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Taxonomic adjustments in the systematics of the southern African lacertid lizards (Sauria: Lacertidae)

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Abstract

Molecular phylogenetic analyses of southern African lacertid lizards (Eremiadini) using mitochondrial and nuclear markers revealed two examples of generic assignments incompatible with monophyletic clades. *Australolacerta* Arnold 1989, a genus endemic to South Africa and to which two isolated species have been referred, is paraphyletic at the generic level. In addition, the species *Ichnotropis squamulosa* Peters 1854 was found to be embedded within the genus *Meroles.* To resolve the paraphyly in *Australolacerta* we erect a new genus, *Vhembelacerta* Edwards, Branch, Herrel, Vanhooydonck, Measey, & Tolley, **gen. nov.**, to accommodate *Lacerta rupicola* FitzSimons 1933. To maintain a monophyletic *Ichnotropis* Peters 1854, *Ichnotropis squamulosa* Peters 1854 is transferred to *Meroles* Gray 1838, now named *Meroles squamulosus* **comb. nov.** Where necessary the genera affected by these actions are re-characterized.

Key words: Lacertidae, Eremiadini, *Ichnotropis squamulosa*, *Australolacerta,* paraphyly, mitochondrial and nuclear DNA

Introduction

Lacertids are a diverse group of lizards, ubiquitous throughout much of the Old World and occur in a wide variety of habitats; e.g. high mountain tundra, heath lands, Mediterranean scrub, tropical forest, semi-desert and desert (FitzSimons 1943; Arnold 1989; Branch 1998). However, they have an unusual distribution, with only a limited penetration into south-east Asia, and are absent from Australia and Oceania. Lacertids are also absent from Madagascar but occur throughout mainland Africa, with high regional endemism at both genus and species level (Branch 1998; Spawls *et al.* 2002). Although diverse lacertid faunas occur in southern Africa (at least 8 genera and 37 species; Branch 1998; Conradie *et al.* 2012) and eastern Africa (10 genera, 19 species; Spawls *et al.* 2002; Greenbaum *et al.* 2011), only three species (*Nucras ornata* (Gray 1864)*, Ichnotropis capensis* (Smith 1838) and *I. squamulosa* Peters 1854) occur in both regions and then only marginally, with the southern African species just entering the southern parts of East Africa.

Early classification of lacertids, as with that of most organisms, relied almost exclusively on morphological characteristics, occasionally supplemented with other types of biological data. Phylogenetic hypotheses of lacertid

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relationships were originally based on morphology, and Arnold (1986; 1989) presented a generic level phylogeny which recognised two Afrotropical groups: a South African clade containing *Tropidosaura* Fitzinger 1826, *Pedioplanis* Fitzinger 1843, *Meroles* Gray 1838 and *Ichnotropis* Peters 1854; and another comprising *Nucras* Gray 1838 and a subclade consisting of *Latastia* Bedriaga 1884, *Heliobolus* Fitzinger 1843 and *Philochortus* Matschie 1893, referred to as the Northeast African group.

The use of molecular phylogenetics as a tool for systematics has revealed some surprising relationships for lizards, which are often incongruent with taxonomy based on morphological characters (e.g. lack of genetic distinction between morphologically different agamids: *Agama agama* and *A. finchi*; Leaché *et al*. 2009; *Agama boueti* and *A. castroviejoi*; Gonçalves *et al*. 2012). Morphological traits can be labile, and the phenotype may be influenced by factors such as microhabitat and environment (e.g. Vanhooydonck & Van Damme 1999; Herrel *et al.* 2002; Revell *et al.* 2007; Barros *et al.* 2011; Hopkins & Tolley 2011; Edwards *et al.* 2012; Herrel *et al*. 2013), dietary preferences (e.g. Measey *et al.* 2009), sexual selective pressures (Herrel *et al.* 2011), or a combination of these factors. If a particular environment places a selective pressure on a lizard to evolve a specific trait, then lizards living in similar environments may evolve convergent phenotypes (e.g. Revell *et al.* 2007; Edwards *et al*. 2012), confounding taxonomy. Arnold (1991) investigated why phylogenies based on morphology varied considerably in quality, based (in part) on what he considered to be a "robust and explicit morphological phylogeny" for *Meroles* and a poorly-supported morphological phylogeny for *Pedioplanis*. He found the former to most likely result from exposure to different ecological conditions, resulting in pectinate phylogenies or what is often termed an 'adaptive radiation'. In *Meroles* this was postulated to reflect the increasing acquisition of morphological synapomorphies in species inhabiting increasingly more aeolian habitats.

