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Phylogeny of the Genus *Chondrodactylus* (Squamata: Gekkonidae) with the Establishment of a Stable Taxonomy

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PHYLOGENY OF THE GENUS *CHONDRODACTYLUS* (SQUAMATA: GEKKONIDAE) WITH THE ESTABLISHMENT OF A STABLE TAXONOMY

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Abstract. Despite being among the largest and most conspicuous geckos across southern and eastern Africa, the toe-padded species of *Chondrodactylus* have remained one of the most taxonomically difficult groups of African lizards, due chiefly to their overall morphological conservativeness accompanied by high intraspecific variation. Current recognition of taxa is based on recent molecular phylogenetic analyses, but the application of the currently recognized nomina to particular populations has not yet been presented. We present a much-expanded multigene analysis of 234 representatives of the genus *Chondrodactylus* that supports the recognition of 6 species-level taxa, one without toepads, *C. angulifer,* as sister to five with pads: *C. bibronii, C. turneri, C. laevigatus, C. pulitzerae,* and *C. fitzsimonsi*. In general, the species can be recognized on the basis of the relative size of chin and gular scales, dorsal scalation, and head shape. However, the most widespread species, *C. laevigatus* is only very subtly distinct from *C. turneri,* with which it is likely parapatric in East Africa (although western populations of *C. laevigatus* are unambiguously diagnosable from all other congeners). Intraspecific divergences are high in some of the species. In *C. fitzsimonsi* there is evidence of shared nuclear haplotypes with *C. pulitzerae* and potential morphological evidence for hybridization or introgression with *C. laevigatus*. *Chondrodactylus turneri* exhibits a mitochondrial gene rearrangement that is unique among all geckos followed by an insertion of roughly 200 base pairs that do not correspond to known sequences. Most *Chondrodactylus* species are primarily distributed in arid to semiarid southwestern Africa, where as many as 4 species occur in sympatry in northern Namibia. In contrast, *C. turneri* is limited to the lowlands of the southeast and *C. laevigatus* follows the "arid-corridor" traversing sub-Saharan Africa southwest to northeast.

Key words: Reptilia, Gecko, Africa, Systematics, Biogeography

INTRODUCTION

Geckos of the genus *Chondrodactylus* are among the largest and most conspicuous nocturnal lizards in southern Africa. The genus was erected by Peters (1870) to accommodate a large ground-dwelling lizard, *C. angulifer,* initially found at Hantam, Oorlogsrivier, near the town of Calvinia, in what is now the Northern Cape Province of South Africa. The then-monotypic genus was distinguished by its short digits and absence of adhesive pads, with the toes clad instead by distinctive small pointed scales (Fig. 1 left and inset). The name is derived from the Greek χόνδρος *khóndros,* meaning, in this instance, "grain"—in reference to the small grain-like scales under the toes, not cartilage, the more frequent zoological meaning. *Chondrodactylus weiri* Boulenger, 1887 was described from an unspecified locality in the Kalahari but was quickly relegated to the synonymy of *C. angulifer* (Boulenger, 1910). No further taxa were allocated to *Chondrodactylus* until the description of *C. angulifer namibensis* by

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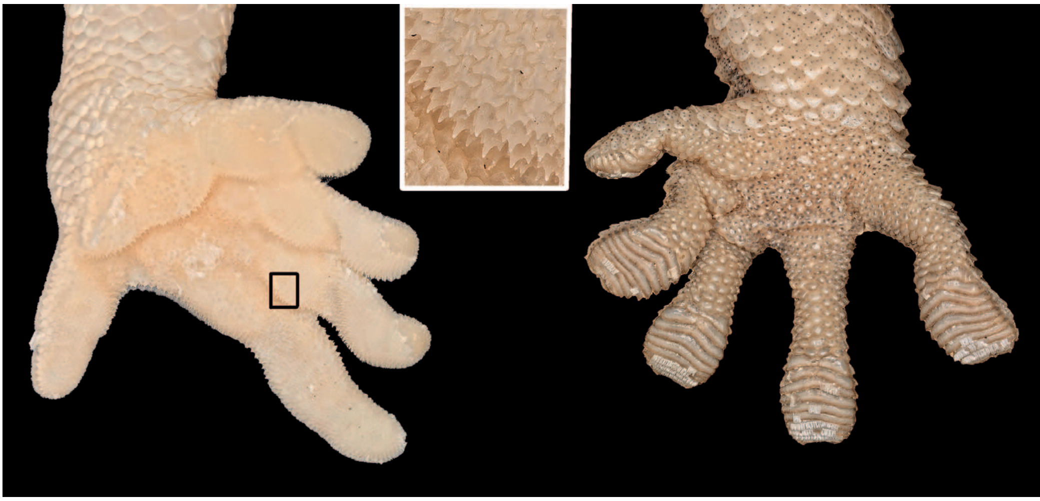

Figure 1. Left pes of *Chondrodactylus angulifer* (CAS 200011) and right pes of *C. bibronii* (CAS 266390) illustrating the radically different subdigital ornamentation of the terrestrial type species and the earliest described of the toe-padded members of the genus. Inset shows an enlargement of the spiny subdigital scales that give the genus its name.

Haacke (1976a). Despite a trend in herpetology for several decades to either synonymize or elevate non-nominotypic subspecies (Frost and Hillis, 1990), this taxon has retained its subspecific rank (e.g., Branch, 2014).

Chondrodactylus was subsequently recognized as a member of a proposed evolutionary unit within African geckos, the *Pachydactylus* group, that also included *Pachydactylus* Wiegmann, 1834, *Colopus* Peters, 1869, *Rhoptropus* Peters, 1869, *Elasmodactylus* Boulenger, 1895, *Palmatogecko* Andersson, 1908, and *Kaokogecko* Steyn and Haacke, 1966 in southern Africa and *Tarentola* Gray, 1825 and *Geckonia* Mocquard, 1895 in North Africa, the Mediterranean, and parts of the New World. All of these were united by the putative synapomorphy of hyperphalangy of digit I of both the manūs and pedes (Haacke, 1968, 1976b; Russell, 1972, 1976). Joger (1985), using immunological data, argued that the two geographic units did not comprise a monophyletic group, although morphologically derived phylogenies (e.g., Bauer, 1990; Kluge and Nussbaum, 1995) retrieved them as members of a single clade. Subsequently, *Kaokogecko* was synonymized with *Palmatogecko* (Kluge and Nussbaum, 1995) and *Geckonia* with *Tarentola* (Carranza et al., 2002). A series of molecular phylogenies (Lamb and Bauer, 2002, 2006; Bauer and Lamb, 2005) assumed *Tarentola* as an outgroup to the remaining hyperphalangic geckos and established a number of well-supported species groups within *Pachydactylus sensu stricto*. Lamb and Bauer (2002) confirmed the monophyly of 2 large-bodied clades within *Pachydactylus,* both of which had been previously recognized on morphological grounds, the *P. namaquensis* group (Branch et al., 1996), and the *P. bibronii* group.

More taxonomically inclusive analyses, incorporating *Chondrodactylus angulifer* (Bauer and Lamb, 2005; Lamb and Bauer, 2006), however, revealed that the *P. bibronii* group was, in reality, sister to *C. angulifer* and resulted in the reallocation of its constituent species to an expanded *Chondrodactylus,* which was recovered as the sister clade to *Pachydactylus* + *Colopus*.

The same work demonstrated that *Palmatogecko* was deeply embedded in *Pachydactylus,* with which it was formally synonymized. With near complete gekkotan sampling at the generic level (Gamble et al., 2008, 2012, 2015), *Tarentola* has been shown to have evolved hyperphalangy independently of *Pachydactylus* and its relatives, thus vindicating Joger (1985), and to belong to a trans-Atlantic clade, the Phyllodactylidae (Gamble et al., 2008), which is sister to the Gekkonidae *sensu stricto* (to which the *Pachydactylus* group belongs). The most recent phylogeny of the *Pachydactylus* group (Heinicke et al., 2017), with near taxon-complete sampling at the species level, recovered a topology similar to that of Bauer and Lamb (2005), except that the two species of *Colopus, C. wahlbergi* and *C. kochi,* have been subsumed into the *P. rangei* and *P. mariquensis* species groups, respectively. *Chondrodactylus,* now incorporating its highly autapomorphic padless terrestrial type species as sister to a clade of scansorial species (Fig. 1 right), is strongly and unambiguously supported as the immediate sister to *Pachydactylus* (Heinicke et al., 2017).

Heinicke et al. (2017) included six species of *Chondrodactylus* in their tree, *C. angulifer, C. bibronii, C. pulitzerae, C. fitzsimonsi, P. laevigatus,* and *P. turneri*. However, they provided no explanation for why these nomina were employed. Indeed, standard herpetological species lists for southern Africa in the preceding decades (e.g., Branch, 1998; Griffin, 2000; Alexander and Marais, 2007; Herrmann and Branch, 2013; Bates et al., 2014) would have typically acknowledged only 4 constituent taxa, one variably under 2 different names (*C. turneri* and *C. laevigatus*). The senior author of this paper bears responsibility for this disconnect because he and his colleagues used the names consistent with a series of ongoing taxonomic revisions of the group, which, over time, revealed a shifting landscape of more-and-more complete phylogenies, available names, and associated distributions. Although parts of the results of the taxonomic revision of *Chondrodactylus* have been used in the literature, sometimes extensively, the justification for the recognition of the six species included by Heinicke et al. (2017) has yet to be presented. In addition to creating uncertainties regarding the application of names in the technical literature and for conservation purposes, this situation has also caused confusion in the popular literature (e.g., Schleicher, 2018) and among the online citizen scientist community (e.g., iNaturalist; Reptile Atlas of Africa; Atlasing in Namibia). With this paper we take the opportunity to clarify the application of names to units within the genus and to evaluate both inter- and intraspecific patterns of *Chondrodactylus* diversity across southern Africa and, to the extent possible, provide morphological markers that may serve to identify specimens of the recognized species in this highly conservative genus.

MATERIALS AND METHODS

Molecular Sampling

Taxon sampling comprises 234 individuals representing all recognized species of *Chondrodactylus*. The majority of the distributional range of the genus in Angola, Namibia, and South Africa is well-represented, but north central and northeastern populations of *Chondrodactylus* spp. from Botswana, Zambia, Mozambique, and East Africa are poorly sampled. Zimbabwe is intermediate in this regard. Although this lack of sampling precludes investigating details of population substructure in parts of the continent, our results suggest that our ultimate taxonomic interpretations will be unaffected by the poorer sampling in the east. All samples sequenced, along with locality data, voucher information, and GenBank accession numbers, can be found in Table 1. For some samples represented

Table 1. Specimens of *Chondrodactylus* used in the molecular phylogenetic analysis of the genus and their corresponding GenBank numbers. Specimens marked "fragment" in one of the GenBank columns were represented by sequence data adequate to verify species identity but not sufficiently informative for meaningful placement within a species-level clade. These specimens have neither been included in Figure 2 nor have their sequences been deposited in GenBank. See Materials and Methods for most museum collection abbreviations. Additional museum identifiers are: INBAC = Instituto Nacional da Biodiversidade e Áreas de Conservação, Luanda; ISCED = Instituto Superior de Ciências de Educação da Huíla, Lubango; LSUMZ = Louisiana Museum of Natural History, Baton Rouge; LUN = Lúrio University, Nampula; NMB = National Museum Bloemfontein; NMZB = Natural History Museum of Zimbabwe, Bulawayo; TNHC = Texas Natural History Collections, University of Texas at Austin; UF = University of Florida, Florida State Museum of Natural History, Gainesville. Collection ID refers to field or tissue numbers: AMB = Aaron M. Bauer; ANG = PEM Angola; DGB = Donald G. Broadley; ESP = Elizabeth Scott Prendini; JB = Jon Boone; JET = James E. Titus-McQuillan; JM = Johan Marais; JVV = Jens V. Vindum; KHH = Koanaka Hills Expedition, Sam Houston State University; KTH = Krystal Tolley; LMH = Vincent Egan; MB, MBUR = Marius Burger; MCZ F, MCZ A, MCZ Z = MCZ field series; MDH = Morgan D. Heinz; MH = Michael Cunningham; PEM FN = PEM field number series; WC, WCDNA = Werner Conradie; WRB = William R. Branch . Country abbreviations: ANG = Angola, BOT = Botswana, MOZ = Mozambique, NAM = Namibia, RSA = Republic of South Africa, ZAM = Zambia, ZIM = Zimbabwe.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID		
							ND2	RAG1	PDC
C. angulifer									
MCZ F27515	—	Gobabeb	Erongo	NAM	−23.562	15.042	OK563256	—	—
MCZ F27516	—	Gobabeb	Erongo	NAM	−23.562	15.042	OK563257	—	—
MCZ F38623	MCZ R184984	Klein Aus Vista	Karas	NAM	−26.638	16.216	KM073687	JQ945289	JQ945357
MCZ F38624	MCZ R184985	Klein Aus Vista	Karas	NAM	−26.638	16.216	KY224209	KY224307	KY224257
MCZ F38631	MCZ R184992	13.2 km W Klein Aus Vista	Karas	NAM	−26.627	16.124	OK563258	OK563257	—
MCZ Z23096	MCZ R185978	Gaias Spring	Erongo	NAM	−20.767	14.02	OK563259	OK563258	—
JB 243	—	Prince Albert	W Cape	RSA	−33.23	22.02	OK563255	OK563463	—
AMB 4669	PEM R12426	Kodas Ruins, Richtersveld Natl. Pk.	N Cape	RSA	−28.235	16.942	JX041320	—	—
—	PEM R17498	Tankwa Karoo Natl. Pk.	W Cape	RSA	−32.585	19.558	OK563260	OK563259	—
C. bibronii									
JM 1554	—	Boegoeberg, Sperrgebeit	Karas	NAM	−27.9	15.92	OK563269	OK563472	—
AMB 5033	CAS 201900	Kerbe-Huk, 40km N Orjanemund	Karas	NAM	−28.229	15.99	OK563263	—	—
AMB 7647	MCZ R183771	Klein Aus Vista	Karas	NAM	−26.65	16.25	OK563265	—	—
MCZ F38644	MCZ R185004	Geister Schlucht, Klein Aus Vista	Karas	NAM	−26.677	16.228	OK563277	OK563269	—
MCZ F38645	MCZ R185005	Geister Schlucht, Klein Aus Vista	Karas	NAM	−26.677	16.228	OK563278	OK563261	—
MCZ A27045	NMNW 11139	Farm Zonderput, Gochas	Hardap	NAM	−24.822	18.772	OK563276	OK563266	—
MH 1499	—	Oorlogskloof Nat. Res.	N Cape	RSA	−31.445	19.07	OK563279	—	—
PEM FN1106	—	Pakhuis Pass	W Cape	RSA	−33.071	24.866	OK563280	—	—
PEM FN1204	CAS 197916	8.5 km S Plathuis	W Cape	RSA	−33.69	20.971	OK563283	OK563260	—
AMB 4805	CAS 200113	Pakhuis Pass	W Cape	RSA	−33.071	24.866	OK563262	—	—
AMB 4853	CAS 201841	28.3 km E Pofadder	N Cape	RSA	−29.021	19.652	JN543886	JN543930	KY224258
AMB 6205	CAS 214463	Farm Avondschijn, Askham	N Cape	RSA	−26.906	21.089	OK563264	OK563283	—
AMB 4510	LSUMZ 57285	Nicodaemus, Richtersveld Natl. Pk.	N Cape	RSA	−28.353	16.967	OK563261	—	—

TABLE 1. CONTINUED.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID ND2	GenBank ID RAG1	GenBank ID PDC
AMB 8169	MCZ R184392	Farm Newstead	E Cape	RSA	−32.101	26.255	OK563266	OK563264	—
JM 1592	NMB R09442	Farm no. 139, Askham, Gordonia Dist.	N Cape	RSA	−26.97	20.76	OK563270	OK563275	—
MB 21159	NMB R10429	Farm Lemoenkloof	N Cape	RSA	−30.879	23.66	OK563271	OK563265	—
MBUR 00719	PEM pending	Farm Tierberg	W Cape	RSA	−33.131	22.27	OK563275	OK563477	—
PEM FN1147	PEM R11196	Molteno Pass, Karoo Natl. Pk.	W Cape	RSA	−32.253	22.569	OK563281	OK563277	—
PEM FN1165	PEM R11242	Farm Rietvallei	W Cape	RSA	−33.636	21.681	OK563282	—	—
JM 1372	PEM R17759	130 km N Sutherland	N Cape	RSA	−31.595	20.02	OK563268	OK563278	—
JM 1339	PEM R17770	Koingaas	N Cape	RSA	−30.158	17.282	OK563267	OK563279	—
MB 21392	PEM R21045	9.2 km NW Bothithong	N Cape	RSA	−27.019	23.751	OK563272	OK563270	—
MB 21393	PEM R21046	9.2 km NW Bothithong	N Cape	RSA	−27.019	23.751	OK563273	—	—
MBUR 00572	PEM R24915	25 km WNW Jansenville	E Cape	RSA	−32.846	24.423	OK563274	OK563271	—
C. fitzsimonsi									
JVV 8691	CAS 254756	7.35 km NW Pico Azevedo	Namibe	ANG	−15.476	12.463	OK563289	—	—
JVV 8487	CAS 254833	Omauha Lodge, Iona NP	Namibe	ANG	−16.199	12.4	—	fragment	—
JVV 8511	CAS 254841	N Tambor, Iona NP	Namibe	ANG	−15.996	12.407	OK563322	OK563281	—
AMB 10611	CAS 266380	near Virei	Namibe	ANG	−16.091	12.836	OK563284	OK563282	—
AMB 10612	CAS 266381	near Virei	Namibe	ANG	−16.091	12.836	OK563285	OK563268	—
KTH 09-282 MBUR 2316	ISCED	Espinheira	Namibe	ANG	−15.914	12.395	OK563296	OK563491	—
KTH 09-281	PEM R17952	Espinheira	Namibe	ANG	−15.914	12.395	OK563295	OK563310	—
KTH 09-283	PEM R17954	Espinheira	Namibe	ANG	−15.914	12.395	OK563297	OK563311	—
JET 165/ ANG 330	PEM R21612	45 km SSE Bentiaba	Namibe	ANG	−14.658	12.527	fragment	—	—
JB 162	—	Henties Bay	Erongo	NAM	−22.17	14.31	OK563292	OK563488	—
JB 211	—	Opuwo	Kunene	NAM	−18.07	13.86	OK563293	OK563489	—
AMB 5994	CAS 206981	34 km S Epupa	Kunene	NAM	−17.249	13.224	OK563286	OK563280	—
MCZ F38576	MCZ R 184937	W Grootberg Pass	Kunene	NAM	−19.84	14.114	OK563300	OK563322	—
AMB 7546	MCZ R183733	Brandbergwesmyn	Erongo	NAM	−21.075	14.166	OK563288	OK563274	—
MCZ Z37876	MCZ R184191	Gaias	Kunene	NAM	−20.779	14.075	OK563319	OK563287	—
MCZ Z37879	MCZ R184194	False Gaias	Kunene	NAM	−20.787	14.112	OK563320	OK563286	—
MCZ F38575	MCZ R184936	W Grootberg Pass	Kunene	NAM	−19.84	14.114	OK563299	OK563289	—
MCZ F38600	MCZ R184961	Swakop River	Erongo	NAM	−22.638	14.728	OK563301	OK563284	—
MCZ F38601	MCZ R184962	Swakop River	Erongo	NAM	−22.638	14.728	OK563302	OK563285	—
MCZ F38602	MCZ R184963	Swakop River	Erongo	NAM	−22.638	14.728	OK563303	OK563292	—
MCZ F38603	MCZ R184964	Swakop River	Erongo	NAM	−22.638	14.728	OK563304	OK563293	—
MCZ F38944	MCZ R185694	101km N Opuwo	Kunene	NAM	−17.464	13.328	OK563305	—	—
MCZ F38961	MCZ R185695	Okongwati Rd	Kunene	NAM	−17.29	13.159	OK563306	OK563294	—

Table 1. Continued.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID		
							ND2	RAG1	PDC
MCZ Z23044	MCZ R185709	Gaias	Kunene	NAM	−20.779	14.075	OK563309	OK563296	—
MCZ Z23063	MCZ R185710	Gaias	Kunene	NAM	−20.779	14.075	OK563310	OK563288	—
MCZ Z23064	MCZ R185711	Gaias	Kunene	NAM	−20.779	14.075	OK563311	OK563319	—
MCZ Z23091	MCZ R185712	Gaias Spring	Kunene	NAM	−20.767	14.02	JN393945	KY224308	KY224259
MCZ Z23092	MCZ R185713	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563312	OK563320	—
MCZ Z23093	MCZ R185714	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563313	OK563299	—
MCZ Z23097	MCZ R185715	Gaias	Kunene	NAM	−20.779	14.075	OK563314	OK563300	—
MCZ Z23098	MCZ R185716	Gaias	Kunene	NAM	−20.779	14.075	OK563315	OK563301	—
MCZ Z23099	MCZ R185717	Gaias	Kunene	NAM	−20.779	14.075	OK563316	OK563302	—
MCZ Z23100	MCZ R185718	Gaias	Kunene	NAM	−20.779	14.075	OK563317	OK563303	—
MCZ Z23026	MCZ R185813	19.4 km E Coast on Rd to Brandberg Wesmyn	Erongo	NAM	−21.358	13.959	OK563307	OK563304	—
MCZ Z23027	MCZ R185814	19.4 km E coast on Brandbergwesmyn Rd.	Erongo	NAM	−21.358	13.959	OK563308	—	—
AMB 5995	NMNW	34 km S Epupa	Kunene	NAM	−17.249	13.224	OK563287	OK563486	—
JVV 1850	NMNW	30 km N Swakopmund	Erongo	NAM	−22.432	14.463	OK563294	EU293645	EU293712
MCZ A27673	NMNW	Epupa Falls	Kunene	NAM	−17.002	13.246	—	fragment	—
MCZ F37848	NMNW 11154	False Gaias	Kunene	NAM	−20.731	14.127	OK563298	OK563306	—
MCZ Z37849	NMNW 11171	False Gaias	Kunene	NAM	−20.731	14.127	OK563318	OK563309	—
MCZ Z37880	NMNW 11008	False Gaias	Kunene	NAM	−20.787	14.112	OK563321	OK563305	—
AMB 7547	NMNW 10602	Brandbergwesmyn	Erongo	NAM	−21.075	14.166	fragment	—	—
ESP 894	TM 85199	Hartmann's Valley, 1 km S Cunene River	Kunene	NAM	−17.183	12.147	OK563291	—	—
ESP 801	TM 85201	Ga'aseb Kloof, Brandberg	Erongo	NAM	−21.237	14.581	OK563290	—	—
C. laevigatus									
AMB 10171	CAS 266365	Infotur Hotel, Namibe City	Namibe	ANG	−15.209	12.102	—	fragment	—
AMB 10173	INBAC	Infotur Hotel, Namibe City	Namibe	ANG	−15.209	12.102	—	fragment	—
ANG 303	PEM R20478	Mpupa Falls	Cuando Cubango	ANG	−17.509	20.066	OK563352	—	—
JET 130/ANG 295	PEM R21618	47 km SSE Bentiaba	Namibe	ANG	−14.658	12.527	—	fragment	—
MCZ Z37837	PEM pending	Ghanzi	Ghanzi	BOT	−21.734	21.657	OK563401	OK563582	—
MCZ Z37838	PEM pending	Ghanzi	Ghanzi	BOT	−21.734	21.657	OK563402	OK563583	—
KHH 007	TNHC 68750	Koanaka Hills	North West	BOT	−20.158	21.195	OK563356	OK563361	—
JVV 2993	CAS 198952	20.4 km N Kajiado	Rift Valley	KEN	−1.924	36.628	OK563353	—	—
WCDNA 1013	LUN	20 km E Ribaue	Nampula	MOZ	−14.98	38.505	OK563408	—	—
WCDNA 997	LUN	20 km E Ribaue	Nampula	MOZ	−14.98	38.505	OK563409	—	—
MDH 02	—	Namutoni, Etosha	Oshikoto	NAM	−18.807	16.941	OK563354	OK563543	—
MDH 03	—	Namutoni, Etosha	Oshikoto	NAM	−18.807	16.941	OK563355	OK563544	—
AMB 6881	AMS	East Kamanjab	Kunene	NAM	−19.751	15.094	OK563332	OK563523	—

TABLE 1. CONTINUED.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID		
							ND2	RAG1	PDC
AMB 3095	CAS 176265	Farm Franken, Kamanjab	Kunene	NAM	−19.605	14.763	OK563323	—	—
AMB 5875	CAS 206930	Farm Daweb, Maltahöhe	Hardap	NAM	−24.863	16.992	OK563326	OK563316	—
AMB 5882	CAS 206933	Oanab Dam, Rehoboth	Hardap	NAM	−23.32	17.001	OK563327	OK563317	—
AMB 6002	CAS 206984	4.3 km S Luhebu	Otjozondjupa	NAM	−19.469	19.728	OK563328	OK563307	—
AMB 6844	CAS 223896	Farm Narudas	Karas	NAM	−27.37	18.858	OK563331	OK563308	—
AMB 6919	CAS 223916	Para Camp, Sesfontein	Kunene	NAM	−19.132	13.589	—	fragment	—
MCZ Z23089	MCZ R185822	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563399	OK563580	—
AMB 7564	MCZ R183742	22.4 km N Ugab R on Gaias Rd.	Kunene	NAM	−20.764	14.092	OK563335	OK563290	—
AMB 7618	MCZ R183763	Kamanjab Lodge	Kunene	NAM	−19.629	14.815	OK563338	OK563325	—
MCZ A38262	MCZ R184227	19 km S Helmeringhausen	Karas	NAM	−26.125	16.8	OK563364	—	—
MCZ Z37891	MCZ R184281	8.5 km N Palmwag	Kunene	NAM	−19.832	13.886	OK563403	OK563332	—
MCZ Z37942	MCZ R184313	Jct. Marienfluss and Orupembe Rds.	Kunene	NAM	−18.068	12.629	OK563404	OK563337	—
MCZ Z37943	MCZ R184314	Jct. Marienfluss and Orupembe Rds.	Kunene	NAM	−18.068	12.629	OK563405	OK563323	—
MCZ A38480	MCZ R184819	Farm Savanna	Karas	NAM	−27.376	18.493	KY224211	KY224310	KY224260
MCZ F38488	MCZ R184827	Avis Dam	Khomas	NAM	−22.579	17.101	OK563380	OK563354	—
MCZ F38492	MCZ R184831	Avis Dam	Khomas	NAM	−22.579	17.101	OK563381	OK563355	—
MCZ F38496	MCZ R184835	Avis Dam	Khomas	NAM	−22.579	17.101	OK563382	OK563399	—
MCZ F38497	MCZ R184836	Avis Dam	Khomas	NAM	−22.579	17.101	OK563383	OK563366	—
MCZ F38498	MCZ R184837	Windhoek	Khomas	NAM	−22.577	17.089	OK563384	OK563367	—
MCZ F38499	MCZ R184838	Windhoek	Khomas	NAM	−22.577	17.089	OK563385	OK563372	—
MCZ F38503	MCZ R184859	4.9 km E Waterberg Guest House	Otjozondjupa	NAM	−20.645	17.136	OK563386	OK563335	—
MCZ F38504	MCZ R184860	6 km E Waterberg Guest House	Otjozondjupa	NAM	−20.642	17.154	OK563387	OK563338	—
MCZ F38523	MCZ R184877	Farm Uisib	Otjozonjupa	NAM	−19.553	17.217	OK563388	OK563364	—
MCZ F38524	MCZ R184878	Farm Uisib	Otjozonjupa	NAM	−19.553	17.217	OK563389	OK563403	—
MCZ F38550	MCZ R184912	22.4 km E Kamanjab	Kunene	NAM	−19.666	15.042	OK563390	OK563404	—
MCZ F38674	MCZ R185063	32 km W Guruchab Pass	Karas	NAM	−26.605	18.478	OK563391	OK563405	—
MCZ Z23045	MCZ R185815	Gaias	Kunene	NAM	−20.779	14.075	OK563392	OK563373	—
MCZ Z23046	MCZ R185816	Gaias	Kunene	NAM	−20.779	14.075	OK563393	OK563374	—
MCZ Z23047	MCZ R185817	Gaias	Kunene	NAM	−20.779	14.075	OK563394	OK563375	—
MCZ Z23077	MCZ R185819	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563396	OK563376	—
MCZ Z23087	MCZ R185820	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563397	OK563377	—
MCZ Z23088	MCZ R185821	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563398	OK563378	—
MCZ Z23090	MCZ R185823	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563400	OK563379	—
AMB 8743	MCZ R188210	Shamvura	Kavango	NAM	−18.035	20.861	OK563339	OK563410	—

