardless, there are gaps remaining in our understanding, especially centred on the geographic area around the Cunene River (the border between Angola and Namibia), as well as north of Namibe Province (central and northern Angola), particularly in the succulent-rich northern Pro-Namib region. While this study focuses on a single genus of lacertid lizard, the results may be indicative of greater herpetofaunal diversity in Angola. Elsewhere, we present the description of a new hyperoliid frog discovered in the Serra da Chela escarpment during the same survey (Conradie *et al.* 2012). Further, the results demonstrate that voids in knowledge of species richness, evolutionary relationships and taxonomic status can be partially revealed through the use of basic surveys. There is a need not only to conduct more surveys, but to build networks and capacity in Angola to document and protect the rich biodiversity as this area comes under intense developmental pressure.

Taxonomy

Pedioplanis haackei sp. nov. (Fig 3A,B)

Synonymy.—*Eremias undata undata* (part) Laurent 1964.

Type material.—The type series comprises 15 specimens. All have small ventral incisions where liver tissue was excised for molecular studies. They were fixed in 10% formalin in the field and thereafter transferred to 50% iso-propanol for long-term storage at the PEM.

Holotype.—An adult male (PEM R18465) with a partially everted hemipenis, collected by W.R. Branch, W. Conradie, G.J. Measey and K.A. Tolley, 19 January 2009, along the road to Tambo, Namibe Province, Angola (15°52′33.8″ S, 12°12′21.0″ E, 1512CC, 196 m a.s.l.). Field number KTH09–161.

Allotype.—An adult gravid female (PEM R18461) with broken tail, collected by W.R. Branch, W. Conradie, G.J. Measey and K.A. Tolley, 18 January 2009, Red Canyons, Namibe Province, Angola (15°44′45.5′ S, 12°8′23.6″ E, 1512CA, 81 m a.s.l.). Field number KTH09–136.

Paratypes.—Thirteen specimens (five females: PEM R18463, −18467, −18469, −18470 and −18472; eight males: PEM R18462, −18464, −18466, −18468, −18471, −18473, −18474 and −18475), all collected by W.R. Branch, W. Conradie, G.J. Measey and K.A. Tolley, at various localities on the road between Namibe and Espinheira (see Online Supplementary Material for further details), 12–23 January 2009.

Diagnosis.—Distinguished from all other species of *Pedioplanis,* except *P. benguellensis*, *P. undata, P. rubens*, *P. gaerdesi*, *P. inornata* and *P. huntleyi* sp. nov., in possessing 10 longitudinal rows of ventral scale; in having a semi-transparent lower eyelid with a brille formed of two large scales (only a single scale brille in *P. benguellensis* and