To ensure that systematics and taxonomy reflect evolutionary history, molecular phylogenies are routinely used as a guide. Recent molecular studies have indicated primary divisions within the Lacertidae, although there has been debate as to the taxonomic hierarchy assigned to the divisions. Harris *et al.* (1998) divided the family into three subfamilies: Gallotiinae, Eremiainae and Lacertinae, but it now seems more appropriate to recognize Gallotiinae as a clade sister to Lacertinae. The latter contains the tribes Eremiadini Szczerbak 1975 and Lacertini Oppel 1811 (Arnold *et al.* 2007; Kapli *et al.* 2011; Salvi *et al.* 2011), of which only the Eremiadini occurs in sub-Saharan Africa.

Various phylogenies, based on molecular markers, have generally agreed on relationships between southern African lacertid genera within Eremiadini (Mayer & Pavlicev 2007; Hipsley *et al.* 2010; Kapli *et al.* 2011), and Salvi *et al.* (2011) showed a sister-group relationship within the Eremiadini of *Australolacerta* Arnold 1989 and *Tropidosaura*. However, these phylogenies used only a few representatives from each genus, and thus interspecific relationships within genera remained largely unknown. To date only phylogenies for the southern African genera *Meroles* (Harris *et al.* 1998; Lamb & Bauer 2003; Edwards *et al*. 2012) and *Pedioplanis* (Makokha *et al.* 2007; Conradie *et al.* 2012) have been investigated. The evolutionary history of both genera, as well as of other lizards in the subcontinent (Lamb *et al.* 2003; Bauer & Lamb 2005), was thought to be driven by habitat changes induced by climate aridification during the Mid-Miocene (Siesser 1978; 1980).

Southern African lacertid lizards inhabit a wide variety of microhabitats, differing in substrate, openness, elevation and inclination (or slope) (Branch, 1998). In instances where unrelated species are convergent in morphology due to occurrence in similar habitats, species may be incorrectly classified. Recent molecular phylogenies using mitochondrial and nuclear markers for southern African lacertid lizards (Eremiadini) revealed two examples of existing generic assignments incompatible with evolutionary history (Edwards *et al.* 2012; Engleder *et al.* 2013). The first was that *Ichnotropis squamulosa*, a species previously not included in higher level phylogenies, grouped within a clade containing nearly all of the described *Meroles*. This species did not group with other *Ichnotropis* previously incorporated in phylogenies, including the type species *I. capensis.* The second was that the two known *Australolacerta* species, *A. australis* Hewitt 1926 and *A. rupicola* FitzSimons 1933, showed high levels of genetic divergence and were paraphyletic with respect to *Tropidosaura, Ichnotropis,* and *Meroles*. These unexpected results were interpreted to be due to convergence in morphology between species from different lineages (Edwards *et al.* 2012). These phylogenetic results have taxonomic consequences. We therefore conducted a re-analysis of evolutionary relationships within southern African lacertids within a taxonomic framework.

Material and methods

Sampling and laboratory protocols. We obtained complete genus level taxon sampling of southern African Eremiadini (*Meroles*, *Australolacerta*, *Pedioplanis*, *Tropidosaura*, *Ichnotropis, Nucras* and *Heliobolus*), which included complete sampling for *Australolacerta*, and near complete species level taxon sampling for *Meroles*. In order to re-investigate the phylogenetic relationships of all southern African lacertid lizard taxonomic groups, individuals used in Edwards *et al.* (2012) were included and additional individuals from *Pedioplanis* and *Nucras* (highlighted in grey in Table 1) were sequenced using standard PCR techniques for four genes (mitochondrial: 16S, ND4 and nuclear: RAG1, KIAA2018) as in Edwards *et al.* (2012). Sequences were aligned using Clustal Omega v.1.1.0 (Sievers *et al.* 2011) and checked in BioEdit Sequence Alignment Editor v. 7.0.5.2 (Hall 1999). All sequences have been deposited in EMBL-Bank (see Table 1 for all voucher information, with corresponding EMBL-Bank accession numbers).