TABLE 1. CONTINUED.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID ND2	GenBank ID RAG1	GenBank ID PDC
AMB 8786	MCZ R188220	Shamvura	Kavango	NAM	−18.035	20.861	OK563344	OK563380	—
AMB 8809	MCZ R188229	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563351	OK563381	—
MCZ A27059	MCZ R188271	Kobos	Hardap	NAM	−23.626	16.693	OK563358	OK563382	—
AMB 8062	MCZ R190219	Epupa Falls	Kunene	NAM	−17.002	13.246	—	fragment	—
AMB 8067	MCZ R190222	Epupa Falls	Kunene	NAM	−17.002	13.246	—	fragment	—
AMB 8162	MCZ R190228	Epupa Falls	Kunene	NAM	−17.002	13.246	—	fragment	—
MCZ F28714	MCZ R193185	Farm Omandumba	Erongo	NAM	−21.495	15.628	OK563368	—	—
MCZ F28715	MCZ R193186	Farm Omandumba	Erongo	NAM	−21.495	15.628	OK563369	—	—
MCZ F28778	MCZ R193235	Farm Ohange	Otjozondzupa	NAM	−19.516	17.572	OK563370	—	—
MCZ F28815	MCZ R193263	Farm Namases	Otjozondjupa	NAM	−21.968	16.926	OK563371	—	—
AMB 5874	NMNW	S Maltahöhe	Hardap	NAM	−24.864	16.992	OK563325	OK563516	—
AMB 7617	NMNW	Kamanjab Lodge	Kunene	NAM	−19.629	14.815	OK563337	OK563528	—
MCZ A38930	NMNW	58 km W Kamanjab	Kunene	NAM	−19.542	14.258	OK563366	OK563553	—
MCZ F28655	NMNW	Farm Omandumba	Erongo	NAM	−21.495	15.628	OK563367	—	—
MCZ F28816	NMNW	Farm Namases	Otjozondjupa	NAM	−21.968	16.926	OK563372	—	—
MCZ Z23048	NMNW	Gaias	Kunene	NAM	−20.779	14.075	OK563395	OK563576	—
AMB 7119	NMNW 10575	25 km WNW Usakos	Erongo	NAM	−21.62	14.985	OK563334	OK563390	—
AMB 7118	NMNW 10578	25 km WNW Usakos	Erongo	NAM	−21.62	14.985	OK563333	OK563391	—
AMB 7565	NMNW 10606	22.4 km N Ugab R on Gaias Rd.	Kunene	NAM	−20.764	14.092	OK563336	OK563392	—
AMB 8805	NMNW 10847	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563347	OK563393	—
AMB 8807	NMNW 10848	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563349	OK563394	—
AMB 8783	NMNW 10849	10.7 km E Mbwata Rd. Jct.	Kavango	NAM	−18.028	20.99	OK563342	OK563396	—
AMB 8785	NMNW 10851	Shamvura	Kavango	NAM	−18.035	20.861	OK563343	OK563397	—
AMB 8806	NMNW 10852	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563348	OK563398	—
AMB 8808	NMNW 10853	Gaias Spring	Kunene	NAM	−20.767	14.02	OK563350	OK563400	—
MCZ Z37944	NMNW 10858	Jct. Marienfluss and Orupembe Rds.	Kunene	NAM	−18.068	12.629	OK563406	OK563339	—
MCZ A27060	NMNW 10859	Kobos	Hardap	NAM	−23.626	16.693	OK563359	OK563344	—
MCZ A38263	NMNW 10860	19 km S Helmeringhausen	Karas	NAM	−26.125	16.8	OK563365	OK563351	—
AMB 8792	NMNW 10861	36 km W Rundu	Kavango	NAM	−18.155	19.526	OK563346	OK563358	—
AMB 8745	NMNW 10862	Shamvura	Kavango	NAM	−18.035	20.861	OK563340	OK563362	—
AMB 8791	NMNW 10863	36 km W Rundu	Kavango	NAM	−18.155	19.526	OK563345	OK563363	—
AMB 8746	NMNW 10864	Shamvura	Kavango	NAM	−18.035	20.861	OK563341	OK563360	—
WC12-A012	PEM R20027	Rundu	Kavango	NAM	−17.874	19.832	OK563407	—	—
ESP 878	TM 85231	17 km SW Okandombo	Kunene	NAM	−17.165	13.373	—	fragment	—
AMB 3843	CAS 186363	16 km S Khuboes Jct.	N Cape	RSA	−28.587	16.943	OK563324	OK563315	—
MCZ F38437	MCZ R184775	91.4 km E Springbok	N Cape	RSA	−29.339	18.731	OK563373	OK563324	—
MCZ F38438	MCZ R184776	91.4 km E Springbok	N Cape	RSA	−29.339	18.731	OK563374	OK563353	—

TABLE 1. CONTINUED.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID		
							ND2	RAG1	PDC
MCZ F38439	MCZ R184777	Aggeneyes	N Cape	RSA	−29.246	18.838	OK563375	OK563326	—
MCZ F38440	MCZ R184779	Aggeneyes	N Cape	RSA	−29.246	18.838	OK563376	OK563327	—
MCZ F38460	MCZ R184800	Farm Daberas	N Cape	RSA	−28.495	19.954	OK563377	OK563328	—
MCZ A38463	MCZ R184803	3km N Pofadder	N Cape	RSA	−29.081	19.414	OK563378	OK563331	—
MCZ F38469	MCZ R184809	19 km N Pofadder	N Cape	RSA	−28.968	19.394	OK563379	OK563329	—
MB 404	ZFMK 88662	Lusaka	Lusaka	ZAM	−15.39	28.32	OK563357	—	—
AMB 6182	CAS 266395	Elim Mission	Manicaland	ZIM	−17.604	32.776	OK563329	OK563321	—
AMB 6183	CAS 266396	Elim Mission	Manicaland	ZIM	−17.604	32.776	OK563330	OK563298	—
MCZ A27630	MCZ R190542	Chilila Camp, Lake Kariba	Matabeleland North	ZIM	−17.601	27.411	OK563362	OK563383	—
MCZ A27640	MCZ R190550	Chilila Camp, Lake Kariba	Matabeleland North	ZIM	−17.601	27.411	OK563363	OK563384	—
MCZ A27292	MCZ R190572	Chilila Camp, Lake Kariba	Matabeleland North	ZIM	−17.601	27.415	OK563360	OK563385	—
MCZ A27294	MCZ R190573	Chilila Camp, Lake Kariba	Matabeleland North	ZIM	−17.601	27.411	OK563361	OK563386	—
C. pulitzerae									
JVV 8413	CAS 254791	Iona Natl. Park	Namibe	ANG	−16.812	12.271	OK563437	OK563368	—
JVV 8360	CAS 254796	Espenhierra, Iona NP	Namibe	ANG	−16.786	12.358	—	fragment	—
JVV 8385	CAS 254808	Espenhierra, Iona NP	Namibe	ANG	−16.785	12.355	—	fragment	—
JVV 8421	CAS 254814	Espenhierra, Iona NP	Namibe	ANG	−16.787	12.358	—	fragment	—
JVV 8430	CAS 254815	Espenhierra, Iona NP	Namibe	ANG	−16.787	12.358	—	fragment	—
JVV 8431	CAS 254816	Espenhierra, Iona NP	Namibe	ANG	−16.788	12.357	—	fragment	—
JVV 8434	CAS 254817	Espenhierra, Iona NP	Namibe	ANG	−16.787	12.358	—	fragment	—
JVV 8435	CAS 254818	Espenhierra, Iona NP	Namibe	ANG	−16.788	12.357	—	fragment	—
JVV 8339	CAS 254830	Omauha Lodge, Iona NP	Namibe	ANG	−16.199	12.401	—	fragment	—
JVV 8330	CAS 254843	Omauha Lodge	Namibe	ANG	−16.198	12.401	OK563422	OK563369	—
JVV 8611	CAS 254915	1.8 km W Caraculo	Namibe	ANG	−15.016	12.642	OK563436	OK563370	—
AMB 9930	CAS 263056	Chimalavera	Benguela	ANG	−12.834	13.17	OK563417	OK563371	—
AMB 9931	CAS 263057	Chimalavera	Benguela	ANG	−12.834	13.17	OK563418	OK563395	—
AMB 9933	CAS 263058	Chimalavera	Benguela	ANG	−12.834	13.17	OK563419	OK563401	—
AMB 10027	CAS 263080	Chimalavera	Benguela	ANG	−12.792	13.127	OK563412	OK563402	—
MCZ A36430	CAS 263108	Quiçama National Park	Luanda	ANG	−9.184	13.371	—	fragment	—
MCZ A36496	CAS 263109	Quiçama National Park	Luanda	ANG	−9.184	13.371	OK563411	—	—
AMB10199	CAS 266367	Serra Da Neve	Namibe	ANG	−13.777	13.259	OK563433	OK563334	—
AMB10201	CAS 266368	Serra Da Neve	Namibe	ANG	−13.777	13.259	OK563434	—	—
AMB10244	CAS 266371	Dolondolo	Namibe	ANG	−13.813	13.136	OK563435	—	—
AMB10486	CAS 266372	Virei	Namibe	ANG	−16.120	12.835	—	fragment	—
AMB10487	CAS 266373	Virei	Namibe	ANG	−16.120	12.835	fragment	—	—
AMB 10029	INBAC	Chimalavera	Benguela	ANG	−12.792	13.127	OK563413	OK563589	—
AMB 10030	INBAC	Chimalavera	Benguela	ANG	−12.792	13.127	OK563414	OK563590	—
AMB 10035	INBAC	Chimalavera	Benguela	ANG	−12.792	13.127	OK563415	—	—
AMB 10170	INBAC	Infotur Hotel, Namibe City	Namibe	ANG	−15.209	12.102	—	fragment	—

Table 1. Continued.

							GenBank ID		
Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	ND2	RAG1	PDC
AMB 9948	INBAC	Chimalavera	Benguela	ANG	−12.834	13.17	OK563421	—	—
KTH 09-210/ MBUR 2237	ISCED	Omauha Lodge, Iona Nat. Pk.	Namibe	ANG	−16.201	12.402	OK563427	OK563601	—
KTH 09-248/ MBUR 2280	ISCED	Espinheira	Namibe	ANG	−16.789	12.358	OK563428	OK563602	—
KTH 09-199	PEM R17955	Rd. to Omauha Lodge	Namibe	ANG	−15.99	12.358	OK563425	OK563348	—
KTH 09-249	PEM R17957	Espinheira	Namibe	ANG	−16.789	12.358	OK563429	OK563350	—
KTH 09-148	PEM R17958	50 km E Namibe	Namibe	ANG	−15.017	12.557	OK563424	OK563406	—
KTH 09-275	PEM R17959	20 km N Omauha	Namibe	ANG	−16.074	12.433	OK563430	OK563359	—
KTH 09-209	PEM R17960	Omauha Lodge, Iona Nat. Pk.	Namibe	ANG	−16.201	12.402	OK563426	OK563365	—
JET 85/ ANG 248	PEM R21611	Cambambe	Cuanza Norte	ANG	−9.751	14.514	OK563423	OK563346	—
AMB 9932	UF 187180	Chimalavera	Benguela	ANG	−12.834	13.17	OK563420	OK563340	—
AMB 9918	UF 188782	Chimalavera	Benguela	ANG	−12.834	13.17	OK563416	OK563345	—
JVV 1759	CAS 193828	Munutum River	Kunene	NAM	−18.159	12.178	KY224210	KY224309	—
MCZ Z37921	MCZ R184202	Sesfontein	Kunene	NAM	−19.132	13.589	OK563432	OK563342	—
MCZ A38203	MCZ R184328	10 km N Red Drum	Kunene	NAM	−17.771	12.551	OK563431	OK563343	—
MCZ Z37913	NMNW 10850	Para Camp, Sesfontein	Kunene	NAM	−19.132	13.589	—	fragment	—
ESP 874	TM 85202	7 km E Swartboosdrift	Kunene	NAM	−17.358	13.883	—	fragment	—
C. turneri									
WRBbots1	—	Mashatu	Central	BOT	−22.116	29.091	OK563460	OK563630	—
MCZ Z38876	CAS 234213	Matlala	Limpopo	RSA	−23.753	29.023	OK563458	OK563341	—
MCZ Z38879	CAS 234214	Matlala	Limpopo	RSA	−23.753	29.023	OK563459	OK563407	—
LMH 000049	CAS 234232	Mont Blanc, Makgabeng	Limpopo	RSA	−24.265	28.776	OK563449	OK563352	—
MBUR 02850	CAS 248767	Cleveland Nat. Res.	Limpopo	RSA	−24.014	31.206	OK563450	OK563356	—
MBUR 02851	CAS 248768	Cleveland Nat. Res.	Limpopo	RSA	−24.014	31.206	OK563451	OK563408	—
MCZ A27190	CAS 248787	Farm Vrieden	Limpopo	RSA	−22.706	29.829	OK563454	OK563409	—
MCZ A27191	CAS 248788	Farm Vrieden	Limpopo	RSA	−22.706	29.829	OK563455	OK563357	—
MCZ A27172	CAS 248792	7.2 km W of Percy Fyfe-Mokopane junction	Limpopo	RSA	−23.97	29.052	OK563452	OK563437	—
MCZ A27173	CAS 248793	7.2 km W of Percy Fyfe-Mokopane junction	Limpopo	RSA	−23.97	29.052	OK563453	OK563422	—
AMB 6132	CAS 266394	Tshipise	Limpopo	RSA	−22.606	30.176	OK563438	OK563436	—
AMB 8187	MCZ R184410	Farm Lilie	Limpopo	RSA	−24.066	30.832	KM073688	KM073525	KM073612
AMB 8201	MCZ R184419	Farm Lilie	Limpopo	RSA	−24.066	30.832	OK563439	OK563418	—
AMB 8300	MCZ R184445	Farm Vrieden	Limpopo	RSA	−22.705	29.828	OK563440	OK563419	—
AMB 8336	MCZ R184483	Waterpoort	Limpopo	RSA	−22.908	29.618	OK563441	OK563412	—

TABLE 1. CONTINUED.

Collection ID	Museum ID	Locality	Region/ Province	Country	Latitude	Longitude	GenBank ID		
							ND2	RAG1	PDC
AMB 8606	PEM R17564	Platinum Mine	Limpopo	RSA	−24.614	30.124	OK563442	OK563413	—
AMB 8607	PEM R17565	Platinum Mine	Limpopo	RSA	−24.614	30.124	OK563443	OK563414	—
MCZ A27565	—	Malilangwe	Masvingo	ZIM	−21.053	31.931	OK563456	—	—
MCZ A27566	—	Malilangwe	Masvingo	ZIM	−21.053	31.931	OK563457	OK563627	—
DGB 693	NMZB 17871	Malilangwe	Masvingo	ZIM	−21.003	31.807	OK563445	OK563411	—
DGB 701	NMZB 17879	Malilangwe	Masvingo	ZIM	−21.044	31.917	OK563446	OK563433	—
DGB 733	NMZB 17912	Chilo Lodge	Manicaland	ZIM	−21.25	32.351	OK563447	OK563434	—
DGB 734	NMZB 17913	Chilo Lodge	Manicaland	ZIM	−21.25	32.351	OK563448	OK563435	—
AMB 8886	PEM R18277	Bulawayo	Bulawayo	ZIM	−20.197	28.623	OK563444	OK563415	—

by partial data, molecular data were used to confirm species identity, but missing data precluded meaningful intraspecific placement. These samples, including 24 represented by RAG1 data only and an additional 7 with limited ND2 data, were included in initial phylogenetic analyses but were ultimately excluded from the final analyses and, thus, are not represented in trees nor are they included in calculations of support values or patristic distances. To root the tree we included 2 outgroup species, *Pachydactylus bicolor* and *Pachydactylus rangei*.

Molecular and Phylogenetic Methods

Genomic DNA was isolated from ethanol-preserved tissues via Qiagen DNeasy blood and tissue kit (Valencia, California, USA). We chose to target mitochondrial and nuclear loci that have proven useful in assessing inter- and intraspecific relationships among gekkotans, providing us the opportunity to take advantage of preexisting sequence data. For samples unique to this study, segments of the mitochondrial locus ND2 (NADH dehydrogenase subunit 2; 1,052 base pairs [bp]), and nuclear loci RAG1 (recombination activating gene 1; 1,068 bp) and PDC (Phosducin; 394 bp), were amplified under standard protocols in 25-mL reactions with published and novel primer pairs (see Table 2). Amplified products were visualized on 1.5% agarose gels and purified using AMPure magnetic bead system (Agencourt Bioscience). Sequencing reactions used ABI Prism BigDyeTerminator (Applied Biosystems), and product was purified using Agencourt CleanSeq magnetic bead system (Agencourt Bioscience). Sequencing was carried out on an automated ABI 3730 for electrophoresis, and electropherograms were imported into Geneious 9.0 (https://www.geneious.com) for assembly and subsequent alignment via MAFFT. We inspected all alignments by eye and made adjustments as needed.

Table 2. Primers used for PCR amplification and sequencing.

Gene	Primer	Sequence	Source	Use
ND2	ND2 f17	5′-TGACAAAAAATTGCNCC-3′	Macey et al. (2000)	Sequencing
ND2	CO1 R1	5′-AGRGTGCCAATGTCTTTGTGRTT-3′	Macey et al. (1997)	Amplification and Sequencing
ND2	CO1 R8	5′-GCTATGTCTGGGGCTCCAATTAT-3′	Weisrock et al. (2001)	Amplification and Sequencing
tRNATrp	Trp R3	5′-TTTAGGGCTTTGAAGGC-3′	Greenbaum et al. (2007)	Sequencing
tRNAMet	Met F1	5′-AAGCTTTCGGGCCCATACC-3′	Macey et al. (1997)	Amplification and Sequencing
ND2	Chondro ND2 r870	5′-CGGGTRTARAAGTAWAGGCTKGGKAGGCT-3′	This study	Amplification and Sequencing
ND2	Chondro ASN r1	5′-TYGTGGGATAGARGCCCKYC-3′	This study	Amplification and Sequencing
ND2	Chondro ND2 f174	5′- MCACCACCCHCGAGCAACAGA-3′	This study	Sequencing
RAG1	RAG1 pf1	5′-YAWGAAATTTKCTGGAAATTCAAGCT-3′	Portik et al. (2013)	Amplification and Sequencing
RAG1	RAG1 pr1	5′-GTCTYGGTCGGCCACCTTTGTT-3′	Portik et al. (2013)	Amplification and Sequencing
RAG1	RAG1 f700	5′-GGAGACATGGACACAATCCATCCTAC-3′	Bauer et al. (2007)	Sequencing
RAG1	RAG1 r700	5′-TTTGTACTGAGATGGATCTTTTTGCA-3′	Bauer et al. (2007)	Sequencing
PDC	PHOf2	5′-AGATGAGCATGCAGGAGTATGA-3′	Bauer et al. (2007)	Amplification and Sequencing
PDC	PHOr1	5′-TCCACATCCACAGCAAAAAACTCCT-3′	Bauer et al. (2007)	Amplification and Sequencing

To estimate phylogenetic relationships we used IQTree 2 (Minh et al., 2020). To start we analyzed each locus individually using a single representative of each species to investigate among-locus concordance. In addition to the 3 loci forming the core of this study, we also included data from the nuclear gene KIF24 (kinesin family member 24; 592 bp) from the data set of Heinicke et al. (2017). Following this exercise, we concatenated the fully sampled alignments and implemented a concatenated partition-by-locus model (option *-q*; Chernomor et al., 2016) with preferred substitution models determined by ModelFinder (Kalyaanamoorthy et al., 2017). We estimated branch support using the ultrafast bootstrap (BS) approximation with 1,000 replicates (option *-bb 1000*; Hoang et al., 2018). Uncorrected pairwise p-distances (mean and range) for the mitochondrial locus ND2 were calculated for ingroup taxa using Geneious 9.0.

Morphology and Species Concept

We use genetic data in combination with morphology in an integrative taxonomic framework (Padial et al., 2010) to apply names to taxa within the genus *Chondrodactylus*. We adopt the general lineage species concept (de Queiroz, 1999) and recognize species based on a combination of characters suggesting evolutionary independence. Padded members of the genus share a highly conservative morphology and a previous attempt to delimit species within *Chondrodactylus* by applying a morphometric or statistical approach (Benyr, 1995) did not adequately discriminate among the constituent taxa. As a consequence, for morphological evidence we focused on discrete diagnostic characteristics and grossly observable proportional differences to try to identify features associated with the genetic lineages identified. When possible, we have provided numerical estimates of proportional values, such as head width, but these may vary with sex and age. Head depth, another potentially useful diagnostic trait is even more difficult to meaningfully quantify, as variation due to the position of fixation far exceeds lineage-specific differences.

Note that preserved specimen images have been digitally altered to provide a uniform background and optimize contrast and brightness. Features of the specimens have not been altered.

We examined and confirmed the specific identity of available specimens, including all known primary type material, of toepad-bearing *Chondrodactylus* in the collections of the California Academy of Sciences, San Francisco (CAS); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); National Museum of Namibia, Windhoek (NMNW); Ditsong National Museum of Natural History, Pretoria (TM); Museum für Naturkunde, Berlin (ZMB); Zoologisches Museum Hamburg (ZMH); Carnegie Museum of Natural History, Pittsburgh (CM); Academy of Natural Sciences of Drexel University, Philadelphia (ANSP); The Natural History Museum, London (NHM, but the older BMNH retained here for continuity with respect to older specimen references); Muséum d'Histoire Naturelle, Genève (MHNG); Musée d'Histoire Naturelle de La Chaux-de-Fonds (MHNC); Zoologische Staatssammlung München (ZSM); Naturhistorisches Museum, Wien (NMW); Museu Regional do Dundo (MD); Port Elizabeth Museum (PEM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SMF); Senckenberg Naturhistorische Sammlungen, Dresden (MTD); Natural History Museum of Los Angeles County (LACM); American Museum of Natural History, New York (AMNH); Iziko South African Museum, Cape Town (SAM); Hungarian Natural History Museum, Budapest (HNHM); McGregor Museum, Kimberley (MMK); and Australian Museum, Sydney (AMS). We also gathered additional museum and other records for mapping purposes. Haacke (1976a) provided a lengthy list of specimens and localities for *C. angulifer*. In cases of uncertain specific identity, the relevant curators and collections managers were consulted and, when possible, photos or other verification allowing assignment to species were obtained.

Distribution

Chondrodactylus as a whole extends throughout Africa from near the Equator in Kenya through to South Africa, exclusive of near coastal areas of the southwestern Cape (although there is an introduced population in the Kommetjie area of Cape Town; Rose, 1962; Branch, 2014) and the grassland biome that is largely coincident with the Highveld and Drakensberg of South Africa and Lesotho. They are also absent from most of the east coastal regions south of Zululand, KwaZulu-Natal. The records mapped here are not exhaustive, but they provide an adequate picture of the distribution of the members of the genus. When available, decimal latitude/longitude records were used or records were georeferenced as precisely as possible using the WGS84 map datum. Quarter degree square (QDS) records (see Bates et al., 2014) were plotted as points in the center of each QDS grid square, which is adequate for the subcontinental level of mapping used herein.

Distributional data were obtained from South Africa and Swaziland chiefly from Bates et al. (2014), data from Namibia have been gathered by AMB in the course of the preparation of a forthcoming book on the herpetofauna of Namibia (data available from authors). Angolan records include those from Marques et al. (2018) and from a JRS Biodiversity Foundation sponsored project. Records from Zambia, Zimbabwe, Botswana, and Malawi were kindly provided

TABLE 3. UNCORRECTED INTERSPECIFIC AND INTRASPECIFIC PATRISTIC DISTANCES (AS PERCENTAGES) FOR THE MITOCHONDRIAL LOCUS ND2 AMONG *CHONDRODACTYLUS* SPECIES AND POPULATIONS. MEAN DISTANCE IS SHOWN IN PARENTHESES ALONGSIDE RANGES. VALUES WERE CALCULATED ONLY ON THE BASIS OF SPECIMENS FOR WHICH ND2 DATA WERE SUBSTANTIALLY COMPLETE.

	C. angulifer	*C. bibronii*	*C. pulitzerae*	*C. fitzsimonsi*	*C. laevigatus*	*C. turneri*
C. angulifer	0–16 (11)					
C. bibronii	27–30 (28)	0–8 (6)				
C. pulitzerae	31–33 (32)	22–24 (23)	1–17 (12)			
C. fitzsimonsi	30–33 (32)	21–24 (22)	18–19 (18)	0–12 (8)		
C. laevigatus	29–32 (31)	21–24 (23)	18–21 (20)	15–17 (16)	0–14 (8)	
C. turneri	28–33 (31)	22–24 (23)	18–21 (20)	16–22 (18)	13–20 (17)	0–10 (7)

by the late Donald G. Broadley, who had accumulated them as part of the "Reptilia Zambesiaca" project stemming from his doctoral work. This has been supplemented by localities provided by Harith Farooq (Mozambique) and Darren Pietersen (Zambia, Malawi, Mozambique). Records from Kenya were provided by Steven Spawls. These records were augmented by data from GBIF, including photo-vouchered records, and from the literature, particularly Loverdige (1947) and the unpublished thesis of Benyr (1995). Records of *C. angulifer* were mapped without typically checking identity because the distinctiveness of this taxon effectively precludes misidentification. Records of some padded *Chondrodactylus* were accepted without examination of the associated vouchers if they derived from areas that support only a single species (e.g., most of South Africa and southeastern Africa north of the Zambezi River).

RESULTS

Molecular Phylogenetics

The final mito-nuclear data set included 3,110 bases, 807 of which were parsimony-informative (ND2–672; RAG1–104; PDC–20; KIF24–11). ModelFinder selected the GTR model for all 4 locus partitions. Individual nuclear markers alone provided little resolution but no strong conflict among loci and were thus combined in a single concatenated analysis. The resultant maximum-likelihood tree of the locus partitioned concatenated alignment (Fig. 2) provides support (BS >95%) for interspecific relationships among *Chondrodactylus* species, as well as the monophyly of all six recognized taxa (BS 100%). This includes well-supported divergent subclades in *C. pulitzerae, C. fitzsimonsi, C. turneri,* and *C. laevigatus*. Patristic distances among these clades, as well as all species, are reported in Table 3.