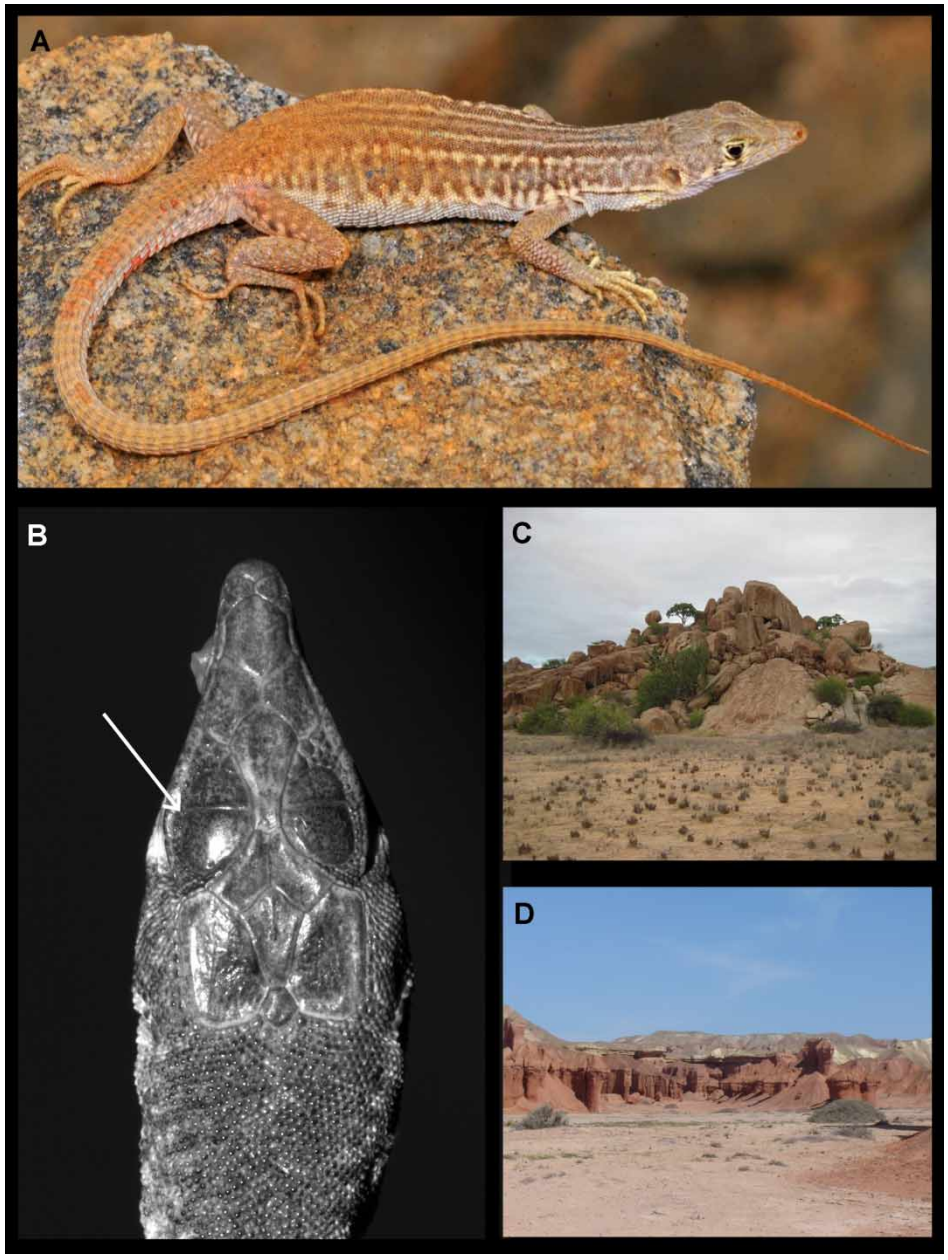

Figure 3. A – Paratype *Pedioplanis haackei* sp. nov. (PEM R18472) in life; B – close-up of head of holotype (PEM R18465) showing scalation; C & D – general habitat photo of *P. haackei* sp. nov., Namibe province, Angola.

P. gaerdesi, lower eyelid opaque to semi-transparent with 10–15 scales in *P. burchelli, P. namaquensis* and *P. laticeps;* opaque to semi-transparent with eight opaque scales in *P. husabensis* and opaque and scaly in *P. breviceps*); possessing a small tympanic shield (may be absent in *P. breviceps* and absent in *P. burchelli*, *P. laticeps*, *P. l. lineoocellata*,

P. l. inocellata and *P. l. pulchella*); in having 5–6 supralabials (mostly five) anterior to the subocular (four supralabials in *P. benguellensis*); in having numerous small granules (12–32) anterior to the first supraocular (6–15 in *P. undata*); and two rows of small granules between the SO and supraciliaries (only one in *P. undata*).

Its typical colouration of three faint dorsal-lateral dark stripes with white borders and reticulated flanks is also distinct from *P. gaerdesi* (no longitudinal stripes with scattered black spots), *P. rubens* (uniform brick-red with weak greyish band on the flanks) and *P. undata* (five distinct darker longitudinal stripes).

