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A phylogenetic analysis of the southern African gecko genus *Afroedura* Loveridge (Squamata: Gekkonidae), with the description of nine new species from Limpopo and Mpumalanga provinces of South Africa

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Abstract

A molecular phylogeny of the largely rupicolous geckos of the gekkonid genus *Afroedura* is presented based on a combination of mitochondrial and nuclear gene sequence data. Previously recognized species groups are only partly recovered, with *A. pondolia* retrieved as very distantly related to the congeners to which it was previously considered allied. *Afroedura hawequensis* forms a monotypic group that is sister to all other species, which are allocated to the *A. nivaria*, *A. transvaalica*, *A. africana*, *A. multiporis*, *A. marleyi*, and *A. langi* groups. The taxonomic status of species occurring in the former Transvaal province of South Africa (now Limpopo and Mpumalanga provinces) is reviewed based on morphological and molecular evidence. *Afroedura rupestris* **sp. nov.** is described in the *A. multiporis* group, *A. maripi* **sp. nov.**, *A. pongola* **sp. nov.**, and *A. rondavelica* **sp. nov.**, are described in the *A. marleyi* group, and *A. broadleyi* **sp. nov.**, *A. granitica* **sp. nov.**, *A. leoloensis* **sp. nov.**, *A. pienaari* **sp. nov.**, and *A. waterbergensis* **sp. nov.** are described in the *A. langi* group. In addition, *A. haackei*, *A. namaquensis*, and *A. tirasensis*, are all raised to specific status. The description of nine new species highlights Limpopo and Mpumalanga provinces as previously unrecognized centers of diversity for the genus *Afroedura*. A key to the species of *Afroedura* is provided.

Key words: *Afroedura*, *Afroedura broadleyi* **sp. nov.**, *Afroedura granitica* **sp. nov.**, *Afroedura leoloensis* **sp. nov.**, *Afroedura maripi* **sp. nov.**, *Afroedura pienaari* **sp. nov.**, *Afroedura pongola* **sp. nov.**, *Afroedura rondavelica* **sp. nov.**, *Afroedura rupestris* **sp. nov.**, *Afroedura waterbergensis* **sp. nov.**, South Africa, molecular phylogenetics, description, taxonomy, biogeography

Introduction

Southern Africa supports one of the most diverse gecko-faunas in the world and recent phylogenetic studies (Bauer & Lamb 2005; Lamb & Bauer 2006; Gamble *et al.* 2012) have verified the monophyly of a large clade of chiefly southern African gekkonid geckos that includes the highly speciose genus *Pachydactylus* Wiegmann and its satellite genera, *Colopus* Peters, *Chondrodactylus* Peters, *Elasmodactylus* Boulenger, and *Rhoptropus* Peters. These taxa have long been hypothesized as close relatives, on the grounds of shared features of digital morphology, most notably hyperphalangy of the first digit of both manus and pes (Haacke 1968, 1976; Russell 1972, 1976; Joger 1985; Bauer 1990). In this instance, this putative synapomorphy of these geckos has been validated by independent (molecular) data. However, the presumed sister group relationship of the North African/Mediterranean *Tarentola* Gray, to the *Pachydactylus* group, also based on shared hyperphalangy, has been falsified and this genus is now known to belong to a different gekkotan family, the Phyllodactylidae (Gamble *et al.* 2008). Rather, a multi-gene phylogenetic analysis of nearly all gekkotan genera (Gamble *et al.* 2012) reveals that the *Pachydactylus* group is part of a more inclusive clade of Afro-Malagasy gekkonids. The closest relatives of the *Pachydactylus* group include not only genera characterized by broad toepads—the clade *Geckolepis* Grandidier (*Blaesodactylus* Boettger, *Homopholis* Boulenger) (Greenbaum *et al.* 2007), but also taxa with so-called leaf-toed digital morphologies, i.e., *Goggia* Bauer, Good & Branch and *Afroedura* Loveridge, demonstrating the plasticity of digital morphology within gekkotans as a whole (Gamble *et al.* 2012). Although these latter two African leaf-toed genera share some features in common (Bauer 1990), existing data suggest a closer relationship of *Afroedura* to the *Geckolepis* + *Blaesodactylus* + *Homopholis* clade (Gamble *et al.* 2012).

Afroedura species are typically distinctly dorsoventrally flattened and usually occupy rock cracks and crevices, although *A. loveridgei* is arboreal and the facultative use of arboreal and/or edificarian habitats has been reported in *A. marleyi*, *A. haackei*, and *A. pondolia* (Hewit 1937; Bruton & Haacke 1980; Onderstall 1984; Alexander 1990; Bauer 2014f,h,i). Like many rupicolous taxa, their distributions are highly disjunct, being dependent on the availability of suitable substrates. The majority of the species occur in eastern southern Africa, with a single species in Angola and extreme northern Namibia (Loveridge 1944; Branch 1998), another, with several subspecies from Little Namaqualand to central Namibia (Haacke 1965), and one species in the Cape Fold Mountains of the southwestern Western Cape (Mouton & Mostert 1985). In the northeast of the range two additional species extend north of the Limpopo, one in Mozambique, the other in Zimbabwe (Visser 1984; Branch 1998).

Until the advent of molecular phylogenetic analyses, the relationships of *Afroedura* had been particularly

perplexing, as the only other geckos sharing its multiple rows of expanded leaf-like digital scensors were *Oedura* Gray, an Australian diplodactylid, with which *Afroedura* was confused until Loveridge (1944) demonstrated their distinctness, and *Calodactylodes* Strand (formerly *Calodactylus* Beddome), a genus of two species from India and Sri Lanka (Russell & Bauer 1989; Bauer & Das 2001). This latter genus is now known to belong to an even more inclusive, mostly Afro-Malagasy group, but has no particularly close relationship to *Afroedura* (Gamble *et al.* 2012).

Relationships within *Afroedura* have long been obscured by the relative morphological conservatism within the genus. The majority of species in the group are very similar to one another in general appearance and historically it has been difficult to identify specific boundaries between certain members of the chiefly allopatric members of the genus. Early herpetologists lumped rather different animals, often from greatly distant localities within single species (Roux 1907; Boulenger 1910; Hewitt 1910). FitzSimons (1943) recognized 14 species and subspecies of *Afroedura* (as *Oedura*), the majority of which were distributed from the Drakensburg to the inland Western Cape. Only three of these were considered to occur in the former Transvaal: *A. t. transvaalica* (Hewitt, 1925), *A. pondolia multiporis* (Hewitt, 1925), and *A. langi* (FitzSimons, 1930).

Loveridge (1947) considered only 12 taxa, including *A. karroica bogerti* Loveridge, 1944 but treating *A. karroica wilmoti* (Hewitt, 1926) as a synonym of *A. k. karroica* (Hewitt, 1925), *A. amatolica* (Hewitt, 1925) as a synonym of *A. nivaria* (Boulenger, 1895 [1894]), and *A. langi* as a synonym of *A. p. pondolia* (Hewitt, 1925).

The next substantial work on the genus was that of Onderstall (1984), who described two new taxa, *A. pondolia haackei* Onderstall, 1984 and *A. p. major* Onderstall, 1984, and also resurrected *A. langi* as a subspecies of *A. pondolia* and elevated *A. bogerti* to a full species. Onderstall (1984) separated the genus into three species groups: the *transvaalica* group (*A. t. transvaalica*, *A. t. loveridgei* Broadley, 1963, *A. bogerti*), characterized by two pairs of scensors per digit and a verticillate tail; the *pondolia* group (*A. p. pondolia*, *A. p. marleyi* (FitzSimons, 1930), *A. p. major*, *A. p. haackei*, *A. p. langi*, *A. p. multiporis*), with two pairs of scensors per digit but without a verticillate tail; and the *africana* group (*A. a. africana* (Boulenger, 1888), *A. a. tirasensis* Haacke, 1965, *A. a. namaquensis* (FitzSimons, 1938), *A. nivaria*, *A. amatolica*, *A. tembulica* (Hewitt, 1926), *A. k. karroica*, *A. k. halli* (Hewitt, 1935)), with three pairs of scensors per digit and a verticillate tail. This basic grouping was followed by Mouton and Mostert (1985) who described the most morphologically distinctive species, *A. hawaquensis* Mouton & Mostert, 1985, placing it in the *A. africana* group, although they pointed out that the affiliations assumed by this approach were not necessarily phylogenetic.

Jacobsen (in Branch *et al.* 1988) first signalled the probable occurrence of undescribed species in *A. pondolia* (as then construed) in the former Transvaal. Jacobsen (1990) subsequently reviewed all taxa from this region and provided data on both described and undescribed forms. Later he re-evaluated the diagnostic characters then in use and concluded that the taxa hitherto included in *A. pondolia sensu lato* actually comprised three species groups (Jacobsen 1992a, 1997). An *A. pondolia* subgroup distinguished from the *A. langi* subgroup based on the presence of an internasal, and an *A. multiporis* complex, distinguished by the presence of keeled dorsal scales. Jacobsen (1997) also provided a summary of the taxonomic history of the genus.

Most recently Makhubo *et al.* (2011) and Makhubo (2013) examined molecular phylogenetic relationships within the *A. nivaria* complex, including *A. nivaria*, *A. amatolica*, *A. karroica*, *A. tembulica*, and *A. halli*, (Bates & Branch 1998). They concluded that *A. karroica* is not a member of this group, but that *A. pondolia*, previously not considered closely related to the *nivaria* group, was indeed embedded within this radiation.

Onderstall (1984) signalled the existence of undescribed *Afroedura* in the Soutpansberg region of the then Transvaal province of South Africa. In the course of his survey of the Transvaal herpetofauna, Jacobsen (1990, 1992a) identified twelve putative additional taxa of *Afroedura*, including those from the Soutpansberg. These taxa were identified by informal names and even keyed out and mapped by Jacobsen (1992a). He included *A. pondolia* ‘Godlwayo’ and *A. ‘Maripi’* along with *A. p. marleyi* as the Transvaal members of the *A. pondolia* complex, *A. multiporis* ‘Abel Erasmus’ and *A. ‘Lebombo’* along with *A. m. multiporis* and *A. m. haackei* in the *A. multiporis* complex, and eight putatively new taxa (*A. langi* ‘Lillie,’ *A. l. ‘Shinokwen,’ A. l. ‘Tshipise,’ A. l. ‘Waterpoort,’ A. l. ‘Soutpansberg,’ A. l. ‘Leolo,’ A. l. ‘Waterberg,’* and *A. ‘Matalala’*) along with *A. l. langi* in his *A. langi* complex. Subsequent investigation (Jacobsen 1997) has suggested that *A. l. ‘Soutpansberg* and *A. ‘Matalala’* represent disjunct populations of the same species, and that *A. l. ‘Shinoken,’ A. l. ‘Tshipise,’* and *A. l. ‘Waterpoort’* are likewise synonyms. He also signalled the existence of an additional putative species occurring on the Three Rondavels, along the Blyde River Canyon in Mpumalanga.

Although none of these species have since been described, the informal names and the existence of these taxa has long been acknowledged by southern African herpetologists. However, their unofficial status has been problematic and they were not included in the recent conservation assessment of South African reptiles (Bates *et al.* 2014). Indeed, of all South African reptile genera, *Afroedura* was recently ranked third in a list of priority taxa in need of further systematic study (Branch 2006).

In this paper we use a multi-gene approach to generate a preliminary molecular phylogeny of *Afroedura*, representing 16 of 18 currently recognized taxa, as well as six of Jacobsen's (1990, 1992a) new species. We evaluate previous interpretations of intrageneric relationships in light of our phylogeny and take this opportunity to describe nine of the new species previously identified by Jacobsen. We also allocate currently recognized taxa to monophyletic species groups and elevate several taxa currently regarded as subspecies to full specific status.

Material and methods

Species concepts. Previous studies of *Afroedura* have recognized some taxa as specifically distinct and others as subspecifically distinct, generally without explicit justification for rank differences. Although subspecies continue to be described in herpetology, most modern workers subscribe to the viewpoint that most or all described subspecies represent either "pattern clades" that do not reflect evolutionary units, or valid species as recognised by prevailing species concepts (Frost *et al.* 1992; Grismer *et al.* 1994; Grismer 1999). In most instances in which genetic data has been incorporated into assessments of described reptile subspecies, the result has been elevation to full specific status (Torstrom *et al.* 2014). We here accept a general lineage-based species concept (Frost & Hillis 1990; Mayden 1997; de Queiroz 1998) and treat as species those entities that represent independent historical lineages. Practically, we are concerned with the operational criteria that permits us to infer species boundaries (Wiens & Penkrot 2002; Sites & Marshall 2003, 2004; Bauer 2006; Camargo & Sites 2013). Such criteria may be either tree-based or character-based and where possible we employ both approaches in this paper. In addition, although distribution patterns alone should not be used in erecting initial hypotheses of species boundaries, geographic concordance (as reflected by allopatry) with other evidence of lineage independence may be corroborative of taxonomic decisions based on tree- and character-based delimitations (Bergmann & Russell 2007). Specifically, we follow the recommendations proposed for the establishment of a stable alpha level taxonomy for the reptiles of South Africa (Bauer 2006) in the context of a coordinated plan for phylogenetic studies of southern African reptiles (Branch *et al.* 2006).

Morphology. Most *Afroedura* are morphologically conservative and discrete diagnostic differences are typically limited to a small number of characters, which we use below in the descriptions of the new species here proposed and which serve as the basis for the construction of a key to the *Afroedura* of the former Transvaal and adjacent areas. The number of pairs of enlarged subdigital scancers is one such feature that has historically been used in the systematics of the group (FitzSimons 1943; Loveridge 1947; Onderstall 1984; Jacobsen 1997), but does not vary among taxa occurring in the former Transvaal. Other characters recorded follow Jacobsen (1992a) and include: presence or absence of internasal granules between the nasorostral scales, number of postmental scales, number of scales between the eye and ear, number of supralabials, number of infralabials, shape of dorsal scales (smooth versus keeled), number of midbody scale rows, caudal verticillation, number of supracaudal and subcaudal rows per tail whorl (counted 3–6 verticils posterior to the cloaca due to variation in these values at the base of the tail), and number of precloacal pores in males. Snout-vent length (SVL), tail length (TailL), and mass before preservation were recorded from freshly collected specimens. Maximum size differences are often consistent and informative in gecko systematics, especially in highly morphologically conservative lineages (e.g., Bauer *et al.* 2006, 2012). Descriptive terminology follows Onderstall (1984).

Student's t-tests were used to test for significant differences in various characters between putative taxa. Differences were considered to be significant at $P < 0.05$.

Specimens. A total of 456 *Afroedura* specimens from the former Transvaal housed in the Ditsong Museum of Natural History (formerly Transvaal Museum, TM), including those collected during the herpetofaunal survey of the former Transvaal (Jacobsen 1990) were examined morphologically. Also examined were extralimital material of *A. marleyi* from Kwazulu-Natal, *A. major* (Onderstall) from Swaziland and *A. pondolia* (Hewitt) from the eastern Cape Province and Kwazulu-Natal (material all housed in the Ditsong Museum of Natural History except the types of *A. pondolia*, which are in the collection of Bayworld, formerly the Port Elizabeth Museum, PEM).

In order to avoid the inconvenience of referring to the many undescribed taxa as ‘species 1,’ etc. we here provide the names applied herein to new taxa along with the informal names by which they have been known for the last 20 years. These formal names are then used throughout the remainder of the manuscript.

Afroedura rupestris **sp. nov.** = *Afroedura multiporis* ‘Abel Erasmus’

Afroedura maripi **sp. nov.** = *Afroedura* ‘Maripi’

Afroedura pongola **sp. nov.** = *Afroedura pondolia* ‘Godlwayo’

Afroedura rondavelica **sp. nov.** [not treated by Jacobsen 1992a]

Afroedura granitica **sp. nov.** = *Afroedura langi* ‘Lillie’

Afroedura leoloensis **sp. nov.** = *Afroedura langi* ‘Leolo’

Afroedura soutpansbergensis **sp. nov.** = *Afroedura langi* ‘Soutpansberg,’ *A. langi* ‘Matlala’

Afroedura waterbergensis **sp. nov.** = *Afroedura langi* ‘Waterberg’

Afroedura pienaari **sp. nov.** = *Afroedura langi* ‘Waterpoort,’ *A. langi* ‘Tshipise,’ *A. langi* ‘Shinokwen’

The specimens examined for morphological analysis and used in the descriptions of new taxa were collected prior to 1990 and were formalin-fixed, precluding their use in molecular analyses. Specimens of the species newly described herein used in the molecular phylogeny were either collected specifically for this study at or near the type localities of these taxa, or were obtained as a result of general collecting or surveys, including those directly associated with the South African Reptile Conservation Assessment (SARCA) (Bates *et al.* 2014). Specimens used for sequencing (Table 1) were compared to the corresponding type material to ensure their conspecificity.

The following institutional or field series acronyms are used in this paper: AMB (field series, Aaron M. Bauer), FGZC (Frank Glaw field series), Griffin (Mike Griffin, field series), GVH (Gerald V. Haagner field series), JM (Johan Marais, field series), JS (Jay Sommers private living collection), KTH (Krystal Tolley field series), LMH (Limpopo frozen collection, Vincent Egan), MBarts (Mirko Barts, private collection), MBUR (Marius Burger, field series), MH (Michael Cunningham), NKW (Nasionale Kruger Wildtuin = Kruger National Park Collection, Skukuza), NMZB (National Museum of Zimbabwe, Bulawayo), PEM (Port Elizabeth Museum, Bayworld), RCBS (Richard Boycott field series), TM (Distsong Museum, Pretoria).

Locality data have been taken from collector or museum collection records. For localities without precise coordinates determined using a GPS or topographic map we have determined quarter degree square references (QDS). The QDS system has been nearly universally used in large scale mapping of the southern African biota and remains a convenient approach to dealing with distributions (De Waal 1978; Bates *et al.* 2014). Under this system of notation, each single degree square is subdivided into four quarter degrees, designated A-D (A=NW quadrant, B=NE quadrant, C=SW quadrant, D=SE quadrant). Each quarter degree is in turn divided into four similarly designated divisions, yielding a basic unit one sixteenth of a degree square, or one quarter of a degree on a side (e.g., 3015Ac represents the unit bounded by 30°15’S and 30°30’S and 15°00’E and 15°15’E). All QDS references are to degrees South and East. Unfortunately, locality data for some SARCA specimens used in the molecular phylogeny were unobtainable from the collector. In addition, localities listed for many specimens include farm number designations. Many farm names are used by multiple farms in South Africa, these designators help to identify the correct locality. Locality names, exclusive of provincial names, reflect the place names in use at the time of museum accession. We employ the standard abbreviation KNP for Kruger National Park. Vegetation types follow Mucina & Rutherford (2006).

Molecular systematics. Taxon and gene sampling—Sequences were obtained from 72 tissue samples representing 16 of the 18 known species of *Afroedura* as well as representative individuals for six new species: *A. granitica* **sp. nov.**, *Afroedura pienaari* **sp. nov.**, *A. maripi* **sp. nov.**, *A. pongola* **sp. nov.**, *A. broadleyi* **sp. nov.**, and *A. waterbergensis* **sp. nov.** Representatives of the probable sister group to *Afroedura*, including *Blaesodactylus*, *Homopholis*, and *Gekkolepis* were also included, as well as individuals from the *Pachydactylus* radiation (*Pachydactylus*, *Chondrodactylus*) and its closest relatives (*Rhoptropus*, *Goggia*) (Bauer & Lamb 2005; Gamble *et al.* 2012).

TABLE 1. Specimens used in molecular phylogeny. The column "No." corresponds to specimen identifier numbers in Table 2 (GenBank accession numbers). Coordinates are provided for ingroup taxa only and these localities are plotted on Figures 4 and 6.

No.	Genus/species	ID No.	Locality	Latitude	Longitude
1	<i>Afroedura africana</i>	GRIFIN 300	Namibia, Erongo Region	21° 27' 40.78" S	15° 52' 32.77" E
2	<i>Afroedura africana</i>	MCZ R186011	Namibia, Erongo Region, near Omaruru	21° 10' 47" S	14° 33' 16" E
3	<i>Afroedura africana</i>	TM 84996	Namibia, Erongo Region, Brandberg	32° 06' 04" S	26° 15' 19" E
4	<i>Afroedura amatolica</i>	AMB 8167	South Africa, Eastern Cape, Farm Newstead	33° 02' 05" S	26° 49' 05" E
5	<i>Afroedura amatolica</i>	PEM FN1190	South Africa, Eastern Cape, Double Drift Game Reserve	16° 12' 22" S	12° 24' 06.6" E
6	<i>Afroedura bogerti</i>	KTH 09196	Angola, Namibe Province, Omauha Lodge	16° 12' 22" S	12° 24' 06.6" E
7	<i>Afroedura bogerti</i>	KTH 09197	Angola, Namibe Province, Omauha Lodge	16° 04' 00" S	12° 26' 00" E
8	<i>Afroedura bogerti</i>	MBARTS 001	Angola, Namibe Province, Tambor	23° 00' 00" S,	30° 07' 00" E
9	<i>Afroedura broadleyi</i> sp. nov.	LMH 000073	South Africa, Limpopo, Bergplaats	23° 00' 00" S,	30° 07' 00" E
10	<i>Afroedura broadleyi</i> sp. nov.	LMH 000092	South Africa, Limpopo, Bergplaats	22° 58' 40" S,	29° 19' 57" E
11	<i>Afroedura broadleyi</i> sp. nov.	MBUR 01753	South Africa, Limpopo Province	22° 58' 40" S	29° 19' 57" E
12	<i>Afroedura broadleyi</i> sp. nov.	MBUR 01754	South Africa, Limpopo Province	24° 03' 59" S	30° 49' 56" E
13	<i>Afroedura granitica</i> sp. nov.	AMB 8199	South Africa, Limpopo, Farm Lillie	24° 03' 59" S	30° 49' 56" E
14	<i>Afroedura granitica</i> sp. nov.	MCZ R184411	South Africa, Limpopo, Farm Lillie	24° 03' 59" S	30° 49' 56" E
15	<i>Afroedura granitica</i> sp. nov.	MCZ R184416	South Africa, Limpopo, Farm Lillie	24° 03' 59" S	30° 49' 56" E
16	<i>Afroedura haackei</i>	MBUR 00109	South Africa, Mpumalanga Province	25° 27' 31" S	30° 41' 48" E
17	<i>Afroedura haackei</i>	PEM R16805	South Africa, Mpumalanga, Nelspruit	25° 29' 54.1" S	31° 00' 23.4" E
18	<i>Afroedura halli</i>	MBUR 00429	South Africa, Eastern Cape Province, Farm Bamboeshoek	31° 36' 39" S	26° 18' 53" E
19	<i>Afroedura halli</i>	MBUR 00486	South Africa, Eastern Cape Province, Farm Bamboeshoek	31° 36' 52" S	26° 18' 50" E
20	<i>Afroedura halli</i>	MBUR 00490	South Africa, Eastern Cape Province, Farm Bamboeshoek	31° 36' 39" S	26° 18' 53" E
21	<i>Afroedura halli</i>	MBUR 00502	South Africa, Eastern Cape Province, Farm Bamboeshoek	31° 36' 39" S	26° 18' 53" E
22	<i>Afroedura halli</i>	MBUR 00503	South Africa, Eastern Cape Province, Farm Bamboeshoek	31° 36' 39" S	26° 18' 53" E
23	<i>Afroedura halli</i>	MBUR 00535	precise locality data lacking		
24	<i>Afroedura halli</i>	MBUR 00536	precise locality data lacking		
25	<i>Afroedura halli</i>	MBUR 00537	precise locality data lacking		
26	<i>Afroedura halli</i>	MBUR 00541	precise locality data lacking		
27	<i>Afroedura</i> aff. <i>halli</i>	MBUR 1429	South Africa, Free State, Farm Merrimetsi, near Excilsior	28° 50' 52.46" S	27° 14' 11.70" E
28	<i>Afroedura hawequensis</i>	MH 0221	South Africa, Western Cape Province, Suurvlakte Farmstead	33° 41' 12.98" S	19° 06' 28.01" E
29	<i>Afroedura hawequensis</i>	MH 0894	South Africa, Western Cape Province, Summit Road	33° 40' 52" S	19° 05' 17" E
30	<i>Afroedura karroica</i>	MCZ R184391	South Africa, Western Cape Province, Farm Newstead	32° 06' 04" S	26° 15' 19" E
31	<i>Afroedura karroica</i>	PEM FN1112	South Africa, Eastern Cape Province, Farm Newstead	32° 01' 38" S	24° 08' 26" E
32	<i>Afroedura karroica</i>	PEM FN1113	South Africa, Eastern Cape Province, 41 km SE of Murraysburg.	32° 01' 38" S	24° 08' 26" E
33	<i>Afroedura langi</i>	MBUR 01488	South Africa, Limpopo Province, Kruger National Park	24° 01' 44" S	31° 10' 30" E