Chondrodactylus is recovered as strongly monophyletic, with *C. angulifer* as sister to all padded members of the genus (100% BS). Although specimens assignable (based on distribution) to the nominotypical form are monophyletic, they make *C. a. namibensis* paraphyletic (Fig. 2A). On this basis, and modest intraspecific pairwise genetic distances (Table 3), we tentatively regard the species as monotypic.

Chondrodactylus bibronii was recovered as basal to all other samples of scansorial *Chondrodactylus*. There is well-supported substructure within *C. bibronii*, although divergences are relatively shallow, with a general trend of specimens from the northwestern portion of the range (southern Namibia and northern Northern Cape, South Africa) being basal to more easterly and southerly clades (Fig. 2A).

Among remaining members of the genus, *C. pulitzerae* is sister to its congeners, receiving strong support (100% BS). There are deep divergences within the *C. pulitzerae* clade, with one well-supported (100% BS) lineage including all specimens from Benguela as well as some individuals from

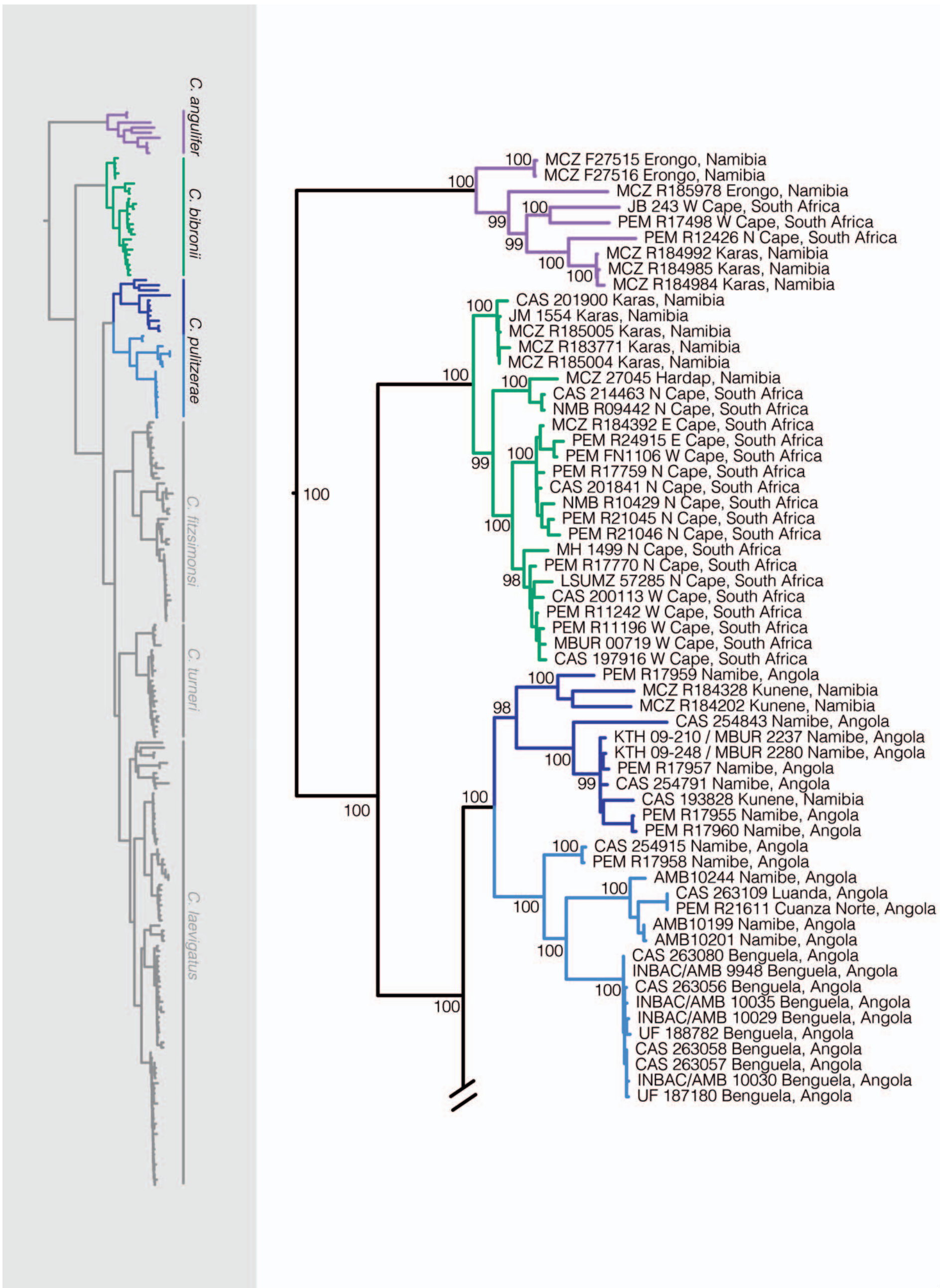

Figure 2. Maximum likelihood tree, concatenated and partitioned by locus, of the genus *Chondrodactylus,* outgroups not shown. Values subtending nodes are ultrafast bootstrap values. (A) *Chondrodactylus angulifer, C. bibronii, C. pulitzerae*, (B) *C. fitzsimonsi, C. turneri,* (C) *C. laevigatus*. Branches are color coded by species with different hues indicating major sublineages within a species.

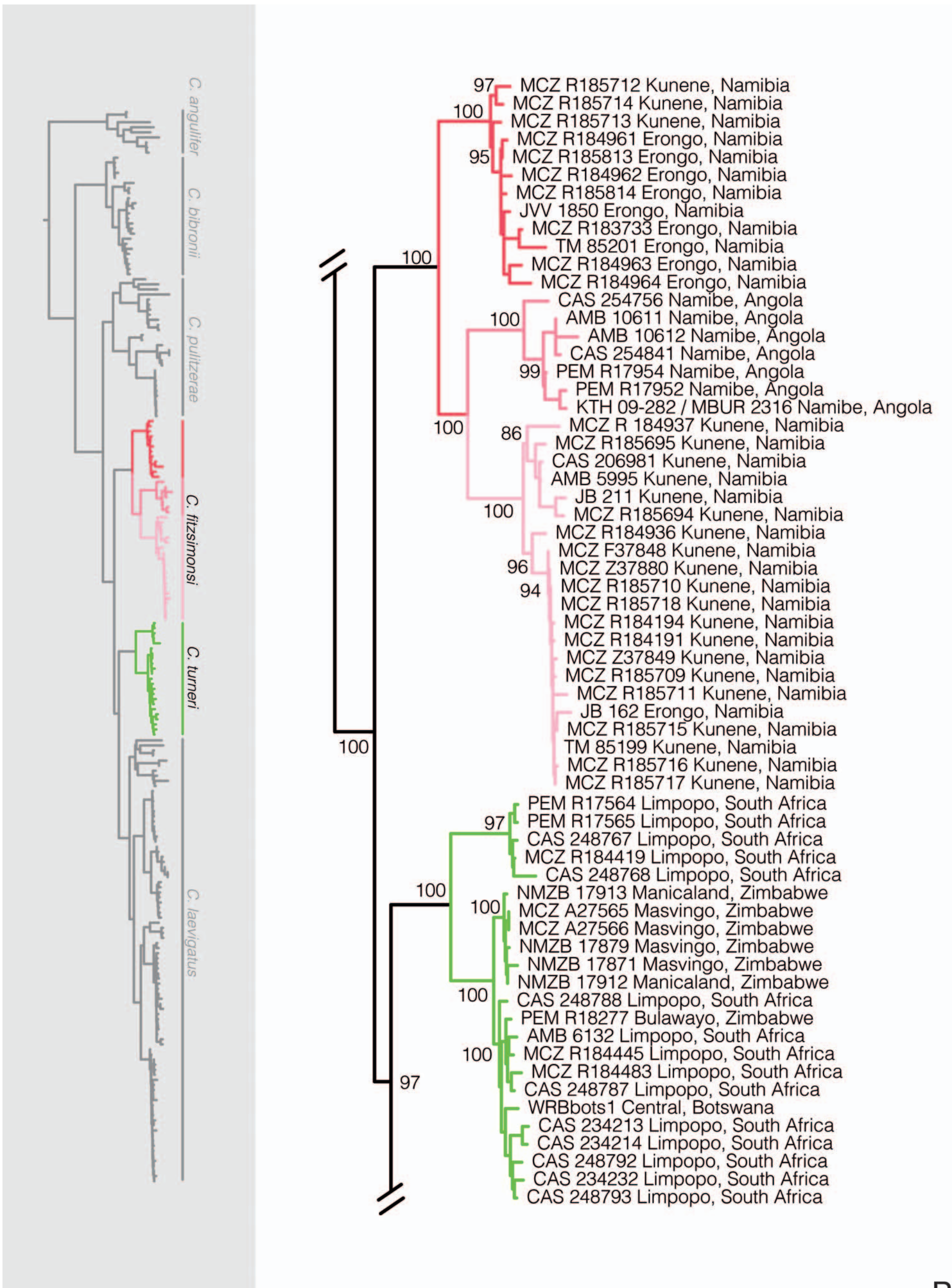

Figure 2. Continued.

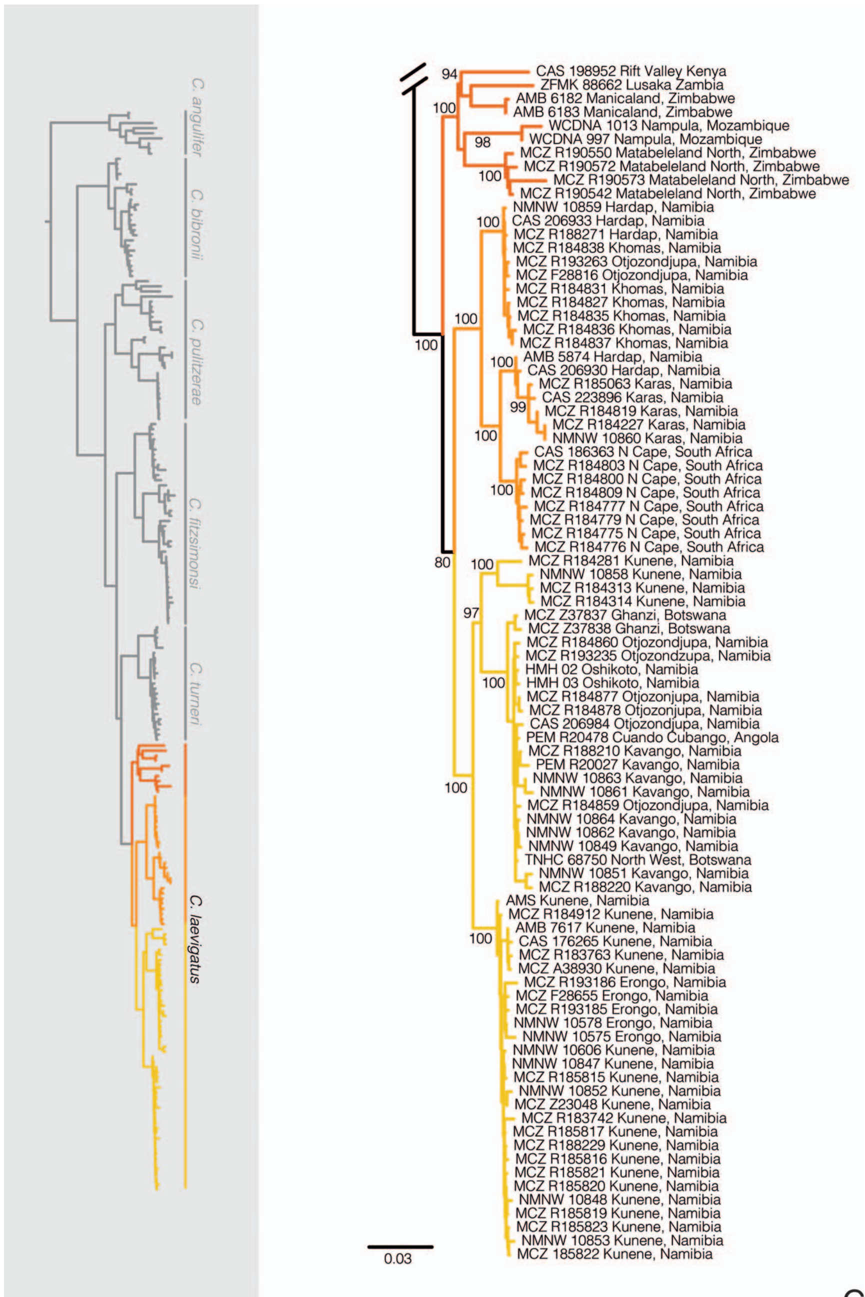

Figure 2. Continued.

Namibe, Luanda, and Cuanza Norte provinces. Support is also high (98% BS) for the other large group of *C. pulitzerae,* which includes individuals from Namibe Province in Angola and from the Kunene Region in Namibia (Fig. 2A).

The clade *C. laevigatus* + *C. turneri* + *C. fitzsimonsi* is recovered with 100% bootstrap support, with each species also receiving 100% bootstrap support and the sister group relationship of *C. laevigatus* and *C. turneri* receiving 97% bootstrap support (Fig. 2B).

Within *Chondrodactylus fitzsimonsi* there are 3 relatively deeply divergent clades, all with 100% bootstrap support. One clade is exclusively Angolan. A second chiefly comprises specimens from the western Kunene Region of Namibia, which includes the type locality, and a third includes most specimens from the Erongo Region of Namibia, as far south as the Swakpmund area. However, both Namibian clades include some individuals from the other Namibian region. Specimens from <2 km apart in the Gaias region in the southwestern Kunene Region are represented in both the Kunene and Erongo clades (Fig. 2B).

Chondrodactylus turneri is represented by 2 relatively deeply divergent, well-supported clades, each with little substructure. One of these includes specimens only from Limpopo Province south of the Soutpansberg and the other includes specimens from northernmost Limpopo, as well as from southern and western Zimbabwe and far eastern Botswana (Fig. 2B).

Finally, within *C. laevigatus* there are 3 subclades, each with 100% bootstrap support. One includes all specimens from the Northern Cape of South Africa as far north as the Khomas Hochland in central Namibia. A second clade includes all material from the Erongo Region northward to the Kunene River and thence northward into Angola and eastward across northeastern Namibia (including the Zambezi Region, formerly known as the Caprivi Strip) and western Botswana. The third subclade is more poorly sampled than the others and includes specimens from northern and eastern Zimbabwe, northern Mozambique, Zambia, and Kenya (Fig. 2C).

Gene Rearrangement

All individuals of *C. turneri* have a mitochondrial gene rearrangement that is unique among all gekkotans. The region coding for the alanine tRNA (*trnA*) is replaced by the proline tRNA gene (*trnP*). Then, following an insertion of roughly 200 base pairs that do not correspond to known sequences, the typical gene order is resumed: *trnN, trnC, trnY,* and the beginning of the CO1 gene. All *C. turneri* individuals sequenced for the region following ND2 exhibit the rearrangement. Trees of the phylogeographic portion of this study did not include the tRNAs downstream of ND2, so this rearrangement did not affect topologies or support of the presented trees and may be interpreted as independent verification of the monophyly of *C. turneri*.

SYSTEMATICS

The pattern of species relationships retrieved here, with large sample sizes, is fully congruent with that previously reported by Heinz (2011) and Heinicke et al. (2017) based on less dense and exemplar-only sampling, respectively.

The scansorial *Chondrodactylus* (*Pachydactylus* until 2005) have long been taxonomically problematic because they share a similar body size, color pattern, and habitus (Bauer et al., 1993). They exhibit significant variation in aspects of dorsal scalation, however, ranging from flattened, almost pavement-like dorsal scales, through so-called "button scales," to strongly keeled or mucronate tubercles, with virtually all possibilities on the spectrum of rugosity expressed. This variation traditionally formed the basis for species recognition within the group (Fischer, 1888; Werner, 1910; FitzSimons, 1938, 1943; Loveridge, 1947).

Benyr (1995), in a seminal but unpublished thesis, dismissed dorsal scalation alone as a diagnostic and, based on broad sampling across the entire distribution of the *P. bibronii* group (padded *Chondrodactylus*), instead recognized 3 species on the basis of size of the scales bordering the mental relative to the width of the paravertebral dorsal tubercles: *P. bibronii* (Smith, 1846), *P. laevigatus* (Fischer, 1888), and *P. fitzsimonsi* Loveridge, 1947. Likewise, multivariate analysis of morphometric data could not distinguish among any *C. bibronii* complex clades recognized here on the basis of eye, head, limb, body, or toe measures (Heinz, 2011), echoing the conclusions of Benyr (1995) and emphasizing the morphological conservatism of this group and the need for molecular data in determining clade boundaries and guiding the search for distinguishing characters.

With the well-established phylogeny supported by the combined mitochondrial and nuclear data presented here, it is now possible to revisit the existing morphological and distributional data for *Chondrodactylus* and to attempt to identify diagnostic characters consistent with the species-level units we have identified. Previous morphometric approaches have thus far proved inadequate (see above), so we have chosen to focus on discrete characters of potentially diagnostic value. These are based on the examination of approximately 3,000 specimens.

In the accounts that follow a partial chresonymy is provided for each species. This includes all newly proposed names and the first occurrence of new combinations.

Chondrodactylus Peters, 1870

Homodactylus Gray, 1864:59 (non *Homodactylus* Fitzinger, 1843 = Gerrhosauridae). Type species: *Homodactylus turneri* Gray, 1864, by monotypy.

Chondrodactylus Peters, 1870:110. Type species: *Chondrodactylus angulifer* Peters, 1870 by monotypy.

Content. *Chondrodactylus angulifer* Peters, 1870, *C. bibronii* (Smith, 1846), *C. turneri* (Gray, 1864), *C. laevigatus* (Fischer, 1888), *C. pulitzerae* (Schmidt, 1933), *C. fitzsimonsi* (Loveridge, 1947).

Although Bauer and Lamb (2005) transferred *Pachydactylus bibronii* group taxa to *Chondrodactylus,* they did not provide a revised diagnosis for the significantly expanded genus. We take the opportunity to do so here.

Diagnosis. Large sized gekkonid geckos (adult snout-to-vent length [SVL] typically >75 mm) with or without adhesive toepads. Manus and pes with hyperdactyly of digit I; phalangeal formulae (3-3-4-5-3 manus, 3-3-4-5-4 pes). Head large, body robust, tail short (63.2% SVL; Haacke 1976a) to moderate (110% SVL) in length. Claws minute or absent. Precloacal and femoral pores absent in both males and females. Dorsum gray to brown or reddish/orange-brown, usually banded, although this pattern may be weak or the bands disrupted. Venter immaculate white. All species are typically sexually dichromatic with males exhibiting distinct white spots, particularly in the shoulder region (these may be absent in some *C. angulifer*; Haacke, 1976a), as first noted by Schmidt (1933) for *C. pulitzerae*.

Distribution. *Chondrodactylus* has a broad distribution in sub-Saharan Africa, occupying desert, semidesert, savanna, woodland, and other habitats from southern South Africa, northward through Namibia, Botswana, Zimbabwe, and Mozambique, to southern and western Angola, and thence eastward to southern and eastern Zambia, Malawi, Tanzania, and southern Kenya. A controversial record from Rwanda is considered to be in error (see *C. laevigatus* species account). Within this broad area members of the genus are absent only from the extreme coastal south of the Eastern and

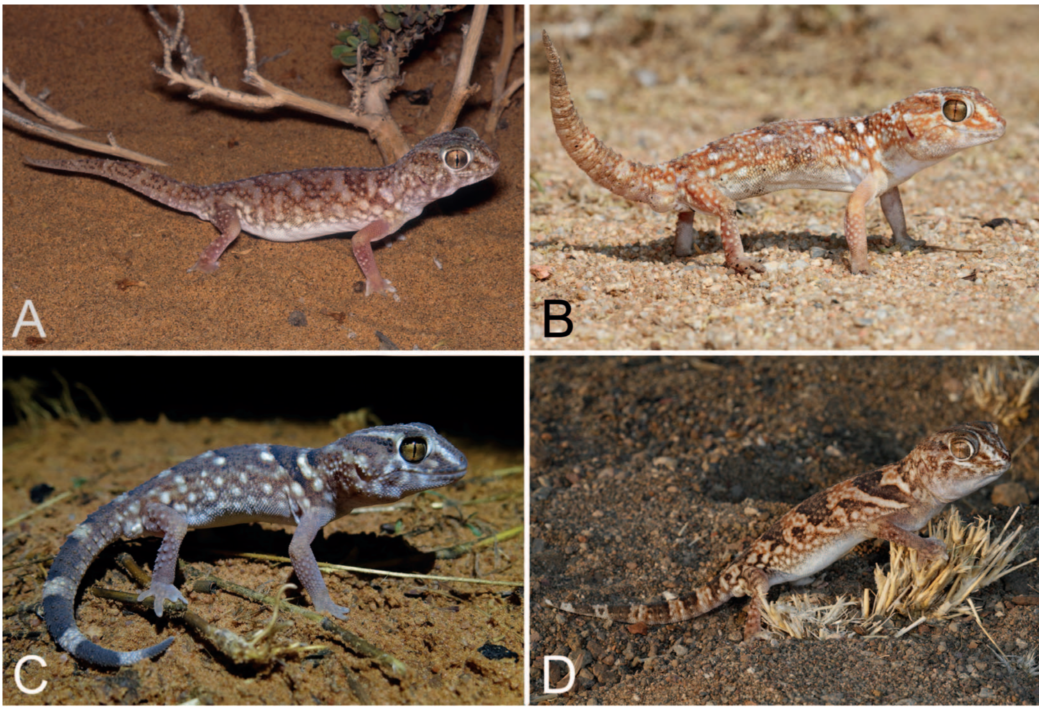

Figure 3. *Chondrodactylus angulifer* life photos. (A) Sesriem, Hardap Region, Namibia; –24.48529°, 15.79713°; (B) Springbok, Namaqualand, Northern Cape Province, South Africa; (C) Witsand Reserve, Northern Cape Province, South Africa, –28.568368°, 22.493221°; (D) Gaias, Kunene Region, Namibia. Based on distribution, D would be a typical *C. a. namibensis* and the remaining specimens would represent the nominate form. The characteristic white spots, especially on the shoulder, identify males (B, C). Photo credits: (A) Randall Babb; (B, D) Johan Marais; (C) Ryan van Huyssteen.

Western Cape provinces and higher elevations and grassland areas in Lesotho and adjacent parts of South Africa. Sparse and scattered records at the periphery of the range result in an imprecise knowledge of distribution at the northern margins of the distribution.

Comments. *Homodactylus* Gray, 1864, with *H. turneri* its type species by monotypy, would have temporal priority over *Chondrodactylus* Peters, 1870 when *turneri* and *angulifer* are included in the same genus. However, Gray's generic name is a junior homonym of *Homodactylus* Fitzinger, 1843 (Gerrhosauridae), with *Caitia africanus* Gray, 1838 = *Tetradactylus africanus* (Gray, 1838) as its type species by original designation.

***Chondrodactylus angulifer* Peters, 1870**

Figure 3.

Chondrodactylus angulifer Peters, 1870: Monatsb. Akad. Wiss. Berlin 1870:111, pl., fig. 1. Lectotype: ZMB 6750 (formerly ZMB 6750A; collector H. Meyer), designated by Bauer and Günther (1991). Paralectotypes: ZMB 90588–89 (formerly 6750B and 6750C). ZMB 6749, also a paralectotype, could not be located (F. Tillack, in litt., 7 June 2021) and an additional specimen in Zoological Institute, Russian Academy of Sciences, Saint Petersburg (ZISP) 2632 is also a member of the type series. Type locality: "Hantam, Oorlogsrivier, S. W. Africa" [= Calvinia, Northern Cape Province, South Africa].

Chondrodactylus weiri Boulenger, 1887:340. Type locality: "Kalahari Desert." Holotype: BMNH 1946.8.23.58 (formerly BMNH 87.3.15.1; collector J.J. Weir).

Chondrodactylus angulifer angulifer Haacke (1976a:54, pls. 4, 5–top, 6–right, 7–left, 8–bottom).

Chondrodactylus angulifer namibensis Haacke, 1976a: Ann. Transvaal Mus. 30(5):64, pls. 5 (bottom), 6 (left), 7 (right), 8 (top). Holotoype: TM 32632 (collector W.D. Haacke). Type locality: "Amichab (= Anigab) Mountain, Namib Park, central Namib Desert, South West Africa (±23°11′S, 15°30′E. Altitude about 1,000 m)." See Mashinini and Mahlangu (2013) for data on paratypes.

Diagnosis. A large *Chondrodactylus* (SVL to ≥113 mm; Haacke 1976a). This taxon is unambiguously distinguishable from all of its congeners by the absence of adhesive toepads under all digits. Its short, stubby, digits, as well as plantar surfaces, appear puffy and bear raised spiny scales (Fig. 1 inset), which appear to be one type of pedal specialization for movement in loose sand (see Bauer and Russell, 1991). Distal 2 phalanges of each digit greatly reduced in size and recurved. Digits of manus clawless. Body cylindrical, tail cylindrical, not depressed. Head large, deep, rounded; eyes large (Fig. 3). Extrabrillar "fringe" above eye prominent. Dorsum and flanks covered with rows of low, pointed, though non-keeled tubercles. Original tail shorter than body length (63.2–80.5% SVL; Haacke, 1976a), distinctly verticillate. Dorsal pattern more-or-less uniform, speckled, or weakly to strongly banded and may be predominantly brownish, reddish, burnt orange or pale cream. Consistent pattern elements include a dark saddle across the shoulders and white to cream lines from the snout, through the dorsal part of the eye to the upper temporal region (Fig. 3). Iris bronze to coppery. See Haacke (1976a) for a detailed description of the species and variation in pattern.

Distribution. *Chondrodactylus angulifer* occupies most of arid and semiarid western southern Africa (Fig. 4, top), mostly in areas within the 300 mm isohyet (Haacke, 1976a). In South Africa it occurs west of 24°E throughout most of the Northern Cape Province, and in adjacent regions of the Western Cape Province (although not south of the Cape Fold Mountains), as well as the far west of the Eastern Cape (Branch, 2014). It reaches its southernmost point near Touwsrivier (Haacke, 1976a). In Botswana it is known only from the southwestern corner of the country and in Namibia it occurs broadly south of the Tropic of Capricorn, but north of the lower Kuiseb River it occurs chiefly in the far west of the country (Haacke, 1976a). A significant range extension of the species into the Omaheke Region of Namibia has been documented since the previous revision of the species. Its northernmost occurrence has been recorded near Orupembe in the Kunene Region (Haacke, 1976a).