Description of holotype.—Body relatively slender (SVL four times the HL), with hindlimbs larger than forelimbs (femur of hind limb approximately half interlimb length, tibia one third); head narrow and elongated (60% longer than wide) with narrow pointed snout (width at level of rear of frontonasal half width at front of eye), that is a little longer than distance from back of eye to rear of ear opening. Tail two and half times SVL. Prefrontals in broad median contact with one another; parietals longer than broad, with large, pentagonal interparietal that is longer than prefrontals and frontoparietals, in contact posteriorly with a small subtriangular occipital; two larger rounded SO, both in contact with the frontal, with anterior supraocular preceded by a group of 12 granules (three largest in contact with prefrontals) on both sides and posterior supraocular bordered by a region of 27R/25L granules (six largest in contact with frontoparietals and parietals); three small scales between last supracilliars and parietal; six supraciliaries on each side, first longest and separated from SO by granules; nasals slightly swollen and directed slightly upwards, infralabial in contact with rostral and first supralabial; five supralabials anterior to subocular and three supralabials posterior to subocular, on both sides; subocular keeled below and bordering the lip, its lower border being shorter than the upper; no upper temporal shield, temporal scales all small, granular and slightly tubercular; tympanic shield narrow on upper border of ear opening; no ear lobes, although a few granules may project slightly; lower eyelid with transparent brille formed of two larger, black-edged scales; 7R/6L infralabials; four enlarged pairs of chin shields, last largest and first three in median contact; 31 gular scales in a straight line between symphysis of chin shields and median collar plate; collar free, comprising eight enlarged plates (median subtriangular) and extending onto side of neck as a crease; dorsal scales small, juxtaposed, granular, smooth, larger on sides towards ventrals; 63 scales across midbody; ventral plates 10 longitudinal and 29 transverse rows (from collar to groin); plates of the outermost rows longer than broad, with outer row notably smaller than other rows; transverse row of ventrals across chest just behind collar longer than broad; preanal scales irregular, median ones larger; scales on upper surface of forearm large, smooth or slightly keeled; scales on lower surface of forearm with a series of enlarged plates, at least twice width of scales on upper forearm; scales on upper surface of tibia rhombic, subimbricate, keeled and much larger than dorsals; tibia below with a series of large plates; subdigital lamellae under fourth toe 26R/27L; 13R/12L femoral pores; dorsal scales on tail oblique, strongly keeled diagonally and truncate behind, ventral scales on tail obtusely keeled.

Colouration (in life).—Head uniform grey, dorsally greyish anterior and reddish-brown ventrally, three fine dorso-lateral stripes with white interlinking, flanks are reticulated with white markings, a line of small blue/yellow lateral spots, white

ventrally, limbs light greyish, hind limbs with unpigmented circles, tail reddish above and white below.

Variation.—Measurements for the type series of *Pedioplanis haackei* sp. nov. are summarised in Table 1. Allotype and paratypes have similar scalation to holotype, except: prefrontals separated by single small azygous shield in allotype and PEM R18462, −18463, −18464, −18466, −18467 and −18470; in allotype interparietal separated from occipital by small azygous shield; in PEM R18467 anterior subocular is separated by frontal by a single row of small granules; usually four pairs of chin shields, first three at least partially in median contact; supralabials anterior to subocular 4–6 (mostly five); infralabials: 6–8 (mostly six); supraciliaries 6–8 (mostly six); small scales in front of anterior supraocular touching frontal 3–6 (mostly four); number of granules in group preceding anterior supraocular 12–23 (average 16); rows of granules between supraciliaries and SO 1–3 (mostly two, 88%); midbody scales 57–70; collar plates 8–10; gular scales in a straight line between symphysis of chin shields and median collar plate 27–31; ventral transverse rows 25–31; subdigital lamellae under fourth toe 26–32; femoral pores 11–16 on each side. **Size.**—Males larger than females (males 47.5 + 108.9 = 156.4 mm; females, 46.6 + 93.7 = 140.5 mm. Maximum SVL = 50.8 mm (PEM R18473: paratype female) and maximum tail = 126.8 mm (PEM A18468: paratype male). **Colouration (in life).**—Similar to holotype and allotype. Juvenile colouration unknown.

Etymology.—The specific epithet is a patronym honouring the now retired curator of the herpetology collection at the former TM (now the Ditsong: National Museum of Natural History), Wulf Haacke, whose herpetological surveys in Angola in the early

Table 1. Morphological measurements (mm) of Angola *Pedioplanis* (tail and total length was only taken of specimens with intact tails).