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TABLE 1. (Continued)

No.	Genus/species	ID No.	Locality	Latitude	Longitude
34	<i>Afroedura lovenidgei</i>	GVH 3969	Mozambique, Tete District, 7km West of Songa turn-off	16° 20' 49" S	33° 27' 89" E
35	<i>Afroedura major</i>	RCBS 2130	Swaziland, Hhohho, Nkomati River Valley, Maguga Dam	26° 07' 30" S	31° 22' 30" E
36	<i>Afroedura maripi</i> sp. nov.	MBUR 01525	South Africa, Mpumalanga, Mariepskop	24° 34' 11" S	30° 53' 19" E
37	<i>Afroedura maripi</i> sp. nov.	MBUR 01527	South Africa, Mpumalanga, Mariepskop	24° 34' 11" S	30° 53' 19" E
38	<i>Afroedura maripi</i> sp. nov.	MCZ R184421	South Africa, Mpumalanga, Mariepskop	24° 33' 00" S	30° 51' 53" E
39	<i>Afroedura marleyi</i>	MBUR 01187	South Africa, KwaZulu-Natal, Manyiseni region	26° 54' 55" S	32° 03' 04" E
40	<i>Afroedura marleyi</i>	MBUR 01231	South Africa, KwaZulu-Natal, Manyiseni region	26° 54' 55" S	32° 03' 04" E
41	<i>Afroedura marleyi</i>	MBUR 01232	South Africa, KwaZulu-Natal, Manyiseni region	26° 54' 55" S	32° 03' 04" E
42	<i>Afroedura marleyi</i>	MBUR 01240	South Africa, KwaZulu-Natal, Manyiseni region	26° 54' 55" S	32° 03' 04" E
43	<i>Afroedura marleyi</i>	PEM R17576	South Africa, Mpumalanga Prov., Komati River Valley, The Hippos	25° 28' 36" S	31° 58' 15" E
44	<i>Afroedura multiporis</i>	MBUR 01620	South Africa, Limpopo Province, Wolkberg Wilderness Area	24° 00' 22" S	30° 00' 05" E
45	<i>Afroedura multiporis</i>	MBUR 01669	South Africa, Limpopo Province, Wolkberg Wilderness Area	24° 00' 22" S	30° 00' 05" E
46	<i>Afroedura multiporis</i>	MBUR 01690	South Africa, Limpopo Province, Wolkberg Wilderness Area	24° 00' 41" S	30° 04' 24" E
47	<i>Afroedura nivaria</i>	TM 83237	South Africa, Kwazulu-Natal, Royal Natal Nml Parkr	28° 43' 38.9" S	28° 53' 27.18" E
48	<i>Afroedura pienaari</i> sp. nov.	MBUR 00935	South Africa, Limpopo, Nwanedi Nature Reserve	22° 37' 46" S	30° 24' 42" E
49	<i>Afroedura pienaari</i> sp. nov.	MBUR 00937	South Africa, Limpopo, Nwanedi Nature Reserve	22° 37' 46" S	30° 24' 42" E
50	<i>Afroedura pienaari</i> sp. nov.	MBUR 00975	precise locality data lacking		
51	<i>Afroedura pienaari</i> sp. nov.	MBUR 00976	precise locality data lacking		
52	<i>Afroedura pienaari</i> sp. nov.	MBUR 01052	precise locality data lacking		
53	<i>Afroedura pienaari</i> sp. nov.	MCZ R184480	South Africa, Limpopo, Farm Waterpoort	22° 54' 29" S	29° 37' 03" E
54	<i>Afroedura pienaari</i> sp. nov.	MCZ R184481	South Africa, Limpopo, Waterpoort	22° 54' 29" S	29° 37' 03" E
55	<i>Afroedura pienaari</i> sp. nov.	PEM R17362	South Africa, Limpopo, Waterpoort	22° 54' 29" S	29° 37' 03" E
56	<i>Afroedura pondolia</i>	JM 1036	South Africa, KwaZulu-Natal, Durban, Glenwood, Pigeon Valley	29° 51' 52.57" S	30° 59' 12.89" E
57	<i>Afroedura pongola</i> sp. nov.	PEMR 17585	South Africa, KwaZulu-Natal, near KwaMlimisi, Godlwayo Hill	27° 19' 41" S	31° 25' 59" E
58	<i>Afroedura pongola</i> sp. nov.	PEMR 17586	South Africa, KwaZulu-Natal, near KwaMlimisi, Godlwayo Hill	27° 19' 41" S	31° 25' 59" E
59	<i>Afroedura tembulica</i>	PEM R16927	South Africa, Eastern Cape Province, Indwe Region, Guba coal mine	31° 31' 13" S	27° 16' 03" E
60	<i>Afroedura tembulica</i>	PEM R16926	South Africa, Eastern Cape Province, Indwe Region, Guba coal mine	31° 31' 13" S	27° 16' 03" E
61	<i>Afroedura tembulica</i>	PEM R16928	South Africa, Eastern Cape Province, Indwe Region, Guba coal mine	31° 31' 13" S	27° 16' 03" E
62	<i>Afroedura transvaalica</i>	JM 1709	South Africa, Limpopo, near Musina, Vele Coal Mine	22° 10' 40.3" S	29° 39' 20.3" E
63	<i>Afroedura transvaalica</i>	JM 1730	South Africa, Limpopo, near Musina, Vele Coal Mine	22° 10' 12.8" S	29° 40' 22.1" E
64	<i>Afroedura transvaalica</i>	MBUR 01714	South Africa, Limpopo Province	22° 12' 53" S	29° 24' 49" E

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TABLE 1. (Continued)

No.	Genus/species	ID No.	Locality	Latitude	Longitude
65	<i>Afroedura transvaalica</i>	MCZ R190438	Zimbabwe, Matabeleland South, Farm Driefontein	20° 33' 42.4" S	28° 20' 09.8" E
66	<i>Afroedura transvaalica</i>	MCZ R190473	Zimbabwe, Matabeleland South, Farm Driefontein	20° 33' 42.4" S	28° 20' 09.8" E
67	<i>Afroedura transvaalica</i>	NMZB 17703	Zimbabwe, Manicaland, 1 km S of Avila Mission	17° 28' 31" S	32° 46' 30" E
68	<i>Afroedura transvaalica</i>	NMZB 17850	Zimbabwe, Matabeleland South, Western Matopos, Stone Hills	20° 37' 30" S	28° 10' 30" E
69	<i>Afroedura transvaalica</i>	NMZB 17861	Zimbabwe, Masvingo, Malilangwe, near Kwali Camp	21° 03' 27" S	31° 52' 36" E
70	<i>Afroedura transvaalica</i>	NMZB 17862	Zimbabwe, Masvingo, Malilangwe, near Kwali Camp	21° 03' 27" S	31° 52' 36" E
71	<i>Afroedura waterbergensis</i> sp. nov.	MBUR 01548	South Africa, Limpopo, Farm Fancy	23° 52' 41" S	27° 38' 43" E
72	<i>Afroedura waterbergensis</i> sp. nov.	MBUR 01550	South Africa, Limpopo, Farm Fancy	23° 52' 41" S	27° 38' 43" E
73	<i>Blaesodactylus antongilensis</i>	ZSM 410/2005	Madagascar, Toamasina Province, Nosy Mangabe		
74	<i>Blaesodactylus boivini</i>	FGZC 506	Madagascar, Antsiranana Province, Montagne des Français		
75	<i>Chondrodactylus angulifer</i>	MCZF38623	Namibia, Karas Region, Klein Aus Vista		
76	<i>Chondrodactylus turneri</i>	AMIB 8187	South Africa, Limpopo, Farm Lillie		
77	<i>Geckolepis maculata</i>	FGZC 463	Madagascar, Antsiranana Province, Montagne d'Ambre		
78	<i>Geckolepis typica</i>	FGZC 2343	Madagascar, Antsiranana Province, Montagne des Français		
79	<i>Goggia braacki</i>	AMB 4265	South Africa, Eastern Cape Province, Karoo National Park		
80	<i>Goggia lineata</i>	MB 20705	South Africa, Northern Cape Province, Farm Donkiedam		
81	<i>Homopholis fasciata</i>	JS 004	captive specimen, locality unknown		
82	<i>Homopholis mulleri</i>	MCZ F38772	South Africa, Limpopo, Farm Brenhilda		
83	<i>Homopholis wahlbergii</i>	AMB 8123	South Africa, Limpopo Province		
84	<i>Pachydactylus carinatus</i>	JM 1155	South Africa, Northern Cape Prov. Richtersveld Transfrontier NP		
85	<i>Pachydactylus gataasensis</i>	AMIB7596	Namibia, Kunene Region, Gai-As		
86	<i>Pachydactylus montanus</i>	MCZ A38340	Namibia, Karas Region, Grüttau, Savanna Guest Farm		
87	<i>Pachydactylus oreophilus</i>	KTH09264	Angola, Namibe Province, 100 km N of Espinheira		
88	<i>Pachydactylus purcelli</i>	MCZA38455	South Africa, Northern Cape Province, 31 km E of Upington		
89	<i>Pachydactylus scutatus</i>	MCZ A38220	Namibia, Kunene Region, Kaoko Otavi		
90	<i>Pachydactylus werneri</i>	MCZ R183725	Namibia, Erongo Region, north bank of Swakop River		
91	<i>Rhopropus afer</i>	AMB 7138	Namibia, Erongo Region, Rössing Mountain		
92	<i>Rhopropus bradfieldi</i>	AMB 7136	Namibia, Erongo Region, Rössing Mountain		

TABLE 2. GenBank accession numbers for specimens used in this study. Specimen identifier numbers correspond to the “No.” column in Table 1.

No.	Genetic Markers													
	ND2	RAG-1	MFSD4	MAP-1A	CGNL1	CASC5	KCNMB4	KIF24	PDC	TET1	PRUNE2	KIAA1107		
1	KM073618	KM073460	—	KM073719	—	KM073896	KM073853	KM073751	KM073573	KM073436	KM073537	KM073807		
2	KM073619	KM073461	—	—	—	KM073895	—	KM073752	KM073574	KM073437	KM073538	KM073808		
3	KM073620	KM073462	—	—	—	—	—	—	KM073575	—	—	—		
4	—	KM073463	—	—	—	KM073897	—	KM073753	—	—	KM073539	—		
5	KM073622	KM073464	KM073693	KM073721	—	—	—	KM073754	KM073576	—	KM073540	KM073809		
6	KM073623	—	—	—	—	—	—	KM073755	KM073577	—	—	—		
7	KM073624	KM073465	—	—	KM073867	—	—	KM073756	KM073578	—	KM073541	—		
8	KM073625	KM073466	—	KM073722	KM073868	KM073898	—	—	KM073579	KM073439	KM073542	KM073810		
9	KM073626	—	—	—	—	—	—	—	—	—	—	—		
10	KM073627	KM073467	—	—	—	—	—	—	KM073603	—	KM073543	—		
11	KM073628	KM073468	KM073694	—	KM073869	—	—	KM073757	KM073604	KM073440	—	—		
12	KM073629	KM073469	—	KM073723	KM073870	—	—	KM073758	KM073605	—	KM073544	KM073811		
13	EU054231	KM073470	—	—	—	—	KM073854	—	—	—	—	—		
14	KM073630	KM073471	—	KM073724	KM073871	—	—	KM073759	KM073580	—	—	—		
15	KM073631	KM073472	KM073695	—	KM073872	—	—	—	KM073581	KM073441	—	KM073812		
16	KM073632	—	KM073696	KM073725	KM073873	KM073899	KM073855	KM073760	KM073582	—	—	KM073813		
17	KM073633	KM073474	—	KM073726	KM073874	KM073900	—	KM073761	—	—	KM073545	—		
18	KM073634	KM073475	—	KM073727	—	—	—	—	KM073583	KM073442	KM073546	KM073814		
19	KM073635	KM073476	—	—	—	KM073901	—	—	KM073584	—	—	—		
20	KM073636	KM073477	—	—	—	—	—	KM073763	—	—	—	KM073815		
21	KM073637	KM073478	—	—	—	—	—	KM073764	—	—	—	—		
22	KM073638	KM073479	—	—	—	—	—	KM073765	—	—	—	—		
23	KM073639	KM073480	—	—	—	—	—	KM073766	—	—	—	KM073816		
24	KM073640	KM073481	—	—	—	—	—	—	—	—	—	—		
25	KM073641	—	—	—	—	—	—	—	—	—	—	—		
26	KM073642	KM073482	—	—	—	—	—	—	—	—	—	—		
27	KM073643	—	—	—	—	—	—	KM073762	—	—	—	—		
28	KM073644	KM073483	KM073697	—	—	—	—	KM073767	KM073585	—	KM073547	KM073817		
29	KM073645	KM073484	—	—	—	—	—	KM073768	—	—	KM073548	—		
30	KM07362	—	KM073698	KM073720	KM073875	—	—	KM073769	KM073586	KM073443	—	—		

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TABLE 2. (Continued)

No.	Genetic Markers												
	ND2	RAG-I	MFSD4	MAP-1A	CGNLI	CASC5	KCNMB4	KIF24	PDC	TET1	PRUNE2	KIAA1107	
31	JX041302	KM073485	—	KM073728	—	—	—	—	KM073587	—	—	KM073818	
32	—	KM073486	—	—	—	—	—	—	—	—	—	—	
33	KM073646	—	—	KM073729	KM073876	—	—	KM073770	KM073588	—	KM073549	KM073819	
34	JX041303	KM073487	KM073699	KM073730	KM073877	—	KM073856	KM073771	KM073589	KM073444	KM073550	KM073820	
35	KM073647	—	—	KM073731	KM073902	—	—	KM073772	KM073590	—	—	KM073821	
36	KM073648	KM073488	KM073700	KM073732	KM073878	KM073910	KM073857	KM073591	KM073773	KM073445	—	KM073822	
37	KM073649	KM073489	—	—	—	—	—	—	—	—	—	—	
38	KM073650	KM073490	—	—	—	—	—	—	KM073592	—	—	—	
39	KM073651	KM073491	—	—	—	—	—	KM073774	KM073593	—	—	—	
40	KM073652	—	—	—	—	—	—	—	KM073594	KM073446	—	KM073823	
41	KM073654	KM073492	KM073701	—	—	—	KM073858	KM073775	—	—	KM073551	—	
42	KM073653	—	—	—	—	—	—	KM073776	—	—	KM073552	—	
43	KM073655	KM073493	—	—	KM073879	—	—	KM073777	KM073595	KM073447	KM073553	KM073824	
44	KM073656	KM073494	—	—	—	—	—	—	—	—	—	KM073825	
45	KM073657	KM073495	KM073702	KM073734	KM073881	KM073903	KM073859	KM073778	KM073596	—	KM073554	KM073826	
46	KM073658	KM073496	KM073703	KM073880	KM073733	KM073904	—	KM073779	KM073597	—	—	KM073827	
47	KM073659	KM073497	—	—	—	—	—	KM073780	KM073598	—	—	—	
48	KM073660	KM073498	—	—	—	—	—	—	—	—	—	—	
49	KM073661	KM073499	—	—	KM073882	KM073905	KM073860	KM073781	—	—	KM073555	KM073828	
50	KM073662	KM073500	—	—	KM073735	—	—	—	—	—	KM073556	KM073829	
51	KM073663	KM073501	—	KM073736	—	—	—	—	—	—	—	KM073830	
52	KM073664	KM073502	—	KM073883	—	—	—	—	—	—	—	—	
53	KM073665	KM073503	KM073704	—	KM073884	KM073906	KM073861	KM073782	KM073599	KM073448	KM073557	KM073831	
54	KM073666	KM073504	—	—	—	—	—	—	—	—	—	—	
55	KM073667	KM073505	KM073737	—	—	—	—	—	—	—	—	—	
56	KM073668	KM073506	—	—	—	—	—	—	KM073600	—	—	—	
57	KM073669	KM073507	—	—	—	—	—	KM073784	KM073601	KM073449	KM073558	KM073832	
58	KM073670	KM073508	KM073705	KM073738	KM073885	—	—	KM073785	KM073602	—	KM073559	KM073833	
59	KM073672	KM073510	—	KM073740	—	KM073907	—	—	—	—	KM073561	—	
60	KM073671	KM073509	KM073706	KM073739	—	—	KM073862	—	KM073606	KM073450	KM073560	—	
61	KM073673	KM073511	—	—	—	—	—	KM073787	—	—	KM073562	KM073834	
62	KM073674	KM073512	KM073708	—	—	—	—	KM073793	—	—	—	KM073836	

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TABLE 2. (Continued)

No.	Genetic Markers												
	ND2	RAG-1	MFS4	MAP-1A	CGN1	CASC5	KCNMB4	KIF24	PDC	TET1	PRUNE2	KIAA1107	
63	KM073675	KM073513	KM073709	—	—	—	—	KM073794	—	—	—	KM073837	
64	KM073682	—	—	KM073741	—	—	—	—	KM073608	KM073451	—	—	
65	KM073676	KM073514	KM073710	—	—	—	—	—	—	—	—	KM073838	
66	KM073677	KM073515	KM073711	—	—	—	—	KM073796	—	—	—	KM073839	
67	KM073683	KM073516	KM073712	KM073742	—	KM073908	—	KM073797	KM073607	KM073452	—	KM073840	
68	KM073678	KM073517	KM073713	—	—	—	—	KM073788	—	—	—	KM073841	
69	KM073679	KM073518	KM073714	—	—	—	—	KM073789	—	—	—	—	
70	KM073680	KM073519	KM073715	—	—	—	—	KM073790	—	—	—	KM073842	
71	KM073684	KM073520	—	—	KM073886	—	—	KM073798	KM073609	—	—	—	
72	KM073685	KM073521	—	KM073743	KM073887	KM073909	KM073863	KM073799	KM073610	—	—	KM073844	
73	KM073686	KM073522	—	—	—	KM073911	—	—	KM073611	KM073453	KM073563	KM073845	
74	—	KM073523	—	—	—	—	—	—	—	—	—	—	
75	KM073687	KM073524	—	KM073744	—	—	—	—	—	—	KM073564	—	
76	KM073688	KM073525	—	KM073745	KM073888	—	—	KM073800	KM073612	KM073454	KM073565	KM073846	
77	EU054235	KM073526	—	—	—	—	—	—	—	—	—	—	
78	EU054233	KM073527	—	KM073746	KM073889	KM073912	—	KM073801	KM073613	KM073455	KM073566	KM073847	
79	KM073689	KM073528	—	KM073747	KM073890	KM073913	—	KM073802	KM073614	KM073456	KM073567	KM073848	
80	KM073690	KM073529	—	—	—	—	—	—	—	—	—	—	
81	EU054249	KM073530	—	—	—	—	—	—	—	—	—	—	
82	EU054241	EU054217	—	—	KM073891	—	—	—	EU054193	—	KM073568	—	
83	EU054248	KM073532	—	KM073748	KM073892	—	KM073864	KM073803	—	KM073457	KM073569	KM073849	
84	—	—	—	—	—	—	KM073865	—	—	—	—	—	
85	JX041391	JQ945322	—	KM073749	KM073893	—	—	—	JQ945390	KM073458	KM073570	KM073850	
86	—	—	KM073717	—	—	—	KM073866	—	—	—	—	—	
87	—	—	—	—	—	—	—	KM073804	—	—	—	—	
88	—	—	KM073718	—	—	—	—	—	—	—	—	—	
89	KM073691	KM073534	—	—	—	—	—	KM073805	—	—	—	—	
90	—	—	—	KM073750	—	—	—	—	—	—	KM073571	—	
91	JX041430	JQ945336	—	—	—	KM073914	—	KM073806	JQ945405	KM073459	—	KM073851	
92	KM073692	KM073536	—	—	KM073894	—	—	—	KM073617	—	KM073572	KM073852	

TABLE 3. Primers used in this study.

Gene	Primer Name	Sequence (5' to 3')	Reference
PRUNE2	PRUNE2PF1	5'-RACTCCACCAACCCCAATGA-3	This paper
PRUNE2	PRUNE2PR1	5'-CTYTRTATGASAGGAAGGGATCTWCCCA-3'	This paper
PRUNE2	PRUNE2PF2	5'-TGGGWAGATCCCTTCTSTCATAYARAG-3'	This paper
PRUNE2	PRUNE2PR2	5'-TCCAAGCATCMAGWATTTGGGACAATTCA-3'	This paper
PDC	PHOF1	5'-CCATCCAACATCTCAGCATGATGAA-3'	Bauer <i>et al.</i> (2007)
PDC	PHOR1	5'-CCCTCAGAATGATATTTGTCTCA-3'	Bauer <i>et al.</i> (2007)
KIF24	KIF24 F1	5'-SAAACGTRTCTCCMAAACGCATCC-3'	Portik <i>et al.</i> (2012)
KIF24	KIF24 R1	5'-WGGCTGCTGRAAYTGCTGGTG-3'	Portik <i>et al.</i> (2012)
KIAA1107	KIA1107F1	5'-RTGCCATGATTTYCTTGGWAGAAGCAG-3'	Portik <i>et al.</i> (2012)
KIAA1107	KIAA1107R1	5'-WCGTATTCAGTAGRTGCTGGTTSACT-3'	Portik <i>et al.</i> (2012)
TET1	TET1PF1	5'-SAGCAGTGTMACCAAAGCCT-3'	This paper
TET1	TET1PR1	5'-ATCCGGTGGCTYGTGTTTGCG-3'	This paper
CASC5	CASC5PF1	5'-SAAAATGAAATGGATATGACATCTGGTCACAC-3'	This paper
CASC5	CASC5PR1	5'-MAATKTTCTTCCCAGRYTAAACCTGTRCAATT-3'	This paper
CGNL1	CGNL1F1	5'-WGTCAGCATYMGWGTCCAAGGRATMGATGG-3'	Portik <i>et al.</i> (2012)
CGNL1	CGNL1R1	5'-ACCAGTGTCAATATCACGACC-3'	Portik <i>et al.</i> (2012)
MAP-1A	MAP-1APF1	5'-SAACAGYATMCCTTCTCTCGRAC-3'	This paper
MAP-1A	MAP-1APR1	5'-CCTCTGGAAACCACACTTTCTTCTCA-3'	This paper
MAP-1A	MAP-1AafroedF378	5'-GAGCCCTGACGACAGCACCG-3'	This paper
MAP-1A	MAP-1AafroedR850	5'-CSTGCAAGTTCCTCCCACCC-3'	This paper
MFSD4	MFSD4F200	5'-RACTRAGRGAMAAGCARAATYCTAGA-3'	This paper
MFSD4	MFSD4R1140	5'-GGGTGCATACCCATGCAACAT-3'	This paper
KCNMB4	KCNMB4R547	5'-ACCAYAMTTTGGGCACAMWYTGTCT-3'	This paper
ND2	METF1 L4437	5'-AAGCTTTCGGGCCATAACC-3'	Macey <i>et al.</i> (1997)
ND2	ND2R102	5'-CAGCCTAGGTGGGCGATTG-3'	Greenbaum <i>et al.</i> (2007)
ND2	CO1R1	5'-AGRGTGCCAATGTCTTTGTGRTT-3'	Macey <i>et al.</i> (1997)
Trp tRNA	TRPR3 H5540	5'-TTTAGGGCTTTGAAGGC-3'	Macey <i>et al.</i> (1997)
ND2	ND2afroedF450	5'-RCCGMCTAAACCAGACACAAACRCG-3'	This paper
ND2	ND2afroedR475	5'-TCGYGTTTGTGTCTGGTTTAGKCC-3'	This paper
ND2	ND2afroedF32	5'-MGCCTGACTYGGMTAGAACTWAAYAC-3'	This paper
ND2	ND2afroedR915	5'-YATGGTTGGTTTTTCAYTTKTGTTC-3'	This paper
RAG-1	RAG-1F700	5'-GGAGACATGGACACAATCCATCCTAC-3'	Bauer <i>et al.</i> (2007)
RAG-1	RAG-1R700	5'-TTTGTACTGAGATGGATCTTTTGCA-3'	Bauer <i>et al.</i> (2007)
RAG-1	RAG-1F396	5'-TCTGAATGGAAATCAAGCTGTT-3'	Groth & Barrowclough
RAG-1	RAG-1R397	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'	Groth & Barrowclough
RAG-1	RAG-1PF1	5'-YAWGAAATTKCTGGAAATTCAAGCT-3'	Portik <i>et al.</i> (2013)
RAG-1	RAG-1PR1	5'-GTCTYGGTCGGCCACCTTTGTT-3'	Portik <i>et al.</i> (2013)

The sequence data set (Table 2) includes mitochondrial NADH dehydrogenase sub- unit 2 gene (ND2, 1027 bp aligned) nuclear protein-coding genes phosphatidylinositol 3-kinase (PDK; 395 bp aligned), recombination activating gene 1 (RAG-1; 1038 bp aligned), prune homolog 2 (PRUNE2, 890 bp aligned), uncharacterized protein KIAA1107 (KIAA1107,

986 bp aligned), Ten-eleven translocation 1 gene (TET1, 1354 bp aligned), cancer susceptibility candidate 5 (CASC5, 901 bp aligned), cingulin-like 1 (CGNL1, 905 bp aligned), microtubule-associated protein 1A (MAP-1A, 1545 bp aligned), and kinesin family member 24 (KIF24 589- bp aligned), as well as two 3' UTR genes major facilitator superfamily domain containing 4 (MFSD4, 883 bp aligned) and large conductance calcium-dependent potassium ion channel beta 4 subunit (KCNMB4, 415 bp aligned).