Comments. The name *Chondrodactylus a. namibensis* was previously applied to populations north of the Kuiseb River as well as for coastal or near coastal populations as far south as northern Namaqualand. The occurrence of specimens ostensibly attributable to both *C. a. angulifer* and *C. a. namibensis* in near sympatry in the Sperrgebiet (Branch, 1994) and in the Richtersveld (Bauer and Branch, "2001" 2003), as well as "intermediate populations" in and around the Richtersveld (Haacke, 1976a), suggests that the two named forms may reflect variation, primarily in color pattern, along a steep west-to-east cline in the driest regions of the distribution. Our genetic sampling showed no evidence of a clear divergence between the nominal subspecies. We here regard *C. angulifer* as a monotypic species, but caution that a much more deeply and broadly sampled phylogeographic study is needed to adequately assess genetic variation across the vast distribution of this taxon. In particular, we lack genetic material from the Kgalagadi region. Although *C. weiri* Boulenger, 1887 continued to be recognized by Sternfeld (1911) for animals from this area, all authors

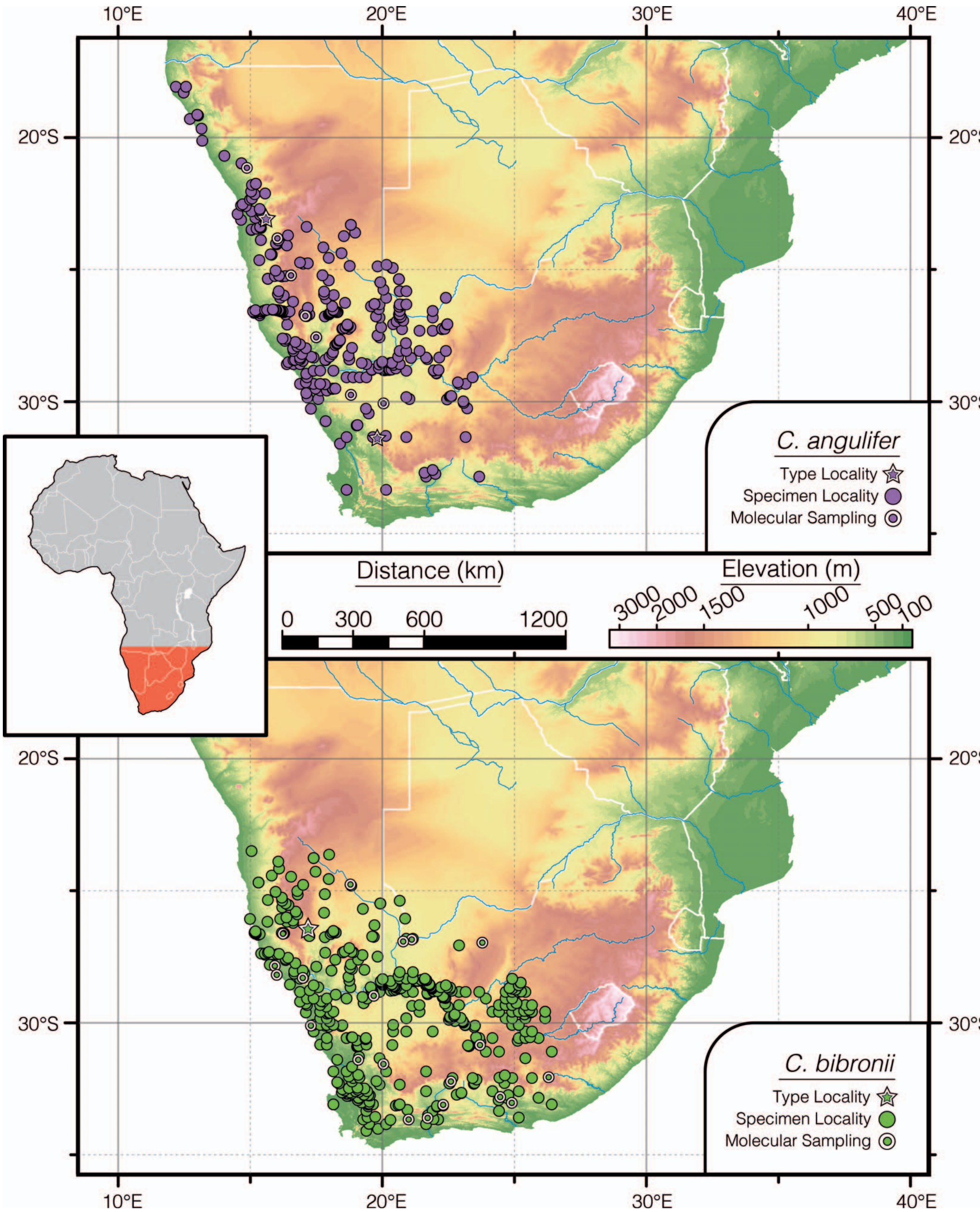

Figure 4. Distribution of *Chondrodatylus angulifer* (top) and *C. bibronii* (bottom). In this and following maps, localities from which sequenced specimens were derived are indicated by a white ring around the locality dot and type localities are indicated by a star. For *C. angulifer* the type localities of the nominate form (in South Africa) and *C. a. nambiensis* (in central Namibia) are indicated. The type locality of *C. weiri* is too vague to plot. The type locality plotted for *C. bibronii* is that of *Pachydactylus stellatus*.

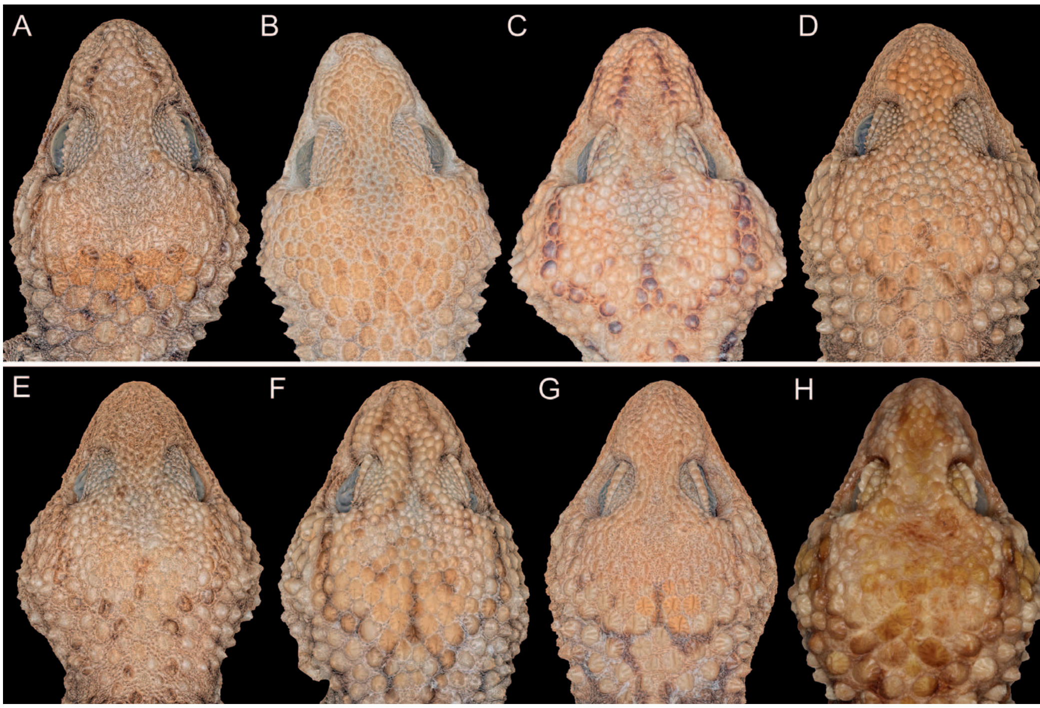

Figure 5. Comparative dorsal views of heads of adult *Chondrodactylus* spp. (A) *C. bibronii* (CAS 223900), 99.2 km N of Helmringhausen, Hardap Region, Namibia; (B) *C. pulitzerae* (CAS 254790), Iona National Park, Namibe Province, Angola; (C) *C. fitzsimonsi* (CAS 175392), 49.2 km N of Cape Cross Rd., Erongo Region, Namibia; (D) *C. turneri* (CAS 266390), Farm Harmony, Hoedspruit District, Limpopo Province, South Africa; (E) *C. laevigatus*—western clade (CAS 266423), Farm Garub, Karas Region, Namibia; (F) *C. laevigatus*—Kgaligadi clade (MCZ Z37838), Ghanzi, Ghanzi District, Botswana; (G) *C. laevigatus*—eastern clade (CAS 266396), Elim Mission, Manicaland, Zimbabwe; (H) *C. laevigatus*—"Vulkangegiet" [Rwanda, see comments in text] (ZMB 24300). Images standardized to similar size for ease of comparison. Photos (A–G) A.M. Bauer, (H) Frank Tillack (ZMB).

since have accepted Boulenger's (1910) synonymization with *C. angulifer* and morphological data (Haacke, 1976a) have not suggested noteworthy variation.

Toepad-bearing *Chondrodactylus*

All remaining species of *Chondrodactylus* retain the plesiomorphic condition (for the *Pachydactylus* group *sensu* Bauer and Lamb 2005) of adhesive scansorial pads under all of the digits (Fig. 1 right). The species are highly conservative with respect to most aspects of external morphology. All are large members of the broader *Pachydactylus* group with robust, somewhat depressed bodies and large subtriangular heads (Fig. 5). The dorsum bears longitudinal rows of enlarged scales or tubercles, which range from completely flattened and juxtaposed to raised and strongly keeled to mucronate (Fig. 6). The dorsal pattern is mostly stereotypic; all have a predominantly brownish to grayish dorsum with variably developed transverse bands or markings that are a darker brown to blackish that may be bordered or marked with cream to bright white tubercles. In adult males there are bright white markings that are typically larger and more conspicuous on the shoulder region and nape than elsewhere. Hatchlings and juveniles have bolder patterns than adults and scale features, like keels and mucrones, are poorly developed in younger animals.

Early attempts to make sense of the various names applied to members of the

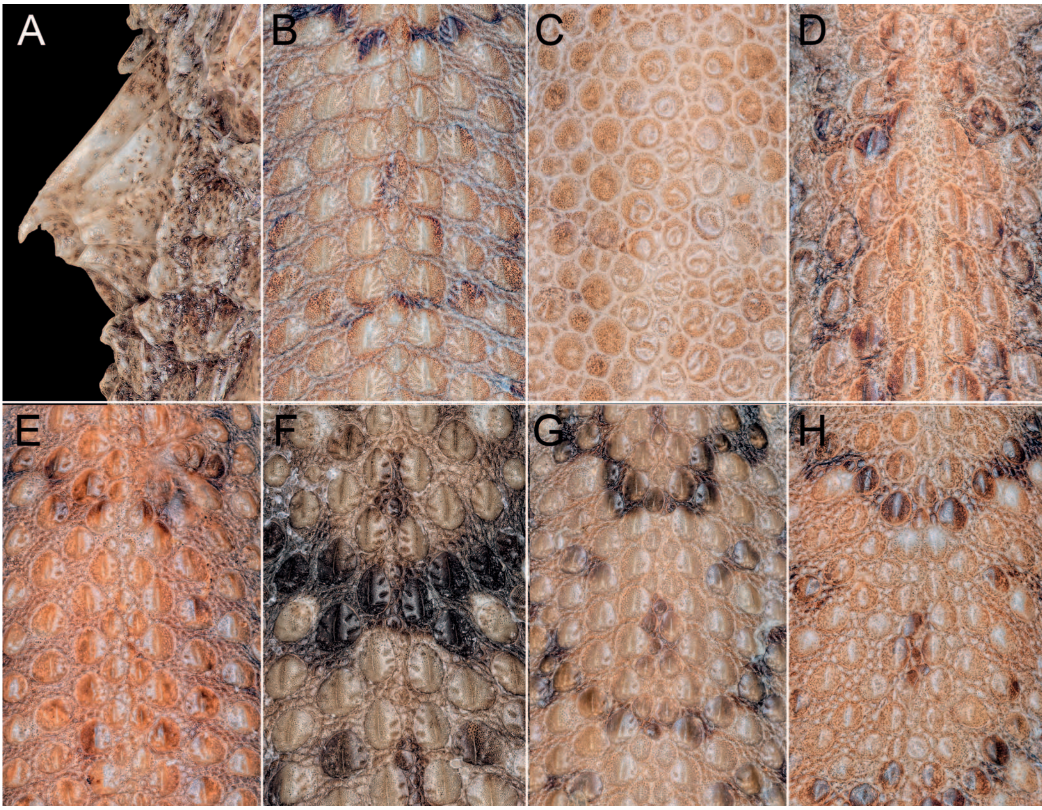

Figure 6. Comparative dorsal scalation of *Chondrodactylus* spp. (A) Close up of a single strongly mucronate upper flank tubercle of *Chondrodactylus bibronii* (CAS 223900); dorsal scalation in the shoulder and thoracic region, centered on the vertebral midline: (B) *C. bibronii* (CAS 223900), 99.2 km N of Helmringhausen, Hardap Region, Namibia; (C) *C. fitzsimonsi* (CAS 266381), near Virei, Namibe Province, Angola; (D) *C. pulitzerae* (CAS 223916), 4 km N of Sesfontein, Kunene Region, Namibia; (E) *C. turneri* (CAS 266390), Farm Harmony, Hoedspruit District, Limpopo Province, South Africa; (F) *C. laevigatus*—eastern clade (CAS 266396), Elim Mission, Manicaland, Zimbabwe; (G) *C. laevigatus*—Kgaligadi clade (MCZ Z37838), Ghanzi, Ghanzi District, Botswana; (H) *C. laevigatus*—western clade (CAS 266423), Farm Garub, Karas Region, Namibia. Images standardized to similar size for ease of comparison. Photos A.M. Bauer.

"*Pachydactylus bibronii*" complex were largely unsuccessful and most earlier workers lumped all specimens from across southern Africa into a single, highly variable *C. bibronii* (e.g., Roux, 1907). Despite the ubiquity of these geckos in most of southern Africa, material from Namibia was very poorly represented in museum collections prior to the German colonial period commencing in 1884 and Central and East African material remained scarce until well into the 20th century. Werner (1910) and Parker (1936), amongst others, attempted to interpret the taxonomy of the group in light of the growing number of specimens available, but their interpretations relied too heavily on dorsal scalation and resulted in decades of confusion. Indeed, Schmidt (1933), Parker (1936), FitzSimons (1943), Loveridge (1947), and Mertens (1955) all found the distribution and allocation of names within this group to be difficult. Parker (1936) devised a method of species delimitation that was largely followed by FitzSimons (1943), Loveridge (1947), and Mertens (1955); but, in reality, this resulted in all four authors thoroughly confounding *P. bibronii, P. turneri,* and *P. laevigatus*.

Figure 7. Comparative chin and gular region of (A) *Chondrodactylus bibronii* (CAS 223900), 99.2 km N of Helmringhausen, Hardap Region, Namibia; (B) *C. turneri* (CAS 266390), Farm Harmony, Hoedspruit District, Limpopo Province, South Africa; and (C) *C. fitzsimonsi* (CAS 266381), near Virei, Namibe Province, Angola. Images standardized to similar size for ease of comparison. Photos A.M. Bauer.

Indeed, FitzSimons (1943:109) stated "in South Africa at least, *turneri* appears to preponderate in the West, while eastwards *bibronii* is the dominant form"—precisely the opposite of the actual situation. He (FitzSimons, 1946:360) clarified that he regarded *turneri* as "the more heavily keeled variety" of *P. bibronii*. The work of Benyr (1995) summarized the features reported for each species by all previous authors and identified 3 character states pertaining to the size of the scales bordering the mental relative to the size of the paravertebral dorsal tubercles (Fig. 7). In over 25 years of field and museum work, we have found this character to be reliable for distinguishing *C. bibronii* and *C. fitzsimonsi* from all other taxa, but *C. laevigatus, C. pulitzerae,* and *C. turneri* share the same (intermediate) character state.

Chondrodactylus bibronii **(Smith, 1846)**
Figures 5A, 6A,B, 7A, 8, 9, 10.

Tarentola bibronii Smith, 1846: Illustr. Zool. S. Afr. Pl. L, fig. 1 and 2 accompanying unnumbered text pages. Lectotytpe: BMNH 1946.8.26.20 (collector Andrew Smith) here designated (see Comments below). Paralectotypes: BMNH 1946.8.26.21–28 (collector Andrew Smith). Type locality: "Southern Africa," here restricted to Southern Africa (South Africa or Namibia) south of –26.4°S and west of 26.4°E.

Pachydactylus bibronii Smith (1849: unpaginated index and errata slip).

Homodactylus bibronii (part) Gray (1865:612).

Pachydactylus bibroni (part) Boulenger (1910:460).

Pachydactylus bibronii **var.** ***stellatus*** Werner, 1910:309. Lectotype: NMW 17995:4 (collector Leonhard Schultze, 1903–1905; from the collection of Franz Werner) here designated (see Comments below). Type locality: "Groß-Namaland," [= Great Namaqualand] Namibia. On the basis of the lectotype locality, the type locality is here restricted to "Bethanien" [Karas Region, Namibia]. Paralectotypes: See Comments below.

Pachydactylus stellatus Hewitt (1911:43).

Pachydactylus bibroni stellatus Hewitt (1927:401).

Pachydactylus bibronii bibronii (part) FitzSimons (1935a:527).

Pachydactylus bibronii stellatus FitzSimons (1935a:528).

Pachydactylus bibronii turneri (part) Parker (1936:129).

Pachydactylus bibronii var. *turneri* (part) FitzSimons (1943:109).

Chondrodactylus bibronii Bauer and Lamb (2005:117).

Diagnosis. A large *Chondrodactylus* (SVL to 108 mm, TM 18185) bearing prominent subdigital lamellae. Body very robust, somewhat depressed, habitus most similar to *C. turneri* among its congeners. Head large, subtriangular, both wide and high, area behind orbits squarish, with nearly parallel lateral sides (Fig. 5A), in contrast to the wide rectangular parietal table of *C. fitzsimonsi* and more rounded shape of other congeners; snout short and rounded with a shallow midline concavity. Canthus rostralis moderately well-developed, scales on snout and canthal region smooth, domed, equal to or larger than those on parietal region but smaller than those on occiput, which are heterogeneous, strongly keeled and stellate, with prominent striae radiating from the central keel. Circumauricular scales prominent and strongly keeled to mucronate. Scales between posterior rim of orbit and ear greatly enlarged, oblong, with prominent keels. Chin and gular scales minute and granular (Fig. 7A), approximately 5 contained within half the diameter of a paravertebral dorsal tubercle. Dorsal tubercles large, round, and very strongly keeled or mucronate (Fig. 6B), largest in paravertebral position just posterior of midbody, becoming mucronate on flanks (Fig. 6A) and in lumbar region; tubercles in 14–16 longitudinal rows (several shorter rows continue onto the flanks, but only near the midbody), tubercles within a single row usually separated by granular scales from each other, but tubercles of adjacent longitudinal rows often in touch with one another. Vertebral midline covered by a series of small keeled tubercles alternating with even smaller smooth scales, each several times the size of intertubercular granules (Fig. 6B). Scales on dorsal surfaces of thighs, shanks, upper arms, and forearms mucronate. Tail approximately equal to or slightly greater than SVL, strongly verticillate, each whorl at tail-base bearing 6–8 enlarged, raised mucronate tubercles; tubercles per whorl decreasing distally. Across the body as a whole, the scalation of *C. bibronii* is typically more heavily sculptured than in its congeners giving it a distinctly rugose appearance that contrasts strongly with the button-scaled morphology of western clade *C. laevigatus*, the only toe-padded congener with which it is sympatric.

Dorsal coloration usually light to mid-brown or grayish with moderately well-developed to bold dark brown dorsal crossbars, especially dark on the nape and shoulders. Basic pattern similar to congeners with nape, shoulder, mid-body, mid-abdomen, and hip bands, which may appear as wide bands, each becoming paler anteriorly or as a series of chevrons or zigzag lines formed only by the darker posterior border of each band. Bright white markings, when present, typically immediately posterior to dark bands. Tail banded, with 7–8 dark bands fading ventrolaterally (Fig. 9). Iris bronze to coppery.

Distribution. *Chondrodactylus bibronii* has a temperate distribution, occurring from the southern Eastern and Western Cape Provinces of South Africa, northward through most of the Northern Cape and the far western Free State, as well as sporadically along the western periphery of North West Province. In Namibia it occurs south of the Kuiseb River, although it is absent from the southern sand sea except for some rocky isolates. It enters extreme southwestern Botswana along the Nossob River and near the junction of the Nossob and Molopo River (Fig. 4, bottom). It is broadly sympatric and even syntopic with *C. laevigatus* in southern Namibia (Methuen and Hewitt, 1914) and the Richtersveld of the far northern Northern Cape (Bauer and Branch, “2001” 2003). Although its range approaches that of *C. turneri* in North West Province, South Africa, there are no known examples of sympatry or parapatry.

Comments. The syntypes of *Tarentola bibronii* Smith, 1846 are without specific locality. Although the majority of Smith’s period in South Africa (1821–1837) was spent within the bounds of the then Cape

Figure 8. Representative *Chondrodactylus bibronii* life photos. (A) Gochas, Hardap Region, Namibia; (B) Springbok, Namaqualand, Northern Cape Province, South Africa; (C) Southern Sperrgebiet, Karas Region, Namibia, –27.90622, 15.90694; (D) Vicinity of Prince Albert, Western Cape, South Africa. Photo credits: (A–C) Johan Marais; (D) Tyrone Ping.

Colony, which would have harbored only *C. bibronii,* his expedition to Namaqualand in 1828 would have brought him into the extreme southern limits of the range of *C. laevigatus*. In 1831 on his expedition to Natal, he reached Zululand and Delagoa Bay at the southern limit of *C. turneri* and on his expedition to the interior of South Africa (1834–1835) any northeastern localities visited after departing Kuruman (Kirby, 1965) would have all been in the range of *C. turneri*. Boulenger (1885) listed Smith's types but did not provide the precise number of specimens present. At the time of Boulenger's writing *Pachydactylus laevigatus* had not yet been described and *Homodactylus turneri* was regarded by him as a synonym of *Tarentola bibronii*. Later, FitzSimons (1937) reported on the status of Smith's type material in London and Edinburgh. As of 1935 he recorded 9 surviving specimens in the type series. Following World War II these were reregistered as BMNH 1946.8.26.20–28, and these specimens were examined by one of us (AMB) in 2016. As reported by FitzSimons (1937), of the 9 specimens 5 are adult, 1 is a subadult, and 3 are juveniles. FitzSimons found one of the adults to be a good match for the larger animal in Smith's (1846) plate L, fig. 1 and considered it "quite probably the type." However, FitzSimons did not indicate which specimen this was, nor did he, or any previous or subsequent author formally designate a lectotype for the taxon (Uetz et al., 2019).

Smith's (1846) illustration shows an adult and a juvenile. The latter is not rendered in sufficient detail to determine much. The adult, however, clearly has strongly keeled

Figure 9. Lectotype of *Tarentola bibronii* Smith, 1846 (BMNH 1946.8.26.20), here designated, part of a composite type series, including both *C. bibronii* and *C. turneri*. (Top): entire specimen with broken original tail and scale bar (20 mm). Photograph A.M. Bauer. (Bottom): enlargement of head and trunk to show details of dorsal scalation. Photograph Patrick Campbell © *The Trustees of the Natural History Museum, London*. Differences in color reflect different lighting conditions.

tubercles, a feature not found in Namaqualand *C. laevigatus*. The written description, while relatively detailed, is insufficient to unambiguously distinguish *C. bibronii* from *C. turneri,* although the reference to the chin and gular scales as "minute" is certainly consistent with the former species. Smith's illustrated adult has an original tail. This characterizes only 2 of the adult syntypes, BMNH 1946.8.26.20 and BMNH 1946.8.26.22. Both Specimens unambiguously exhibit the diagnostic minute chin and gular scales of *C. bibronii*. In contrast, the other members of the type series are referable to *C. turneri*. Given that the syntype series is composite, we here designate a lectotype to stabilize the established use of the name *Chondrodactylus bibronii* for the primarily western South African species. BMNH 1946.8.26.20 is in good condition (Fig. 9), with the original tail broken, but present with the specimen. BMNH 1946.8.26.22 is in poor to fair condition with the tail still attached, but with the body discolored and the skin somewhat pulpy with the tubercles mostly flattened. It is likely that the latter specimen is that figured by Smith because the tail of the former is distinctive in its prominent tubercles, whereas that illustrated is more typical and similar to BMNH 1946.8.26.22. Given the somewhat deteriorated state of the other specimen, we here select BMNH 1946.8.26.20 as the lectotype of *Tarentola bibronii*. Although it is highly likely that the specimen was collected within the confines of the Cape Colony as it existed in Smith's time, the possibility that it was collected beyond the bounds of the colony remains, and there even exists the possibility that it was collected outside of the present Republic of South Africa because Smith's journey to Namaqualand crossed the Orange (Gariep) River into extreme southern Namibia. Thus, it is possible to restrict the type locality only slightly from the original ''Southern Africa'' to Southern Africa (South Africa or Namibia) south of –26.4°S and west of 26.4°E.

Werner (1910) described *Pachydactylus bibronii* var. *stellatus* as a subspecies from Great Namaqualand, southern Namibia, recognizing it as distinct from both *P. laevigatus* and the nominotypical form. Parker (1936) subsequently synonymized *P. b. stellatus* with *P. turneri* based on their shared widespread stellate tubercles. Parker assigned Namibian material from 4 localities to *P. turneri*. In fact, 3 of these (Otjosongombe, Otavifontein, and Lake Otjikoto) represent a clade of *C. laevigatus* that is characterized by particularly spinose scalation (see *C. laevigatus* species account), whereas the fourth, Maltahöhe, supports some of the most northerly populations of *C. bibronii* (Fig. 7A). Indeed, all southern Namibian *Chondrodactylus* that have stellate tubercles anywhere on the body are, in fact, referable to *C. bibronii*. Thus, Werner's (1910) types from Great Namaqualand are also *C. bibronii* and the synonymization of *P. stellatus* with *P. turneri* by Parker (1936) and followed by FitzSimons (1943) and Loveridge (1947) was in error. This name is here allocated to the synonymy of *C. bibronii* (Smith, 1846). This has been confirmed by examination of NMW 17995.4 (Gemel et al., 2019), which is unambiguously referable to this species (Fig. 10). In order prevent future instability should another member of the original syntype series be found to be referable to *C. laevigatus*, we here designate NMW 17995.4 as the lectotype of *Pachydactylus bibronii stellatus*. The identification of some of Franz Werner's type material can be difficult because he was not based at a museum himself, and largely described material housed in a diversity of collections (other than that in Vienna, from which he was barred until 1919; see Adler, 1989) or material from his own large private collection, portions of which were sold to institutions around the world. Delisle et al. (2013, 2016) listed BMNH 1923.3.16.7 (collector Leonhard Schultze) and NMW 17995:1–2 as syntypes. However, the BMNH registers indicate no specimen with the registration number listed and no corresponding specimen could be located among either the type or non-type material in London (P. Campbell, pers. comm. 1 June 2021). The solution seems to be that 23.3.16.7 was the Werner collection number associated with NMW 17995:3 and 17995:4. NMW 17995:1, 17995:2, and 17995:3 were all collected by Schltze and at least the last two came from the Werner collection, but only 17995:4 is listed as part of the type series by Gemel et al. (2019). It is certainly

Figure 10. Lectotype of *Pachydactylus stellatus* Werner, 1910 (NMW 17995:4), here designated, from Bethanien, Karas Region, Namibia. Photo Georg Gassner (NMW).

possible that these additional specimens, all of which bear only the locality "Deutsch SW-Afrika," may be paralectotypes.

The chin scale/paravertebral dorsal tubercle ratio is sufficient to unambiguously identify specimens to *Chondrodactylus bibronii*. Intraspecific divergences in *C. bibronii* are particularly shallow, with no evidence of taxonomically relevant variation. Benyr (1995) illustrated examples of variation in the species and we illustrate the very minor variation seen across the range of the species (Fig. 8).

***Chondrodactylus fitzsimonsi* (Loveridge, 1947)**

Figures 5C, 6C, 7C, 11.

Pachydactylus laevigatus Schmidt (1933:5, pl. I, second from left).