		P. benguellensis (n = 11)		*P. haackei* sp. nov. (n = 15)		*P. huntleyi* sp. nov. (n = 16)	
Measurement		Mean	SD	Mean	SD	Mean	SD
Snout Vent Length (SVL)	males	44.0	1.68	47.3	2.06	55.3	1.46
	females	43.2	2.07	46.8	3.94	53.7	2.76
Tail	males	103.3	NA	108.9	13.64	130.4	12.33
	females	77.1	11.47	96.1	8.10	104.0	18.16
Total length	males	149.7	NA	143.6	8.91	185.7	11.81
	females	121.1	8.65	148.7	16.68	157.4	19.67
Head length		10.6	0.55	11.7	0.78	13.2	1.05
Head width		6.2	0.39	6.6	0.41	7.9	0.62
Lower jaw length		10.5	0.78	11.8	0.86	13.7	1.39
Inter-limb length		21.9	2.38	22.4	1.9	25.8	1.39
Body length		27.6	0.72	29.8	1.97	35.1	1.71
Collar-snout length		15.5	2.55	18.0	1.62	20.1	1.67
Forelimb length		5.2	0.41	6.0	0.47	7.1	0.57
Finger		4.8	0.53	5.3	0.73	5.8	1.19
Hindlimb length		8.8	0.57	10.6	1.22	12.4	1.39
Toe		9.1	0.67	10.1	0.67	11.4	1.13

1970s prepared the way for this study. The name is constructed in the masculine genitive.

Distribution.—Found in the drier south-western desert area of Namibe Province, Angola, south of Lake Arco and north of Espinheira.

Habitat.—Mainly sandy plains surrounding granite outcrops, with varying degrees of short grass cover and scattered *Acacia mellifera* thorn bush. Other vegetation included small *Commiphora* sp., *Boscia foetida* and *Salvadora persica*. Vegetation is classified as semi-desert shrubland.

Conservation.—During the expedition, specimens were found to be abundant and common. More fieldwork is required to determine the full range of the species and potential habitat threats in order to assess its conservation status.

Pedioplanis huntleyi sp. nov. (Fig 4A,B)

Synonymy.—*Eremias undata* (part) Boulenger 1921; *Eremias undata undata* (part) Laurent 1964.

Type material.—The type series comprises 16 specimens. All have a small ventral incision where liver tissue was excised for genetic studies; they were fixed in 10% formalin in the field and transferred to 50% iso-propanol for long-term storage at the PEM.

Holotype.—An adult male (PEM R18479), collected by W.R. Branch, W. Conradie, G.J. Measey and K.A. Tolley, 21 January 2009, road to Oncocua, 7 km from Iona, Namibe Province, Angola (16°51′29.9″ S, 12°36′45.9″ E, 1612DC, 803 m a.s.l.). Field number KTH09–245.

Allotype.—An adult female (PEM R18487), collected by W. Conradie, 24 January 2009, 14 km west of Moimba, Namibe Province, Angola (16°40′46.1″ S, 12°58′26.3″ E, 1612DB, 684 m a.s.l). Field number WC09–29.

Paratypes.—Thirteen specimens (six females: PEM R18476, −18477, −18485, −18486, −18489, −18490; eight males: PEM R18478, −18480, −18481, −18482, −18483, −18484, −18486, −18488), collected by W.R. Branch, W. Conradie, G.J. Measey and K.A. Tolley, near Espinheira and eastward to Ruacana (see Online Supplementary Material for further details), 20–25 January 2009. All with full tail, except PEM R18482, −18484 and −18490.

Diagnosis.—It shares similar scalation features to *P. haackei*, and can therefore be diagnosed in these features from all other *Pedioplanis*, except for the following differences: having 7–13 small granules anterior to the first supraocular (12–23 in *P. haackei* sp. nov.); having only one row (rarely two rows) of small granules between the supraocular and supraciliaries (two in *P. haackei* sp. nov.) and 2–4 (mostly three) small scales in front of the first supraocular touching the frontal (3–6, mostly four in *P. haackei* sp. nov.).

Its typical colouration of five dark ventral lines, with clear white borders and which fade on the latter half of the body, is distinct from *P. gaerdesi* (no longitudinal stripes, but with scattered black spots), *P. rubens* (uniform