DNA extraction, amplification and sequencing—Liver, toe and tail samples taken were stored in 95–100% ethanol. Genomic DNA was isolated from ethanol-preserved tissue samples with a Qiagen DNeasy blood and tissue kit. Polymerase chain reaction (PCR) was then performed on isolated DNA in 25- μ L reactions with the published primers KIF24F1, KIF24R1, ND2F117, ND2R102, PHOF2, PHOR1, RAG1F700, RAG1R700 (Greenbaum *et al.*, 2007; Bauer *et al.*, 2007, Portik *et al.*, 2012) and a battery of novel primers (Table 3).

Standard reaction conditions were as follows: denaturation at 95°C (2 min), then 32–34 cycles of denaturation at 95°C (35 s), annealing at 50°C (35 s), and extension at 72°C (initially 150 s, with 4 s added per cycle). Annealing temperature was adjusted as necessary for poor-yielding samples and specific primer pairs (see Table 3). Amplified products were visualized on 1.5% agarose gels. The AMPure magnetic bead system (Agencourt Bioscience) was used to purify amplified DNA. ABI Prism BigDye Terminator chemistry was used for cycle sequencing (Applied Biosystems), followed by purification with CleanSeq magnetic bead system (Agencourt Bioscience). An ABI automated 3730 sequencer was used for electrophoresis and analysis of targeted gene regions.

Alignment and phylogenetic analyses—Resulting chromatograms were translated to check for premature stop codons using MacClade v4.08 (Maddison & Maddison 2005). Initial alignments were performed with Geneious v5.6 (Drummond *et al.* 2012) and manually edited to account for codon deletions and sequencing error. Preliminary maximum likelihood estimations (GARLI v0.951, Zwickl 2006; RAxML v7.2.8 ALPHA, Stamatakis *et al.*, 2005) were performed with independent nuclear and mitochondrial datasets to assess phylogenetic congruence between mitochondrial and nuclear data prior to concatenation for comparison with both a taxon-reduced 12-gene concatenated dataset (59 individuals, including samples lacking one or more nuclear gene datasets) as well as and two-gene concatenated dataset for which all mitochondrial and nearly all nuclear data was available for all 72 ingroup samples (ND2, RAG1).

Maximum likelihood (RAxML v7.2.8 ALPHA, Stamatakis *et al.*, 2005), Bayesian inference (MrBayes 3.2.1, Ronquist *et al.*, 2012) and maximum parsimony (PAUP* v4.0, Swofford 2002) analyses were used for phylogenetic reconstruction for both concatenated datasets. Both analyses treated gaps as missing data. Estimates of evolutionary divergence between ND2 sequences were calculated as uncorrected pairwise differences using MEGA6 (Tamura *et al.* 2013).

Two-gene concatenated dataset—For likelihood and Bayesian analyses, the mitochondrial dataset was partitioned by codon position for the protein-coding region of ND2. Protein-coding nuclear genes were partitioned by codon position and non-coding nuclear genes were not partitioned, giving a total of seven partitions (three mitochondrial codon, three nuclear codon and one nuclear non-coding). The parsimony analyses were run using a stepwise addition starting tree with 3 random addition replicates for 1,000 non-parametric bootstrapping iterations with one tree held at each step. A tree bisection-reconnection (TBR) branch-swapping algorithm was used with a reconnection limit of 8. Zero-length branches were collapsed to yield polytomies, and gaps were treated as missing data.

For the likelihood analyses, branch support was assessed by running 1,000 bootstrap replicates using a general time reversible (GTR) model with gamma distributed rate variation among sites (Γ). For the Bayesian analysis, the model was estimated simultaneously with the run by using the nst=mixed option in MrBayes (v3.2.1). Analyses were performed with random starting trees and run for 10,000,000 generations with sampling every 1,000 generations yielding 10,000 trees for each parallel run. Burn-in was taken at 25% resulting in 7,500 trees for each parallel run. Accuracy of post burn-in convergence was checked using Tracer (v1.5). The final majority rule consensus tree contained posterior probabilities for each node recovered in the analysis.

Twelve-gene concatenated dataset: Prior to concatenation, preliminary likelihood trees were evaluated for each gene. All instances of incongruence amongst topologies were at poorly supported nodes (<60 BSS). Parsimony starting trees were obtained via stepwise addition, and analyses followed a TBR branch-swapping algorithm with a reconnection limit of 8 for 1000 bootstrap replicates. Trees were unrooted with no topological constraints and where maximum branch length was zero, branches were collapsed. Two parallel Bayesian runs were performed with random starting trees for 10 million generations each with sampling every 1,000 generations

to ensure that at least 10,000 samples were acquired from the posterior probability distribution using a GTR substitution model with gamma-distributed rate variation across sites and a proportion of invariable sites. Diagnostics were calculated every 5,000 generations. Average standard deviation of split frequencies = 0.004431, and average PSRF for parameter values = 1.00. The program AWTY (Nylander *et al.* 2008) was used to confirm convergence in both runs. A conservative approach to burn-in time was taken at 25%, discarding the first 2,500 trees produced in each run, leaving a total of 15,000 trees in the combined analyses from which the 50% majority rule consensus tree was calculated. The likelihood analysis was conducted using the GTR + Γ + I substitution model and partitioned by gene. For each analysis, 1,000 nonparametric bootstrap replicates were performed and a 50% majority-rule consensus tree was estimated.

Results

Molecular phylogeny

The most complete taxon sampling (72 ingroup taxa) is represented in the combined ND2 and RAG1 dataset, incorporating a total of 2104 bp, of which 1238 sites are variable and 968 are parsimony-informative. MP, ML and BI analyses of the combined dataset recovered highly concordant phylogenies. *Afroedura* as a whole is strongly supported as monophyletic (Fig. 1). Interspecific relationships with *Afroedura* are fully congruent between the maximum likelihood and Bayesian inference analyses and most basal branches and many intermediate branches in the tree are recovered under maximum parsimony as well. All species are monophyletic and moderate to high levels of support were found for each of the species groups recognized, except for the *A. africana* group, which was not retrieved under parsimony and was not well supported by the likelihood and Bayesian analyses. *Afroedura hawequensis* is unambiguously found to be the sister to all its congeners. Among remaining species, there is a strongly supported *A. nivaria* clade, in turn divided into two strongly supported subclades: *Afroedura halli* and an undescribed species (*A. aff. halli*—divergent by 21.13–23.84% from true *A. halli*) on the one hand and (*A. amatolica* + *A. tembulica*) + (*A. nivaria* + *A. pondolia*) on the other. Within this group all internal relationships except *A. amatolica* + *A. tembulica* are strongly supported by the model-based analyses (ML bootstraps 78% or higher, Bayesian posterior probabilities ≥ 0.98).

All remaining *Afroedura* constitute a monophyletic group within which a species-rich, strongly supported diverse clade of mostly former Transvaal (Limpopo and Mpumalanga) taxa is sister to a poorly supported group that includes the strongly supported *A. transvaalica* subgroup (*A. transvaalica* as sister to the pair *A. loveridgei* + *A. bogerti*) as sister to a weakly linked *A. karroica* + *A. africana* group. There is clear and well supported genetic substructure within both *A. transvaalica* and *A. africana*. Uncorrected p distances within the former taxon range from 0.60 to 15.33% are and in the latter they are 15.99–19.34%.

Relationships within the former Transvaal clade are mostly well supported (bootstraps > 75%, pp > 0.98). *Afroedura multiporis* and *A. haackei* (both recognized here as full species) are sister taxa, but highly divergent from one another (14.60%), and in turn group with *A. major*. Collectively these species are here recognized as the *A. multiporis* group and are sister to remaining congeners, which include only two recognized species, *A. marleyi* and *A. langi*, but seven undescribed lineages corresponding to a subset of those described as new herein. *A. marleyi* is sister to *A. pongola* **sp. nov.** and together these are sister to *A. maripi* **sp. nov.** The remaining taxa constitute a very strongly supported *A. langi* group consisting of a southern clade (*A. langi*, *A. waterbergensis* **sp. nov.**, *A. granitica* **sp. nov.**) and a northern clade (*A. broadleyi* **sp. nov.**, *A. soutpansbergensis* **sp. nov.**, *A. pienaari* **sp. nov.**). Divergences among species in the *A. langi* group are roughly comparable to those between *A. haackei* and *A. multiporis* (12.33% between *A. granitica* **sp. nov.** and *A. waterbergensis* **sp. nov.** and 14.16% between *A. broadleyi* **sp. nov.** and *A. pienaari* **sp. nov.**).

The 12-gene concatenated dataset had a great deal of missing data (Table 2), but nonetheless recovered a nearly congruent topology, with only three instances of incongruence, all occurring at poorly supported nodes (<60 BSS). We used the preferred topology of the more complete two-gene concatenated estimation as the reference tree for species relationships within *Afroedura* and plotted onto it the nodes that were strongly supported by the full 12-gene analysis and the individual genes that were able to recover the preferred relationships on a node-by-node basis (Fig. 2).

In some cases, this expanded nuclear phylogeny was able to provide greater support for certain relationships than the two-gene mitochondrial and nuclear phylogeny. For example, the monophyly of the *A. africana* and *A. transvaalica* groups collectively is well supported by CASC5 and is also retrieved by five other nuclear genes, but receives only 32% ML bootstrap support and a posterior probability of 0.49 in the two-gene tree. Similarly, the monophyly of *A. amatolica* + *A. tembulica*, which is weakly supported in the two-gene analyses, is well supported by CASC5, KIAA1107 and MAP1A, with three additional nuclear genes also supporting this relationship. On the other hand, some nodes (e.g., the *A. africana* group and the *A. marleyi* + *A. langi* groups) were poorly supported in both data sets.

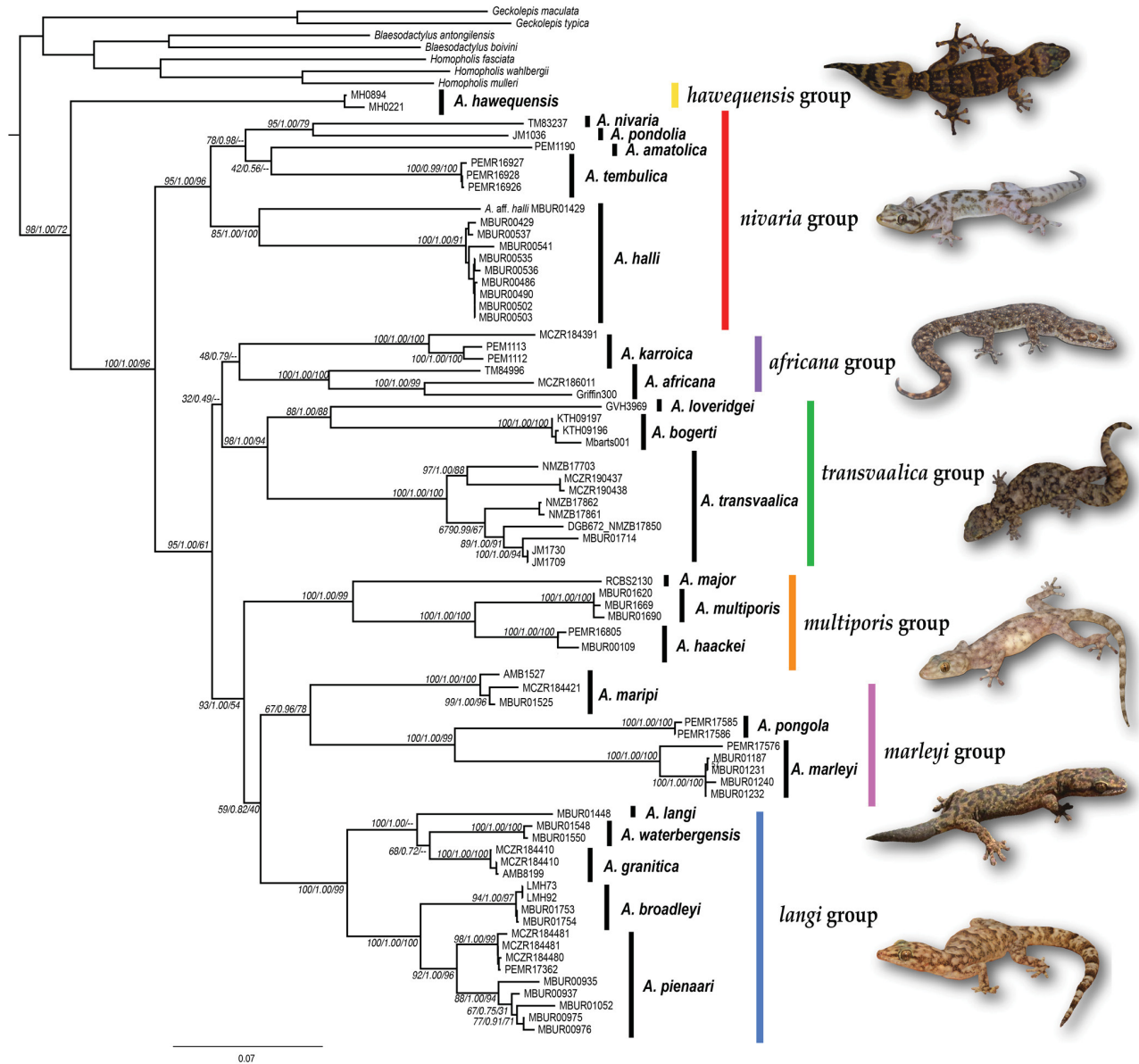


FIGURE 1. Maximum likelihood phylogram of *Afroedura* relationships derived from two genes (ND2, RAG1). Support values are presented as maximum likelihood bootstraps (MLBS)/ Bayesian posterior probabilities (BPP)/ parsimony bootstraps (PBS). Only most closely related outgroup taxa are shown. Images (top to bottom) of representative *Afroedura* species groups: *A. havequensis*, *A. pondolia*, *A. karroica*, *A. loveridgei*, *A. haackei*, *A. marleyi*, *A. granitica* sp. nov.

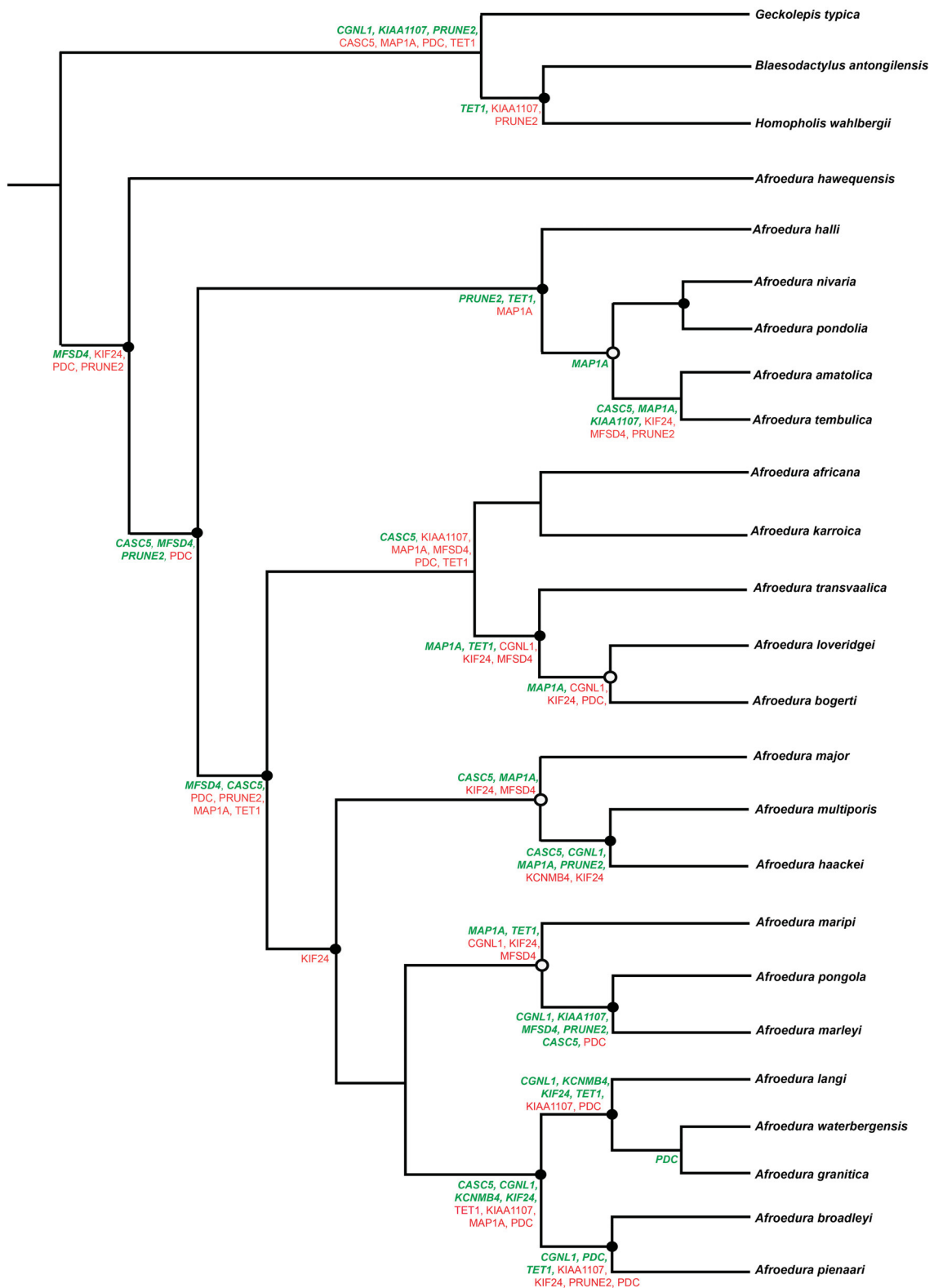


FIGURE 2. Results of the 12-gene concatenated phylogenetic analysis and 10 individual nuclear gene trees. The tree shows the topology as estimated in the two-gene (ND2, RAG1) concatenated analysis. Outgroup taxa (not shown) include *Chondrodactylus*, *Pachydactylus*, *Rhoptropus*, and *Goggia*. The tree has been pruned from the full dataset (72 ingroup taxa) to indicate species-level relationships only (22 ingroup taxa). Solid circles indicate >90 MLBS/1.0 BPP for the 12-gene concatenated analysis at the node, and open circles indicate 70–90 MLBS/9.0–9.9 BPP. Each individual nuclear gene not used in the two-gene concatenated analyses that was able to recover the same species relationship as in the two-gene analysis (Fig. 1) is listed on a node-by-node basis. Bold italic black names indicate >70 MLBS for that particular gene, and gray names in normal font indicate <70 MLBS.

Systematics

Afroedura Loveridge, 1944

Afroedura hawequensis Group

Diagnosis. Large sized (maximum SVL 83 mm), three pairs of enlarged scansors on digits II–V, first digit with a single scansor, tail verticillate and flattened, precloacal pores > 25.

A. hawequensis Mouton & Mostert, 1985

(Fig. 3A)

Distribution. Restricted to the fynbos habitats in Hawequa Mountains of the southwestern Western Cape Province, South Africa (Bauer 2014c) (Fig. 4).

Remarks. This species is the sister to all remaining congeners. It was previously considered a member of the *A. africana* group (Mouton & Mostert 1985). The species was previously listed in the *South African Red Data Book* as “Restricted” (Mouton 1988) and is currently considered as Near Threatened under IUCN assessment criteria (Bauer 2014c).

Afroedura transvaalica Group

Diagnosis. Two pairs of enlarged scansors per digit, tail strongly verticillate and flattened.

A. bogerti Loveridge 1944

(Fig. 3B)

Distribution. Namibe Province, Angola and adjacent northern Kaokoveld of northern Namibia (Branch 1998; Griffin 2003) (Fig. 4).

Remarks. This distinctive species was originally described by Loveridge (1944) as *A. karroica bogerti*, and was only elevated to specific status by Onderstall (1984). *Afroedura bogerti* and *A. karroica* possess the diagnostic features of different species groups and are separated from one another by a disjunction of approximately 2000 km; that they were previously considered conspecific is illustrative of the fact that herpetologists were reluctant to erect new specific level taxa for geckos of this genus, presumably because of their general morphological conservatism (Jacobsen 1997). Barts & Haacke (2010) provided data about reproduction in captivity.

A. loveridgei Broadley, 1963

Distribution. Tete district, Mozambique (Onderstall 1984) (Fig. 4).

Remarks. This species was originally described as a subspecies of *A. transvaalica*, but was elevated to specific status without comment by Branch (1998), although Kluge (2001) continued to recognize it as a subspecies.

Afroedura transvaalica (Hewitt, 1925)

(Fig. 3C)

Distribution. Zimbabwe and adjacent northern Limpopo province, South Africa, central Mozambique and possibly extreme eastern Botswana (Bauer 2014k) (Fig. 4).