Pachydactylus laeviegatus tessellatus FitzSimons, 1938:172, fig. 6. Holotype: TM 17202 (collector V. F. M. FitzSimons). Type locality: "Kamanyab" [= Kamanjab], Kunene Region] Namibia. See Mashinini and Mah-

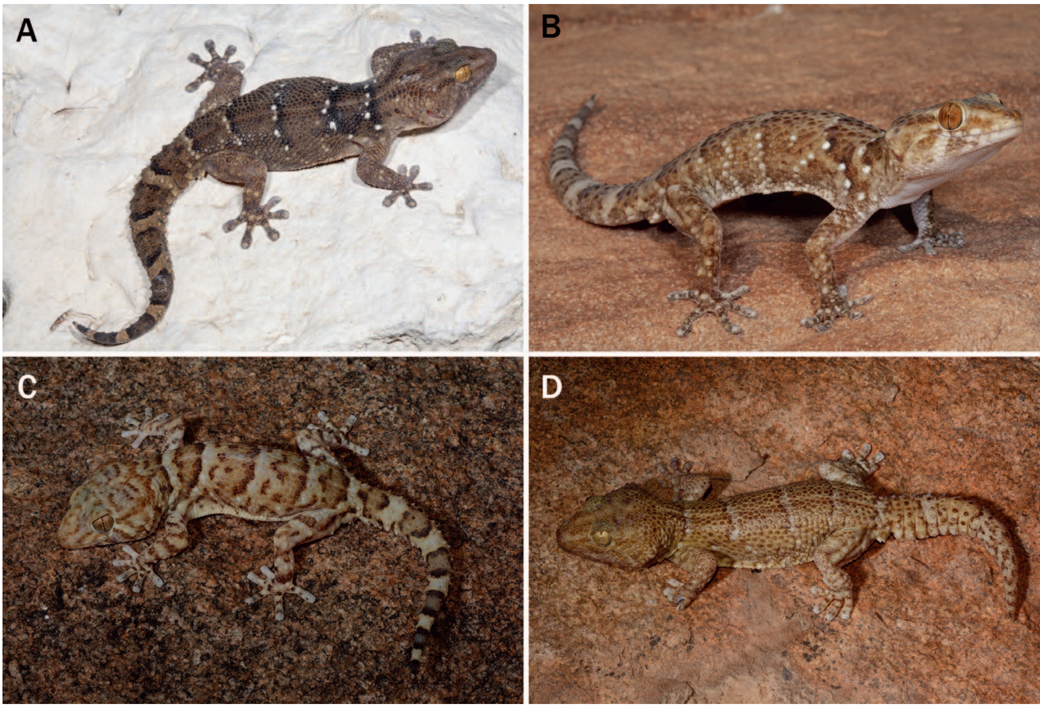

Figure 11. *Chondrodactylus fitzsimonsi* life photos. (A) Northern Kaokoveld, Kunene Region, Namibia; (B) Gaias, Kunene Region, Namibia; (C) Virei, Namibe Province, Angola, –16.09130, 12.83568; (D) Virei, Namibe Province, Angola, –16.09130, 12.83568. Photo credits: (A–B) Johan Marais; (C–D) Ishan Agarwal. (A) Illustrates the typical darker and bolder pattern of northern and inland populations, whereas (B) shows the paler "oatmeal-colored" pattern typical of the western, near-desert populations.

langu (2013) for additional data on the type series.

Pachydactylus laevigatus laevigatus (part) FitzSimons (1943:109).

Pachydactylus laevigatus fitzsimonsi Loveridge, 1947:400. *Nomen substitutum* (see below).

Pachydactylus fitzsimonsi Benyr (1995:50); Branch (1998:255).

Chondrodactylus fitzsimonsi Bauer and Lamb (2005:117).

Diagnosis. A moderate-sized *Chondrodactylus* (SVL to ≥89.3 mm SVL; CAS 176273; Bauer et al., 1993) bearing prominent subdigital lamellae. Body robust, somewhat depressed; head large, triangular, very broad across adductor musculature and angle of jaws (approximately as broad as long), snout moderately elongate, rounded (Fig. 5C), canthus rostralis relatively prominent, interorbital region weakly concave. Crown of head wide, flat; parietal table rectangular. Chin and gular scales enlarged, juxtaposed, either rounded or polygonal, a row of 5 chin scales approximately twice the width of a paravertebral dorsal tubercle (Fig. 7C). Dorsal head scales large, flattened (chiefly in midline) weakly domed (laterally), never keeled, larger on loreal region than on crown, largest above ears and across occiput. Anterior margin of ear bearing 3–4 enlarged conical tubercles. No discrete rows of enlarged dorsal tubercles. Dorsal scales large, heterogeneous in size, flat, and juxtaposed, rounded to polygonal, in some cases forming a virtual pavement of juxtaposed scales; interstitial granules absent or rare in northern specimens. Dorsal scales rounded, slightly raised but flat-topped in southern populations, never bearing a keel or mucro; interstitial granules often present (Fig. 6C). Scales on thighs flattened to weakly conical, smooth, not keeled or mucronate. Tail weakly (Fig. 11C) to strongly (Fig. 11D) verticillate, each whorl at tail-base bearing six enlarged conical (dorsal) to mucronate (lateral) tubercles, less prominent than in congeners; tubercles per whorl decreasing distally.

Dorsal coloration either dark, with almost black cross-barring or pale, oatmeal-colored with darker dorsal markings. Typically with a dark band on nape ventrolaterally coalescent (or nearly so) with a wide band across shoulders, the space between enclosing a lighter brown area. Additional broad bands at midbody, above mid-abdomen, and across hips, posterior border of each band darkest, anterior border from bold to diffuse, intermediate area paler; in some specimens only the dark posterior borders of these markings remain in adults. Small dark spots present or absent within pale spaces between body bands. White scales, when present, adjacent to darkest posterior borders of dorsal bands. Tail with alternating light and dark bands. Light bands more-or-less uniform; dark bands with bold anterior and especially posterior borders and fading to intermediate brown centrally. Approximately 7–8 dark bands on original tails. Pale lines from nostril through eye and on to upper temporal region less pronounced and more diffuse than in congeners. Iris bronze to coppery.

Distribution. *Chondrodactylus fitzsimonsi* is restricted to the western regions of northern Namibia and adjacent southern Angola (Fig. 12, right). In Namibe Province, Angola it is found south of Moçâmedes (formerly Namibe) to the Namibian border in Iona National Park (Ceríaco et al., 2016; Marques et al., 2018) with a single record from Ongueria, just above the escarpment in Huíla Province (Laurent, 1964). The distribution commonly reported for the species (e.g., Branch, 1998) extends southward in the Kunene Region of Namibia at least as far as the Grootberg Pass and the type locality at Kamanjab. A phenotypically distinctive morph has a far western distribution extending from the northern Kaokoveld southward to the west of the Brandberg and thence to Henties Bay in the Erongo Region. The species is absent from the northern Namib dunefields and in much of its range is associated with boulder landscapes.

Comments. *Pachydactylus laevigatus fitzsimonsi* Loveridge, 1947 was proposed to replace the name *P. l. tessellatus* FitzSimons, 1938, which was preoccupied by *P. tessellatus* (Werner, 1910), which is currently regarded as a synonym of *Pachydactylus capensis* (Smith, 1846). Schmidt's (1933) plate image of "*P. laevigatus*" from Pico Azevedo reveals that his specimens were, in fact, *C. fitzsimonsi,* and we have subsequently confirmed this through examination of the relevant specimen (CM 5621). Benyr (1995) treated *C. fitzsimonsi* as a full species in his unpublished thesis, and this was followed by Branch (1998) and subsequent authors. The identification of *C. fitzsimonsi* has generally been nonproblematic because of its restricted range and highly distinctive morphology.

There is deep divergence within *C. fitzsimonsi*. A chiefly Erongo Region clade from near the Brandberg and in near coastal regions north of Henties Bay is sister to remaining populations. This includes specimens from Gaias Spring in the southwestern Kunene Region, adjacent to the Brandberg. A more widely distributed clade (the chiefly Kunene subclade) occurs in near sympatry with the Erongo clade (within 2 km of each other near Gaias) but extends northward to the Angolan border and inland to the top of the escarpment. A single sequenced specimen from Henties Bay falling within this subclade may represent a translocated specimen. *Chondrodactylus fitzsimonsi* from the area of Gaias are morphologically identical regardless of clade membership and differ from speci-

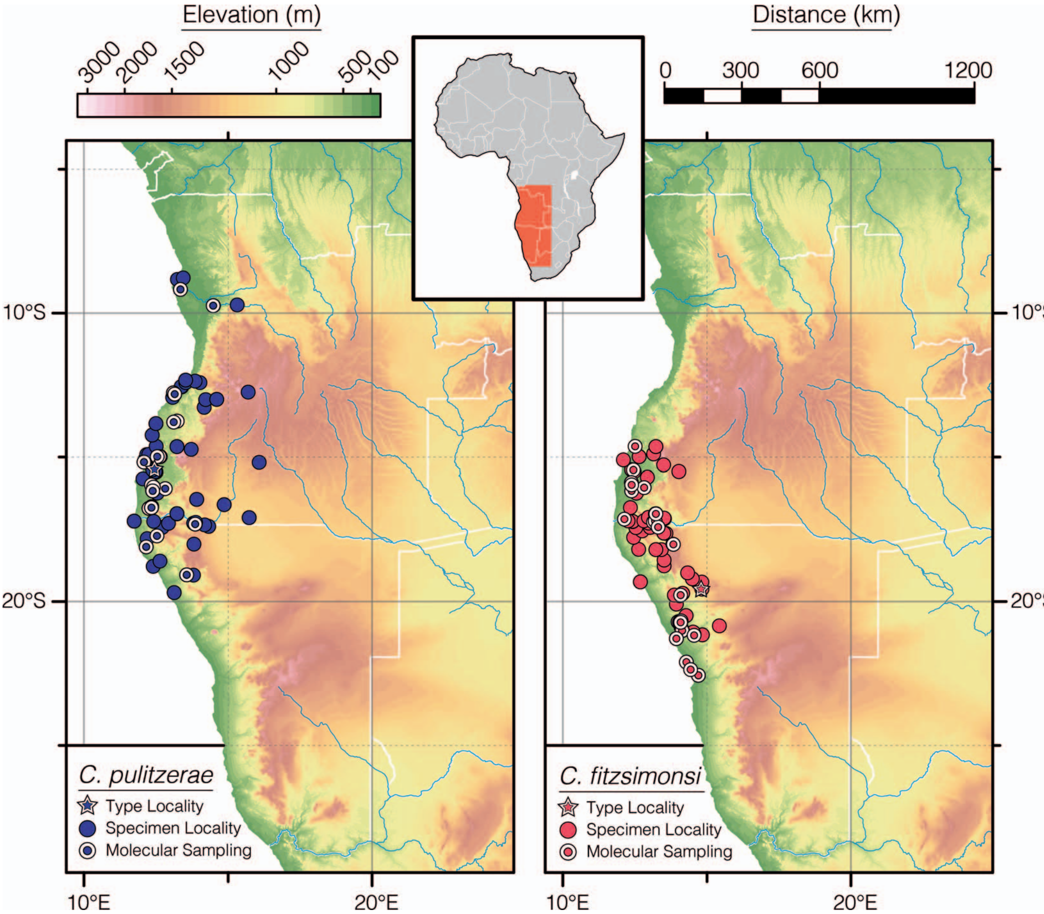

Figure 12. Distribution of *Chondrodatylus pulitzerae* (left) and *C. fitzsimonsi* (right). Stars represent the type localities of *Pachydactylus bibronii pulitzerae* (purple) and *P. laevigatus tessellatus* (rose).

mens from the type locality and other more inland and northerly areas (see Fig. 11). The morphological and genetic variation within *C. fitzsimonsi* will be the subject of a subsequent study. The most common nuclear haplotype of *C. fitzsimonsi* is shared by both morphs of the species; however, 2 *C. fitzsimonsi* haplotypes found in the southwest of the distribution are close to haplotypes of *C. pulitzerae* (Heinz, 2011). Along the western edge of the species' distribution occasional specimens with head shapes and dorsal scalation intermediate between *C. fitzsimonsi* and either *C. pulitzerae* or *C. laevigatus*, with which they may be sympatric or even syntopic, are encountered.

Chondrodactylus pulitzerae (Schmidt, 1933)

Figures 5B, 6D, 13.

Homodactylus bibroni Bocage (1867a:220).

Pachydactylus bibronii (part) Boulenger (1885:201).

Pachydactylus bibroni (part) Boulenger (1910:460).

Pachydactylus bibronii pulitzeræ Schmidt (1933:6, pl. 1, far left). Holotype: CM 5619

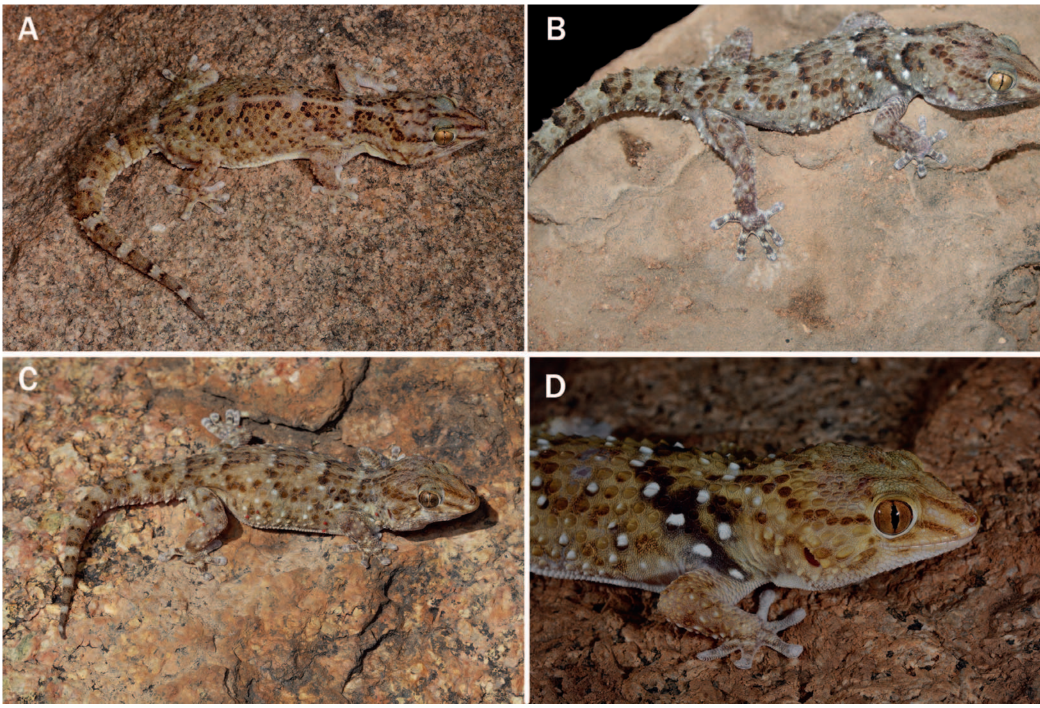

Figure 13. *Chondrodactylus pulitzerae* life photos. (A) Rocky outcrop near Virei, Namibe Province, Angola, –16.05543, 12.82340; (B) Chimalavera, Benguela Province, Angola; (C) 22 km west of Caraculo, Namibe Province, Angola, –15.01558, 12.55503; (D) Quiçama National Park, Luanda Province, Angola. Photo credits: (A) Ishan Agarwal; (B) Luis M.P. Ceríaco, (C) Johan Marais; (D) John Cavagnaro.

(collectors R. and L. Boulton). Type locality: "Pico Azevedo," Namibe Province, Angola (McCoy and Richmond, 1966). The 2 paratypes are FMNH 18478 [formerly CM 5620] (Marx, 1958) and MCZ R39728 [formerly CM 5622] (Barbour and Loveridge, 1946).

Pachydactylus bibroni pulitzerae Parker (1936:129).

Pachydactylus laeviegatus laeviagatus (part) Loveridge (1947:398).

Pachydactylus bibronii pulitzerae (part) Loveridge (1947:403).

Pachydactylus bibronii turneri (part) Loveridge (1947:405).

Pachydactylus laevigatus pulitzerae Benyr (1995:50).

Pachydactylus turneri (part) Branch (1998:254).

Pachydactylus turneri pulitzerae Bauer ("1999" 2000:56).

Chondrodactylus pulitzerae Heinz (2011:55), Ceríaco et al. (2014:670).

Chondrodactylus cf. *pulitzerae* (part) Conradie et al. (2016:24).

Diagnosis. A large *Chondrodactylus* (to ≥102.2 mm SVL; PEM R21610) bearing prominent subdigital lamellae. Body robust and somewhat depressed. Head large and triangular, not as broad as long (usually <90% broad as long), inflection at ear relatively angular when viewed from above, snout more pointed than in congeners, elongate, canthus rostralis relatively well-developed, loreal region somewhat inflated, interorbital region strongly concave. Scales from parietal region forward small (smallest medially), smooth to weakly keeled, contrasting strongly with the very large stellate scales on the occiput and nape. Unlike congeners, most dorsal head scales, except those of snout, are separated from one another by minute granules (Fig. 5B). Enlarged tubercles of nape becoming more conical to mucronate laterally. Prominent spiny tubercles over ears. Chin and gular scales small and granular, approximately 5 chin scales contained within the diameter of a single paravertebral dorsal tubercle. Dorsal tubercles large, oval, and weakly to strongly keeled, usually separated by smaller granular scales, becoming conical to mucronate on flanks. A "naked" mid-vertebral line, at least on the occiput, nape and shoulders, although often extending well down the trunk or to the tail base, several granular scale rows wide and appearing at a distance as a pale mid-vertebral stripe (Fig. 6D). This may be clearly evident along the entire trunk (Fig. 13A), or part thereof (Fig. 13B, C) or may be relatively subtle (Fig. 13D) but is always present. A similar "naked" area, although always limited to the nape is present in some *C. turneri*. 16–18 regular to irregular longitudinal rows of relatively flattened, smooth to keeled, but rarely stellate, oval to rounded, dorsal tubercles. Trunk tubercles almost always separated from one another in all directions by small granules. Tubercles on dorsum of thigh very large, flattened to weakly inflated, becoming keeled or mucronate on shank. Tail distinctly verticillate, each whorl at tail-base bearing 6–8 enlarged, though not strongly projecting, keeled or conical (dorsal) to strongly mucronate (lateral) tubercles; tubercles per whorl decreasing distally.

Dorsal coloration usually buff to light brown with indistinct to moderately well-developed reddish-brown to dark brown dorsal crossbars, especially anteriorly. Basic pattern similar to congeners, with nape, shoulder, mid-body, mid-abdomen, and hip bands. White tubercles, when present, typically immediately posterior of dark bands. Pale interspaces in between darker bands may form a regular pattern of oval markings connected by the pale middorsal granular line (Fig. 13A). Thick pale line from snout to dorsal portion of eye generally distinct and bordered above and below by thinner dark lines. Tail banded, with 8–9 dark bands fading laterally; boundaries between pale and dark bands usually marked by complete or incomplete dark brown edges; some darker bands may be reduced to middorsal blotches.

Distribution. The species is known from southwestern and western Angola as far north as Capanda in Malanje Province (Ceríaco et al., 2014) and Luanda and Cacuaco, Luanda Province (Ceríaco et al., 2017; Marques et al., 2018; Fig. 12, left). Both the Capanda record and one from Huambo Province are above the Angolan Escarpment. Loveridge (1947) followed by Mertens (1955, 1971) tentatively assigned material (e.g., MCZ R43401) from the Erongo Mountains in Namibia to this taxon, although he suggested they might alternatively represent an undescribed species. In fact, only *C. laevigatus* occurs in this region. Ceríaco et al. (2016) noted the presence of *C. pulitzerae* in far northwestern Namibia but did not provide details. It occurs from the border at the Kunene River south as far as Sesfontein (entire Namibian distribution in the Kunene Region) with a single locality further south at "10 km N of the Hunkab River" (but unknown where along the river, TM 52910–11). Throughout most of its range in Namibia it is sympatric with *C. laevigatus* and *C. fitzsimonsi,* although its easternmost occurrences in both Angola and Namibia are out of the range of the latter species.

Comments. Prior to its description by Schmidt (1933), specimens referable to this taxon were assigned to *P. bibronii* (Bocage, 1867a, b, 1887a, b, 1895; Boulenger, 1885; Mertens, 1926), based on overall similarity and the presence of mostly strongly keeled or mucronate scales across the dorsum. Parker (1936) and later authors (Mertens, 1937, 1938; Barbour and Loveridge, 1946; Loveridge, 1947; Hellmich, 1957a, b; Marx, 1958; Laurent, 1964) accepted Schmidt's trinomial and regarded *P. b. pulitzerae* as an

Angolan endemic (but see comments about Erongo populations above), although Monard (1937) used only the binomen *C. bibronii* and Loveridge (1947) used not only Schmidt's name but also *P. l. laevigatus* and *P. b. turneri* in referring to some Angolan specimens. *Pachydactylus bibronii pulitzerae* was subsequently referred to by Mertens (1955, 1971) and Wermuth (1965) but otherwise the name then went largely unused in the published literature for 5 decades. It was regarded as a valid subspecies of *P. laevigatus* by Benyr (1995) and as a full species of *Chondrodactylus* by Heinz (2011) in their respective unpublished theses. Ceríaco et al. (2014) first used *C. pulitzerae* as a specifically valid name on the basis of Heinz's (2011) molecular data, and it has since been used consistently (e.g., Ceríaco et al., 2016, 2017; Conradie et al., 2016; Heinicke et al., 2017; Marques et al., 2018; Branch et al., 2019).

Specimens genetically sampled fall into a more northern clade, extending northward of the Giraul River in Namibe Province, Angola, and a southern clade occurring southward into Namibia. The genetic identity of a specimen from Quiçama (CAS 263109) with one from Cambambe (PEM R21611), 150 km distant, and their high similarity to specimens from northern Namibe, approximately 450 km away, along with the sporadic distribution of *C. pulitzerae* north of Lobito, raises the possibility that some northern records may represent introductions, although Bocage (1895) stated that the species (as *Pachydactylus bibronii*) was common south of the Kwanza River. More extensive sampling is needed both north and east of Namibe Province to determine whether the range is contiguous and whether there is genetic substructure consistent with geography.

***Chondrodactylus turneri* (Gray, 1864)**
Figures 5D, 6E, 7B, 14, 15.

Homodactylus turneri Gray, 1864: Proc. Zool. Soc. London 1864:59, pl. 9, fig. 2. Lectotype: BMNH 1946.8.26.7 (collector J. Kirk), here designated (see Comments below). Paralectotypes: BMNH 1946.8.26.8, 64.1.9.10–13, 64.1.9.15 (collector J. Kirk). Type locality: "southeastern Africa," (restricted to "Tette" [=Tete], Mozambique fide Loveridge 1947:405; see Comments below).

Pachydactylus Bibronii (part) Peters (1865:457).

Homodactylus bibronii (part) Gray (1865:612).

Pachydactylus bibronii bibronii (part) FitzSimons (1935b:336).

Pachydactylus bibronii turneri (part) Parker (1936:129).

Pachydactylus bibronii var. *turneri* (part) FitzSimons (1943:109).

Pachydactylus bibronii turneri (part) Loveridge (1947:405).

Pachydactylus laevigatus turneri Benyr (1995:50)

Pachydactylus turneri Branch (1998:254).

Pachydactylus turneri turneri Griffin (2003:30).

Chondrodactylus turneri Bauer and Lamb (2005:117).

Diagnosis. A moderately sized *Chondrodactylus* (to ≥95 mm SVL, MCZ R190407) bearing prominent subdigital lamellae. Body robust and somewhat depressed. Head large, relatively deep, and subtriangular, nearly as broad as long, inflection at ear gently curved when viewed from above (contrasting with *C. pulitzerae*), snout typically shorter and broader than in congeners, canthus rostralis moderately developed more variable than in congeners; loreal region moderately to strongly inflated, interorbital region flattened to weakly concave. Tubercles on occipital region very large and keeled to stellate, becoming smaller on the crown and interorbital region and slightly larger again on the dorsum of the snout; interorbital and especially snout scales distinctly domed, most bearing weakly defined keels. Most anterior dorsal head tubercles in contact with one another, whereas tubercles of the occiput and nape usually well-separated from one another by tiny granules (Fig. 5D). Tubercles around ear heterogeneous, generally less massive than in other congeners. Chin and gular scales small and granular, becoming progressively smaller postero-medially (Fig.

Figure 14. *Chondrodactylus turneri* life photos. (A) Tete, Tete Province, Mozambique. (B) Gaza, Gaza Province, Mozambique. (C) Lephalale, Limpopo Province, South Africa. (D) Steelpoort, Limpopo Province, South Africa. (E) Alldays, Limpopo Province, South Africa. Photo credits: (A–C) Luke and Ursula Verburgt (Enviro-Insight); (D–E) Johan Marais.

7B), approximately 5 chin scales contained within the diameter of a single paravertebral dorsal tubercle. Dorsal tubercles large, oval to rounded, strongly keeled, variably bearing small peripheral pustules or short to long radiating ridges in a stellate pattern, becoming smaller and more conical to mucronate on flanks. Trunk tubercles usually well-separated by smaller granular scales, forming 14–18, usually very regular longitudinal rows of enlarged tubercles (Fig. 14). In addition, mid-vertebral line with much smaller, rounded, keeled tubercles separated from one another by alternating pairs of paravertrebral keeled tubercles intermediate in size between the tubercles of the mid-dorsal and more lateral tubercle rows (Fig. 6E). Tubercles on dorsum and postaxial surface of thigh and shank large, somewhat flattened, keeled or stellate.

Scales on upper arm non-tuberculate, imbricating, becoming tubercular on forearm, keeled to mucronate, but much smaller than tubercles of shank. Tail distinctly verticillate, each whorl at tail-base bearing six (eight close to tail base) enlarged, though not strongly projecting, keeled or conical (dorsal) to strongly mucronate (lateral) tubercles; tubercles per whorl decreasing to 4 then 2 on distal portion of tail.

Dorsal coloration buff to light to medium brown, sometimes with reddish or grayish tones with indistinct to moderately well-developed dark brown to almost black dorsal crossbars, especially prominent anteriorly. Basic pattern similar to congeners, with nape, shoulder, mid-body, mid-abdomen, and hip bands. White tubercles, when present, typically immediately posterior to or within dark bands. Tail banded, boldly or obscured, with 8–10 dark bands fading laterally; boundaries between pale and dark bands usually marked by complete or incomplete dark brown edges; some darker bands may be reduced to middorsal blotches.

Additionally, *C. turneri* exhibits a genetic autapomorphy—a rearrangement of the genes coding for transfer RNAs downstream of ND2 (see Discussion), which is not only unique among its congeners, but also among all gekkotans.

Distribution. *Chondrodactylus turneri* occupies most of the southeastern margin of the distribution of the genus (Fig. 16). Its range in South Africa and Eswatini (formerly Swaziland) has been presented by Branch (2014; only records east of 25°E apply to this species, others are actually *C. laevigatus*). It occurs in northern KwaZulu-Natal (i.e., Zululand), central and eastern Eswatini, throughout most of Mpumalanga and Limpopo (except parts of Sekhukuneland), in northern Gauteng and in northeastern North West Province. In Botswana *C. turneri* occurs along the southeast margins of the country and in Zimbabwe it occupies the southern and central parts of the country. Nearly all *Chondrodactylus* records in southern Mozambique are also likely referable to this species, although this is based on biogeographic grounds and weak support from morphology. The precise dividing line between *C. laevigatus* and *C. turneri* in Zimbabwe and central and northern Mozambique remains unclear but, based on morphology and limited genetic sampling, the division in the former country may roughly correspond to the division between the Zambezi and Limpopo drainages.