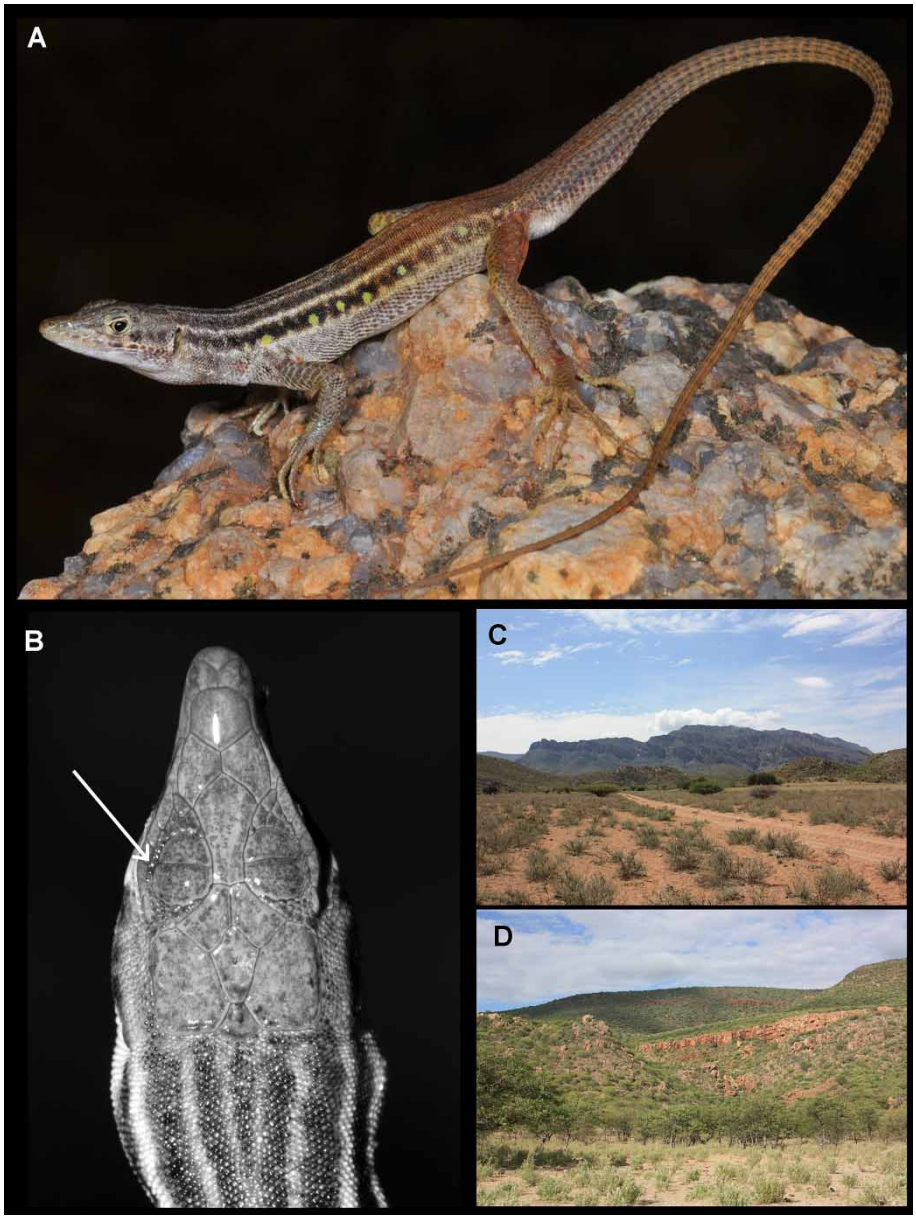

Figure 4. A – Holotype *Pedioplanis huntleyi* sp. nov. (PEM R18479) in life; B – close-up of head of holotype showing scalation; C & D – general habitat photo of *P. huntleyi* sp. nov., Cunene and Namib province, Angola.

brick-red with weak greyish band on the flanks), *P. haackei* sp. nov. (three faint dorsolateral stripes), *P. undata*-N (stripes on back often pale or obsolete; Mayer & Berger-Dell'Mour 1987) and *P. undata*-S (five distinct dark longitudinal strips: Mayer & Berger-Dell'Mour 1987). It further differs from Namibian *P. undata* by its

distribution (north of the Cunene River), colouration and by significant molecular divergence (Fig 2).