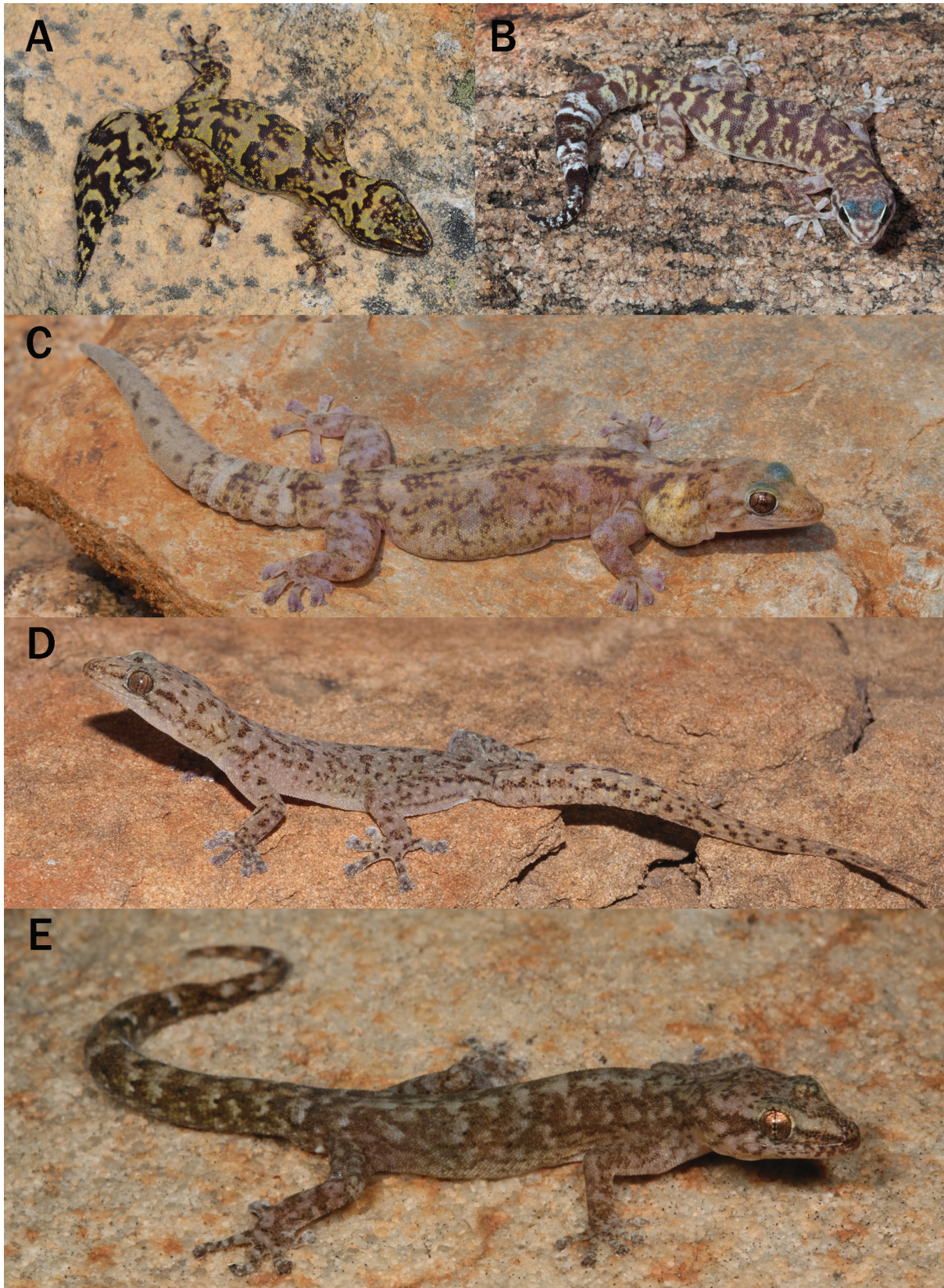


FIGURE 3. Representatives of the species groups of *Afroedura*. (A) *A. hawequensis* group: *A. hawequensis* (Limietberg, Western Cape, South Africa); (B) *A. transvaalica* group: *A. bogerti* (Iona National Park, Namibe Province, Angola); (C) *A. transvaalica* group: *A. transvaalica* (30 km west of Musina, Limpopo, South Africa); (D) *A. africana* group: *A. karroica* (Sneeuberg Mountains, Eastern Cape, South Africa); (E) *A. nivaria* group: *A. pondolia* (Durban, ZwaZulu-Natal, South Africa). Note the strongly verticillate original tail base in *A. transvaalica* and the bulbous regenerated tail in *A. hawequensis*. Photo A: Marius Burger, Photos B–C, E: Johan Marais, Photo D: Stuart V. Nielsen.

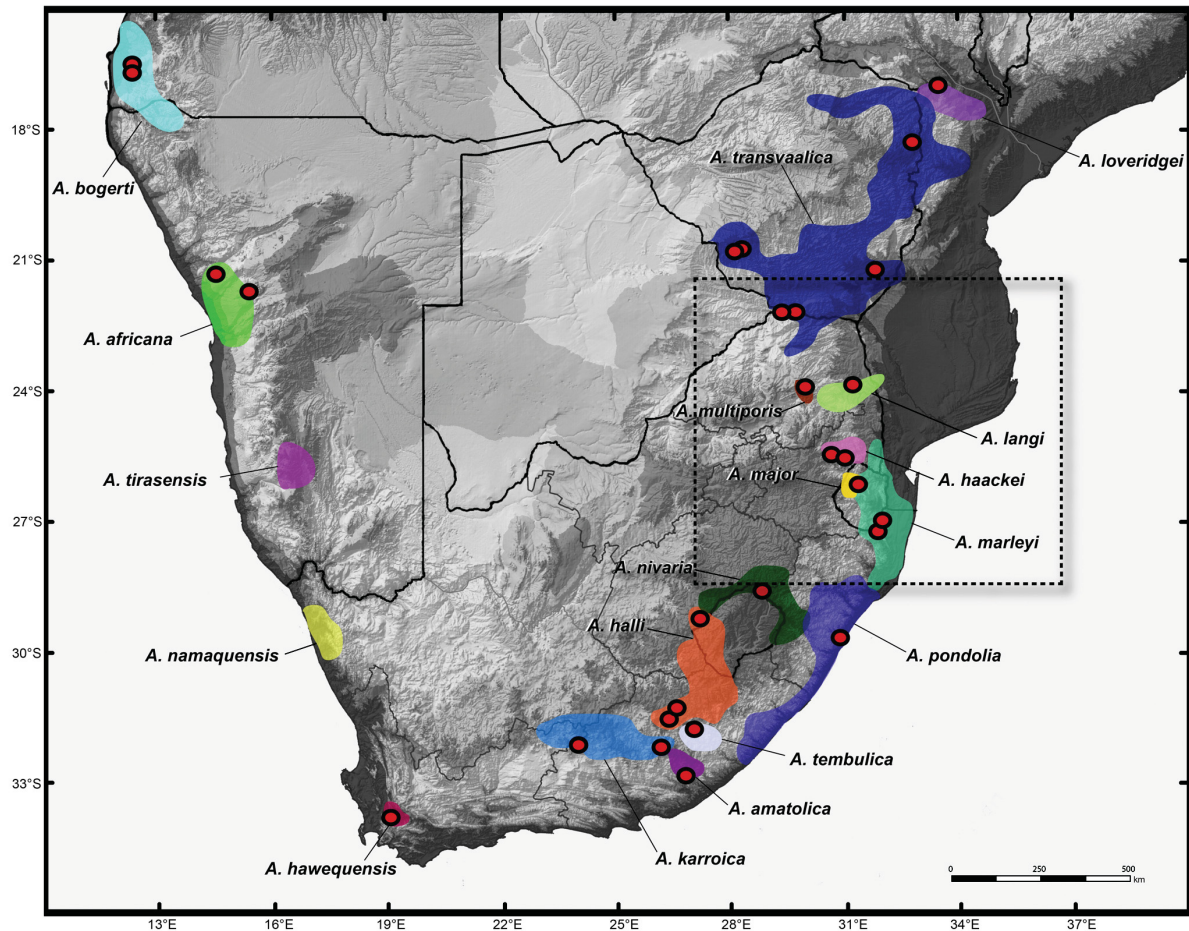


FIGURE 4. Map of southern Africa showing the approximate distributional ranges of previously described species of *Afroedura*. Red dots represent localities sampled for the genetic portion of the study. Ranges based on Branch (1998) and Bates *et al.* (2014) as well as unpublished data. Taxon names follow the conclusions of this paper. Area demarcated by a dashed line is presented in more detail in Figure 6.

Remarks. Our molecular phylogeny reveals relatively deep divergences among the samples, with Limpopo samples clustered with southern Zimbabwean ones and more northerly populations more distinct (Fig. 1). Previous interpretations of distributional data for this taxon reflected three disjunct populations (e.g., Onderstall 1984; Branch 1998), however, more complete sampling across Zimbabwe suggests that there may be no significant gaps between these (D.G. Broadley, pers. comm.) and this is reflected in our approximation of the species' range (Fig. 4).

Afroedura africana Group

Diagnosis. Small to medium sized (SVL < 65 mm), three pairs of enlarged scancers on each digit, tail verticillate and flattened, nasorostrals in contact with one another, preloacal pores < 20.

Remarks. The monophyly of this group is poorly supported and we recognize this group only tentatively. Additional genetic markers might help to support the union of *A. karroica* and the arid western taxa, or may reveal alternative placements of these species within the genus.

A. africana (Boulenger, 1888)

Distribution. Erongo Region, west central Namibia (Mouton & Mostert 1985; Griffin 2003) (Fig. 4).

Remarks. Since the work of Haacke (1965) *A. africana* has been considered a polytypic species (e.g., Branch *et al.* 1988; Rösler 2000; Kluge 2001; Griffin 2003). We here consider *A. africana* as a monotypic central Namibian endemic (see below). All three of our genetic samples originate from the Erongo Region of central Namibia and are thus presumably referable to *A. africana sensu stricto*. However, the levels of divergence among these samples (up to 19.34%) are comparable to or greater than interspecific differences elsewhere in the genus (Fig. 1), suggesting that further study of this taxon is required.

***A. karroica* (Hewitt, 1925)**

(Fig. 3D)

Distribution. Karoo of the central-western Eastern Cape and adjacent areas of the Northern and Western Cape provinces (Bauer 2014d) (Fig. 4).

Remarks. Both *A. bogerti* and *A. halli* were previously treated as subspecies of *A. karroica* (Loveridge 1944, 1947; Wermuth 1965; Kluge 2001).

***A. namaquensis* stat. nov. (FitzSimons, 1938)**

Distribution. Known from scattered localities in the Succulent Karoo Biome in the Little Namaqualand region of the Northern Cape Province (Bauer 2014a) (Fig. 4).

Remarks. Haacke (1965), in describing *A. africana tirasensis* considered *A. namaquensis* as a subspecies of *A. africana*, and it has maintained this rank since (Mertens 1971; Branch 1981, 1988, 1998; Onderstall 1984; Bauer 2014a), although chiefly because this poorly known taxon has not been reviewed subsequently. Under modern species concepts, the differences between the supposed subspecies of *A. africana*—including precloacal pore counts, presence of internasal granules, gular scale counts, and color pattern (Haacke 1965) would generally be accepted as evidence of specific distinctness, especially in light of the large disjunctions between the forms and their likely low vagility (Mouton & Mostert 1985; Jacobsen 1997). On this basis we here recognize this taxon at the rank of full species.

***A. tirasensis* stat. nov. Haacke, 1965**

Distribution. Farm Tiras, Lüderitz District, southern Namibia (Mouton & Mostert 1985; Griffin 2003) (Fig. 4).

Remarks. Haacke (1965) originally described this form as a subspecies of *A. africana*, and it has maintained this rank since (Mertens 1971; Branch 1981, 1988, 1998; Onderstall 1984; Branch *et al.* 1988; Griffin 2003), although chiefly because this poorly known taxon has not been reviewed subsequently. Under modern species concepts, the differences between the supposed subspecies of *A. africana* (Haacke 1965) (see above) would generally be accepted as evidence of specific distinctness, especially in light of the large disjunctions between the forms and their likely low vagility (Mouton & Mostert 1985; Jacobsen 1997). On this basis we here recognize this taxon at the rank of full species.

***Afroedura nivaria* Group**

Diagnosis. Small to medium sized (SVL < 65 mm), three pairs of enlarged scapulars on each digit (two in *A. pondolia*), tail faintly to strongly verticillate and flattened, nasorostrals separated by internasal granule(s), precloacal pores < 20.

***A. amatolica* (Hewitt, 1925)**

Distribution. Amatola Mountains, Eastern Cape Province, South Africa (Bauer 2014b) (Fig. 4).

Remarks. Loveridge's (1947) synonymy of *A. amatolica* with *A. nivaria* was accepted by at least some authors as late as the 1980s (Branch 1981), owing to the long-confused application of names to Eastern Cape *Afroedura*, but since 1984 it has generally be regarded as specifically distinct (Visser 1984b).

A. halli (Hewitt, 1935)

Distribution. Western Lesotho and adjacent southeastern Free State and Eastern Cape provinces, South Africa (Bates & Bauer 2014a) (Fig. 4).

Remarks. This species was previously considered a subspecies of *A. karroica* (e.g., Loveridge 1947; Wermuth 1965; Branch *et al.* 1988; Kluge 1991, 1993) but was elevated to specific status by Bates (1996), although without substantial discussion, and some later authors, especially outside of South Africa, have continued to include it within *A. karroica* (e.g., Kluge 2001). One subspecies, *A. k. wilmoti*, has been variously recognized as valid (FitzSimons 1943) or not (Loveridge 1947; Branch 1981). Its status is under review (Bates & Branch 1998). Our sampling included a single specimen resembling *A. halli* that was deeply divergent from all other samples (Fig. 1), supporting the findings of Makhubo (2013), who found multiple divergent clades within the species. Although the distinctiveness of this specimen in our two-gene analysis may be artificially high due to the absence of RAG1 sequence (Table 2), the >20% ND2 divergence from typical *A. halli*, which vary among themselves by 0.20–3.02%, supports the view that this represents a different species.

A. nivaria (Boulenger, 1895 [1894])

Distribution. Drakensberg of the Eastern Cape and Free State provinces, South Africa. Its occurrence in Lesotho is suspected but not yet documented (Bates & Bauer 2014b) (Fig. 4).

Remarks. Loveridge (1947) synonymized *A. amatolica* with *A. nivaria* and this interpretation was long followed (e.g., Wermuth 1965; De Waal 1978; Branch 1981). The two are not sister taxa (Fig. 1) and *A. amatolica* was raised from synonymy by Visser (1984b). *Afroedura nivaria* as currently construed is non-monophyletic (Makhubo *et al.* 2011; Makhubo 2013) and is currently under revision (Bates & Branch 1998).

A. pondolia (Hewitt, 1925)

(Fig. 3E)

Distribution. Low to middle elevations of the eastern Eastern Cape Province and southern and central KwaZulu-Natal (Bauer 2014i) (Fig. 4).

Remarks. *Afroedura pondolia* was long considered polytypic. Onderstall (1984) recognized five non-nominotypic subspecies, all of which are here considered valid species: *A. marleyi*, *A. major*, *A. multiporis*, *A. haackei*, and *A. langi*, and this interpretation was long accepted by most authors (e.g., Branch *et al.* 1988; Kluge 1991, 1993, 2001). All of the new species described herein would also have been placed in *A. pondolia* under Onderstall's concept of the species. To avoid confusion with the *A. pondolia* group of earlier authors, we have here used the term *A. nivaria* group for the clade to which *A. pondolia* belongs.

A. tembulica (Hewitt, 1926)

Distribution. Queenstown region of the Eastern Cape province, South Africa (Bauer 2014j) (Fig. 4).

Remarks. Although considered poorly differentiated from *A. amatolica* and *A. nivaria* by Branch *et al.* (1988), this taxon has never been synonymized with any of its congeners.

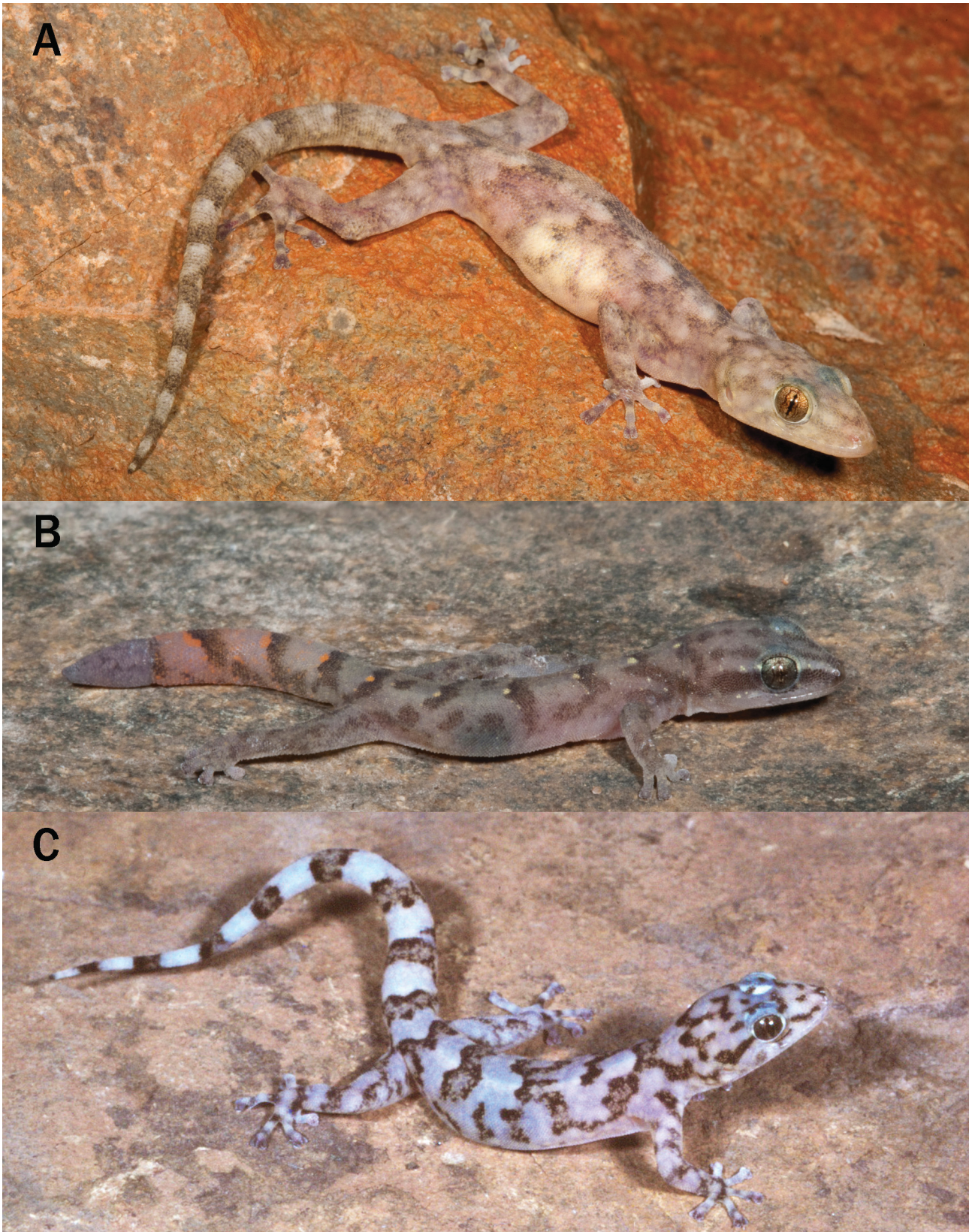


FIGURE 5. Representatives of the species groups of *Afroedura*. (A) *A. multiporis* group: *A. haackei* (Schoemanskloof, Mpumalanga, South Africa); (B) *A. marleyi* group: *A. marleyi* (The Hippos, Mpumalanga, South Africa); (C) *A. langi* group: *A. langi* (Farm Harmony, Hlaralumi River, Limpopo, South Africa). Photos A–B: Johan Marais, Photo C: N.H.G. Jacobsen.

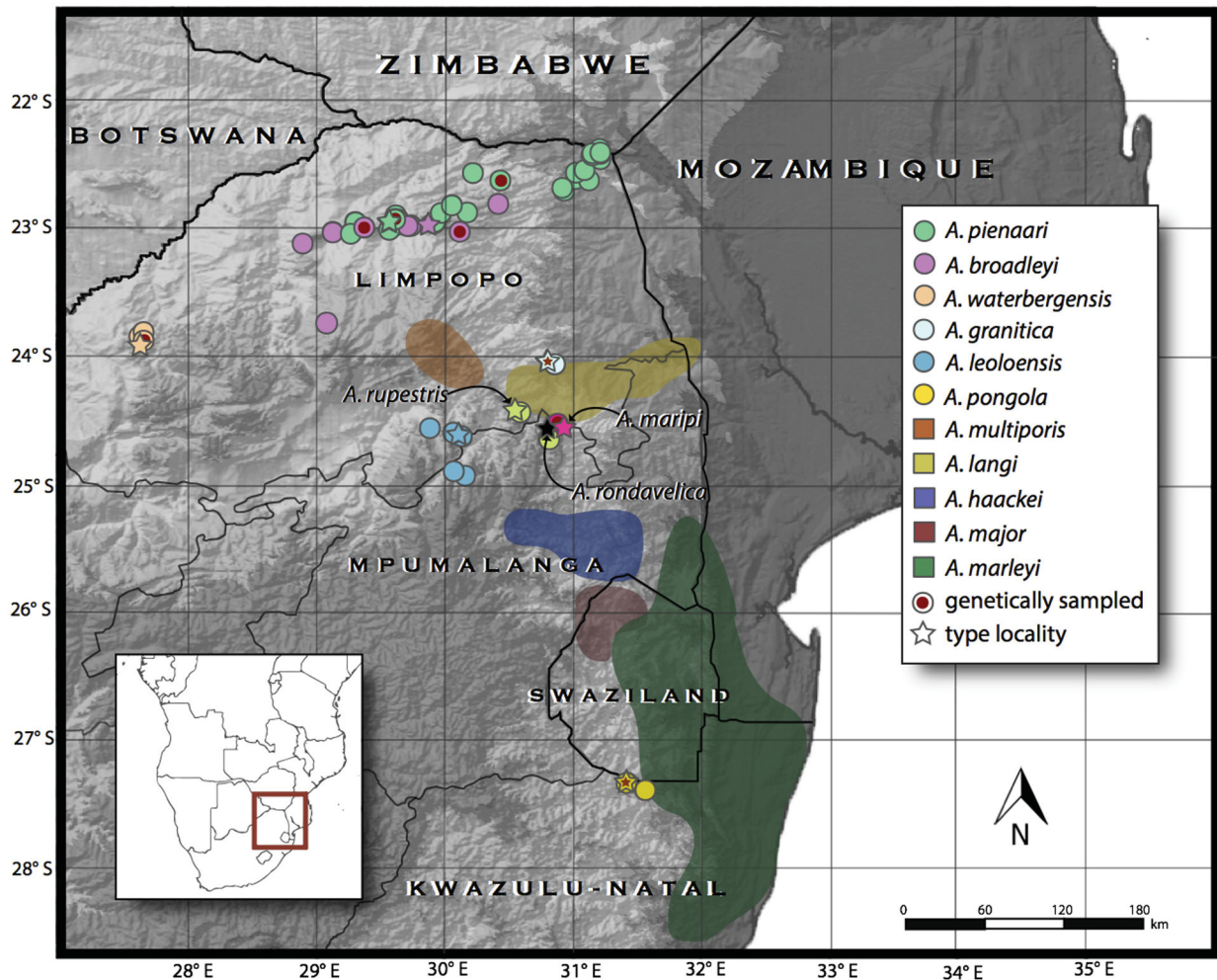


FIGURE 6. Map of Limpopo and Mpumalanga provinces, South Africa and adjacent regions showing the distributions of previously described species of *Afroedura* endemic to this region and known localities of the nine new species described in this paper. For previously recognized forms an approximate outline of the range based on Bates *et al.* (2014) is shown; genetically sampled localities are marked by circles in Figure 4. For new species all known localities are plotted as dots (see relevant species accounts), with genetically sampled site marked by circles with a red center, type locality marked by a star, and all other localities indicated by open circles colored to correspond to the key in the figure. The very restricted distributions of *A. maripi* sp. nov., *A. rondavelica* sp. nov., and *A. rupestris* sp. nov. are indicated by arrows and are labeled directly on the map.