Sampling in Mozambique is uneven and genetic material is derived only from Nampula in the north of the country. Specimens from throughout the northern provinces of Niassa, Cabo Delgado, and Nampula provinces all appear to be *C. laevigatus*. Specimens from south of Beira are conspecific with those in Masvingo and southern Manicaland in Zimbabwe and with those in the South African lowveld (i.e., *C. turneri*). This is supported by the relatively contiguous lowland habitat and, to the extent possible, in the absence of unambiguous diagnostic features, by morphology. Specimens from the type locality of *Homodactylus turneri* Gray, 1864 at Tete and from lowland localities downstream of there are also almost certainly referable to this species. However, specimens from closer to Cahora Bassa in western Tete Province and from northern portions of Manhica and Sofala provinces are problematic. Geographically, they lie between *C. laevigatus* from the Vumbas in Zimbabwe (genetically confirmed) to the southwest and Malawi (morphologically determined) and northern Mozambique to the northeast. However, the Zambezi Valley provides a low-elevation riparian corridor deep into the inland of Tete Province, with Tete itself lying at only 140 m. Elevation may explain some aspect of the distribution boundary between *C. laevigatus* and *C. turneri,* but it is clearly not the sole factor because *C. laevigatus* occurs at quite low elevations in some

Figure 15. Lectotype of *Homodactylus turneri* Gray, 1864 (BMNH 1946.8.26.7), here designated, from Tete, Tete Province, Mozambique. Photograph by A.M. Bauer © *The Trustees of the Natural History Museum, London.*

places, whereas *C. turneri* is present in Bulawayo and the Waterberg Massif of Limpopo, both >1,000 m in elevation.

Comments. The published type locality for *C. turneri* (Gray, 1864) is "South-Eastern Africa," interpreted to be Tette (=Tete), Mozambique by Loveridge (1947) and entered as such in the British Museum of Natural History (now The Natural History Museum, London) re-registration catalogue. In fact, Gray (1864) explicitly listed Tette (now Tete) as a locality for only some of the specimens collected by Kirk. The rest of the specimens, including *Homodactylus turneri,* are associated only with the general locality "South-Eastern Africa," which could be anywhere within the area visited by John Kirk on the Zambezi Expedition during the period 1858–1863. Although Kirk spent a good deal of time at Tete and in the Shire Highlands in what is today Malawi, he also collected specimens below Tete on the Lower Zambezi, including near Sena (Senna) and the mouth of the Shire River. In addition, during the early period of the expedition, Kirk was stationed in the Zambezi Delta and on numerous occasions during the expedition he returned to the river mouth. Other biological specimens returned by Kirk have the localities Quellimane (now Quelimane) and Gorongoza (Günther, 1864; Hill, 1922; Dritsas, 2005). When locality data were available for Kirk's material, he apparently did provide it to the scientists who were working with the material (Dritsas, 2005). The absence of a specific locality suggests that either the specimens represented something widespread in the area covered by Kirk's journeys or that the data were not recorded or were subsequently lost. It must also be remembered that Kirk's primary natural history interest was in botany (Hill, 1922), so it is perhaps not surprising that herpetological material, largely collected incidentally to plants, might not be as carefully recorded. Based on a lack of explicit locality data accompanying the syntypes of *H. turneri,* we think it likely that the type series of *H. turneri* may have originated from multiple sites in the lower Zambezi Valley.

All 7 syntypes of *Homodactylus turneri* are in good condition, nonetheless, their specific identity is still difficult to establish with certainty. All appear to be referable to *Chondrodactylus turneri* as recognized here on the basis of ≥1 morphological traits;

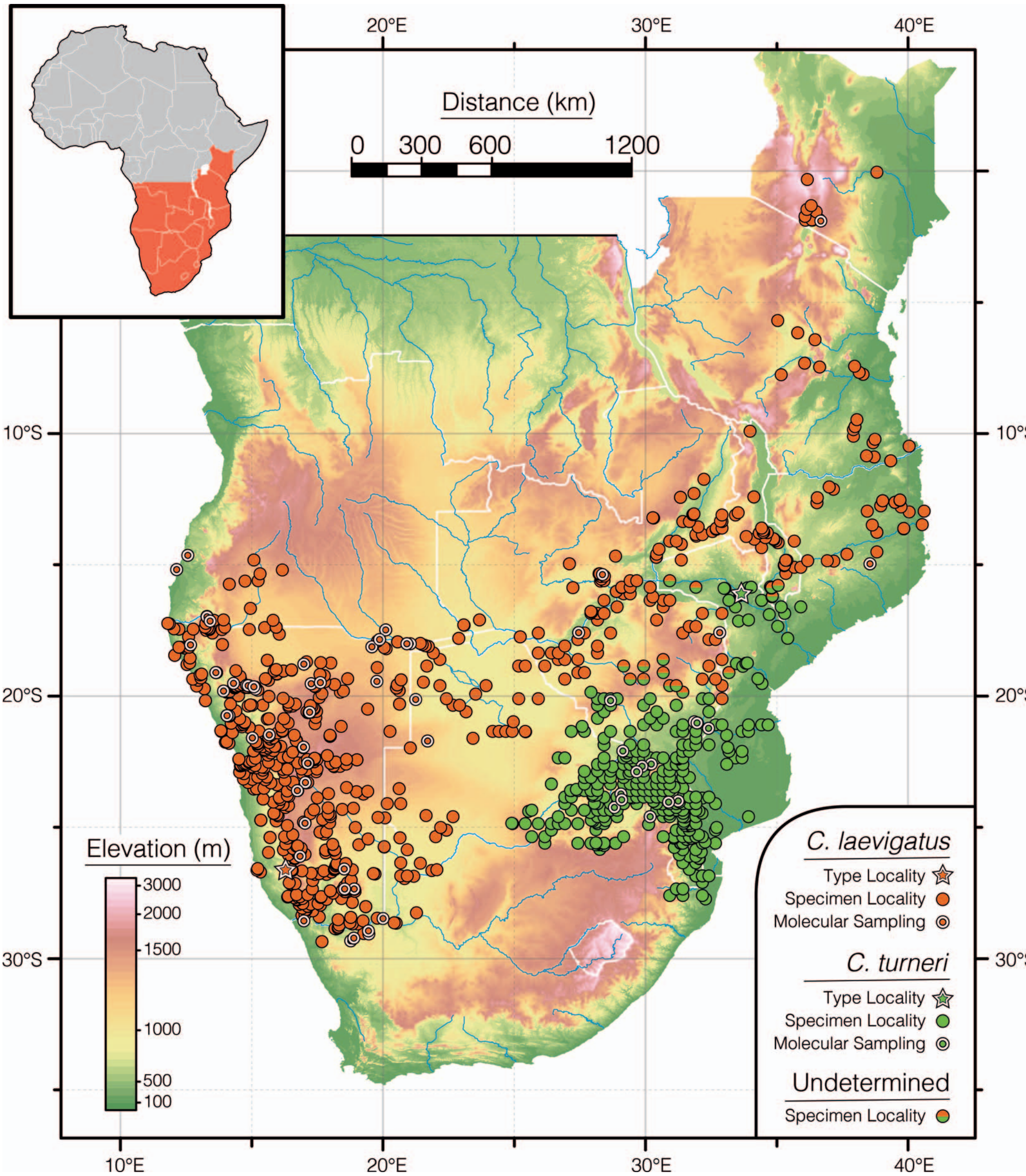

Figure 16. Distribution of *Chondrodactylus turneri* (green) and *C. laevigatus* (brown). Scattered genetic samples in the east of the range of *C. laevigatus* provide an indication of the approximate southern boundary of the species east of 20°E. Split green/brown symbols indicate specimens from near the boundary zone between the two taxa that have not been genotyped and which were examined prior to the "discovery" of relevant diagnostic features, or which have not been examined by the authors. Stars represent the type localities of *Homodactylus turneri* (green) and *Pachydactylus laevigatus* (brown).

however, there is overlap with *C. laevigatus* in each of these traits. Given the extreme similarity of these two congeners and the uncertainty surrounding their precise distributional limits (as well as the extent of the area from which the types were collected), we consider it prudent to select a lectotype to stabilize the current use of the name *C.*

turneri. We here designate BMNH 1946.8.26.7 (Fig. 15) as the lectotype of *Homodactylus turneri* on the basis that it is characterized by the greatest number of *C. turneri* features, specifically, head deep, snout short and broad, lores inflated, and relatively extensive exposed granular skin on occiput, nape, and anterior midline of the back.

This species was synonymized with *Pachydactylus bibronii* by Peters (1865) and, for the majority of the period since, it has remained in the synonymy of this species (see synonymies of FitzSimons, 1943 and Loveridge, 1947). Gray (1865) himself, noted that he had somehow overlooked Smith's (1846) description and illustration of *Tarentola bibronii* and sank *H. turneri* into its synonymy; however, he retained the generic name *Homodactylus,* believing the species to be generically distinct. Gray (1865) further acknowledged that Peters, who had examined Smith's types, had pointed out the synonymy. Loveridge (1947), largely following Parker (1936) and FitzSimons (1943), recognized it as a subspecies of *C. bibronii* but included *P. bibronii stellatus* in its synonymy and his concept of the taxon included specimens from Angola and Namibia currently allocated to *C. laevigatus* as well as true *C. bibronii* from the Free State and Northern Cape provinces of South Africa. Benyr (1995), however, identified a reliable scale character (the size of the anterior chin scales relative to the paravertebral dorsal tubercles) that unambiguously separated *P. bibronii* from what he considered to be *P. laevigatus,* with 3 subspecies, the nominotypical form in the Northern Cape and western Namibia, *P. l. pulitzerae* in Angola, and *P. l. turneri* in the east. Benyr (1995), however, had overlooked that *Homodactylus turneri* Gray, 1864 had priority over *Pachydactylus laevigatus* Fischer, 1888 and thus, as corrected by Branch (1998) and discussed by Lamb and Bauer (2002), the taxon names became *P. t. turneri, P. t. pulitzerae,* and *P. t. laevigatus*. Since the transfer of the *P. bibronii* group to *Chondrodactylus* the majority of the literature on Southern African reptiles has applied the name *C. turneri* to scansorial *Chondrodactylus* (other than *C. bibronii*) distributed from Kenya to South Africa (e.g., Branch, 2014).

The genetic distinctiveness of *C. laevigatus* from *C. turneri sensu stricto* was demonstrated by Heinz (2011) in his unpublished thesis; however, the two names were not used in the published literature as specifically valid to refer to different taxa until several years later (see *C. laevigatus* account), although without explicit justification. Phenotypically, *C. laevigatus* from the east of its range strongly resembles *C. turneri;* thus, unambiguous identification of specimens from areas of parapatry, from Botswana and Zimbabwe through East Africa, can be difficult, especially in the case of juveniles.

***Chondrodactylus laevigatus* (Fischer, 1888)**

Figures 5F, G, H, 6E, F, G, H, 17, 18, 19.

Pachydactylus capensis Peters (1854:615). [previously included in the synonymy of *C. turneri,* e.g., Loveridge (1947)].

Platydactylus (*Pachydactylus*) *Bibronii* Peters (1862:15). [previously included in the synonymy of *C. turneri,* e.g., Loveridge (1947)].

Pachydactylus Bibronii Peters (1869:139).

Pachydactylus laevigatus Fischer, 1888:15, pl. 2, fig. 3. Syntypes: BMNH 1946.8.26.1–2 (formerly BMNH 89.12.16.9–10; collector J. Steingröver). Type locality: "bei Aus und auf dem Wege nach Bethanien" [= near Aus and on the way to Bethanien], Karas Region, Namibia.

Pachydactylus bibroni laevigatus Methuen and Hewitt (1914:129, fig. 14).

Pachydactylus stellatus Schmidt (1933:5).

Pachydactylus bibronii laevigatus FitzSimons (1935a:527).

Pachydactylus bibronii bibronii (part) FitzSimons (1935b:336).

Pachydactylus laevigatus laevigatus FitzSimons (1938:172).

Pachydactylus bibronii turneri (part) Parker (1936:129).
Pachydactylus bibronii pulitzerae (part) Loveridge (1947:403).
Pachydactylus bibronii pulitzerae Hellmich (1957b:49)
Pachydactylus turneri (part) Branch (1998:254).
Pachydactylus turneri laevigatus Griffin (2003:30).
Chondrodactylus turneri (part) Bauer and Lamb (2005:117)
Chondrodactylus turneri laevigatus Bauer et al. (2006:90).
Chondrodactylus cf. *pulitzerae* (part) Conradie et al. (2016:24).
Chondrodactylus laevigatus Ceríaco et al. (2014:670).

Diagnosis. A large *Chondrodactylus* (to ≥100 mm SVL, MCZ R190191) bearing prominent subdigital lamellae. Body robust and somewhat depressed. Head large, relatively depressed, and subtriangular, not as broad as long but proportionally wider across adductor region than *C. pulitzerae*; inflection at ear gently curved when viewed from above, snout somewhat longer and more acuminate than in *C. turneri,* canthus rostralis moderately developed, loreal region weakly to moderately inflated, interorbital region flattened to weakly concave or with a narrow furrow. Tubercles on occiput and posterior half of crown large very large and keeled to stellate, becoming smaller on the anterior crown and interorbital region and slightly larger again on the dorsum of the snout; interorbital and especially snout scales flattened or domed, keelless or with only weakly defined keels. Most anterior dorsal head tubercles in contact with one another, whereas tubercles of the crown and nape may be separated from one another by tiny granules (Fig. 5E–H), although typically not as widely spaces as in *C. turneri*. Tubercles anterior and dorsal to ear heterogeneous, generally large and bearing a prominent longitudinal keel. Chin and gular scales small and granular, becoming progressively smaller postero-medially (condition similar to Fig. 7B), approximately 5 chin scales contained within the diameter of a single paravertebral dorsal tubercle. Dorsal tubercles large, oval to rounded, from unkeeled to strongly keeled, if strongly keeled then variably bearing small peripheral radiating ridges, although not as strongly stellate as in *C. bibronii,* becoming smaller and more conical on flanks. Trunk tubercles usually well-separated by smaller granular scales, forming 14–20 (usually 18 in the western clade, 14 in the eastern clade, and 16–18 in the Kgaligadi clade), slightly irregular to very regular longitudinal rows of enlarged tubercles (Fig. 17). In addition, mid-vertebral line with a mixture of granules and smaller, rounded, unkeeled to moderately keeled tubercles (single or in pairs; Fig. 6F–H). Tubercles on dorsum and postaxial surface of thigh and shank large, somewhat flattened, to keeled or mucronate. Scales on upper arm non-tuberculate, flattened, imbricating, becoming tubercular on forearm, conical to mucronate, but smaller and less prominent than tubercles of shank. Tail distinctly verticillate, each whorl at tail-base bearing 6 (8 close to tail base) enlarged, keeled (proximal whorls) or conical to strongly mucronate tubercles; tubercles per whorl decreasing to 4 then 2 on distal portion of tail.

Dorsal coloration buff to light to medium brown, sometimes with reddish or grayish tones with indistinct to well-developed dark brown to almost black dorsal crossbars, especially prominent anteriorly. Basic pattern similar to congeners, with nape, shoulder, mid-body, mid-abdomen, and hip bands. White tubercles, when present, typically immediately posterior to or within dark bands. Tail banded, boldly or obscured, with 8–10 dark bands fading laterally; boundaries between pale and dark bands usually marked by complete or incomplete dark brown edges; some darker bands may be reduced to middorsal blotches.

Variation. Individuals of the western clade of *C. laevigatus* are highly distinctive

Figure 17. *Chondrodactylus laevigatus* life photos. (A) Augrabies Falls National Park, Northern Cape Province, South Africa; (B) Kobos, Hardap Region, Namibia; (C) Otavi Highlands, Otjosondjupa Region, Namibia, –19.32511, 18.39078; (D) Shamvura Lodge, Kavango Region, Namibia; (E) Cuamba Town, Niassa Province, Mozambique; (F) Near Nsanje, Nsanje District, Southern Region, Malawi; (G) Near Mtera Reservoir, Dodoma/Iringa Regions, Tanzania; (H) West of Magadi, Kajiado County, Kenya. A and B represent the Western clade, C and D represent the "Kgaligadi" clade, and E—H represent the Eastern clade. Photo credits: (A) Luke Kemp; (B–D) Johann Marais; (E) Daniel M. Portik; (F–G) Colin Tilbury; (H) Steven Spawls.

and easily distinguished from all other congeners, including members of the "Kgaligadi" and Eastern clades. They are generally more depressed overall (Fig. 17A–B) and have the characteristic button-scale type tubercles, which are typically raised but not, or only weakly, keeled. This clade extends from the southernmost limits of the species to the Otjozondjupa Region of northcentral Namibia. The "Kgaligadi" clade extends northward from the Otjozondjupa and Erongo regions to southern Angola and eastward through the Caprivi Strip and northern Kgaligadi, and the Eastern clade continues from western Zimbabwe and central Zambia to East Africa. We could identify no diagnostic characters distinguishing members of these two clades from one another. Members of these clades usually have the dorsal tubercles more strongly keeled or conical (Fig. 17D) and often bearing transverse stria or having a stellate pattern of keels on at least some scales (particularly on the occiput and nape). Especially strongly keeled specimens of the "Kgaligadi" clade occur in populations near Uis, Takauasa (e.g., NMNW 210), and in the Grootfontein/Tsumeb region of northern Namibia (Fig. 17E). The Eastern clade, likewise, expresses a spectrum of rugosities from moderate to extensive (Figs. 17E, F, H, G and Fig. 18 in order of increasingly large and strongly textured tubercles). The Western clade button-scaled geckos, which share much of their range with the very rugose *C. bibronii* may be exhibiting character displacement in areas of sympatry. The greatest difficulty in the identification of *Chondrodactylus* species from each other is distinguishing the "Kgaligadi" and Eastern clade C. *laevigatus* from *C. turneri*. This is especially difficult in the broad area from central Zimbabwe to central Mozambique in which they likely occur in parapatry or potentially even sympatry (unverified).

Distribution. *Chondrodactylus laevigatus* has by far the broadest range of any member of the genus (Fig. 16). Its distribution in South Africa has been documented (as *C. turneri* [part]) by Branch (2014) and is limited to northern portions of the Northern Cape Province from near Springbok, east along the Orange River as far as Upington, with scattered records near the Molopo and Nossob rivers in the Mier Kalahari and Steinkopf in Namaqualand. It is probably more-or-less continuously distributed throughout this area except for sandy areas that offer no suitable refuge sites, but is most frequently encountered from Lekkersing northward to the Namibian border and in rocky areas along the south shore of the Orange River, where it is syntopic with *C. bibronii* (Methuen and Hewitt, 1914), even occupying refuges beneath the same rock slabs (Bauer and Branch, "2001" 2003). Virtually the whole of Namibia is occupied by *C. laevigatus,* with the exception of the Namib sand seas and portions of the Kalahari that are devoid of rocks and trees. Nonetheless, isolated rocky outcrops surrounded by sand for many kilometers may support populations of *C. laevigatus*. Verified records in Angola are few (Marques et al., 2018) but include records in Cunene (Monard, 1937), Huíla (Baptista et al., 2019; Butler et al., 2019) and Cuando Cubango (Conradie et al., 2016 [as *C.* cf. *pulitzerae*]) provinces, all above the Angolan escarpment. It is likely distributed widely across the southern Angolan Plateau, although the verified records are too few to estimate its northern limits. A record by Schmidt (1933) from Pico Azevedo in the lowlands of Namibe is referable to *C. fitzsimonsi* (Marques et al., 2018); however, we here report several records in coastal Namibe Province (Table 1).

To the east of Namibia and Angola, the distribution of *C. laevigatus* is less precisely known. It occurs throughout suitable habitats in western and northern Botswana, western and northern Zimbabwe, through Zambia and diagonally northeastward as far as southern Kenya. No examples of sympat-

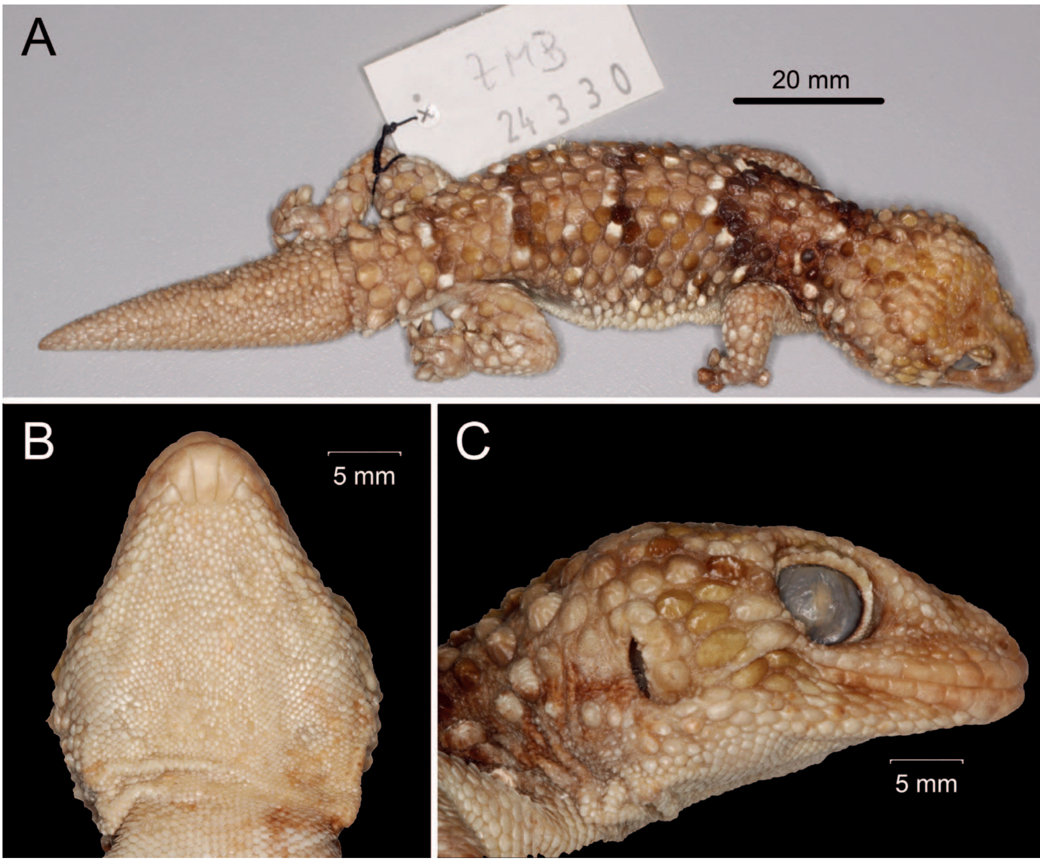

Figure 18. ZMB 24330, a specimen originally reported as *Pachydactylus bibronii* from the "Vulkangebiet" of East Africa by Sternfeld (1912). No further specimens from this area (modern Rwanda) have been reported and it is likely that that this specimen, which is typical of East African *C. laevigatus* in its large body scales (A), mid-sized chin scales (B), and slightly concave snout in profile (C) was collected on the return trip to the coast through central Tanzania.

ry with *C. turneri* are known with certainty, but its ability to co-occur with *C. bibronii* and *C. fitzsimonsi* suggests that this may be possible, perhaps in regions of central Zimbabwe or along the course of the Zambezi River in Mozambique. The eastward extension of *C. laevigatus* roughly follows the Zambezi Valley and in Zambia is mostly bracketed by the Zambezi and Luangwa rivers (Simbotwe and Mubamba, 1993). Sampling in central Mozambique is poor, but existing records suggest that lowland records south of the Pungwe River are *C. turneri,* whereas those north of the Ligonha River are *C. laevigatus*. The distribution of *C. laevigatus* in Tanzania and Kenya appears to be disjunct and scattered (Loveridge, 1928, 1947, 1951, 1955, 1957a). This may be an artifact of collection effort or bias or it may reflect limited suitable habitats, or perhaps competition with large-bodied *Hemidactylus* spp. and *Elasmodactylus* spp.

An isolated record of a *Chondrodactylus* sp. from Rwanda has often been reported or plotted, albeit with some speculation (de Witte, 1941; Loveridge, 1947, 1957b; Spawls et al., 2006, 2018) and stems from a report by Sternfeld (1912) based on a specimen from the "Vulkangebiet." The single specimen, ZMB 24330 (Fig. 18), was collected by Reinhard Houy on the 1911 expedition led by Hans Heinrich Josef Meyer to the area between Lake Kivu and Lake Victoria (Meyer, 1913). The Museum für Naturkunde catalogue entry for the specimen lists only "Dt. Ost Afrika." Vulkangegiet, the published locality, is more specific but still vague, referring to the area to the northeast of Lake Kivu, in northern Rwanda and adjacent Nord-Kivu Province, Democratic Republic of Congo. This record has never been verified by additional vouchers or by records with specific localities and the species has not been mentioned in more recent regional literature (e.g., Laurent, 1956). In the absence of confirmation of the occurrence of *Chondrodactylus* in the region and in light of the unlikely disjunction from the otherwise more-or-less contiguous distribution of the genus, we regard this record as dubious and consider both the Democratic Republic of Congo and Rwanda to be outside of the range of the genus. ZMB 24330 is typical of *Chondrodactylus laevigatus* from East Africa (see below) and the expedition would have passed through the known range of this species from Kilamatinde to Morogo in east-central Tanzania on its way back to the coast. The mid-sized chin scales (Fig. 18B) and slightly concave snout profile (Fig. 18C) are characteristic of *C. laevigatus* in general, whereas the very large body tubercles (Fig. 18A) are typical of the East African clade specifically.

The exact patterns of distribution of *C. turneri* and *C. laevigatus* in Zimbabwe, central Mozambique, and southernmost Malawi are uncertain. The characters used herein to distinguish eastern (highly tuberculate) *laevigatus* from *turneri* were not yet determined more than a decade ago when this project began. Thus, some specimens were examined before what ultimately proved to be the most diagnostically valuable characters were identified. Further, not all specimens for which we have locality data (i.e., are plotted in Fig. 16) have been examined by us. This applies particularly to specimens from the Natural History Museum of Zimbabwe. From genotyped individuals, we know that *C. laevigatus* extends across northern Zimbabwe from Lake Kariba to the former Elim Mission in the Vumba Mountains, whereas *C. turneri* occurs from Bulawayo east to southern Masvingo and Manicaland provinces. *Chondrodactylus laevigatus* likely occupies the higher elevations throughout the Eastern Highlands of Zimbabwe, but we are currently unsure of the allocation of the populations of the Zimbabwean Midlands. Likewise, we are uncertain where a switch to (or an area of sympatry with) *C. turneri* might occur between the Chimanimani Mountains and the adjacent lowlands. Likewise, the identity of populations between the lower end of Lake Kariba and the vicinity of Tete and between the Lower Zambezi and the Shire Highlands of Malawi remains uncertain.

Comments. The description of *Pachydactylus laevigatus* was by J.G. Fischer, who was the volunteer in charge of the herpetological collections of the Hamburg Museum at the time (Adler, 2007). Fischer (1888) mentioned only 2 specimens of this species received from Steingröver, one of which was illustrated. When Fischer died the following year, his collection was purchased by the British Museum from "Madame Fischer." The collection included a number of other Namibian specimens corresponding to material cited in the same paper. Fischer's (1888) illustration of the dorsum of one of his syntypes matches exactly the color pattern of BMNH 1946.12.26.1 (Fig. 19), as does its regenerated tail and size (89 mm SVL), confirming its identity as a type. Details of the second specimen also correspond well to BMNH 1946.12.26.2. Both syntypes are unambiguously assignable to the same taxon and cannot be mistaken for any other congener.