Description of holotype.—Body relatively stout (SVL four times the HL), with hindlimbs larger than forelimbs (femur of hind limb approximately one third interlimb length, tibia one quarter); head broad (62% longer than wide) with narrow snout (width at level of rear of frontonasal less than half width at front of eye), that is a little longer than distance from back of eye to rear of ear opening. Tail two and two-thirds SVL. Prefrontals in broad median contact with one another; parietals longer than broad, with large, pentagonal interparietal that is longer than prefrontals and frontoparietals, in contact posteriorly with a small subtriangular occipital; two larger rounded SO, both in contact with the frontal, with anterior supraocular preceded by a group of 15R/14L granules (two largest and one small in contact with prefrontals) and posterior supraocular bordered by a region of 22R/23L granules (five largest in contact with frontoparietals and parietals); one large scale between last supracilliars and parietal; six supraciliaries on each side, first longest and separated from SO by granules; nasals slightly swollen and directed slightly upwards, infralabial in contact with rostral and first supralabial; five supralabials anterior to subocular on both sides and four supralabials posterior to subocular on both sides; subocular keeled below and bordering the lip, its lower border being shorter than the upper; no upper temporal shield, temporal scales all small, granular and slightly tubercular; tympanic shield narrow on upper border of ear opening; no ear lobes, although a few granules may project slightly; lower eyelid with transparent brille formed of two larger, black-edged scales; six infralabials; four enlarged pairs of chin shields, last largest and first two in median contact; 35 gular scales in a straight line between symphysis of chin shields and median collar plate; collar free, comprising nine enlarged plates (median subtriangular) and extending onto side of neck as a crease; dorsal scales small, juxtaposed, granular, larger on sides towards ventrals; 55 scales across midbody; ventral plates 10 longitudinal and 29 transverse rows (from collar to groin); plates of the outermost rows longer than broad, with outer row notably smaller than other rows; transverse row of ventrals across chest just behind collar longer than broad; preanal scales irregular, median ones largest; scales on upper surface of forearm large, smooth or slightly keeled; scales on lower surface of forearm with a series of enlarged plates, at least twice width of scales on upper forearm; scales on upper surface of tibia rhombic, subimbricate, keeled and much larger than dorsals; tibia below with a series of large plates; subdigital lamellae under fourth toe 27R/28L; femoral pores 15 beneath each thigh; dorsal scales on tail oblique, strongly keeled diagonally and truncate behind, ventral scales on tail obtusely keeled.

Colouration (in life).—Head uniform olive to slate brown, snout paler, five well-defined dorsal stripes with white interlinking lines, the stripes turn buff or orange-brown posterior, lateral dark stripes extend from the upper labials through the ear to the groin, series of large green to bluish spots on the flanks, three darker dorsalateral stripes, which fade two-thirds down the back, ventral side is white, front legs are light greyish and back legs are reddish-brown, tail is reddish-brown with darker pigmented keels above and white below.

Variation.—Measurements for the type series of *Pedioplanis huntleyi* sp. nov. are summarised in Table 1. Allotype and paratypes have similar scalation to holotype, except: prefrontals separated by single small azygous shield in allotype and PEM R18478, −18481, −18486 and −18490; in allotype and all paratypes the occipital is larger and more trapezoid than in the holotype; right posterior supraocular not in contact with frontal (PEM R18476); usually four pairs of chin shields, first three at least partially in median contact (only first two in contact in holotype), but five in PEM R18483 and 18485, first four in median contact; supralabials anterior to subocular 4–6 (mostly five); infralabials 6–7 (mostly six); supraciliaries 5–7 (mostly six); small scales in front of anterior supraocular touching frontal 2–4 (mostly three); number of granules in group preceding anterior supraocular 7–13 (average nine); rows of granules between supraciliaries and SO 1–2 (mostly one, 69%); midbody scales 57–69; collar plates 8–10; gular scales in a straight line between symphysis of chin shields and median collar plate 26–34; ventral transverse rows 27–30; subdigital lamellae under fourth toe 20–29; femoral pores 12–15 on each side. **Size.**—Males larger than females (males 56.0 + 128.6 = 184.6 mm; females, 53.8 + 107.7 = 161.5 mm. Maximum SVL = 57.41 mm (PEM R18484: male paratype) and maximum tail = 141.5 mm (PEM R18479: male holotype). **Colouration (in life).**—Similar to holotype and allotype. In life, the males are more brightly coloured than females, and in females the dorsal stripes fade higher up on the body to a reddish-brown colour. Juvenile colouration unknown.