Afroedura multiporis Group

Diagnosis. Two pairs of enlarged scansors per digit, tail not, or only faintly verticillate, rounded to slightly flattened, dorsal scales keeled, one or more internasals between nasorostrals.

Remarks. Onderstall (1984) mentioned the presence of keeled scales in members of this group but did not appreciate the phylogenetic value of this character. Jacobsen (1990, 1992a, 1997) identified *A. multiporis* ‘Lebombo’ as another member of this species complex. This putative species remains known from a single juvenile specimen. Although apparently distinctive in several features, the lack of adult material and the imperfect state of the specimen prevent us from describing this form at this time. This form was noted as *Afroedura* sp. nov. ‘Lebombo flat gecko’ by Bourquin (2004).

***A. haackei* stat. nov. Onderstall, 1984**

(Fig. 5A)

Distribution. Granite outcrops of the southern Lowveld of Mpumalanga province, South Africa (Bauer 2014h) (Figs. 4, 6). TM 49920 from Farm Scrutton 23MT (2230AD) (illustrated by Pienaar 1978 as *A. transvaalica*) appears similar or identical to *A. haackei* (Onderstall 1984, Jacobsen 1990) and may represent a translocation.

Remarks. This species was described as a subspecies of *A. pondolia* (Onderstall 1984), but was amended by Jacobsen (1990) to *A. multiporis haackei*. Our molecular data confirm the relationship of the two taxa, but based on substantial genetic differentiation (Fig. 1) as well as differences in body size and precloacal pore counts (see Table 4), and their allopatric distribution, we here formally elevate *A. haackei* to specific rank. The species was previously listed in the *South African Red Data Book* as “Restricted” (Jacobsen 1988a) but is currently considered to be of Least Concern (Bauer 2014h).

***A. major* Onderstall, 1984**

Distribution. Highveld and middleveld areas of western Swaziland (Boycott 1992, 2014) (Figs. 4, 6).

Remarks. This species was originally described as a subspecies of *A. pondolia* and was elevated to specific rank by Branch (1998) without comment, although Kluge (2001) continued to list it as a subspecies. The species is considered Near Threatened (Monadjem *et al.* 2003; Boycott 2014).

***A. multiporis* (Hewitt, 1925)**

Distribution. Restricted to the Haenertsburg and Wolkberg areas of central Limpopo province, South Africa (Bauer 2014g) (Figs. 4, 6).

Remarks. This species was described as a subspecies of *A. pondolia* and long retained this status (e.g., Onderstall 1984; Kluge 2001), but was referred to by Jacobsen (1990) as *A. multiporis multiporis*. Our molecular data confirm its affinities with *A. haackei*. On the basis of substantial genetic differentiation from *A. haackei* as well as differences in body size and precloacal pore counts (see Table 4) we here formally elevate *A. haackei* to specific rank, leaving *A. multiporis* monotypic. The species was previously listed in the *South African Red Data Book* as “Restricted” (Jacobsen 1988b) and is currently considered Vulnerable under the IUCN threat categories (Bauer 2014f).

***Afroedura rupestris* sp. nov.**

(Fig. 7A–B)

Afroedura multiporis ‘Abel Erasmus’ Jacobsen 1992a, 1997

Holotype. TM 81233, adult male, Farm Perkeo 223KT, 24°27'S, 30°35'E, Sekukhuneland District (2430BC), Limpopo Province, Republic of South Africa, collector R.E. Newbery, 28 June 1982.

Paratypes. TM 81224–81228, 81230–81232, 81234–81235, same data as holotype.

Additional material: TM 47504, 52120, 81229, Bourk’s Luck, Pilgrim’s Rest District, Limpopo Province, Republic of South Africa (2430DB).

Etymology. The species name refers to the rupicolous nature of this (and most) members of the genus *Afroedura*.

Diagnosis. A large *Afroedura* (to 62 mm SVL) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail faintly verticillate with three subcaudal rows and usually six supracaudal rows per verticil; dorsal scales bluntly keeled to trihedral; usually a single internasal scale; 20–24 precloacal pores in males.

Description. (based on holotype TM 81233) Adult male; SVL 52.0 mm; tail 61.0 mm; mass in life 3.4 g. A slender elongated, lightly pigmented gecko with a rounded crown to the head. Rostral twice as broad as high,

heptagonal; nostril pierced between rostral, first upper labial and three nasal scales; nasorostrals separated by a granular scale behind rostral. Scales on snout larger than on crown with some keeled scales along canthus rostralis and above and slightly anterior to the eyes; 2–3 supraciliary spines. Scales between the nasals and anterior margin of eye 12 and from posterior margin of eye to ear 20. Supralabials nine. Mental wedge-shaped, pentagonal, longer than broad; postmentals two; infralabials eight.

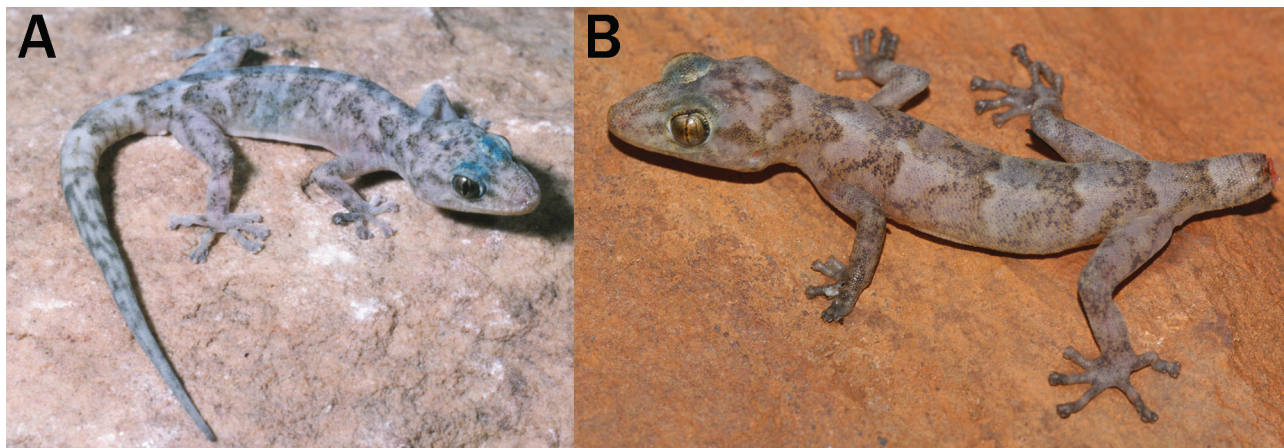


FIGURE 7. *Afroedura rupestris* sp. nov. (A) Farm Perkoe, Limpopo Province, South Africa (Photo N.H.G. Jacobsen). (B) Abel Erasmus Pass, Limpopo Province, South Africa (Photo Marius Burger).

Dorsals granular, heterogeneous, smaller paravertebally, larger dorsolaterally, bluntly keeled to rounded, conical and juxtaposed. Scales rows at midbody 87. Ventral scales smooth, larger than dorsals, imbricate. Digits slender with two pairs of enlarged scansors and some enlarged inferomedian scales under the fourth toe. Other digits lacking enlarged inferomedian scales. Precloacal pores in a continuous row of 24, arranged in a chevron; three postcloacal spurs on each side of tail base. Tail long, somewhat flattened proximally; caudal scales arranged in poorly developed verticils with six dorsal and three ventral rows per verticil; dorsal scales smaller than ventrals and subimbricate; ventrals imbricate.

Color. Olive-brown above with six, rarely seven, blackish wavy and irregular crossbands extending from occiput to sacrum. Pale whitish spots sometimes present at posterior margin of crossbands but may be absent. Limbs pale olive-brown with reticulate darker patterns on the thighs or with wavy stripes and spots. Crown of head paler, mostly without distinct markings. A darkish stripe from nostril to the anterior margin of eye. Two stripes extend from posterior margin of eye to above ear opening. In some individuals a single stripe extends through the eye and is continuous with the occipital bar. Tail with up to 10 crossbars. Body venter whitish, tail venter brownish with darker speckling.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Single internasal typically present but two in paratype TM 81232 and nasorostrals in contact (no internasals) in TM 81234. Scales from eye to ear 16–19. Supraciliary spines four and scales on snout not keeled except above and anterior to the eye in TM 81232. Rostral and mental scales variable in relative proportion and shape. Postmentals generally two, but three in TM 47504, 52120 and 81234 and one in TM 81232. Female specimens lack precloacal pores; males typically with 20–26 pores with the exception of TM 81231 and TM 81225 which have 12, with a series of poreless scales separating left and right pore series. Postcloacal spurs 1–4. Caudal verticils with 6–7 subcaudal rows each. Tail 51.76–54.31% of total length. 45.45 % of individuals (n = 11) exhibit caudal autotomy.

Distribution. Apparently limited to the Eastern Escarpment of Limpopo Province, between the Abel Erasmus Pass and Bourke's Luck (Fig. 6).

Natural history. An exclusively rupicolous species living in crevices between rocks and under flakes of exfoliating rock along sandstone cliffs in Ohrigstad Mountain Bushveld (SVcb 26) (Mucina & Rutherford 2006) at altitudes between 850–1200 m a.s.l. (Fig. 8A). Also found in kloofs and on rocky Blackreef quartzite outcrops on top of cliffs.

Remarks. *Afroedura rupestris* sp. nov. shares with *A. haackei*, *A. multiporis*, and *A. major* bluntly keeled to trihedral dorsal scales and although not sampled in our molecular phylogeny, presumably belongs to the same clade as these taxa (Jacobsen 1992a, 1997). It differs from these species in typically having 20–24 precloacal pores in

males (*versus* 16–17 in *A. multiporis*, generally 25–28 in *A. haackei*, and 18–19 in *A. major*). It may further be differentiated from *A. multiporis* and *A. major* by its lower number of supracaudal scale rows per vertical (6 *versus* 7 and 8, respectively). It is significantly larger (max SVL 62 mm) than *A. haackei* (max SVL 52 mm), from which it also has a significantly higher number of supralabials ($p < 0.05$, t_{28} d.f.) and scales from eye to ear ($p < 0.001$, t_{25} d.f.), and smaller than *A. major* (max SVL 76 mm).

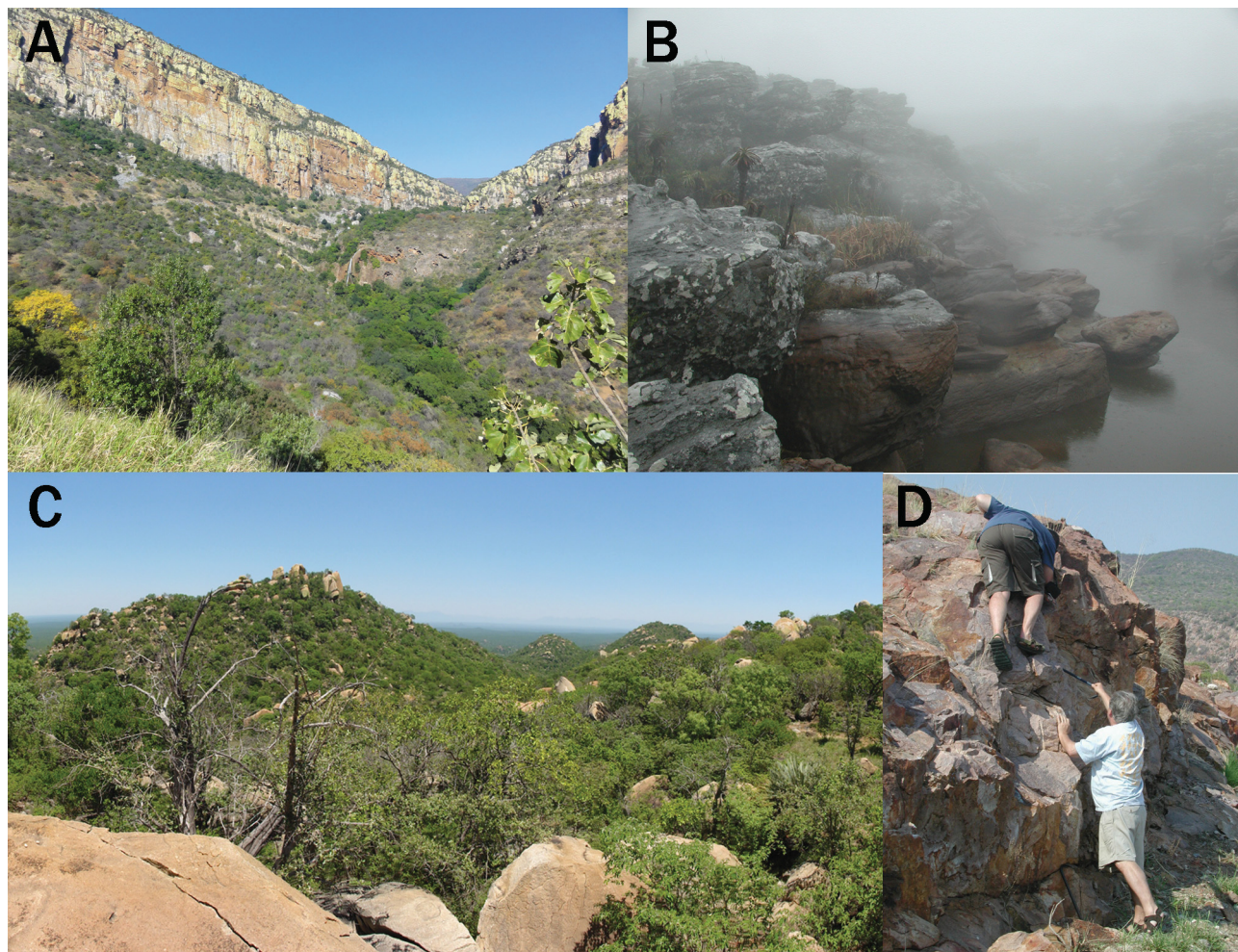


FIGURE 8. Habitats of new species of South African *Afroedura* spp. (A) General view of Abel Erasmus Pass, Limpopo, habitat of *A. rupestris* sp. nov. (B) Habitat of *A. maripi* sp. nov. near the summit of Mariepskop, Mpumalanga Province in heavy mist. (C) Habitat of *A. granitica* sp. nov. at its type locality on Farm Lillie, Limpopo Province. (D) Habitat of *A. pienaari* sp. nov. at Waterpoort on the northern edge of the soutpansberg, Limpopo Province. Photos A and C: Stuart V. Nielsen, Photos B and D: Aaron M. Bauer.

Afroedura marleyi Group

Diagnosis. Two pairs of scansors per digit, tail not or only faintly verticillate, rounded to partially flattened, dorsal scales smooth, one or more internasal granules between nasorostrals.

A. marleyi (FitzSimons, 1930)

(Fig. 5B)

Distribution. Coastal plain of Zululand, Kwazulu-Natal inland to the Lebombo Mountains and through Swaziland to southeastern Mpumalanga, and possibly adjacent Mozambique (Bauer 2014f) (Figs. 4, 6).

Remarks. This species was previously considered a subspecies of *A. pondolia* (Onderstall 1984) until elevated

without comment by Branch (1998). Our samples come from a relatively limited area of the species' range and we suspect that deeper sampling would reveal greater substructure within *A. marleyi*.

***Afroedura maripi* sp. nov.**

(Fig. 9A)

Afroedura 'maripi' Jacobsen 1992a, 1997

Holotype. TM 81262, adult male, Mariepskop, 24°32' S, 30°53' E, Pilgrim's Rest District (2430DB), Limpopo Province, Republic of South Africa, collector R. E. Newbery, 25 June 1982.

Paratypes. (all from same locality as holotype) TM 81248–81249, 81251–81255, 81257–81259, 81261, 81263–81264, same data as holotype; TM 81250, 81256, 81260, 81265, collector N. H. G. Jacobsen, 29 October 1980; TM 58031–58032, collector R. E. Newbery, 5 June 1984; TM 58118, collector R. E. Newbery, 21 November 1984; TM 62907–62909, collector R. E. Newbery, 21 February 1985; TM 64021, collector R. E. Newbery, 1 June 1984.

Etymology. The species name refers to the local name for Mariepskop, the type locality.

Diagnosis. A large *Afroedura* (to 63 mm SVL) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; a single internasal granule between nasorostrals; tail not obviously verticillate, with 4–5 subcaudal rows and 6–8 supracaudal rows per verticil; dorsal scales smooth, in 96–108 rows at midbody; a single internasal scale; 11–13 precloacal pores in males.

Description. (based on holotype TM 81262) Adult male; SVL 57.0 mm; tail 61.0 mm (partly regenerated); mass in life 3.3 g. Head and body dorso-ventally depressed. Head oval and wider than neck, body broad and limbs relatively short, digits stout. Rostral twice as broad as high, more or less octagonal; nostril pierced between rostral, first upper labial and three nasal scales; nasorostrals separated by a single large granular scale. Scales on snout rounded to conical, larger than those on crown. Scales between nasals and anterior margin of eye 12, and from eye to ear 24. Four supraciliary spines at posterodorsal corner of eye. Supralabials 10. Mental wider than deep; postmentals three; infralabials eight.

Dorsals smooth, uniform, each scale raised posteriorly and juxtaposed; scales at midbody 107. Ventral scales smooth, flattened and imbricate. Digits stout with two pairs of enlarged scansors and five enlarged inferomedian scales under fourth toe, not reaching the base. Precloacal pores 13, arranged in a continuous 'V'-shaped pattern. Tail regenerated and constricted at base. Two postcloacal spurs on either side of tail base.

Color. Olive-brown to olive-gray above with variable blackish crossbars extending from occiput to sacrum. Crown of head variably marked, filigreed to reticulate. Interstices between bars are reticulate laterally. Limbs barred or variegated. Tail with approximately 10 black bars, becoming more irregular and diffuse posteriorly. Chin, throat, chest and abdomen whitish. Underside of tail grayish brown, faintly barred.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Endolymphatic sacs distended in adult female paratype TM 81260. Scales between nasals and eye 11–13, from eye to ear 20–23. Supraciliary spines 2–4. Rostral and mental scales variable in relative proportion and shape. Postmentals 2–3. Supralabials 9–10, infralabials 7–8.

Midbody scale rows 96–108. Inferomedian scales under the fourth toe 5–8. Precloacal pores in male paratypes 11–13, females lacking pores. Postcloacal spurs 2–3, rarely four. Original tails 52.1–53.9% of total length and tapered. Tail with 6–8 (mostly seven) dorsal and four (rarely five) ventral scale rows per indistinct verticil. Supracaudals subimbricate with a rounded to pointed posterior margin; subcaudals broad and imbricate. Caudal autotomy evident in 76.3 % of individuals.

Distribution. Restricted to the slopes of Mariepskop and God's Window area of the Eastern Escarpment, in apparently two disjunct populations (Fig. 6). Occurrence in the latter area is verified by a photo voucher.

Natural history. Usually associated with rocky outcrops on west-facing slopes of Mariepskop, frequently in the partial shade of pine plantations but also found on outcrops of Black Reef quartzites on top of the escarpment in the shade of indigenous montane forest. Preferred retreats include crevices under flakes of exfoliating rock and dark overhangs of large boulders. Found in Ohrigstad Mountain Bushveld (SVcb 26) and Northern Escarpment Quartzitic Sourveld (GM 23) (Mucina & Rutherford 2006) at elevations of 1700–1900 m a.s.l.

TABLE 4. Variation in key morphological characters in Limpopo and Mpumalanga Provinces *Afroedura* including, for comparative purposes, values for *A. pondolia* and *A. major*. For size data sample sizes, maxima and adult means \pm 1 S.D. are given by sex for taxa newly described herein; maxima only (regardless of sex) are provided for previously recognized taxa. Internasal and Postmenal counts show the character states recorded and, parenthetically, the number of specimens exhibiting each state. Verticil counts are presented as supra-caudal scale rows followed by sub-caudal scale rows. All other counts are presented as mean \pm 1 S.D. Sample sizes for scale counts are the same as listed for Internasal (Intern) and Postmenal (Postm) conditions.