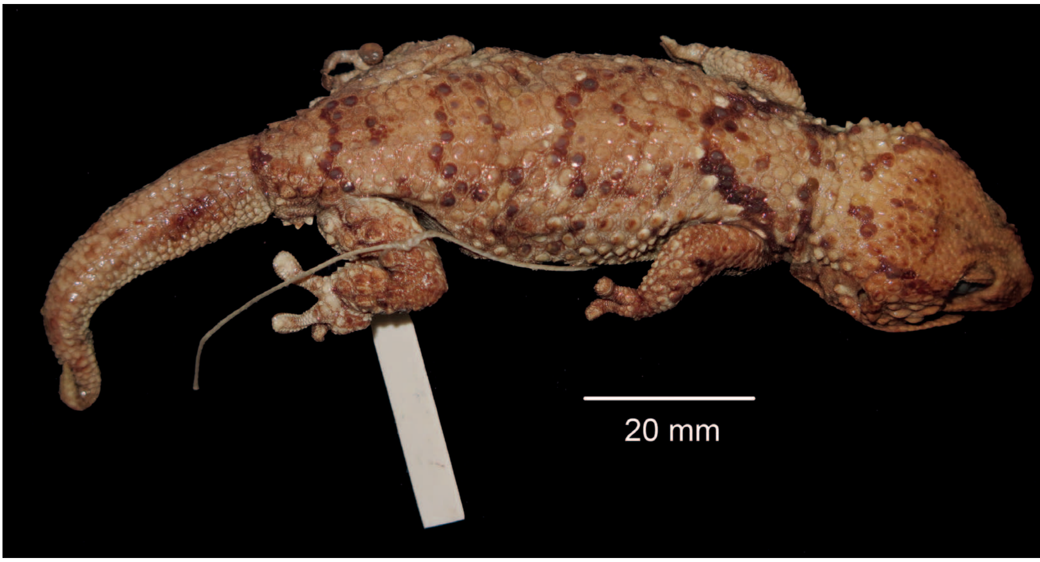

Figure 19. Syntype of *Pachydactylus laevigatus* Fischer, 1888 (BMNH 1946.12.26.1), from the western Karas Region, Namibia. Photograph by A.M. Bauer © *The Trustees of the Natural History Museum, London.*

The type locality of *Pachydactylus laevigatus* Fischer, 1888 lies within the distribution of the southwestern clade and members of this clade are easily diagnosable on morphological grounds, being characterized by the button-scaled morphology, with tubercular keels and mucrones lacking. In both remaining subclades, body scalation is more heterogeneous and some populations are characterized by an extremely acuminate tuberculation, similar to that of *C. turneri* (see above). Given the lack of ambiguity regarding the identity of the syntypes and the fact that no syntypes are unaccounted for, there is no compelling reason to designate a lectotype in this instance.

Prior to the description of *P. laevigatus,* specimens of this species were referred to *P. bibronii* (e.g., Boulenger, 1885). As the specific epithet implies, typical *C. laevigatus* are characterized by their relatively smooth (so-called "button-scaled") tubercles, which easily distinguish them from *C. bibronii,* which have much more strongly keeled or mucronate tubercles. However, although this scale morphology is typical in the western half of Namibia and in adjacent areas of South Africa, the phenotype of *C. laevigatus* becomes decidedly more "*bibronii*-like" from the Namibian Kalahari, Kavango, and Zambezi Regions eastwards. As a consequence, eastern *P. laevigatus* until 1995 had frequently been assigned to *P. bibronii*. Benyr (1995), however, identified a reliable scale character (the size of the gular scales relative to the paravertebral dorsal tubercles) that unambiguously separated *P. bibronii* from what he considered to be *P. laevigatus,* with 3 subspecies—the nominotypical form in the Northern Cape and western Namibia, *P. l. pulitzerae* in Angola, and *P. l. turneri* in the east of the subcontinent. Benyr (1995), however, had overlooked that *Homodactylus turneri* Gray, 1864 had temporal priority over *Pachydactylus laevigatus* Fischer, 1888. Branch (1998), however, who was cognizant of this, recognized a monotypic *P. turneri* for all geckos in the *P. bibronii* group exclusive of

P. bibronii itself and the distinctive *C. fitzsimonsi* from northwestern Namibia. Although Branch (1998) provided no justification for the resurrection of *P. turneri,* the rationale was subsequently explained by Lamb and Bauer (2002), and the taxon names subsequently recognized in light of Benyr's (1995) work were *P. t. turneri, P. t. pulitzerae,* and *P. t. laevigatus*. Most subsequent authors did not use trinomials; therefore, the name *Pachydactylus turneri* (and, after 2005, *Chondrodactylus turneri*) was widely applied *sensu* Branch (1998) until the genetic distinctiveness of *C. laevigatus* and *C. pulitzerae* from *C. turneri sensu stricto* was explicitly demonstrated by Heinz (2011) in his unpublished thesis. However, *C. turneri* and *C. laevigatus* were not recognized in their current sense in the published systematic literature until Ceríaco et al. (2014) and later Heinicke et al. (2017), although again without explicit justification. Marques et al. (2018) likewise used *C. laevigatus* as specifically distinct from *C. turneri,* citing the unpublished phylogeny of Heinz (2011).

Heinz (2011) reported shared nuclear haplotypes amongst individuals from across Namibia, indicating gene flow across the various morphotypes of *C. laevigatus*. Likewise, he found similar haplotypes represented in northeastern Zimbabwean *Chondrodactylus* that we here interpret as *C. laevigatus,* whereas these haplotypes differed markedly from those in southeastern Zimbabwe and eastern South Africa, all of which also share a rearrangement in ND2 and are here interpreted as *C. turneri*. In part because of these shared haplotypes, we choose to recognize *C. laevigatus* as a single species. However, an argument could be made for its subdivision into 3 putative species, based on the deep mitochondrial divergence between the main subclades and their strong support (BS 100%). Under such a scenario *C. laevigatus sensu stricto,* the western clade, would be easily diagnosable, but the difficulties of distinguishing the more eastern forms from *C. turneri* would still remain.

Key to the Species of *Chondrodactylus*

1a. Digits short, without adhesive toepads (Fig. 1 left) .... *C. angulifer*
1b. All digits with toepads bearing broad adhesive lamellae (Fig. 1 right)............ 2
2a. Chin and gular scales large, a row of 5 chin scales approximately twice the width of a paravertebral dorsal tubercle (Fig. 7C); head strongly triangular, about as wide as long (Fig. 5C); dorsal scales flat or weakly raised but never keeled (Fig. 6C) .... *C. fitzsimonsi*
2b. Chin and gular scales small, ≥5 chin scales contained within the width of a single paravertebral tubercle (Fig. 7 and B) 3
3a. Chin and gular scales minute and granular, approximately 5 chin granules contained in half the width of a paravertebral tubercle (Fig. 7A); dorsal tubercles large, always strongly keeled and/or mucronate (Fig. 6B) .... *C. bibronii*
3b. Chin and gular scales small and granular, approximately 5 chin granules contained in the width of a single paravertebral tubercle (Figs. 7B, 18B); dorsal tuberculation variable (Figs. 6D–H)...................4
4a. Head relatively narrow (usually <90% broad as long), snout acuminate; large stellate tubercles on nape and occiput contrasting with smaller, less rugose scales on crown and snout (Fig. 5B); dorsal midline on at least nape and shoulders "naked"—without small tubercles, often giving the appearance of a white vertebral stripe (Fig. 6D) .... *C. pulitzerae*
4b. Head wider (>90% broad as long), snout broader, less acuminate (Figs. 5D–H); anterior middorsum with-

out "naked" stripe, at least some tubercular scales in dorsal midline (Figs. 6E–H) 5

5a. Head and body somewhat depressed (Figs. 17A–B); dorsum with distinctly raised, but keelless or very weakly keeled tubercles (Fig. 6H)..
... *C. laevigatus* (part—Western Clade)

5b. Head and body not depressed; dorsal tubercles strongly keeled to stellate (Figs. 6E–G)............................6

6a. Head deep; snout short and broad, head approximately as wide as deep, lores moderately to strongly inflated (Fig. 5D); snout deep (less steeply sloped; Fig. 14) and slope of snout sometimes with a slight convexity when viewed in profile; relatively extensive exposed granular skin on occiput, nape, and anterior midline of the back; [Southeastern Africa, east of 25°E, southern Zimbabwe and Mozambique lowlands and lower Zambezi River Valley]...........................*C. turneri*

6b. Head of intermediate depth; snout of moderate length, broad, lores weakly to moderately inflated (Figs. 5F–H, 18C); snout less deep and slope of snout sometimes with a slight concavity when viewed in profile; exposed granular skin on occiput, nape, and anterior midline of the back not extensive; [Southern Africa, west of 25°E, upper and middle Zambezi Valley, Zimbabwe Highlands, Zambia, Malawi (exclusive of the lower Shire Valley), Mozambique north of the Ligonha River through eastern Tanzania to southern Kenya] ....*C. laevigatus* (Kgaligadi and Eastern Clades)

DISCUSSION

Chondrodactylus geckos are the largest and among the most frequently encountered geckos in Southern Africa, where they are often seen in and around human dwellings (Cott, 1934; FitzSimons, 1943; Loveridge, 1947). They share a convoluted taxonomic history complicated by sympatry across comparatively broad ranges with limited morphological differentiation despite deep genetic divergences (Fig. 2, Table 3). Our genetic data clearly support the recognition of six deeply divergent clades, which we here recognize as species. The pattern of relationships we found among these six species is congruent with that reported by Heinicke et al. (2017) based on just a single representative each. Our much deeper sampling, however, has revealed previously unreported patterns of intraspecific variation.

Divergence within each of the species is relatively deep, up to 17% intraspecific divergence in ND2, with interspecific divergences of approximately 30% between *Chondrodactylus angulifer* and all its congeners and 13–24% between the toe-padded species (Table 3). These values are high with respect to intrageneric divergences in some other gekkotans, but similar to divergences seen among *Pachydactylus* species (e.g., Bauer et al., 2002; Heinicke et al., 2017). However, unlike *Pachydactylus* and most other geckos, *Chondrodactylus* spp. are large-bodied habitat-generalists, occupying either large areas of more-or-less contiguous sandy terrestrial environments (*C. angulifer*) or almost any type of rocky, vegetative or anthropogenic climbing surfaces (toe-padded species; Heinz, 2011). The vagility of the constituent climbing species is attested to by their occurrence in small patches of rock, isolated by kilometers by open sand (Haacke, 1975; pers. obs., A.M. Bauer) and by their propensity for inadvertent translocation (see *C. pulitzerae* and *C. laevigatus* accounts), whereas their adaptability is shown by the ability of most species to survive and flourish in and around human habitation (Rose, 1962; Branch, 2014). On first principles, these attributes would appear to promote genetic connectivity across geographic distance and decrease the rate of speciation. Heinicke et al. (2017) verified this within the broader *Pachydactylus* clade to which *Chondrodactylus* belongs, showing that diversification rates increased only in lineages combining small size (associated with low vagility) and habitat specialization. Such taxa typically also have small distributional ranges (Dynesius and Jansson, 2000). Consequently, *Chondrodactylus,* as well as *Elasmodactylus* and the large-bodied *Pachydactylus namaquensis* group (Branch et al., 1996), are relatively species-poor in comparison with small-bodied clades, within which individual species specialize on particular substrate types (Bauer, 1999 "2000", 2010; Branch et al., 2011).

Large pairwise distances among *Chondrodactylus* species correspond to deep interspecific splits, with divergence dates estimated by Heinicke et al. (2017) falling between the mid-Oligocene for the split between the padless *C. angulifer* and padded relatives to the late Miocene for the split between *C. turneri* and *C. laevigatus*. Miocene speciation events may have been influenced by climatic and habitat turnover through this period (Porknoy et al., 2015) as historic pulses of aridity in southern Africa led to the repeated contraction, expansion, and shifting movement of the borders of the Kalahari and Namib deserts (van Zinderen Bakker, 1975; Lancaster, 1981; Stokes et al., 1997; Goudie, 1999). This pattern has been proposed to have contributed to speciation in chameleons (Tolley et al., 2008). With the expansion of the Namib and Kalahari and the development of the "arid corridor" connecting the southwest to the Horn of Africa (Wagner, 2010) *C. laevigatus* likely also expanded its range. Ties between the southwest and Horn have been noted in birds (Winterbottom, 1967), plants (Verdcourt,1969; de Winter, 1971; Jürgens, 1997), mammals (Lorenzen et al., 2006; Montgelard and Matthee, 2012), amphibians (Poynton, 1995) and scorpions (Prendini, 2005), as well as in snakes (Wüster et al., 2007) and other lizards (Wagner, 2010; Kissling et al., 2016; Freitas et al., 2018; Wagner et al., 2018). However, biogeographic expansions via the arid corridor among disparate groups are not necessarily temporally congruent, because it is likely that such a corridor has been intermittently "open" and "closed." This repeated isolation and secondary contact may also have contributed to the diversification of this group and close relatives like *Pachydactylus*.

Of course, any interpretation of diversification rates is dependent on the knowledge base for the constituent taxa. Is it possible that the genus *Chondrodactylus* is, in fact, more species-rich than we acknowledge? Are they undercounted? Toe-padded *Chondrodactylus* are conspicuous wherever they occur and, with the exception of *C. fitzsimonsi,* are commonly commensal, at least under some circumstances. Although the possibility of localized undocumented endemism exists, we are aware of only a single population that we suspect to represent an additional valid species. This is a dwarf *Chondrodactylus,* apparently endemic to inselbergs in the southern Namib dune sea (Haacke, 1975) and it will be described elsewhere. Given the relatively deep genetic divergences within some of the species recognized herein, others might consider the elevation of major subclades to species rank. However, identifying diagnostic features of these less-inclusive units may be difficult and shared nuclear haplotypes (Heinz, 2011) argue against further splitting.

Nonetheless, further investigation is warranted, particularly in *C. pulitzerae,* in which the deepest divergences are seen (although unaccompanied by obvious morphological differences), and in *C. laevigatus,* which exhibits, by far, the greatest phenotypic diversity across its range. We identified 3 major subclades within *C. laevigatus*.

One of these, the western clade, from which the type specimens derive, is morphologically distinctive, exhibiting the button-scaled tuberculation with little variation across most of its range in the Northern Cape and southern and central Namibia. However, to the north and east, *C. laevigatus* becomes much more spiny or rugose, with the dorsal pholidosis resembling that of *C. bibronii* or *C. turneri*. This difference may reflect character displacement, because *C. laevigatus* is especially smooth-scaled when it is sympatric with *C. bibronii,* but becomes spinier when it occurs by itself (Figs. 6, 17). Alternatively, tubercle size and scale number may be related to environmental variables. It has been demonstrated in a diversity of lizards that body scale size and, reciprocally, number may vary with hydric conditions as a means to reduce water loss in xeric environments (e.g., Thorpe and Baez, 1987, 1993; Malhotra and Thorpe, 1997; Calsbeek et al., 2006). By and large, smaller tubercles and more exposed granules are typical of *C. laevigatus* in the most arid portions of its distribution in the south and west of its distribution, whereas the Kgadigadi and East African clades occupy areas of higher rainfall and exhibit larger tubercles. This runs counter to the predicted trend, but this exception in desert geckos has been previously noted (Calsbeek et al., 2006). Certainly a quantitative assessment of scalation variation and its possible association with environmental variables is warranted, though beyond the scope of the present study.

How robust the 3 subclades of *C. laevigatus* are remains uncertain. Although our genetic sampling covers a large area, more fine-scale sampling is needed, especially in East Africa. Further sampling may reveal whether, in fact, there are 3 discrete subclades, or if these lose clear support with collections from intervening areas. Most importantly, further sampling in the east, particularly in the Midlands of Zimbabwe, in Tete and other central provinces of Mozambique, and in southern Malawi, will help to more unambiguously determine the range limits of both *C. laevigatus* and *C. turneri*. As discussed in the accounts for these two species, the morphological differences between the two in these areas are subtle at best. Our estimations of the species ranges (Fig. 16) are based on the sparse genetic sampling east of about 25°E and largely on the gestalt of preserved specimens, informed by the examination of many hundreds of individuals. More for simplicity than any reflection of reality, we have assumed that these two species occur in allopatry or parapatry, but intensive sampling in critical regions could reveal otherwise because it is clear from the situation in the west of the continent that toe-padded *Chondrodactylus* can occur in broad sympatry and even syntopy.

Two species are of particular interest genetically. *Chondrodactylus turneri* is characterized by a mitochondrial genome rearrangement. Such rearrangements are known from most major vertebrate taxa, including gekkotans (Kumazawa et al., 2014), probably arising via a "duplication-random loss" model (Moritz et al., 1987; Boore, 2000; San Mauro et al., 2006). Rearrangement is strongly associated with the loss of the origin of light-strand replication (between -trnaN and -trnaC) among vertebrates including squamate reptiles (Macey et al., 2005), suggesting this loss is a precursor to rearrangement (Macey et al., 1997, 1998). A complete sequence of the rearranged genome of *C. turneri* is highly desirable to determine the location of the alanine tRNA, as well as to determine whether the inserted proline tRNA is a duplicate. The 200 base-pair insert following *trnP* is likely a copy of a portion of the mitochondrial control region, the section immediately adjacent in the typical vertebrate mitochondrial genome. Five other rearrangements, duplications, and/or deletions within gekkotans include two in the genus *Uroplatus,* rearrangements within the genera *Tropiocolotes* and *Stenodacylus* (Kumazawa et al., 2014), and duplications in *Heteronotia* (Fujita et al., 2007).

Chondrodactylus fitzsimonsi is also of interest because some individuals share nuclear genes with *C. pulitzerae* and specimens appearing to show a phenotype intermediate between *fitzsimonsi* and *laevigatus* are known from inland of the Skeleton Coast of northern Namibia. Circumstantial evidence suggests that hybridization may occur along the edge of the Namib, or perhaps that there has been past introgression. Increased sampling of individuals and more nuclear markers should be able to distinguish between current hybridization and past introgression or a possible combination of the two (Twyford and Ennos, 2012).

Four species of *Chondrodactylus* (*C. angulifer, C. fitzsimonsi, C. laevigatus, C. pulitzerae*) can occur in sympatry in northwestern Namibia. This area corresponds to the Kaokoveld–Damaraland center of diversity and endemism, noted in plants (Jürgens, 1991, 1997; Craven and Vorster, 2006) and scorpions (Prendini, 2005) as well as reptiles (Simmons et al., 1998), including the speciose ''northwestern group'' of *Pachydactylus* geckos (Bauer and Lamb, 2005; Bauer, 2010). The region's rugged topology and complex geology, as well as its position bordering the arid lowlands and the more mesic mopane transition zone upland, are thought to contribute to high levels of diversity and endemism (Irish, 2002; Prendini, 2005), and in this instance may facilitate the co-occurrence of multiple congeners that seem to share very similar niche parameters. The significant overlap of the ranges of *Chondrodactylus* spp. in southwestern Africa indicates that features such as the Kunene River in the north and the Orange (Gariep) River in the south do not seem to represent significant barriers to most of the regional herpetofauna (Simmons et al., 1998; Bauer et al., 2006). Although they tend to be extremely common lizards where found, there are few reports on the natural history or ecology (beyond isolated reports of predators and prey, see e.g., Cott, 1934; FitzSimons, 1943; Loveridge, 1947) of members of the genus. With little ecological data to draw from, it is difficult to determine how species remain discrete from one another in sympatry, or even syntopy (FitzSimons, 1938; Bauer and Branch, "2001" 2003). *Chondrodactylus bibronii* have been noted to display gregarious aggregation behavior, with multiple full-grown adults of both sexes found in the same rock crevices (FitzSimons, 1943; Branch, 1998; Meyer and Mouton 2007). Though a study as to whether this aggregation is induced by limited availability of optimal shelters or whether it is the result of mutual conspecific attraction was inconclusive (Meyer and Mouton 2007), these observations suggest behavioral cues may mediate interactions, hinting at the possibility that behavioral isolation may be reinforcing species-level boundaries. These limited ecological insights highlight how much more there is to learn about *Chondrodactylus* and Africa's herpetofauna in general.

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LITERATURE CITED

Adler, K. 1989. Herpetologists of the past, PP. 5–141 IN: K. Adler, editor. *Contributions to the History of Herpetology*. Oxford, Ohio: Society for the Study of Amphibians and Reptiles.

Adler, K. 2007. Herpetologists of the past, PP. 7–273 IN: K. Adler, editor. *Contributions to the History of Herpetology*, Vol. 2. St. Louis, Missouri: Society for the Study of Amphibians and Reptiles.

Alexander, G., and J. Marais. 2007. *A Guide to the Reptiles of Southern Africa*. Cape Town: Struik Publishers.

Baptista, N. L., T. António, and W. R. Branch. 2019. The herpetofauna of Bicuar National Park and surroundings, southwestern Angola: a preliminary checklist. *Amphibian and Reptile Conservation* 13(2): 96–130 (e203).

Barbour, T., and A. Loveridge. 1946. First supplement to typical reptiles and amphibians. *Bulletin of the Museum of Comparative Zoology at Harvard College* 96: 59–214.

Bates, M. F., W. R. Branch, A. M., Bauer, M., Burger, J. Marais, G. J. Alexander, and M. S. de Villiers, editors. 2014. *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*. Suricata 1. Pretoria, South Africa: South African National Biodiversity Institute.

Bauer, A. M. 1990. Phylogeny and biogeography of the geckos of southern Africa and the islands of the western Indian Ocean: a preliminary analysis, PP. 275–284 IN: G. Peters and R. Hutterer, editors. *Vertebrates in the Tropics*. Bonn, Germany: Zoologisches Forschungsinstitut und Museum A. Koenig.

Bauer, A. M. "1999" 2000. Evolutionary scenarios in the *Pachydactylus*-group geckos of southern Africa: new hypotheses. *African Journal of Herpetology* 48: 53–62.

Bauer, A. M. 2010. A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia. *Bonn Zoological Journal* 57: 257–266.

Bauer, A. M., and W. R. Branch. "2001" 2003. The herpetofauna of the Richtersveld National Park, and the Adjacent Northern Richtersveld, Northern Cape Province, Republic of South Africa. *Herpetological Natural History* 8: 111–160.

Bauer, A. M., W. R. Branch, and W. D. Haacke. 1993. The herpetofauna of the Kamanjab area and adjacent Damaraland, Namibia. *Madoqua* 18: 117–145.

Bauer, A. M., and R. Günther. 1991. An annotated type catalogue of the geckos (Reptilia: Gekkonidae) in the Zoological Museum, Berlin. *Mitteilungen aus dem Zoologischen Museum in Berlin* 67: 279–310.

Bauer, A. M., and T. Lamb. 2005. Phylogenetic relationships of southern African geckos in the *Pachydactylus* Group (Squamata: Gekkonidae). *African Journal of Herpetology* 54: 105–129.

Bauer, A. M., and A. P. Russell. 1991. Pedal specializations in dune-dwelling geckos. *Journal of Arid Environments* 20: 43–62.

Bauer, A. M., T. Lamb, and W. R. Branch. 2002. A revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the description of a new species from northern Namibia. *Proceedings of the California Academy of Sciences* 53: 23–36.

Bauer, A. M., T. Lamb, and W. R. Branch. 2006. A revision of the *Pachydactylus serval* and *P. weberi* Groups (Reptilia: Gekkota: Gekkonidae) of Southern Africa, with the description of eight new species. *Proceedings of the California Academy of Sciences* 57: 595–709.

Bauer, A. M., A. de Silva, E. Greenbaum, and T. R. Jackman. 2007. A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin*, *Zoologische Reihe* 83 (Sonderheft): 22–32.

Benyr, G. 1995. Systematik und Taxonomie der Geckos des *Pachydactylus bibronii-laevigatus* Komplexes (Reptilia: Squamata: Gekkonidae). Diplomarbeit. Vienna, Austria: Universität Wien.

Bocage, B. du, V. 1867a. Segunda lista dos reptis das possessões portuguezas d'Africa occidental que existem no Museu de Lisboa. *Jornal de Sciencias Mathematicas, Physicas e Naturaes* 1(3): 217–228.

Bocage, B. du, V. 1867b. Descriptions of two new saurians from Mossamedes (West Africa). *The Annals and Magazine of Natural History* Series 3, 20: 225–228.

Bocage, B. du, V. 1887a. Mélanges erpétologiques. IV. Reptiles du dernier voyage de MM. Capello et Ivens à travers l'Afrique. *Jornal de Sciencias Mathematicas Physicas e Naturaes* 11(44): 201–208.

Bocage, B. du, V. 1887b. Mélanges erpétologiques. V. Reptiles et batraciens de Quissange (Benguella) envoyés par M. J. Anchieta. *Jornal de Sciencias Mathematicas, Physicas e Naturaes* 6(44): 208–211.

Bocage, B. du, V. 1895. *Herpétologie d'Angola et du Congo*. Lisbonne (Lisbon), Portugal: Ministério da Marinha e das Colónias.

Boore, J. L. 2000. The duplication/random loss model for gene rearrangement exemplified by mitochondrial genomes of deuterostome animals, PP. 133–147 IN: D. Sankoff and J. Nadeau, editors. *Comparative Genomics, Computational Biology Series*, Vol. 1. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Boulenger, G. A. 1885. *Catalogue of the Lizards in the British Museum* (*Natural History*). Volume 1. *Geckonidæ, Eublepharidæ, Uroplatidæ, Pygopodidæ, Agamidæ*. London: The Trustees of the British Museum.

Boulenger, G. A. 1887. On a new gecko, of the genus *Chondrodactylus,* from the Kalahari Desert. *Proceedings of the Zoological Society of London* 1887: 339–340.

Boulenger, G. A. 1910. A revised list of the South African reptiles and batrachians, with synoptictables, special reference to the specimens in the South African Museum, and descriptions of new species. *Annals of the South African Museum* 5: 455–538.

Branch, W. R. 1994. Herpetofauna of the Sperrgebiet region in Southern Namibia. *Herpetological Natural History* 2: 1–11.

Branch, W. R. 1998. *Field Guide to Snakes and Other Reptiles of Southern Africa*, 3rd edition. Cape Town, South Africa: Struik.

Branch, W. R. 2014. *Chondrodactylus,* PP. 102–104 IN: M. F. Bates, W. R. Branch, A. M., Bauer, M. Burger, J. Marais, G. J. Alexander, and M. S. de Villiers, editors. 2014. *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*. Suricata 1. Pretoria, South Africa: South African National Biodiversity Institute.

Branch, W. R., A. M. Bauer, and D. A. Good. 1996. A review of the Namaqua gecko, *Pachydactylus namaquensis* (Reptilia: Gekkonidae) from southern Africa, with the description of two new species. *South African Journal of Zoology* 31: 53–69.

Branch, W. R., A. M. Bauer, T. R. Jackman, and M. Heinicke. 2011. A new species of the *Pachydactylus weberi* complex (Reptilia: Squamata: Gekkonidae) from the NamibRand Reserve, southern Namibia. *Breviora* 524: 1–15.

Branch, W. R., P. Vaz Pinto, N. Baptista, and W. Conradie. 2019. The reptiles of Angola: History, diversity, endemism and hotspots, PP. 283–334 IN: B. J. Huntley, V. Russo, F. Lages, and N. Ferrand, editors. *Biodiversity of Angola. Science and Conservation: A Modern Synthesis*. Cham, Switzerland: Springer.