Etymology.—The specific epithet is a patronym honouring the former CEO of the South African National Biodiversity Institute (SANBI), Brain Huntley, who organised the expedition to Angola, and has made valuable contributions to the conservation of Angolan biodiversity. The name is constructed in the masculine genitive.

Distribution.—Iona National Park, north-west of Espinheira and westward to Ruacana, Namibe and Cunene provinces, Angola.

Habitat.—Prefers more compacted rocky substrate, well-vegetated scrub woodland and shrubland.

Conservation.—During the expedition, specimens were found to be abundant and common. More fieldwork is required to determine the full range of the species and potential threats in order to assess its conservation status.

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APPENDIX: UPDATED KEY TO THE SPECIES OF THE GENUS *PEDIOPLANIS* (ADAPTED FROM MAYER 1989)

1. Ventral plates in 10–14 longitudinal series..... **2**

la. Ventral plates in 14–16 longitudinal series **13**

2. Lower eyelid with 1 or 2 greatly enlarged, black-edged transparent scales, forming a disk ('brille')..... **3**

2a. Lower eyelid opaque to semi-transparent with 7–15 slightly enlarged scales across the middle **11**

3. Tympanic shield present, ventral plates in 10–12 longitudinal series **4**

3a. Tympanic shield absent, ventral plates in 12–14 longitudinal series **9**

4. Three or five darker longitudinal stripes on back and flanks **5**

4a. No longitudinal stripes but scattered black speckles **8**

4b. Uniform brick-red with a weak greyish band on the flanks ..... ***P. rubens***

5. Lower eyelid with 1 transparent scale only, usually 4 upper labials in front of subocular ..... ***P. benguellensis***

5a. Lower eyelid with 2 transparent scales, usually 5–6 upper labials in front of subocular **6**

6. Three faint darker dorsolateral stripes, reticulated pattern on flanks, numerous small granules in front of supraoculars, 2 rows of granules separating supraoculars from supraciliaries ..... ***P. haackei*** **sp. nov.**

6a. Five darker longitudinal stripes on back and flanks, 1 (sometimes 2) row of granules separating supraoculars from supraciliaries **7**

7. Distinct dark longitudinal stripes all the way to the tail; restricted to Namibia, ... ***P. undata***

7a. Longitudinal stripes distinct only midway down body, then replaced by uniform brick red colouration; restricted to Angola,..... ***P. huntleyi* sp. nov.**

8. Lower eyelid with 1 transparent scale only ..... ***P. gaerdesi***

8a. Lower eyelid with 2 transparent scales ..... ***P. inornata***

9. A series of colourful lateral spots present **10**

9a. No series of colourful lateral spots present ..... ***P. l. inocellata***

10. Dorsal scales on posterior part of back rhombic, subimbricate and distinctly keeled, subequal in size to scales on tibia ..... ***P. l. lineoocellata***

10a. Dorsal scales on posterior part of back granular, juxtaposed, not or feebly keeled and much smaller than scales on tibia ..... ***P. l. pulchella***

11. Usually 4 or 5 upper labials anterior to subocular shield; 5 more or less distinct longitudinal stripes on back and flanks; if uniform then no reddish colouration discernible **12**

11a. Usually 5 or 6 upper labials anterior to subocular shield; head dorsally and anterior part of back greyish, posterior part and tail russet to brick-red; no longitudinal stripes but scattered black speckles ..... ***P. husabensis***

12. 5 more or less distinct longitudinal stripes in both sexes, the dorsolateral stripe being broadest; size of tympanic shield moderate to large, scales on tibia large and distinctly keeled ..... ***P. namaquensis***

12a. 5 more or less distinct longitudinal stripes in juveniles and females only, the lateral stripe being broadest; males light brown to bluish grey dorsally, with irregular white mottles; tympanic shield small or absent; scales on tibia small, smooth or feebly keeled ..... ***P. breviceps***

12b. 5 more or less distinct stripes in juveniles, that fade in adults or become broken rows of white spots; tympanic shield absent **13**

13. 48–62 scales across middle of dorsum, nasals usually not in contact behind rostral; 16–18 longitudinal ventral plates; juveniles 5 white stripes ..... ***P. laticeps***

13a. 62–75 scales across middle of dorsum; nasals usually in contact behind rostral; 14–16 longitudinal ventral plates; juveniles 7 white stripes ..... ***P. burchelli***