Taxon	SVL (mm)	Mass (g)	Intern (n)	Postm (n)	Supralabials	Infralabials	Eye-Ear	Midbody Rows	Scale	Verticils supra/sub	Precaudal Pores	
<i>A. transvaalica</i> group												
<i>transvaalica</i>	64.0	5.4	0(35) 1(2)	2(28) 3(9)	9.60 \pm 0.80	8.81 \pm 0.70	18.13 \pm 0.81	109.13 \pm 3.83	7-8 5		6.20 \pm 0.83	
<i>A. nivaria</i> group												
<i>pondolia</i>	58.0	—	1(8) 2(5)	1(2) 2(14) 3(4)	9.27	8.30	23.86	102.92	6-7 4		14.50	
<i>A. multiporis</i> group												
<i>haackei</i>	52.0	2.3	0(3) 1(13) 2(3)	2(16)	9.06 \pm 0.68	8.38 \pm 0.62	16.86 \pm 0.86	90.36 \pm 4.27	6-7 3-4		25.83 \pm 1.64	
<i>major</i>	76.0	—	2(3)	2(3)	11.00	9.33	22.17	106.50	8 4		18.50	
<i>multiporis</i>	66.5	5.5	1(11)	1(1) 2(10)	9.10 \pm 0.70	8.60 \pm 0.67	20.60 \pm 1.51	99.60 \pm 4.33	6-7 3-4		16.67 \pm 0.58	
<i>rupestris sp. nov.</i>												
	9♂,3♀	8♂,3♀	0(1)	1(1)	9.79 \pm 1.05	8.36 \pm 0.63	18.77 \pm 1.17	90.14 \pm 4.90	6-7 3		22.12 \pm 1.96	
	62.0♂,56.0♀	5.8♂,3.9♀	1(11)	2(10)								
	54.5 \pm 4.0♂	3.5 \pm 1.1♂	2(2)	3(3)								
	54.7 \pm 1.5♀	3.0 \pm 1.0♀										
<i>A. marleyi</i> group												
<i>marleyi</i>	36.0	1.2	1(17)	2(14) 3(3)	8.47 \pm 0.87	8.18 \pm 0.64	19.1 \pm 1.68	88.77 \pm 3.00	6-7 4-5		13.40 \pm 0.89	
<i>maripi sp. nov.</i>												
	7♂,9♀	7♂,9♀	1(13)	2(13) 3(8)	9.59 \pm 0.67	8.18 \pm 0.73	21.81 \pm 1.38	102.56 \pm 3.81	7-8 4-5		12.29 \pm 0.95	
	63.0♂,63.0♀	3.8♂,6.5♀										
	56.7 \pm 5.2♂	3.0 \pm 0.5♂										
	56.7 \pm 5.1♀	3.3 \pm 1.4♀										
<i>pongola sp. nov.</i>												
	5♂,5♀	5♂,3♀	1(12)	2(8)	9.00 \pm 0.58	8.08 \pm 0.28	20.77 \pm 1.42	98.22 \pm 3.07	6-7 4-5		22.40 \pm 0.89	
	35.0♂,40.0♀	1.0♂,0.9♀	2(1)	3(5)								
	34.1 \pm 0.6♂	0.8 \pm 0.2♂										
	38.0 \pm 1.4♀	0.8 \pm 0.1♀										

.....continued on the next page

TABLE 4. (Continued)

Taxon	SVL (mm)	Mass (g)	Intern (n)	Postm (n)	Supralabials	Infralabials	Eye-Ear	Midbody Rows	Scale	Verticils supra/sub	Precloacal Pores
<i>rondevelica</i> sp. nov.	2♂ 55.0♂ 54.0 ± 1.4♂	1♂, 2.4♂ —	1(2)	2(2)	9.00±1.41	8.00 ± 0.00	22.00± 0.00	101.00± 4.24	7	7	8.00±1.41
<i>A. langi</i> group											
<i>langi</i>	7♂,15♀ 44.0♂,46.0♀ 40.6±-3.3♂ 41.3±-4.0♀	2♂,5♀ 1.9♂,1.8♀ 1.8±-0.1♂ 1.4±-0.3♀	0(29)	1(1) 2(28)	8.52± 0.74	7.43±0.50	18.50±1.06	98.00±2.62	6-7 4	6-7 4	14.75±1.16
<i>granitica</i> sp. nov.	8♂,2♀ 58.0♂,54.0♀ 51.4 ± 4.5♂ 52.8 ± 1.8♀	7♂,2♀ 3.0♂,3.6♀ 2.4 ± 0.6♂ 3.0 ± 0.8♀	0(8) 1(2)	1(2) 2(8)	9.10±0.88	7.70±0.48	19.10±1.79	100.78±3.03	7 4	7 4	14.13±1.13
<i>leoloensis</i> sp. nov.	10♂,6♀ 39.0♂,40.5♀ 35.6 ± 2.4♂ 38.8 ± 1.4♀	10♂,6♀ 1.2♂,1.1♀ 0.7 ± 0.2♂ 0.9 ± 0.1♀	0(16) 1(1)	2(15) 3(1)	9.10±0.83	8.00±0.93	16.50±0.81	88.69±3.48	6-7 4	6-7 4	32.78±1.86
<i>broadleyi</i> sp. nov.	27♂,33♀ 56.0♂,55.0♀ 46.8 ± 5.7♂ 45.9 ± 5.4♀	27♂,33♀ 3.6♂,4.5♀ 2.2 ± 0.8♂ 2.1 ± 0.9♀	0(71) 1(4)	1(18) 2(52) 3(2)	8.95± 0.80	8.16± 0.77	19.16± 1.39	96.74± 4.64	6-8 4	6-8 4	9.78±1.22
<i>waterbergensis</i> sp. nov.	2♂,5♀ 41.0♂,46.0♀ 41.0 ± 1.0♂ 44.4±1.1♀	2♂,4♀ 1.8♂,2.8 1.75±0.1♂ 2.2±0.4♀	0(8)	2(8)	9.24 ± 0.92	7.80± 0.89	17.50± 1.31	96.60± 3.41	7 4	7 4	5.33± 1.53
<i>pianaari</i> sp. nov.	16♂,16♀ 51.0♂,52.0♀ 44.6 ± 3.1♂ 47.1 ± 3.7♀	15♂,16♀ 3.3♂,2.6♀ 1.9 ± 0.6♂ 2.1 ± 0.5♀	0(108) 1(6)	1(16) 2(90) 3(8)	9.57±0.79	8.06± 0.74	16.2± 1.33	95.23±5.34	6-7 4	6-7 4	16.52±1.60

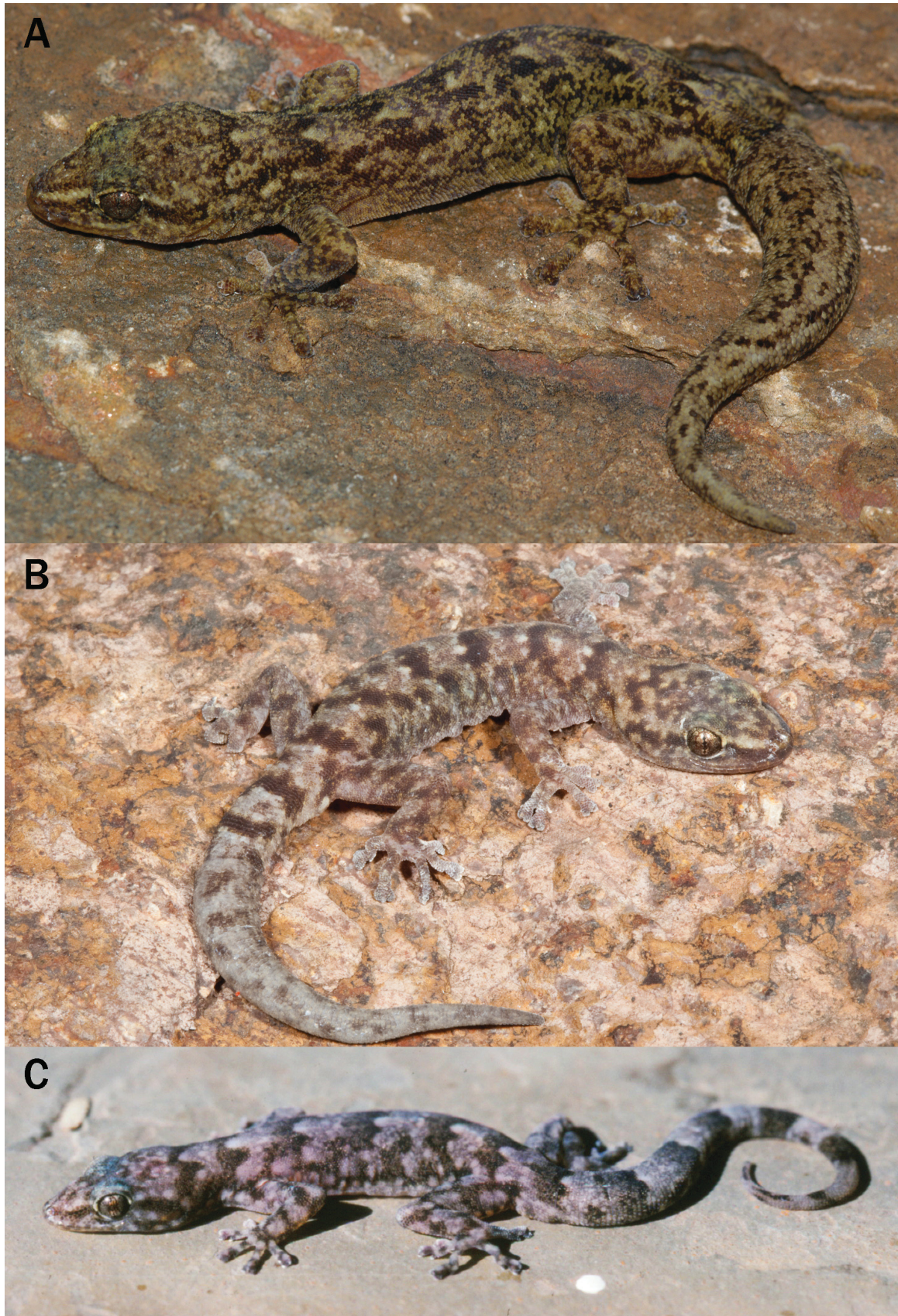


FIGURE 9. New species in the *Afroedura marleyi* group. (A) *Afroedura maripi* **sp. nov.** from Mariepskop, Mpumalanga, South Africa (Photo Marius Burger). (B) *Afroedura pongola* **sp. nov.** from from west of Pongola, KwaZulu-Natal, South Africa (Photo Johan Marais). (C) *Afroedura rondavelica* **sp. nov.** from the Three Rondavels, Blyde River Nature Reserve, Mpumalanga Province, South Africa (24°34' S, 30°50' E) (Photo by N.H.G. Jacobsen).

Two eggs are laid at a time during August–October. They are soft when laid, adhering to the rock and hardening, as has been reported for *A. halli* (Power 1939). The eggs measure 9.5–10.9 x 7.8–9.3 mm and take approximately two months to hatch. Neonates measure 23.0 mm SVL, 21.0 mm TailL, with a mass of 0.25–0.30 g.

Remarks. *Afroedura maripi* **sp. nov.** was included by Jacobsen (1990, 1992a, 1997) in his *A. pondolia* complex, but our molecular results suggest that while other members of this proposed complex—*A. marleyi*, *A. pongola* **sp. nov.**, and presumably *A. rondavelica* **sp. nov.** (also unsampled genetically), as well as *A. maripi* **sp. nov.**—do form a monophyletic group, referred to as the *A. marleyi* group, *A. pondolia* is only distantly related. It may be distinguished from *A. pongola* **sp. nov.** and especially *A. marleyi* on the basis of its greater number of midbody scale rows (mean of 102.56 *versus* 98.22 and 88.77, respectively) and larger size (maximum SVL 63 mm *versus* 40 mm and 36 mm, respectively) and has substantially fewer precloacal pores than *A. pongola* **sp. nov.** (11–13 *versus* 21–23). It also has significantly more supralabial scales than *A. marleyi* ($p < 0.001$, t37 d.f.). It is larger (60 mm *versus* 55 mm maximum SVL) and has more precloacal pores (11–13 *versus* 7–9) than *A. rondavelica* **sp. nov.**

Afroedura pongola **sp. nov.**

(Fig. 9B)

Afroedura pondolia 'Godlwayo' Jacobsen 1990, 1992a, 1997

Afroedura sp. nov. "Pongola flat gecko" Bourquin 2004

Holotype. TM 81210, adult male, Godlwayo, 27°20' S, 31°25' E, Piet Retief District (2731AD), Kwazulu-Natal, Republic of South Africa, collector R. E. Newbery, 24 May 1981.

Paratypes. TM 81211–81213, 81216 same data as holotype; TM 81208–81209, 81214, 81217–81218, same locality as holotype, collectors R. E. Newbery & W. Petersen, 19 November 1985; TM 81215, 81219–81220, Farm Zwartkloof 60HU, Piet Retief district (2731BC), collector R. E. Newbery, 21 May 1981.

Etymology. The name refers to the Pongola River, along part of which this species occurs. It is used as a noun in apposition.

Diagnosis. A small *Afroedura* (to 40 mm SVL) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail not obviously verticillate, with 4–5 subcaudal rows and 6–7 supracaudal rows per verticil; dorsal scales smooth, 95–103 scale rows at midbody; a single (rarely two) internasal scale; 21–23 precloacal pores in males.

Description. (based on holotype TM 81210) Adult male; SVL 35.0 mm; TailL 32.0 mm (partly regenerated); mass in life 1.0 g. Head oval, wider than neck. Rostral approximately 1.5 times wider than high. Nostril pierced between rostral, first upper labial and three nasal scales. Nasorostrals separated by a single granular scale. Scales on snout round and flattened, decreasing in size posteriorly, smallest on crown. Ten scales between nasals and anterior margin of eye; 21 scales between eye and ear. No enlarged supraciliary spines. Supralabials eight. Mental broadly wedge-shaped, wider than deep and in contact with two postmentals; infralabials eight.

Dorsals relatively uniform, smooth, rounded and flattened, becoming larger laterally. Scales at midbody 101. Ventral scales rounded and imbricate, largest mesially becoming smaller ventrolaterally. Limbs relatively short and feet small; digits with two pairs of enlarged scancers; three enlarged inferomedian scales under the fourth toe. Precloacal pores 21, arranged in a continuous shallow 'V'-shape. Tail flattened at base, becoming more cylindrical distally. Distal half regenerated. Caudal scales in whorls (verticils) with 6–7 scales rows dorsally and 4–5 ventrally. Supracaudals almost square with a rounded posterior margin and subimbricate. Subcaudals large and imbricate. 1–2 postcloacal spurs at base of tail.

Color. Pale to mid-brown with 6–8 dark brown, irregular, wavy crossbands extending from occiput to sacrum. A median white spot or spots adjacent to each crossbar. Crown of head pale with brown to dark brown patches. A dark brown stripe extends from the nostrils through the middle of the eye to link with the occipital bar. In life the eyeballs appear dark gray to blackish through the skin. Limbs spotted and mottled with dark brown. Original tail with nine dark brown crossbands. Venter pinkish white with slightly darker pigmentation under tail.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Nasorostrals separated by two granules in TM 81209. Scales between nasals and eye 10–13, from eye to ear 20–23. Supraciliary spines 2–3 and mental nearly as deep as wide in some paratypes. Postmentals 2–3. Supralabials 8–10,

infralabials 8–9. Midbody scale rows 95–103. Enlarged inferomedian scales under fourth toe mostly 0, rarely 3–5. Precloacal pores in male paratypes 21–23, females lacking pores. Postcloacal spurs 1–2, rarely three. Original tails 50.5–52. 8% of total length. Tail with 6–7 dorsal and 4–5 ventral scale rows per indistinct verticil. 66.7% (8/12) of individuals have regenerated tails.

Distribution. Known only from north of the Pongola River in the far northeast of Kwazulu-Natal (Fig. 6).

Natural history. This gecko retreats into narrow crevices between rocks and under exfoliating flakes of granite. It is found in Granite Lowveld (SVI 3) and Northern Zululand Sourveld (SVI 22) (Mucina & Rutherford 2006) at elevations of 750–850 m a.s.l.

Remarks. *Afroedura pongola* **sp. nov.** was included by Jacobsen (1990, 1992a, 1997) in his *A. pondolia* complex, but our molecular results demonstrate that whereas it forms a clade with other members of this proposed complex, *A. pondolia* is only distantly related. *Afroedura pongola* **sp. nov.** may be distinguished from the similarly sized *A. marleyi* on the basis of its greater number of midbody scale rows ($p < 0.001$, t_{20} d.f.) and from this species and the much larger *A. maripi* **sp. nov.** and *A. rondavelica* **sp. nov.** (maximum SVL 63 mm and 55 mm *versus* 40 mm for *A. pongola* **sp. nov.**) by its greater number of precloacal pores in males (mean of 22.4 *versus* 13.4 or fewer).

Afroedura rondavelica **sp. nov.**

(Fig. 9C)

Unnamed taxon, Jacobsen 1997

Holotype. TM 81238, adult male, Blyde River Nature Reserve, 24°34' S, 30°50' E, Pilgrim's Rest District (2430DB), Mpumalanga Province, Republic of South Africa, collector N. H. G. Jacobsen, 18 December 1991.

Paratype. TM 81237, same data as for holotype.

Etymology. The name refers to the 'Three Rondavels,' prominent mountain peaks in the Blyde River Nature Reserve with the appearance of round thatch roofed huts (= rondavels). The specimens were collected on cliff faces of one of these.

Diagnosis. A mid-sized *Afroedura* (to 55 mm SVL) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail cylindrical, weakly verticillate, with four subcaudal rows and seven supracaudal rows per verticil; dorsal scales smooth, 99–100 scale rows at midbody; a single internasal scale separating the nasorostrals; 7–9 precloacal pores in males.

Description. (based on holotype TM 81238) Adult male; 51.0 mm SVL; TailL 61.0 mm; mass in life 2.4 g. Head and body elongated and dorsoventrally depressed. Tail slightly flattened at base, thereafter cylindrical and tapered. Head ovate and much broader than neck. Rostral approximately twice as broad as high. Nostril pierced between rostral, first upper labial and three nasal scales. Nasorostrals large, raised and separated by a single granular scale behind rostral. Scales on snout large, becoming smaller posteriorly. Eleven scales between nasals and eye and 23 between eye and ear. Two to three supraciliary spines. Supralabials eight. Mental wedge-shaped, much broader than deep and in contact with two postmentals. Infralabials seven.

Dorsal granules smooth, rounded and more or less homogeneous, juxtaposed but becoming oblique laterally and subimbricate. Midbody scales in 99 rows. Ventral scales smooth, imbricate and almost hexagonal, with thin margins. Limbs relatively slender; digits with two pairs of scansors; eight enlarged inferomedian scales under the fourth toe. Seven continuous precloacal pores arranged in a 'V'-shape. Tail mostly cylindrical, only faintly verticillate with 7–8 dorsal and four ventral rows per verticil. Supracaudals square to rectangular and subimbricate; subcaudals imbricate, mostly squarish, with rounded to pointed posterior margins. Two postcloacal spurs on either side of tail base.

Color. Dorsally pale brown to gray-brown with six dark crossbands extending from the crown of the head to the sacrum. Posterior margin of crossbands edged with white. Crown of head similar to the back, bordered laterally by a dark brown stripe extending from the nostrils through the eye and continuous with the occipital bar. Limbs lightly barred with brown with irregular dorsal blotches between the crossbars. Eleven blackish dorsal crossbars extend down the length of the tail. Proximal bars posteriorly edged with white, fading distally. Venter pinkish off-white.

Variation. The sole paratype, TM 81237, another adult male is larger than the holotype (55.0 mm SVL; TailL 68.0 mm). It differs in having 23 scales between eye and ear, 3–4 supraciliary spines, nine supralabials, eight infralabials; 100 midbody scale rows; seven enlarged inferomedian scales under the fourth toe; nine precloacal pores in a shallow forward-directed curve (four left, five right), and three enlarged postcloacal spurs at base of tail.

Distribution. Apparently restricted to the Three Rondavels in the Blyde River Nature Reserve (Fig. 6).

Natural history. This gecko appears to be a cliff dweller, inhabiting horizontal and vertical crevices in sandstone near the base of cliffs. Appears to be gregarious based on the amount of feces observed, but the two individuals collected were solitary in crevices along south-facing cliffs. Occurs in Northern Escarpment Quartzite Sourveld (GM 23) (Mucina & Rutherford 2006) at an elevation of 1300 m a.s.l.

Remarks. *Afroedura rondavelica* **sp. nov.** was not sampled in our genetic analyses, chiefly because of the difficulty in accessing the type locality. Jacobsen (1997) noted the existence of the Three Rondavels population of *Afroedura*, but did not mention its assignment to species complex. However, its weakly verticillate tail, smooth dorsal scales, and internasal as well as its geographic position suggest that it is allied to *A. marleyi*, *A. maripi* **sp. nov.** and *A. pongola* **sp. nov.** It may be distinguished from these taxa by its much lower precloacal pore counts (see **Remarks** under *A. pongola* **sp. nov.**). It is also smaller and less stocky than its nearest neighbour, *A. maripi* **sp. nov.**, and lacks the olive-brown, velvety appearance of that species.

Afroedura langi Group

Diagnosis. Two pairs of enlarged scensors per digit, tail faintly verticillate, rounded to partially flattened, dorsal scales smooth, internasal granules typically absent.

A. langi (FitzSimons, 1930)

(Fig. 5C)

Distribution. Lowveld savannah in northeastern Mpumalanga and northeastern Mpumalanga provinces and adjacent Mozambique (Visser 1984; Jacobsen 1990; Bauer 2014e) (Figs. 4, 6).

Remarks. This species was previously considered a subspecies of *A. pondolia* (e.g., Onderstall 1984) until raised to specific status by Jacobsen (1990, 1992a). Six of the nine new species described herein are related to *A. langi* and earlier references to this species outside of its currently recognized range may refer to one or more of these taxa.

Afroedura granitica **sp. nov.**

(Fig. 10A)

Afroedura langi 'Lillie' Jacobsen 1992a, 1997

Holotype. TM 81187, adult male, Farm Lillie 148KT, 24°04' S, 30°51' E, Letaba district (2430BB), Northern Province, collector R. E. Newbery, 11 November 1985.

Paratypes. TM 81239–81240, 81243–81247, same data as for holotype; TM 81241–81242, same locality as for holotype, collector N. H. G. Jacobsen, 17 May 1980.

Etymology. The specific epithet refers to the decomposing granite hills to which this gecko appears restricted.

Diagnosis. A medium to large *Afroedura* (maximum SVL 58.0 mm) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail not obviously verticillate and weakly flattened, with four subcaudal rows and seven supracaudal rows per verticil; dorsal scales smooth, 99–107 scale rows at midbody; internasal scales typically absent, a deep furrow between nasorostrals; 13–16 precloacal pores in males.

Description. (based on holotype TM 81187) Adult male; 55.0 mm SVL; 62.0 mm TailL; mass before preservation 3.0 g. Dorsoventrally depressed; head ovate, distinctly wider than neck. Forelimbs small, hindlimbs

robust. Rostral more than twice as wide as high; nostril pierced between rostral, first upper labial and three nasal scales; nasorostrals in broad contact behind rostral, with a deep furrow between them. Scales on snout rounded and juxtaposed, much larger than granules on crown of head; ten scales between nasals and eye and 18 scales between eye and ear; three supraciliary spines; supralabials nine. Mental wedge-shaped, much longer than wide and in contact with a single postmental. Infralabials seven.

Dorsal granules uniform, smooth, rounded and juxtaposed. Midbody scales 100. Ventrals lozenge-shaped and imbricate. Digits with two pairs of scancers and four enlarged inferomedian scales under the 4th toe. Fifteen continuous precloacal pores arranged in a curved row. Tail flattened proximally and thickening about one verticil length posterior to the cloaca. Tail inconspicuously verticillate and tapering, with caudal scales in seven dorsal and four ventral rows per verticil; supracaudals subimbricate, squarish to rectangular, with a rounded posterior margin; subcaudals large, squarish to hexagonal with rounded posterior margins, subimbricate. Two postcloacal spurs at base of tail.

Color. The crown of the head is pale brown with dark brown spots and stripes that are also found on the snout. A dark brown stripe extends from the nostril through the eye, and above the ear to communicate with the occipital bar. Pale gray-brown to brown dorsally with six wavy dark brown irregular crossbars between occiput and sacrum. Crossbars are edged with black posteriorly and in their posterior indentations have white or whitish spots, particularly along the vertebral column. Variable pale and dark spots and blotches present between crossbars. The limbs have a variable dark brown reticulate pattern. Original tails with at least 10 dark brown to blackish crossbands with half bands and speckling in the intervening areas. Venter white, subcaudals speckled.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Paratypes TM 81244 and TM 81246 with nasorostrals separated by a single granular scale. Scales between nasals and eye 10–12, from eye to ear 18–22. Postmentals 1–2. Supralabials 7–10. Midbody scale rows 99–107. No enlarged inferomedian scales under the fourth toe in TM 81243. Precloacal pores in male paratypes 13–16, females lacking pores but female paratype TM 81243 with a row of elongate scales in precloacal position. Postcloacal spurs 1–2, absent in some females. Original tails 53.18–58.3% of total length. Degree of distinctness of tail whorls variable; faint, but clearly evident in some specimens. Tail has been autotomized in only 20% of the specimens examined.

Distribution. Restricted to granite hills and outcrops in the eastern Lowveld near Mica, Limpopo Province (Fig. 6).

Natural history. Apparently restricted to decomposing granite outcrops and hillsides on the farm Lillie 148KT in veld type SVI 3 Granite Lowveld (Mucina & Rutherford 2006) at elevations of 600–800 m a.s.l. These geckos inhabit crevices formed by exfoliating sheets on the underside of boulders, as well as crevices between rocks. They are occasionally found occupying the same retreats as large flat rock scorpions (*Hadogenes troglodytes*). The very similar *A. langi* occurs on small schistose outcrops.

Remarks. *Afroedura granitica* **sp. nov.** shares a suite of characters with *A. langi* and four other species described herein as new. The affinities of all but one of these, *A. leoloensis* **sp. nov.** have been confirmed by our molecular phylogeny (Fig. 1). In comparison with other members of this group *A. granitica* **sp. nov.** (maximum SVL 58 mm) is substantially larger than *A. langi* and *A. waterbergensis* **sp. nov.** (both reaching only 46 mm) and *A. leoloensis* **sp. nov.** (40.5 mm maximum SVL). In comparison with the last of these species it also has far fewer precloacal pores (13–16 *versus* typically 31–35), whereas compared to *A. waterbergensis* **sp. nov.** (4–7 pores) and *A. broadleyi* **sp. nov.** (8–12 pores) it has more. In addition, in comparison with the superficially similar *A. langi*, the nasorostrals of *A. granitica* **sp. nov.** form a deep furrow between them (*versus* weakly raised nasorostrals forming a shallow furrow). *Afroedura granitica* **sp. nov.** is most similar in the basic diagnostic features used herein to *A. pienaar* **sp. nov.**, to which it is rather distantly related. It may be distinguished by its larger size (58 *versus* 53 mm maximum SVL and even greater mean differences; Table 4), lower number of male precloacal pores (mean ~14 *versus* ~16), and higher number of eye to ear scales (mean of 19.10 *versus* 16.20), although there is overlap in all characters.