Butler, B. O., L. M. P. Ceríaco, M. P. Marques, S. Bandeira, T. Júlio, M. P. Heinicke, and A. M. Bauer. 2019. Herpetological survey of Huíla Province, southwest Angola, including first records from Bicuar National Park. *Herpetological Review* 50: 225–240.

Calsbeek, R., J. H. Knouft, and T. B. Smith. 2006. Variation in scale numbers is consistent with ecologically based natural selection acting within and between lizard species. *Evolutionary Ecology* 20: 377–394.

Carranza, S., E. N. Arnold, J. A. Mateo, and P. Geniez. 2002. Relationships and evolution of the North African geckos, *Geckonia* and *Tarentola* (Reptilia: Gekkonidae), based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* 23: 244–256.

Ceríaco, L., A. M. Bauer, D. C. Blackburn, and A. C. F. C. Lavres. 2014. The herpetofauna of the

Capanda Dam Region, Malanje, Angola. *Herpetological Review* 45: 667–674.

Ceríaco, L. M. P., A. M. Bauer, M. P. Heinicke, and D. C. Blackburn. 2017. *Chondrodactylus pulitzerae* (Schmidt, 1933), Pulitzer's thick-toed gecko in Angola. *African Herp News* 64: 41–43.

Ceríaco, L. M. P., S. d. A. C., de Sá, S. Bandeira, H. Valério, E. L. Stanley, A. L. Kuhn, M. P. Marquez, J. V. Vindum, D. C. Blackburn, and A. M. Bauer. 2016. Herpetological survey of Iona National Park and Namibe Regional Natural Park, with a synoptic list of the amphibians and reptiles of Namibe Province, southwestern Angola. *Proceedings of the California Academy of Sciences* 63: 15–61.

Chernomor, O., A. von Haeseler, and B. Q. Minh. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–100.

Conradie, W., R. Bills, and W. R. Branch. 2016. The herpetofauna of the Cubango, Cuito, and lower Cuando river catchments of south-eastern Angola. *Amphibian and Reptile Conservation* 10(2): 6–36.

Cott, H. B. 1934. The Zoological Society's expedition to the Zambesi, 1927: no. 5. On a collection of lizards, mainly from Portuguese East Africa, with descriptions of new species of *Zonurus*, *Monopeltis*, and *Chirindia. Proceedings of the Zoological Society of London* 1934: 145–173, pls. I–III.

Craven, P., and P. V. Vorster. 2006. Patterns of plant diversity and endemism in Namibia. *Bothalia* 36: 175–189.

Delisle, H. F., R. A. Nazarov, L. R. Raw, and J. Grathwohl. 2013. *Gekkota, a Catalogue of Recent Species*. Privately published.

Delisle, H. F., R. A. Nazarov, L. R. Raw, and J. Grathwohl. 2016. *Gekkota, a Catalogue of Recent Species*, Second Edition. Privately published.

de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category, PP. 49–89 IN: R. Wilson, editor. *Species. New Interdisciplinary Essays*. Cambridge, Massachusetts: The M.I.T. Press.

de Winter, B. 1971. Floristic relationships between the northern and southern arid areas in Africa. *Mitteilungen der Botanischen Staatssammlung München* 10: 424–237.

de Witte, G. F. 1941. Batraciens et reptiles. *Exploration du Parc National Albert. Mission G. F. de Witte (1933–1935)*. Fascicule 33. Bruxelles [Brussels], Belgium: Institute des Parcs Nationaux du Congo Belge.

Dritsas, L. S. 2005. The Zambezi Expedition, 1858–64, African nature in the British scientific metropolis. Ph.D. Dissertation. Edinburgh, United Kingdom: The University of Edinburgh.

Dynesius, M., and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* 97: 9115–9120.

Fischer, J. G. 1888. Über eine Kollektion Reptilien von Angra Pequenna. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 5: 11–17, pl. II.

Fitzinger, L. J. 1843. *Systema Reptilium. Fasiculus Primus. Amblyglossae*. Vindobonae [Vienna], Austria: Braumüller et Seidel.

FitzSimons, V. F. M. 1935a. Notes on a collection of reptiles and amphibians made in the southern Kalahari, Bushmanland and Great and Little Namaqualand. *Annals of the Transvaal Museum* 15: 519–550.

FitzSimons, V. F. M. 1935b. Scientific results of the Vernay-Lang Kalahari Expedition, March to September, 1930. *Annals of the Transvaal Museum* 16: 295–397.

FitzSimons, V. F. M. 1937. Notes on the reptiles and amphibians collected and described from South Africa by Andrew Smith. *Annals of the Transvaal Museum* 17: 259–46.

FitzSimons, V. F. M. 1938. Transvaal Museum expedition to South-West Africa and Little Namaqualand, May to August 1937. Reptiles and amphibians. *Annals of the Transvaal Museum* 19: 153–209, pls. II–III.

FitzSimons, V. F. M. 1943. The lizards of South Africa. *Memoirs of the Transvaal Museum* 1: i–xv, 1–528, pls. I–XXIV, map.

FitzSimons, V. F. M. 1946. An account of the reptiles and amphibians collected on an expedition to the Cape Province, October to December, 1940. *Annals of the Transvaal Museum* 20: 351–377, pls. XIV–XVII.

Freitas, E. S., A. M. Bauer, C. D. Siler, D. G. Broadley, and T. R. Jackman. 2018. Phylogenetic and morphological investigation of the *Mochlus afer-sundevallii* species complex (Squamata: Scincidae) across the arid corridor of sub-Saharan Africa. *Molecular Phylogenetics and Evolution* 127: 280–287.

Frost, D. R., and D. M. Hillis. 1990. Species in concept and practice: herpetological applications. *Herpetologica* 46: 87–104.

Fujita, M. K., J. L. Boore, and C. Moritz. 2007. Multiple origins and rapid evolution of duplicated mitochondrial genes in parthenogenetic geckos (*Heteronotia binoei*; Squamata, Gekkonidae). *Molecular Biology and Evolution* 24(12): 2775–2786.

Gamble, T., A. M. Bauer, E. Greenbaum, and T. R. Jackman. 2008. Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta* 37:355–366.

Gamble, T., E. Greenbaum, T. R. Jackman, and A. M. Bauer. 2015. Into the light: diurnality has evolved multiple times in geckos. *Biological Journal of the Linnean Society* 115: 896–910.

Gamble, T., E. Greenbaum, A. P. Russell, T. R. Jackman, and A. M. Bauer. 2012. Repeated origin and loss of toepads in geckos. PLoS ONE 7(6): e39429. http://doi:10.1371/journal.pone.0039429

Gemel, R., G. Gassner, and S. Schweiger. 2019. Katalog der Typen der Herpetologischen Sammlung des Naturhistorischen Museums Wien—2018. *Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie* 121: 33–248.

Goudie, A. S. 1999. Climate: past and present, PP. 34–59 IN: W. Adams, A. Goudie, and A. Orme, editors. *The Physical Geography of Africa*. Oxford, United Kingdom: Oxford University Press.

Gray, J. E. 1864. Notes on some new lizards from South-Eastern Africa, with the descriptions of several new species. *Proceedings of the Zoological Society of London* 1864: 58–62, pl. IX.

Gray, J. E. 1865. Descriptions of two new genera of lizards from Damaraland. *Proceedings of the Zoological Society of London* 1865:640–642, pl. XXXVIII.

Greenbaum, E., A. M. Bauer, T. R. Jackman, M. Vences, and R. Glaw. 2007. A phylogeny of the enigmatic Madagascan geckos of the genus *Uroplatus* (Squamata: Gekkonidae). *Zootaxa* 1493: 41–51.

Griffin, M. 2000. The species diversity, distribution and conservation of Namibian reptiles: a review. *Namibia Scientific Society Journal* 48: 116–141.

Griffin, M. 2003. *Annotated Checklist and Provisional National Conservation Status of Namibian Reptiles*. Windhoek, Namibia: Namibia Scientific Society.

Günther, A. 1864. Report on a collection of reptiles and fishes made by Dr. Kirk in the Zambesi and Nyassa regions. *Proceedings of the Zoological Society of London* 1864: 303–313, pls. XXVI–XXVII.

Haacke, W. D. 1968. The burrowing geckos of southern Africa. M.Sc. Thesis. Pretoria, South Africa: University of Pretoria.

Haacke, W. D. 1975. Herpetological investigations in the Sand Sea of the southern Namib. *Bulletin of the Transvaal Museum* 15: 8–10.

Haacke, W. D. 1976a. The burrowing geckos of southern Africa. 4. (Reptilia: Gekkonidae). *Annals of the Transvaal Museum* 30: 53–70, 5 pls.

Haacke, W. D. 1976b. The burrowing geckos of southern Africa. 5 (Reptilia: Gekkonidae). *Annals of the Transvaal Museum* 30: 71–89.

Heinicke, M. P., T. R. Jackman, and A. M. Bauer. 2017. The measure of success: geographic isolation promotes diversification in *Pachydactylus* geckos. *BMC Evolutionary Biology* 17.9. http://doi.org/10.1186/s1286-2-016-0846-2

Heinz, H. 2011. Comparative phylogeography of two widespread geckos from the typically narrow-ranging *Pachydactylus* group in Southern Africa. Master's Thesis. Villanova, Pennsylvania: Villanova University.

Hellmich, W. 1957a. Herpetologische Ergebnisse einer Forschungsreise in Angola. *Veröffentlichungen der Zoologischen Staatssammlung München* 5: 1–92.

Hellmich, W. 1957b. Die Reptilienausbeute der Hamburgischen Angola-Expedition. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 55: 39–80.

Herrmann, H.-W., and W. R. Branch. 2013. Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. *Journal of Arid Environments* 93: 94–115.

Hewitt, J. 1911. Records of South African Lacertilia and Amphibia. Addenda and corrigenda. *Annals of the Transvaal Museum* 3: 42–55.

Hewitt, J. 1927. Further descriptions of reptiles and batrachians from South Africa. *Records of the Albany Museum* 3: 371–415.

Hill, A. W. 1922. Sir John Kirk. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew* 1922: 49–63.

Hoang, D. T., O. Chernomor, A. von Haeseler, B. Q. Minh, and L. S. Vinh. 2018. UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522.

Irish, J. 2002. Namibian mountains: biodiversity potential based on topography. Report for the Mountain Ecosystem Working Group of the National Biodiversity Task Force, Windhoek, Namibia.

Joger, U. 1985. The African gekkonine radiation: preliminary phylogenetic results, based on quantitative immunological comparisons of serum albumins, PP. 479–494 IN: K. L. Schuchmann, editor. *African Vertebrates: Systematics, Phylogeny and Evolutionary Ecology*. Bonn, Germany: Zoologisches Forschungsinstitut und Museum A. Koenig.

Jürgens, N. 1991. A new approach to the Namib region I: phytogeographic subdivision. *Vegetatio* 97: 21–38.

Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6: 495–514.

Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589.

Kirby, P. R. 1965. *Sir Andrew Smith, M.D., K.C.B., His Life, Letters and Works*. Cape Town, South Africa: A. A. Balkema.

Kissling, W. D., A. Blach-Overgaard, R. E. Zwaan, and P. Wagner 2016. Historical colonization and dispersal limitation supplement climate and topography in shaping species richness of African lizards (Squamata: Agamidae). *Scientific Reports* 6: 34014. http://doi:10.1038/srep34014

Kluge, A. G., and R. A. Nussbaum. 1995. A review of African–Madagascan gekkonid lizard phylogeny and biogeography (Squamata). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 183: 1–20.

Kumazawa, Y., S. Miura, C. Yamada, and Y. Hashiguchi. 2014. Gene rearrangements in gekkonid mitochondrial genomes with shuffling, loss, and reassignment of tRNA genes. *BMC Genomics* 15(1): 1–13. http://doi: 10.1186/1471-2164-15-930

Lamb, T., and A. M. Bauer. 2002. Phylogenetic relationships of the large-bodied members of the African lizard genus *Pachydactylus* (Reptilia: Gekkonidae). *Copeia* 2002: 586–596.

Lamb, T., and A. M. Bauer. 2006. Footprints in the sand: independent reduction of subdigital lamellae in the Namib-Kalahari burrowing geckos. *Proceedings of the Royal Society B* 273: 855–864.

Lancaster, N. 1981. Paleoenvironmental implications of fixed dune systems in southern Africa. *Paleogeography, Paleoclimatology, and Paleoecology* 33: 327–346.

Laurent, R. F. 1956. Esquisse d'une faune herpétologique du Ruanda-Urundi. *Les Naturalistes Belges* Novembre–Décembre 1956: 280–287.

Laurent, R. F. 1964. Reptiles et amphibiens de l'Angola. *Publicações Culturais da Companhia de Diamantes de Angola* 67: 1–165.

Lorenzen, E. D., P. Arctander, and H. R. Siegismund. 2006. Regional genetic structuring and evolutionary history of the Impala *Aepyceros melampus*. *Journal of Heredity* 97(2): 119–132.

Loveridge, A. 1928. Field notes on vertebrates collected by the Smithsonian Chrysler East African Expedition of 1926. *Proceedings of the United States National Museum* 73(17): 1–69, pls. 1–4.

Loveridge, A. 1947. Revision of the African lizards of the family Gekkonidae. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* 98: 1–469, pls.1–7.

Loveridge, A. 1951. On reptiles and amphibians from Tanganyika Territory collected by C.J.P. Ionides. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* 106: 175–204.

Loveridge, A. 1955. On a second collection of reptiles and amphibians taken in Tanganyika Territory by C. J. P. Ionides, Esq. *Journal of the East African Natural History Society* 22: 168–198.

Loveridge, A. 1957a. On a third collection of reptiles taken in Tanganyika by C. J. P. Ionides, Esq. *Tanganyika Notes and Records* 43: 1–19.

Loveridge, A. 1957b. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bulletin of the Museum of Comparative Zoölogy at Harvard College* 117: 151–362, i–xxxvi.

Macey, J. R., J. J. Fong, J.V. Kuehl, S. Shafiei, N. B. Ananjeva, T. J. Papenfuss, and J. L. Boore. 2005. The complete mitochondrial genome of a gecko and the phylogenetic position of the Middle Eastern *Teratoscincus keyserlingii*. *Molecular Phylogenetics and Evolution* 36(1): 188–193.

Macey, J. R., A. Larson, N. B. Ananjeva, Z. Fang, and T. J. Papenfuss. 1997. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 14(1): 91–104.

Macey, J. R., J. A. Schulte, II, A. Larson, N. B. Ananjeva, Y. Wang, R. Pethiyagoda, N. Rastegar-Pouyani, and T. J. Papenfuss. 2000. Evaluating Trans-Tethys migration: an example using acrodont lizard phylogenetics. *Systematic Biology* 49(2): 233–256.

Macey, J. R., J. A. Schulte, A. Larson, and T. J. Papenfuss. 1998. Tandem duplication via light-strand synthesis may provide a precursor for mitochondrial genomic rearrangement. *Molecular Biology and Evolution* 15(1): 71–75.

Malhotra, A., and Thorpe, R.S. 1997. Microgeographic variation in scalation of *Anolis oculatus* (Dominica, West Indies): a multivariate analysis. *Herpetologica* 53: 49–62.

Marques, M. P., Ceríaco, L. M. P., Blackburn, D. C., and A. M. Bauer. 2018. Diversity and distribution of the amphibians and terrestrial reptiles of Angola: atlas of historical and bibliographic records (1840–2017). *Proceedings of the California Academy of Sciences* 65, Suppl. II: 1–501.

Marx, H. 1958. Catalogue of type specimens of reptiles and amphibians in Chicago Natural History Museum. *Fieldiana: Zoology* 36: 407–496.

Mashinini, L., and L. Mahlangu. 2013. An annotated catalogue of the types of gekkonid lizards (Reptilia: Squamata: Gekkonidae) in the herpetology collection of the Ditsong National Museum of Natural History, South Africa. *Annals of the Ditsong National Museum of Natural History* 3: 165–181.

McCoy, C. J., and N. D. Richmond. 1966. Herpetological type-specimens in Carnegie Museum. *Annals of the Carnegie Museum* 38: 233–264.

Mertens, R. 1926. Zur Kenntnis der herpetofauna von Angola. *Senckenbergiana* 8: 150–154.

Mertens, R. 1937. Reptilien und Amphibien aus dem südlichen Inner-Afrika. *Abhandlungen der Senck-*

enbergischen Naturforschenden Gesellschaft 435: 1–23.

Mertens, R. 1938. Amphibien und Reptilien aus Angola gesammelt von W. Schack. *Senckenbergiana* 20(6): 425–443.

Mertens, R. 1955. Die Amphibien und Reptilien Südwestafrikas. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 490: 1–172.

Mertens, R. 1971. Die Herpetofauna Südwest-Afrikas. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 529: 1–110.

Methuen, P. A., and J. Hewitt. 1914. Records and descriptions of the reptiles and batrachians of the collection. *Annals of the Transvaal Museum* 4: 118–145, pl. XIV.

Meyer, A., and P. le F. N. Mouton. 2007. Aggregation in Bibron's gecko, *Chondrodactylus bibronii*. *African Journal of Herpetology* 56(2): 137–147.

Meyer, H. 1913. Übersichtskarte. Hans Meyer's Ostafrika-Expedition 1911. *Mitteilungen aus den deutschen Schutzgebieten, Ergänzungsheft* 6. Berlin, Germany: E.S. Mittler & Sohn,

Minh, B. Q., H. A. Schmidt, O. Chernomor, D. Schrempf, M. D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530–1534.

Monard, A. 1937. Contribution à l'Herpétologie d'Angola. *Arquivos do Museu Bocage* 8: 19–154.

Montgelard, C., and C. A. Matthee. 2012. Tempo of genetic diversification in southern African rodents: the role of Plio-Pleistocene climatic oscillations as drivers for speciation. *Acta Oecologica* 42: 50–57.

Moritz, C., T. E., Dowling, and W. M. Brown. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Annual Review of Ecology, Evolution, and Systematics* 18: 269–292.

Padial, J. M., A. Miralles, I. De la Riva, and M. Vences. 2010. The integrative future of taxonomy. *Frontiers in Zoology* **7**: 1–14.

Parker, H. W. 1936. Dr. Karl Jordan's expedition to South West Africa and Angola: herpetological collections. *Novitates Zoologicae* 50: 115–146.

Peters, W. C. H. 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königl. Preuss. *Akademie der Wissenschaften zu Berlin* 1854: 614–628.

Peters, W. C. H. 1862. Übersicht einiger von dem, durch seine afrikanische Sprachforschungen, rühmlichst bekannten, Hrn. Missionär C. H. Hahn bei Neu-Barmen, im Hererolande, and der Westküste von Afrika, im 21° südl. Br. gesammelten Amphibien, nebst Beschreibungen der neue. *Monatsberichte der Königlichen Preussische Akademie der Wissenschaften zu Berlin* 1862: 15–26.

Peters, W. C. H. 1865. Hr. W. Peters lieferte ferneren Nachtrag zu seiner Abhandlung über *Typhlopina. Monatsberichte der Königlichen Preussische Akademie der Wissenchaften zu Berlin* 1895:259–263.

Peters, W. C. H. 1869. Anhang. Uebersicht der Säugthiere und Amphibien des mittleren Ostafrika (Gebiet von Sansibar und Mosambik nebst Binnenland), PP. 137–140 IN: W. C. H. Peters, J. Cabanis, F. Hilgendorf, E. von Martens, and C. Semper, editors. *Baron Claus von der Decken's Reisen in Ost-Afrika in den Jahren 1859–1865*, 3: *Wissenschaftliche Ergebnisse. Erste Abtheilung: Säugthiere, Vögel, Amphibien, Crustaceen, Mollusken und Echinodermen*. Leipzig und Heidelberg, Germany: C. F. Winter'sche Verlagshandlung.

Peters, W. C. H. 1870. Zur Kenntniss der herpetologischen Fauna von Südafrika. *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin* 1870: 110–115, 1 pl.

Porknoy, L., R. Riina, M. Mairal, A. S. Meseguer, V. Culshaw, J. Cendoya, M. Serrano, R. Carbajal, S. Ortiz, M. Heuertz, and I. Sanmartin. 2015. Living on the edge: timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics* 6:154. https://doi.org/10.3389/fgene.2015.00154

Portik, D. M., S. L. Travers, A. M. Bauer, and W. R. Branch. 2013. A new species of *Lygodactylus* (Squamata: Gekkonidae) endemic to Mount Namuli, an isolated 'sky island' of northern Mozambique. *Zootaxa* 3710: 415–435.

Poynton, J. C. 1995. The "arid corridor" distribution in Africa: a search for instances among amphibians. *Madoqua* 19: 45–48.

Prendini, L. 2005. Scorpion diversity and distribution in southern Africa: pattern and process, PP. 25–68 IN: B. A. Huber, B. J. Sinclair, and K. H. Lampe, editors. *African Biodiversity: Molecules, Organisms, Ecosystems*. The Netherlands: Springer Science.

Rose, W. 1962. *The Reptiles and Amphibians of Southern Africa*. Cape Town, South Africa: Maskew Miller Ltd.

Roux, J. 1907. Beiträge zur Kenntnis der Fauna von Süd-Afrika. Ergebnisse einer Reise von Prof. Max Weber im Jahre 1894. VII. Lacertilia (Eidechseb). *Zoologische Jahrbuch, Abteilung für Systematik, Geographie und Biologie der Tiere* 25: 403–444, pls. 14–15.

Russell, A. P. 1972. The foot of gekkonid lizards: a study in comparative and functional anatomy. Ph.D. Dissertation. London, United Kingdom: University of London.

Russell, A. P. 1976. Some comments concerning interrelationships amongst gekkonine geckos, PP. 217–244 IN: A. d'A. Bellairs and C. B. Cox, editors. *Morphology and Biology of Reptiles*. London: Academic Press.

San Mauro, D., D. J. Gower, R. Zardoya, and M. Wilkinson 2006. A hotspot of gene order rearrangement by tandem duplication and random loss in the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 23: 227–234.

Schleicher, A. 2018. *Reptilien Namibias*, überarbeitete Ausgabe. Windhoek, Namibia: Namibia Wissenschaftliche Gesellschaft.

Schmidt, K. P. 1933. The reptiles of the Pulitzer Angola Expedition. *Annals of the Carnegie Museum* 22(1): 1–15, 2 pls.

Simbotwe, M. P. M., and R. Mubamba. 1993. R. Jeffery, editor. *A Guide to the Reptiles, Amphibians, and Fishes of Zambia*. Lusaka, Zambia: Wildlife Conservation Society of Zambia.

Simmons, R. E., M. Griffin, R. E. Griffin, E. Marais, and H. Kolberg. 1998. Endemism in Namibia: patterns, processes and predictions. *Biodiversity and Conservation* 7: 513–530.

Smith, A. 1846. [Plate L and two unnumbered accompanying text pages]. IN: *Illustrations of the Zoology of South Africa; Consisting Chiefly of Figures and Descriptions of the Objects of Natural History Collected During an Expedition to the Interior of South Africa in the Years 1834, 1835, and 1836 Reptilia*. London: Smith, Elder and Co.

Smith, A. 1849. [Unpaginated index and errata slip]. IN: *Illustrations of the Zoology of South Africa: Consisting Chiefly of Figures and Descriptions of the Objects of Natural History Collected during an Expedition into the Interior of South Africa in the Years 1834, 1835 and 1836. Reptilia*. London: Smith, Elder and Co.

Spawls, S., K. Howell, and R. C. Drewes. 2006. *Reptiles and Amphibians of East Africa*. Princeton, New Jersey: Princeton University Press.

Spawls, S., K. Howell, H. Hinkel, and M. Menegon. 2018. *Field Guide to East African Reptiles*, 2nd Edition. London: Bloomsbury Publishing.

Sternfeld, R. 1911. *Die Reptilien (außer den Schlangen) und Amphibien von Deutsch-Südwestafrika. Die Fauna der deutschen Kolonien* IV(2). Berlin, Germany: R. Friedländer & Sohn, Berlin.

Sternfeld, R. 1912. Die Reptilienausbeute der Expedition Professor Hans Meyers nach Deutsch-Ostafrika. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1912(7): 384–388.

Stokes, S., D. S. G. Thomas, and R. Washington. 1997. Multiple episodes of aridity in southern Africa since the last interglacial period. *Nature* 288:154–158.

Thorpe, R. S., and Baez, M. 1987. Geographic-variation within an island—univariate and multivariate contouring of scalation, sze, and shape of the lizard *Gallotia galloti*. *Evolution* 41: 256–268.

Thorpe, R. S., and Baez, M. 1993. Geographic-variation in scalation of the lizard *Gallotia stehlini* within the island of Gran-Canaria. *Biological Journal of the Linnean Society* 48: 75–87.

Tolley, K. A., B. M. Chase, and F. Forest. 2008. Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. *Journal of Biogeography* 35: 1402–1414.

Twyford, A., and R. Ennos. 2012. Next-generation hybridization and introgression. *Heredity* 108: 179–189.

Uetz, P., S. Cherikh, G. Shea, I. Ineich, P. D. Campbell, I. V. Doronin, J. Rosado, A. Wynn, K. A. Tighe, R. McDiarmid, J. L. Lee, G. Köhler, R. Ellis, P. Doughty, C. J. Raxworthy, L. Scheinberg, A. Resetar, M. Sabaj, G. Schneider, M. Franzen, F. Glaw, W. Böhme, S. Schweiger, R. Gemel, P. Couper, A. Amey, E. Dondorp, G. Ofer, S. Meiri, and V. Wallach. 2019. A global catalog of primary reptile type specimens. *Zootaxa* 4695: 438–450.

van Zinderen Bakker, E. M. 1975. The origin and paleoenvironment of the Namib Desert biome. *Journal of Biogeography* 2: 65–73.

Verdcourt, B. 1969. The arid corridor between the north-east and south-west areas of Africa. *Palaeoecology of Africa and the Surrounding Islands* 4: 140–144.

Wagner, P. 2010. Diversity and distribution of African lizards. Ph.D. Dissertation. Bonn, Germany: University of Bonn.

Wagner, P., E. Greenbaum, A. M. Bauer, C. Kusamba, and A. D. Leaché. 2018. Lifting the blue-headed veil—integrative taxonomy of the cryptic *Acanthocercus atricollis* complex (Squamata: Agamidae). *Journal of Natural History* 52: 771–817.

Weisrock, D. W., J. R. Macey, I. H. Ugurtas, A. Larson, and T. J. Papenfuss. 2001. Molecular phylogenetics and historical biogeography among salamandrids of the "true" salamander clade: rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. *Molecular Phylogenetics and Evolution* 18(3): 434–448.

Wermuth, H. 1965. Liste der rezenten Amphibien und Reptilien. Gekkonidae, Pygopodidae, Xantusiidae. *Das Tierreich* 80: I–XXII, 1–246.

Werner, F. 1910. Reptilia et Amphibia, PP. 279–370, pls. VI–XI IN: L. Schultze, editor. Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. Band IV, Systematik und Tiergeographie Vertebrata B. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 16.

Winterbottom, J. M. 1967. Climatological implications of avifaunal resemblances between South Western Africa and Somaliland. *Palaeoecology of Africa and the Surrounding Islands* 2: 77–79.

Wüster, W., S. Crookes, I. Ineich, Y. Mané, C. E. Pook, J.-F. Trape, and D. G. Broadley. 2007. The phylogeny of cobras inferred from mitochondrial DNA sequences: evolution of venom spitting and the phylogeography of the Africa spitting cobras (Serpentes: Elapidae: *Naja nigricollis* complex. *Molecular Phylogenetics and Evolution* 45: 437–453.

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