FIGURE 10. New species in the *Afroedura langi* group. (A) *Afroedura granitica* **sp. nov.** from Farm Lillie, Limpopo Province, South Africa (24°04'S, 30°51'E) (Photo Stuart V. Nielsen). (B) *Afroedura leoloensis* **sp. nov.** from Farm Maandagshoek, Limpopo Province, South Africa (Photo N.H.G. Jacobsen). (C) *Afroedura broadleyi* **sp. nov.** from 22°58'40"S, 29°19'57"E, Limpopo Province, South Africa (Photo Marius Burger).

***Afroedura leoloensis* sp. nov.**

(Fig. 10B)

Afroedura pondolia langi (part) Visser 1984a (fig. p. 61)

Afroedura langi 'Leolo' Jacobsen 1992a, 1997

Holotype. TM 81113, adult male, Farm Hendriksplaats 281KT, 24°38' S, 30°08' E, Lydenburg District, (2430CA) Mpumalanga Province, Republic of South Africa, collectors R. E. Newbery and W. Petersen, 15 November 1985.

Paratypes. TM 81115, TM 81125, 81127, same data as for holotype; TM 81119, 81124, Farm Maandagshoek 254KT, Sekhukhuneland District, Limpopo Province (2430CA) collector N. H. G. Jacobsen, 25 October 1980; TM 81112, 81116–81118, same locality as TM 81119, collector R.E.Newbery, 29 June 1982; TM 81126, Farm Kalkfontein 367KT, Lydenburg District, Mpumalanga Province (2430CC), collector N. H. G. Jacobsen, 23 April 1981; TM 81114, 81121, 81123, 81128, same locality as TM 81126, collectors R. E. Newbery and W. Petersen, 16 November 1985; TM 81122, Kgoloko lokasie, Sekhukhuneland District, Limpopo Province (2429DB), collector R. E. Newbery, 27 October 1980; TM 81120, Farm De Grooteboom 373KT, Lydenburg District, Mpumalanga Province (2430CC), collector N. H. G. Jacobsen, 23 October 1981.

Etymology. The specific epithet refers to the Leolo hills in Sekhukhuneland, Limpopo Province, where it was first discovered.

Diagnosis. A small *Afroedura* (maximum SVL 40.5 mm) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail faintly verticillate and flattened near base, with four subcaudal rows and 6–7 supracaudal rows per verticil; dorsal scales smooth, 87–95 scale rows at midbody; internasal scales typically absent; 31–35 precloacal pores in males.

Description. (based on holotype TM 81113) Adult male; 37.0 mm SVL; 45.0 mm TailL; mass before preservation 0.9 g. Body small and slender, dorsoventrally depressed; head oval, wider than the neck. Rostral approximately 2.5 times wider than high; nostril pierced between rostral, first upper labial and three nasal scales; nasorostrals in moderate contact behind rostral. Scales on snout hexagonal, flattened and much larger than scales on crown of head; nine scales between nasals and eye and 16 scales between eye and ear. Four supraciliary spines. Supralabials 10. Mental wedge-shaped, much longer than wide and in contact with two postmentals. Infralabials eight.

Dorsal scales minute, more-or-less homogeneous, smooth, juxtaposed to subimbricate, rounded to slightly hexagonal. Midbody scales 89. Ventrals large, smooth and imbricate. Digits with two pairs of enlarged scansors and six enlarged inferomedian scales under the fourth toe. Precloacal pores in a continuous, almost straight row of 34. Tail broad and flattened near the base, tapering to a fine tip, faintly verticillate; caudal scales arranged in six dorsal and four ventral rows per verticil. Supracaudals subimbricate, almost rectangular; subcaudals as broad as long and imbricate. Two postcloacal spurs on either side of tail base.

Color. Pale brown to brown dorsally with 7–8 dark brown irregular crossbands extending from the occiput to sacrum. Crossbands with darker posterior margins and, in most specimens, a white vertebral spot just posterior to each crossband. Limbs longitudinally striped or banded. The paler areas between the stripes are spotted dark brown. Crown of head pale brown with darker spotting and other variegations. Tail with 10 blackish crossbands from base to tip. Venter pinkish; tail brownish with darker markings.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Nasorostrals in broad contact behind rostral but separated posteriorly by a single granule in TM 81120. Scales between nasals and eye 9–12, from eye to ear 16–18. Five supraciliary spines in TM 81115. Mental as long as broad in some specimens; postmentals three in TM 81114. Supralabials 8–10. Infralabials 6–10. Midbody scale rows 87–95. 0–8 enlarged inferomedian scales under fourth toe. Precloacal pores in male paratypes 31–35 (except for TM 81126, which has only 11), females lacking pores. Original tails 50.00–55.9% of total length. Supracaudal scales in 6 or 7 rows per tail whorl. Tail has been autotomized in 54.5% of the specimens examined (n=17).

Distribution. Endemic to the Leolo Hills and outcrops above the Steelpoort River on either side of the border between Mpumalanga and Limpopo Provinces (Fig. 6).

Natural history. Exclusively rupicolous, apparently limited to norite and granitic formations. *Afroedura leoloensis* sp. nov. lives in narrow crevices under exfoliating rock. These are usually on the underside of boulders with the openings facing downwards, protecting them from rain. The species is found in Sekhukhune Mountain Bushveld (SVcb 28) and Leolo Summit Sourveld (GM 20) (Mucina & Rutherford 2006) at an elevation of 1200–1800 m a.s.l.

Two eggs are laid at a time and measure 8.9–9.0 x 6.1–6.4 mm with a mass of 0.2 g. The eggs appear to be laid in midsummer and are initially soft-shelled, adhering to the rock and then hardening.

Remarks. *Afroedura leoloensis* sp. nov. is a member of the *A. langi* clade (Figs. 1–2; see **Remarks** under *A. granitica* sp. nov.). This species exhibits the highest number of precloacal pores (31–35) not only in its clade, but in the genus as a whole, and may thus be distinguished from its congeners.

***Afroedura broadleyi* sp. nov.**

(Fig. 10C)

Afroedura langi 'Soutpansberg' Jacobsen 1992a, 1997; Kirchhof *et al.* 2010

Afroedura 'Matlala' Jacobsen 1992a, 1997

Holotype. TM 81316, adult male, Farm Peover 772MS, 22°59' S, 29°44' E, Soutpansberg District (2229DC), Limpopo Province, Republic of South Africa, collector R. E. Newbery, 6 November 1985.

Paratypes. TM 81317–81322, 81341, same data as for holotype; TM 81338–81340, Farm Leek 769MS, Soutpansberg District (2229DC), Limpopo Province, collector R. E. Newbery 6 November 1985.

Additional material examined (all localities in Limpopo Province). TM 81323–81326, Farm Outlook 789MS, Soutpansberg District (2229DD); TM 81327–81329, 81330–81336, Farm Newgate 802MS, Soutpansberg District (2229DD); TM 81337, Mutshenzheni, Sibasa District (2230CD); TM 81300–81307, 81309–81314, Farm Leipzig 264LR, Bochum District (2328BB); TM 81288–81299, 81308, Farm Urk 10LS, Bochum District (2329AA); TM 81188–81207 Matlala Mountain, Seshego District (2329CC).

Etymology. The species is named for our friend and colleague Dr. Donald G. Broadley in honor of his many contributions to African herpetology and in celebration of his 80th birthday.

Diagnosis. A mid-sized *Afroedura* (maximum SVL 56.0 mm) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail moderately verticillate (semi-verticillate) and flattened near base, with four subcaudal rows and 6–8 supracaudal rows per verticil; dorsal scales smooth, 88–106 scale rows at midbody; internasal scales typically absent; 8–12 precloacal pores in males.

Description. (based on holotype TM 81316) Adult male; 45.5 mm SVL; 49.0 mm TailL (part regenerated); mass before preservation 2.3 g. Moderately dorsoventrally depressed; head oval, wider than neck; limbs robust with stout digits; tail depressed, long and tapered, distal portion regenerating. Rostral twice as broad as high; nostril pierced between rostral, first upper labial and three nasals; nasorostrals large and in contact behind rostral. Scales on snout large, heterogeneous and flattened, decreasing in size posteriorly, smallest on crown of head; 10 scales from nasals to eye and 21 scales from eye to ear; three supraciliary spines. Supralabials nine. Mental narrow, wedge-shaped, longer than wide and in contact with two postmentals. Infralabials seven.

Dorsal scales relatively homogeneous, rounded, smooth, slightly flattened and juxtaposed; midbody scales 91. Ventral scales larger, imbricate and almost hexagonal. Digits with two pairs of enlarged scensors and one enlarged inferomedian scale under the 4th toe. Precloacal pores 11, arranged in a shallow curve, separated (five and six) by a poreless scale. Tail semi-verticillate with scales arranged in whorls with six dorsal and four ventral rows per verticil. Supracaudals rectangular with a rounded posterior margin; subcaudals squarish with rounded posterior margins. Two to three cloacal spurs at base of tail.

Color. Pale grey to buff or pinkish brown above with 6–7 dark brown to blackish, very wavy and irregular crossbands extending from occiput to sacrum. Crossbands darkest posteriorly, incompletely edged with white and with a median white spot. Crown of head heavily spotted or mottled with dark brown; a forward pointing darker 'V' extending along the canthus rostralis, whereas a dark streak runs from the nostril through the middle of the eye to above the ear, joining the occipital band. Limbs spotted with white and dark brown. Original tail banded with 10 regular dark brown to blackish crossbars edged with black posteriorly, each followed by a narrow band of white. Venter pale whitish pink; underside of tail mottled and spotted with white and brown.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Nasorostrals separated by a single granular scale in four (of 75) specimens examined. Scales between nasals and eye 10–13, from eye to ear 15–22. Mental from as long to twice as long as broad; one postmental in 18 of 70 specimens. Supralabials 7–10. Infralabials 6–9. Postmentals usually two, but occasionally 1 or 3 (18 and 2 of 72

examined, respectively). Midbody scale rows 88–106. 0–11 enlarged inferomedian scales under the fourth toe. Precloacal pores in males 8–12 (mostly 9–11) often with a median gap; females lacking pores, although exhibiting a row of somewhat enlarged scales in this position. Original tails 50.0–55.5% of total length. Supracaudal scales in 6–7 (rarely 8) rows per tail whorl. 44.7% of specimens have regenerated tails (n=76).

Distribution. Isolated populations are found on the Soutpansberg, Blouberg and Matlala inselberg, Limpopo Province (Fig. 6).

Natural history. The species is nocturnal. It frequents crevices and fissures between rocks as well as under flakes on Waterberg sandstone outcrops, although the Matlala population occurs on granites. May be solitary or can occur in small (presumably family) groups in Soutpansberg Mountain Bushveld (SVcb 21) and Soutpansberg Summit Sourveld (GM 28) (Mucina & Rutherford 2006) at elevations of 1000–1700 m a.s.l.

Two eggs at a time are laid during midsummer. The eggs adhere to the roof of the crevice before hardening. Communal nesting has been observed in the Soutpansberg where more than 20 eggs have been found under a rock.

Remarks. *Afroedura broadleyi* **sp. nov.** shares a suite of characters with *A. langi* and four other species described herein as new. In comparison with other members of this group it differs most obviously in male precloacal pore counts, being much lower than *A. leoloensis* **sp. nov.** and having non-overlapping pore ranges with *A. langi*, *A. pienaari* **sp. nov.** and *A. granitica* **sp. nov.** (more pores) and *A. waterbergensis* **sp. nov.** (fewer pores). In addition it is substantially larger than *A. leoloensis* **sp. nov.**, *A. langi*, and *A. waterbergensis* **sp. nov.** (see Table 4).

Three populations are known, each of which appears to differ slightly from the others. However, there is significant overlap in morphological features and Jacobsen's (1990, 1992a) initial recognition of two putative species ('Soutpansberg' and 'Matlala') cannot be substantiated given available data. Unfortunately, molecular data were available only from Soutpansberg samples. The Soutpansberg form is separated from the others by *A. pienaari* along the Waterpoort Gap, whereas those from Matlala are separated by 70 km from the nearest other population (on the Blouberg). The Matlala and Blouberg forms have the precloacal pores in a continuous row, only exceptionally subdivided by a poreless scale, as is frequently the case in Soutpansberg populations. Precloacal pores on Matlala and in the Blouberg are mostly eight, nine or 10 and on the Soutpansberg nine, 11 or 12. Individuals from the eastern Blouberg tend to be smaller and have a mean midbody scale count of 91.46 ± 2.37 (n = 13), which is considerably lower than that from Soutpansberg individuals— 96.91 ± 4.32 (n = 22), western Blouberg— 97.73 ± 3.49 (n = 15) and Matlala— 99.5 ± 4.19 (n = 18).

Afroedura waterbergensis **sp. nov.**

(Fig. 11A)

Afroedura langi 'Waterberg' Jacobsen 1990, 1992a, 1997

Holotype. TM 81266, adult female, Farm Waterval 601LQ, 23°53' S, 27°39' E, Waterberg District (2327DC), Limpopo Province, collectors N. H. G. Jacobsen & R. E. Newbery, 20 January 1987.

Paratypes. TM 81267, 81269, 81273, Farm Fancy 556LQ, Waterberg District, Limpopo Province (2327DC), collectors N. H. G. Jacobsen & R. E. Newbery, 22 January 1987. TM 81268, 81270, Farm Fourieskloof 557LQ, Waterberg District, Limpopo Province (2327DC), collector R. E. Newbery, 26 September 1979; TM 81271–81272, same data as for holotype.

Etymology. The specific epithet refers to the Waterberg massif, Limpopo Province, to which the species is endemic.

Diagnosis. A small *Afroedura* (maximum SVL 46 mm) differing from all other congeners by the following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail moderately verticillate (semi-verticillate) and flattened near base, with four subcaudal rows and 7 supracaudal rows per verticil; dorsal scales smooth, 92–99 scale rows at midbody; internasal scales absent; 4–7 precloacal pores in males.

Description. (based on holotype TM 81266) Adult female, SVL 44.0 mm; TailL 53.0 mm; mass before preservation 2.2 g. A small to medium-sized, dorsoventrally depressed gecko. Head oval, neck thick, almost as wide as head. Rostral approximately 2.5 times wider than high; nostril pierced between rostral, first supralabial and three nasals; nasorostrals large and in contact behind rostral. Scales on snout rounded but not flattened, decreasing

in size posteriorly to crown of head; 9–10 granular scales between nasals and eye and 18 from eye to ear; 3–4 supraciliary spines; supralabials 11. Mental longer than broad and not wedge-shaped; postmentals two; infralabials nine.

Dorsal scales smooth, juxtaposed, uniform and rounded, becoming larger and oblique laterally. Midbody scales in 101 rows. Ventral scales hexagonal to rounded, smooth and juxtaposed. Hindlimbs robust, feet moderately enlarged. Digits with two pairs of enlarged scancers and 4th toe with six enlarged inferomedian scales. Precloacal pores absent. Tail semi-verticillate, flattened and tapered, constricted at base and widening at the beginning of the first verticil. Caudal scales arranged in verticils with seven dorsal and four ventral rows. Supracaudals subimbricate, more or less square with a rounded posterior margin; subcaudals imbricate wider than or as wide as long. Two postcloacal spurs on either side of tail base.

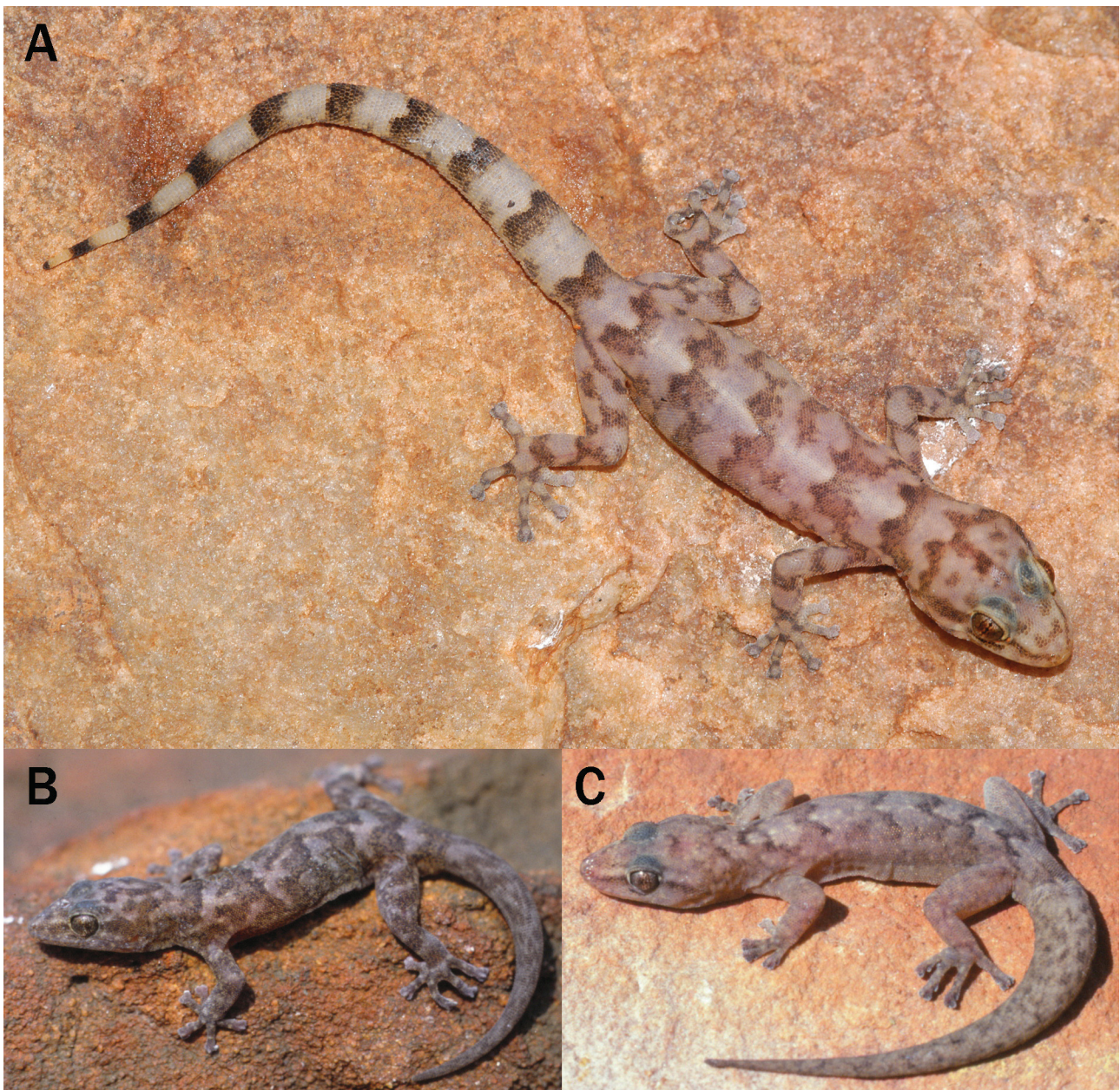


FIGURE 11. New species in the *Afroedura langi* group. (A) *Afroedura waterbergensis* **sp. nov.** from Farm Fancy, Limpopo Province, South Africa (Photo Marius Burger). (B) *Afroedura pienaari* **sp. nov.** from northern Kruger National Park, Limpopo Province, South Africa (Photo N.H.G. Jacobsen). (C). *Afroedura pienaari* **sp. nov.** from Farm Bristol, Waterpoort, Limpopo Province, South Africa (Photo N.H.G. Jacobsen).

Color. Brown to pale brown above with 6–7 wavy dark brown to blackish crossbands extending from the occiput to the sacrum. Posterior margin of crossbands darker and with white spots in indentations. A vertebral row

of white spots is most pronounced. Crown of head marbled with dark brown and a dark brown stripe extending from the nostril through the eye, merging into the occipital crossbar. Limbs striped with dark brown, with interstices spotted and a reticulate pattern on the thighs. Venter white to whitish pink. Tail with seven crossbands at regular intervals. Underside of tail brown with incomplete pale crossbars.

Variation. Paratypes and other specimens agree with the holotype in most features of scalation (Table 4). Scales from eye to ear 16–18. Mental in some specimens only as long as wide. Supralabials 8–11. Infralabials 7–9. Midbody scale rows 92–99. Eight enlarged inferomedian scales under 4th toe in TM 81272. Precloacal pores in males in continuous series of 4–7. 0–3 postcloacal spurs on either side of tail base. Original tails 50.0–56.4% of total length. Supracaudal scales in 6–7 (rarely 8) rows per tail whorl. 33% of specimens have regenerated tails (n=6).

Distribution. Endemic to the western Waterberg massif, Limpopo Province (Fig. 6).

Natural history. *Afroedura waterbergensis* **sp. nov.** is a rupicolous gecko found in crevices between rocks on rocky outcrops and cliff faces of Waterberg sandstone. It inhabits both vertical and horizontal dry crevices. It has only been observed in Waterberg Mountain Bushveld (SVcb 17) (Mucina & Rutherford 2006) at an elevation of 1000 m a.s.l.

Remarks. *Afroedura waterbergensis* **sp. nov.** is the westernmost member of its genus in Limpopo Province. It may be more widespread along the Waterberg than the current records indicate. It is a member of the *A. langi* complex and may be easily distinguished from all other members of this clade on the basis of its low number of precloacal pores (see Table 4).

Afroedura pienaari **sp. nov.**

(Figs. 11B–C)

Afroedura pondolia subsp. nov. Pienaar *et al.* 1983

Afroedura langi 'Waterpoort' Jacobsen 1992a, 1997; Kirchhof *et al.* 2010

Afroedura langi 'Tshipise' Jacobsen 1992a, 1997

Afroedura langi 'Shinokwen' Jacobsen 1992a, 1997

Holotype. TM 81144, adult male, Farm Bristol 760MS, 22°59' S, 29°37' E, Soutpansberg District (2229DC), Limpopo Province, Republic of South Africa, collector R. E. Newbery, 25 July 1981.

Paratypes. TM 81133–81139, 81141–81143, 81145–81146, 81160–81165, same data as holotype; TM 81140, same locality as holotype, collector N. H. G. Jacobsen, 2 February 1979; TM 81175, Farm Crimea 747MS, Soutpansberg District, Limpopo Province (2229DC), collector N. H. G. Jacobsen, 1 February 1979; TM 81147–81153, Farm Robertson 748MS, Soutpansberg District, Limpopo Province (2229DC), collector R. E. Newbery, 24 July 1981; TM 81167–81169, Farm Waterpoort 695MS, Soutpansberg District, Limpopo Province (2229DC), collector R. E. Newbery, 24 July 1981; TM 81170–81173, Farm The Moss 763MS, Soutpansberg District, Limpopo Province (2229DC), collector R. E. Newbery, 7 November 1985.

Additional material examined (all from Limpopo Province). TM 81154–81157, 81174, Farm Zoutpan 459MS, Soutpansberg District (2229CD); TM 81107, Musekwas location 194MT, Dzanani District (2230CC); TM 81103–81104, 81106, 81111 Gumela, Sibasa District (2230CB) TM 81102, 81105, 81110, Lavhalisa, Dzanani District (2230CA); TM 30414, 35 km southwest of Tshipise, Soutpansberg District (2229DD); TM 81342, Vhuswintzhe, Dzanani District (2230CC); TM 81101, 81108–81109, near Shinokwenfontein, KNP (2231AC); TM 77353–77355, Bobomeni, KNP (2231BC); TM 77356–77360, Mashipange, KNP (2230DB); TM 77336–77345, 3 km W of Baobab Hill, KNP (2231AC); TM 77329–77335 Pafuri border gate, KNP (2231AC); TM 77346–77352, 5 km NW of Hutwini, KNP (2231AC); TM 77361–77362, 77363–77367, Madziringwe stream, S of the Trails Camp, KNP (2231CA); TM 77368–77372 Nyala Drive, 4 km W of Bobomeni, KNP (2231AC); TM 77309–77304, Shipudza Spring, KNP (2231CA); TM 77315, 77318–77323, Shidzivani, KNP (2231CA); TM 77324–77328, Xantangalani, KNP (2231CA); TM 47314 Vivo area, Soutpansberg District (2329AB); TM 81129–81132 Farm Calitzdorp 221LS, Soutpansberg District (2329BA).

Etymology. The species is named for the late Dr. U. de V. Pienaar (1930–2011), former Chief Warden of Kruger National Park and former Chief Director of South African National Parks, in recognition of his work in furthering herpetofaunal knowledge of the Kruger National Park.

Diagnosis. A medium-sized *Afroedura* (maximum SVL 53 mm) differing from all other congeners by the

following combination of characters: two pairs of enlarged subdigital lamellae per digit; tail faintly verticillate and flattened near base, with four subcaudal rows and 6–7 supracaudal rows per verticil; dorsal scales smooth, 86–111 scale rows at midbody; internasal scales absent; 13–19 precloacal pores in males.

Description. (based on holotype TM 81144) Adult male; SVL 48.0 mm; TailL 57.0 mm; mass before preservation 2.2 g. A medium sized, dorsoventrally depressed *Afroedura*, with a flat, ovate head, wider than the neck. Rostral 2.5 times wider than high; nostrils pierced between rostral, first upper labial and three nasal scales; nasorostrals raised and in broad contact behind rostral. Scales on snout variable, large and flattened, decreasing in size posteriorly, to being smallest on the crown of the head; 10 scales between nasals and eye and 16 between eye and ear; four supraciliary spines above eye; supralabials nine. Mental wedge-shaped, longer than wide; one postmental. Infralabials seven.

Dorsal scales uniform, rounded, juxtaposed and flattened paravertebrally, becoming larger and oblique laterally. Midbody scales in 93 rows. Ventral scales flat, smooth, imbricate and irregular to hexagonal. Limbs robust; two pairs of enlarged scansors under each digit and four inferomedian scales under 4th toe. Precloacal pores 18, arranged in a shallow ‘V’-shape, with a single median poreless scale interrupting the series. Tail faintly verticillate, widening slightly posterior to the cloaca before tapering. Caudal verticils with seven dorsal and four ventral scale rows. Supracaudals almost square to slightly longer than broad, with a rounded to apical posterior margin; subcaudals almost square with a rounded posterior margin and imbricate; three post cloacal spurs at base of tail.

Color. Gray-brown to brown dorsally with 6–7 irregular dark brown to blackish crossbars occasionally bordered posteriorly by a black edge, followed by a white marking, the latter sometimes evident only as a median spot. Dorsum variegated and mottled with brownish black and off-white. Head mottled dorsally; a dark stripe extending from the nostrils through the eye to the rear of the head, linking to the second crossbar in the neck region. Limbs brownish with pale and dark spotting and marbling. Original tail with 8–13 crossbars, with interstitial areas spotted or marbled. Venter whitish to pinkish mesially.

Variation. There is significant variation in specimens of this species in several features (Tables 4, 5), in part reflecting the very large sample size and its relatively large geographic range. A single internasal is present in TM 81142. 10–14 scales between nasals and eye and 16–22 between eye and ear, 2–4 supraciliary spines. Supralabials 8–12. One or two postmental scales present. Infralabials 7–9. Midbody scale rows 86–98 in type series, up to 111 in other specimens examined. 3–7 enlarged inferomedian scales under 4th toe. Precloacal pores in male paratypes in continuous or interrupted series of 14–18 (12 to 19 in other specimens examined, although 96% of all male specimens have at least 14 pores); no precloacal pores in females. 0–4 postcloacal spurs on either side of tail base. Original tails 50.0–58.4% of total length. 32.2% of specimens have regenerated tails (n=31).

Distribution. Recorded from along the northern Soutpansberg and into the northwestern Kruger National Park, Limpopo Province (Fig. 6). Kirchof *et al.* (2010) reported this species from Lajuma, on the southwestern Soutpansberg, in an area that would be expected to harbour *A. broadleyi*, however, their specimens had the typical precloacal pore counts of *A. pienaari* and on this basis we accept their identification.

Natural history. *Afroedura pienaari* **sp. nov.** is a nocturnal, rupicolous gecko that inhabits crevices and fissures in and between boulders on rocky outcrops and under flakes of exfoliating rock beneath overhangs. It appears to be mostly solitary, but is occasionally found in pairs and rarely three individuals may occupy the same crevice. Found on north and south-facing slopes in Makhuleke Sandy Bushveld (SVI 1), Limpopo Ridge Bushveld (SVmp 2), Soutpansberg Mountain Bushveld (SVcb 21) and Soutpansberg Summit Sourveld (GM 28) (Mucina & Rutherford 2006) at elevations of 800–1200 m a.s.l. Kirchof *et al.* (2010) reported this species from cracks and fissures in vertical rock walls and from caves and found several individuals in an electrical junction box.

Two soft shelled eggs are laid at a time. These are placed on the undersides of rocks, to which they adhere and then harden. Communal nesting takes place in favorable crevices.

Remarks. Jacobsen (1990, 1992a) initially considered each of three discrete populations of this gecko to represent putative species. The western and eastern forms are similar in size but are separated by smaller geckos, with generally lower scale counts, in the central part of the range (Table 5). Genetic divergences between populations of *Afroedura pienaari* **sp. nov.** are also pronounced (Fig. 1). However, further sampling may reveal continuity between populations and existing populational differences in morphological features are largely overlapping, so we here treat all of the northern Soutpansberg/Limpopo Valley *A. langi* complex geckos as a single species.

TABLE 5. Morphological parameters of three populations of *A. pienaar* **sp. nov.** Ranges and means ± 1 S.D. given for most characters, ranges only for caudal verticils, maximums and means ± 1 S.D. for SVLs. Specimens > 34.5 mm SVL were considered adults.

	Waterpoort	Tshipise	KNP
Midbody scales	n = 31 86–107 93.9 \pm 4.71	n = 9 86–102 90.67 \pm 4.8	n = 66 86–111 96.44 \pm 5.29
Eye–Ear scales	n = 33 13–19 16.58 \pm 1.15	n = 9 15–17 15.78 \pm 0.67	n = 62 13–19 16.05 \pm 1.45
Supralabials	n = 38 8–12 9.6 \pm 0.8	n = 10 8–10 9.4 \pm 0.7	n = 59 8–11 9.6 \pm 0.81
Infralabials	n = 42 7–10 8.21 \pm 0.68	n = 10 7–9 7.7 \pm 0.67	n = 62 6–10 8.02 \pm 0.78
Caudal verticils (supracaudals/subcaudals)	7/4–5	6–8/4	6–7/4
Precloacal Pores	n = 16 14–19 16.94 \pm 1.53	n = 7 12–15 14.14 \pm 1.21	n = 27 14–19 16.89 \pm 1.40
Adult male SVL (mm)	n = 16 51.0 44.56 \pm 3.08	n = 5 42.5 39.60 \pm 2.16	n = 27 48.0 43.96 \pm 2.61
Adult female SVL (mm)	n = 16 52.0 47.12 \pm 3.72	n = 2 39.0 34.5 \pm 6.36	n = 31 53.0 44.47 \pm 4.76

This species may be distinguished from the geographically proximate *A. broadleyi* **sp. nov.** and from *A. waterbergensis* **sp. nov.** by its greater number of precloacal pores and from *A. leoloensis* **sp. nov.** by its lower number of pores. In addition, it is substantially larger than *A. leoloensis* **sp. nov.**, *A. langi*, and *A. waterbergensis* **sp. nov.** (see Table 4) and has a significantly greater number of supralabials than *A. langi* ($P < 0.001$, t134 d.f.) and more scales from the eye to ear than *A. broadleyi* **sp. nov.** and *A. langi* ($p < 0.001$, t172 d.f. and $p < 0.001$, t127 d.f., respectively). This species has largely overlapping scale counts with *A. granitica* **sp. nov.**, which is larger (58 versus 53 mm maximum SVL and even greater mean differences; Table 4). The great majority of male specimens, however, have 14 or more precloacal pores (up to 19), averaging more than 16, whereas *A. granitica* **sp. nov.** has a mean of only 14 pores. *Afroedura pienaar* **sp. nov.** also has fewer eye to ear scales than *A. granitica* **sp. nov.**, although not statistically so.

Key to the species of *Afroedura* occurring in northeastern South Africa

(Limpopo, Mpumalanga, and Zululand [northern KwaZulu-Natal Province], Zimbabwe, Mozambique, and Swaziland)

[Note: The extreme morphological conservatism within some species groups can make identification difficult, particularly for juveniles or females. As most species are allopatric, distributions are provided as a useful adjunct to confirm identity.]

1. Original tail flattened and strongly verticillate. 2
Original tail rounded or weakly flattened, not or faintly verticillate 3
2. Rostral in contact with nostril, SVL to > 70 mm *A. transvaalica*
[Zimbabwe, Limpopo River Valley in Limpopo Province]
Rostral excluded from nostril, SVL < 60 mm. *A. loveridgei*
[Tete region of Mozambique]
3. Dorsal scales trihedral to keeled 4
Dorsal scales smooth, rounded to flattened. 7

4.	Eight supracaudal scales per verticil; to 76 mm SVL; precloacal pores in males 18–19	<i>A. major</i>	
	[Swaziland]		
	6–7 supracaudal scales per verticil; < 66 mm SVL; precloacal pores in males < 17 or > 20	5	
5.	Precloacal pores in males 16–17; to 66 mm SVL	<i>A. multiporis</i>	
	[Haenertsburg and Wolkberg areas of central Limpopo]		
	Precloacal pores in males > 20; ≤ 62 mm SVL	6	
6.	Precloacal pores in males usually 20–26 (mean ~22); to 62 mm SVL	<i>A. rupestris</i> sp. nov.	
	[Eastern Escarpment of Limpopo between Abel Erasmus Pass and Bourke’s Luck]		
	Precloacal pores in males 23–28 (mean ~26); adults to 52 mm SVL	<i>A. haackei</i>	
	[southern Mpumalanga Lowveld]		
7.	Internasal present	8	
	Internasal absent (rarely present)	11	
8.	Adults > 50 mm SVL	9	
	Adults ≤ 40 mm SVL	10	
9.	Precloacal pores in males 11–13	<i>A. mariipi</i> sp. nov.	
	[Mariepskop and God’s Window, Mpumalanga]		
	Precloacal pores in males 7–9	<i>A. rondavelica</i> sp. nov.	
	[Three Rondavels, Blyde River, southeastern Limpopo]		
10.	Precloacal pores in males 10–14; midbody scale rows 88–99	<i>A. marleyi</i>	
	[Lebombos and coastal plain of Zululand, through Swaziland to southeastern Mpumalanga; possibly in adjacent Mozambique]		
	Precloacal pores in males 21–23; midbody scales 95–103	[Pongola River area, northern KwaZulu-Natal]	
11.	Adults < 41 mm SVL; precloacal pores in males 30–35	<i>A. leoloensis</i> sp. nov.	
	[Steelpoort Valley and Leolo Mountains, south central Limpopo]		
	Adults to 46 mm SVL and larger; precloacal pores in males < 20	12	
12.	Precloacal pores in males ≤ 12, typically 9–11	13	
	Precloacal pores in males 12–19, typically >13	14	
13.	Precloacal pores in males 4–7	<i>A. waterbergensis</i> sp. nov.	
	[Waterberg, western Limpopo]		
	Precloacal pores in males 8–12	<i>A. broadleyi</i> sp. nov.	
	[Matlala Inselberg, Blouberg and southern Soutpansberg in northern Limpopo]		
14.	Nasorostrals form a shallow V behind rostral; to 46 mm SVL	<i>A. langi</i>	
	[Lowveld near Limpopo/Mpumalanga border and adjacent Mozambique]		
	Nasorostrals form a deep V behind rostral; to > 50 mm SVL	15	
15.	To 53 mm SVL; usually 14–19 precloacal pores in males	<i>A. pienaari</i> sp. nov.	
	[Soutpansberg and northern Kruger National Park, Limpopo]		
	To 58 mm SVL; 13–16 precloacal pores in males	<i>A. granitica</i> sp. nov.	
	[Lowveld near Mica, Limpopo]		

Discussion

The molecular phylogeny of *Afroedura* agrees in part with the morphologically derived groupings proposed by Onderstall (1984) and in great measure with the groupings proposed by Jacobsen (1990, 1992a); the latter treating only taxa occurring in the former Transvaal. Onderstall’s (1984) *transvaalica* group, consisting of *A. transvaalica*, *A. loveridgei*, and *A. bogerti* is retrieved with strong support. However, neither Onderstall’s (1984) *pondolia* group nor his *africana* group is monophyletic. This is consistent with Jacobsen’s (1992a) observations that neither of the latter groups are homogeneous. Onderstall’s (1984) *pondolia* group was broken up by Jacobsen (1992a) into an *A. pondolia* complex, an *A. multiporis* complex, and an *A. langi* complex.

The monophyly of the *A. multiporis* complex is strongly supported by our phylogeny, with the Swazi endemic *A. major* as sister to *A. multiporis* + *A. haackei*. Jacobsen’s (1992a) *A. langi* complex, including *A. langi sensu stricto* plus a series of then undescribed taxa from Limpopo and Mpumalanga provinces, is likewise strongly supported. However, the *A. pondolia* complex of Jacobsen (1992a) is polyphyletic. The three new species signalled as belonging to this group by Jacobsen (1992a, 1997) do indeed form part of a clade (inclusion of the genetically unsampled *A. rondavelica* **sp. nov.** is presumed, based on morphological characters), the *A. marleyi* group, which is weakly supported as sister to the *A. langi* complex.

Afroedura pondolia itself, however, is very distantly related to the taxa occurring in the former Transvaal and receives strong support as the sister of *A. nivaria* and as part of a more extensive clade of southeastern species (chiefly Eastern Cape Province, Free State and KwaZulu-Natal), which we refer to here as the *A. nivaria* clade. Our results are fully consistent with those independently obtained by Makhubo *et al.* (2011) and Makhubo (2013), who,

focusing on relationships in the *Afroedura nivaria* complex, recovered the same pattern of relationships for *A. pondolia*.

Onderstall's (1984) *africana* group had no Transvaal taxa and was not discussed by Jacobsen (1992a). It is also polyphyletic, including the remaining members of the southeastern (*A. nivaria*) clade (*A. nivaria*, *A. amatolica*, *A. tembulica*, *A. halli*) as well as *A. karroica* and *A. africana*, which we recover as sister taxa to one another, albeit without support.

The major clades of *Afroedura* are largely geographically coherent. Together the *A. langi*, *A. marleyi*, and *A. multiporis* groups occupy the area from Zululand north through Swaziland, Mpumalanga, Limpopo, and southern Mozambique. The *A. transvaalica* group is an essentially tropical clade, with *A. bogerti* being highly disjunct from the other members in southeastern Africa. The *A. africana* group as here defined is a western clade, with *A. africana* and its former subspecies ranging from central Namibia to Namaqualand as sister to *A. karroica*, the westernmost of the remaining species, occupying the Karoo of the western Eastern Cape and adjacent regions. Finally, the *A. nivaria* clade includes remaining taxa occurring in Lesotho, the Free State, the Eastern Cape, and KwaZulu-Natal south of Zululand.

Although not entirely congruent with each other, the areas of endemism of the northeastern *Afroedura* are broadly similar to those occupied by other taxa of rupicolous lizards, including *Platysaurus* Smith (Broadley 1978; Jacobsen & Newbery 1989; Jacobsen 1994a; Scott *et al.* 2004), *Lygodactylus* (Jacobsen 1992b, 1994b; Travers 2012), and, on a more limited scale, *Smaug* Stanley, Bauer, Jackman, Branch & Mouton (Stanley & Bates, in press). These distributions suggest that common cladogenic events may have been associated with the evolution of all of these groups. The movement of Kalahari sands in the Plio-Pleistocene has been suggested to play a role in speciation via isolation by Aeolian sands in some lizard groups in southern Africa (Broadley 1978; Jacobsen 1994a), although more recently, older events, chiefly in the Miocene, have been implicated in lineage splitting in cordylids (Scott *et al.* 2004) and geckos (Bauer & Lamb 2002; Broadley *et al.*, in press). This was a period of changing geological (Thomas & Shaw 1993; Partridge & Maud 2000) and climatic conditions (Tyson 1986; van Zinderen Bakker & Mercer 1986; Coetzee 1993; Tyson & Partridge 2000). Uplift of the Great Escarpment continued through the middle to late Tertiary (Thomas & Shaw 1993; Partridge & Maud 2000), providing possible opportunities for vicariance both above and below the Escarpment and along its length.

As has been argued for other geckos (Bauer 2000 [1999]), *Afroedura* species are generally substrate specialists and their distribution has been linked to the availability of particular substrate types (Onderstall 1984). With the exception of *A. marleyi* and *A. loveridgei* which are partially arboreal, most species require rocky substrates with adequate fissures, crevices, overhangs, cliffs and caves, although some species are able to utilize smaller scattered outcrops and even human dwellings. Most taxa inhabit granites, sandstones and quartzitic sandstone but some are found on dolerites and rhyolites which provide similar habitats. Only *A. langi* is known to inhabit schistose outcrops. Restriction to specific rock types increases the likelihood that events such as erosion during pluvial periods would have generated effective barriers to movement and thus genetic continuity among *Afroedura* populations.

The absence of *Afroedura* in most of central inland southern Africa and in the southern Cape Fold Mountains is certainly not due to a lack of suitable substrates (Onderstall 1984), but may indicate that historic barriers prevented movement inland and/or that geological and/or climatic events since the initial diversification of the genus have resulted in the extinction of lineages that once occupied these areas. The isolation of *A. hawequensis* in the southwestern Cape and the highly disjunct distribution of the members of the *A. africana* and *A. transvaalica* groups remain especially puzzling. Alternatively it has been suggested (Branch & Bauer 1997) that other rupicolous leaf-toed geckos of the genera *Goggia* and *Afrogecko*, which have distributions largely complementary to *Afroedura*, may exclude the occurrence of the latter through competition or other biotic mechanisms.

The description of nine additional taxa, and the elevation of three non-nominate subspecies to specific rank raises the total number of species within the genus to 27. These taxa can be placed into seven clades based on our genetic data and these are here recognized as species groups diagnosed on the basis of combinations of characters discussed by Onderstall (1984), Mouton & Mostert (1985) and Jacobsen (1990, 1992a, 1997). Several additional taxa have been signalled (Jacobsen 1992a, 1997; Makhubo 2013), particularly in the *A. nivaria* clade, but require further study and, in some cases, additional material before they can be formalized.

Sixteen species of *Afroedura* occur in the former Transvaal (Limpopo and Mpumalanga provinces) and adjacent areas of northeastern southern Africa, from Zululand north to the Zambezi River. Prior to the description

of the species in this paper, only *A. langi*, *A. multiporis*, *A. haackei*, and peripherally *A. transvaalica* and *A. marleyi* had been known from Limpopo and Mpumalanga themselves. Although the species described herein were known to South African workers since first being identified by Jacobsen (1990, 1992a), without formal description, they have been omitted from most faunal works (e.g., Branch 1998; Bates *et al.* 2014). This has resulted in an artificial underestimation of the true diversity of the genus in northeastern South Africa. As nearly all of the new species have highly restricted ranges it is likely that the conservation status of some will be in the higher threat categories following IUCN assessment criteria.

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APPENDIX. Comparative specimens examined.

- Afroedura haackei* (16 specimens): MPUMALANGA: TM 77390–77392, Farm Broedershoek 129JU (2531AC); TM 77383–77384, Luphisi (2531AD); TM 77385, 77389, Khandizwe, KNP (2531AD); TM 39539–39541, 47806, Farm Rhenosterkop 195JU (2531CA); TM 77393, Eureka City (2531CA); TM 77394, Farm De Hoop 203JU (2531CA); TM 77386, Farm Naude's Rust 272JU (2531CB); TM 77387–77388, Farm Excelsior 211JU (2531CB).
- Afroedura langi* (32 specimens): LIMPOPO: TM 76595, 76604–76605, Farm Harmony 140KT (2430BA); TM 29877–29879, Olifants River Estates (2430BC); TM 12850, 13085, 13134–13135, 29848–298453, 29855–29859, 29862–29863, Farm Venice 40KU (2431AA); TM 76592, Farm Copenhagen 58KU (2431AA); TM 76606–76607, Hlaralumi River, KNP border (2431AB); TM 76608, Tseri River, KNP (2431AB); MPUMALANGA: TM 76593–76594, Mashatumond, KNP (2431BA); NKW 381 Nkomichi mouth, KNP (2431BA).
- Afroedura major* (18 specimens): SWAZILAND: TM 47265, Komati Bridge (2631AA); TM 41947–41949, Black Umbeluzi Falls (2631AC); TM 42530, 42671–42672, 47116, 49642, 50316, Matenga Falls (2631AC); TM 47006, 48170, east slope of Madimba Plateau (2631AC); TM 69334–69335, 78926, Nkomati Gorge.
- Afroedura marleyi* (30 specimens): MPUMALANGA: TM 55699, Komatipoort Border Post (2531BD); TM 57434, Farm The Hippos 192JU (2531BD); TM 81274–81279, Farm Duikerhoek 489JU (2531DB); TM 81280–81281, Mananga (2531DD); TM 81282–81287, Halfkroonspruitmond, KNP (2531BD); KWAZULU–NATAL: TM 62822, Mkuze Game Reserve (2732CA); TM 13184, (Holotype), 21811–21812, False Bay (2732CD); TM 64531–64532, Lister's Point False Bay (2732CD); TM 40064, 42854, 42869, Sodwana Bay (2732DA); TM 42527, Ubombo (2732CA); TM 67668, Ndlozi Peninsula, Lake St Lucia (2832AB); SWAZILAND: TM 47709, Siteki (2631BD); TM 54751, Mlawula Estates (2631BD); TM 55528, Mbuluzi Estates (2631BB).
- Afroedura multiporis* (12 specimens): LIMPOPO: TM 3420, Farm Clearwaters, Haenertsburg (2329DD); TM 77373–77382, Farm Acre 2KT (2430AA); TM 66289, Haenertsburg (2329DD).
- Afroedura pondolia* (20 specimens): EASTERN CAPE: PEM 4897a (holotype), 4897b (paratype), Mbotyi River mouth, Lusikisiki; TM 26645, 69323–69324, 69326–69327, Port St. Johns (3129DA); TM 76520, Silaka Nature Reserve (3129DA); TM 69607–69608, 69611, 69617, Haven Hotel, Gatyana District (3228BD); KWAZULU–NATAL: TM 62728, Stainbank Nature Reserve, Durban (2930DD); TM 53886, Warner Beach, Durban (3030BB); TM 55564, near eastern boundary of Umtamvuna Nature Reserve (3030BC); TM 55175, Oribi Gorge Nature Reserve (3030CB); TM 34750, Ramsgate (3030CD); TM 79357, Mbumbazi Nature Reserve (3030CD). TM 64827, St. Michaels on Sea (3030CD).
- Afroedura transvaalica* (37 specimens): LIMPOPO: TM 55759, 56283–56285, Messina Experimental Farm (2229BD); TM 56290, 56293–56294, Messina Golf Course (2230AC); TM 56291–56292, 56300, 4 km from Messina on Tshipise road (2230AC); TM 56301, Messina (2230AC); TM 57094, Farm Esmefour 29MT (2230AD); TM 3488–3489, 3494, Njelele River (2230AD/CA).