Genetic analyses. We first analysed the mitochondrial (16S vs. ND4) and nuclear (RAG1 vs. KIAA2018) datasets separately and then analyzed the combined dataset (nuclear vs. mitochondrial), using a partition homogeneity test (Farris *et al.* 1994; 1995) in PAUP* v4.0b10 (Swofford 2002), to ensure that there was no conflict in the markers within each genome. The saturation of the codon positions was assessed (Dambe v.5.2.65; Xia *et al.* 2003) and the third codon position of the ND4 gene was found to be saturated, so it was coded as a separate partition in the maximum likelihood and Bayesian analyses using nucleotide substitution models (thus five partitions in total:16S, ND4-1, ND4-2, RAG1 and KIAA2018). Individuals from two genera (*Nucras* and *Heliobolus*) were used as outgroup, as they are nested within the sister clade to the southern African lacertids within the Eremiadini (Mayer & Palicev 2007; Kapli *et al.* 2011). Sequence divergences (uncorrected *p*-distances) were determined in MEGA v.4 (Tamura *et al.* 2007).

Phylogenetic trees were constructed based on the combined total evidence dataset using two different algorithms (Figure 1). Bayesian inference (BI; MrBayes v.3.1.0; Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) was performed using the best-fit models of nucleotide substitution for all five gene partitions (Modeltest v.3.6; Posada & Crandall 1998). The best-fit models of nucleotide substitution for all the mitochondrial gene partitions were GTR+I+G and all the nuclear gene partitions were GTR+G, and uniform priors were kept for all other parameters. A second Bayesian inference was performed, using a codon substitution model for all three partitions of coding genes (ND4, RAG1 and KIAA-2018) and the best-fit model of nucleotide substitution (GTR+I+G) for the 16S gene fragment partition. The nucleotide substitution parameters within the codon models were of the 6-rate variety (inferring different rates for all nucleotide pairs, GTR-like), with empirical codon frequencies. The MCMCs were run with 2 parallel runs for 20 x 10^6 generations each, sampling trees every 1000 generations. The number of generations to discard as burn-in was determined by examining the number of generations 1) at which the standard deviation of split frequencies stabilized (at less than 0.001), 2) at which the log-likelihood tree scores reached stationarity, and 3) the effective sample sizes (ESS) of all parameters which were ≥600 (Tracer v.1.5;Rambaut& Drummond 2007). A 50% majority rule tree was constructed with the burn-in excluded using the 'sumt' command in MrBayes, and nodes with ≥0.95 posterior probability values were considered supported. A partitioned maximum likelihood (ML) analysis was also run in RAxML v.7.2.8 (Stamatakis 2006), at the CIPRES Science Gateway (www. phylo.org/sub_sections/portal/) using the same partitions as the Bayesian analysis, a GTR+I+G model of evolution, and automatic halting of bootstrapping (Stamatakis 2006; Stamatakis *et al.* 2008).

Competing phylogenetic hypotheses of monophyly for *Ichnotropis* and *Australolacerta* were investigated using a Shimodaira–Hasegawa (SH) test (Shimodaira & Hasegawa 1999; Goldman *et al*. 2000) and the approximately unbiased (AU) test (Shimodaira, 2002) generating maximum likelihood scores for the trees (1000 replicates) using PAUP* v.4.0b10 (Swofford 2002) and bootstrapping *p* values for the SH and AU tests in Consel (Shimodaira 2002).The Bayesian consensus topology obtained was compared to a topology which constrained 1) *I. squamulosa* to be within *Ichnotropis,* and 2) *Australolacerta australis* and *A. rupicola* as monophyletic.

Results

Phylogenetic trees were obtained using an aligned sequence dataset of a total of 2683 nucleotide base pairs (bp) from the four genes (16S: 515bp, ND4: 678bp, RAG1: 679bp, KIAA: 813bp) for the 64 taxa. The number of variable sites

for each gene were as follows: 16S = 134, ND4 = 434, RAG1 = 357, KIAA = 199 (1076 total variable sites). The topologies of the phylogenetic trees obtained with the additional taxa were similar to the one obtained by Edwards *et al.* (2012), with the trees obtained using the codon- substitution models being the best resolved with the highest node support values (Figure 1). The generic-level polytomy was again found when nucleotide-substitution models were employed. However the polytomy between *Tropidosaura, Ichnotropis, Australolacerta* and *Meroles* was resolved when a codon-substitution model was used. The two examples of conflict with existing classification observed in the earlier study were again recovered within this phylogenetic study: a) *Ichnotropis squamulosa* falls within *Meroles*, not *Ichnotropis*; and b) the two *Australolacerta* species are genetically distinct and do not form a monophyletic clade.

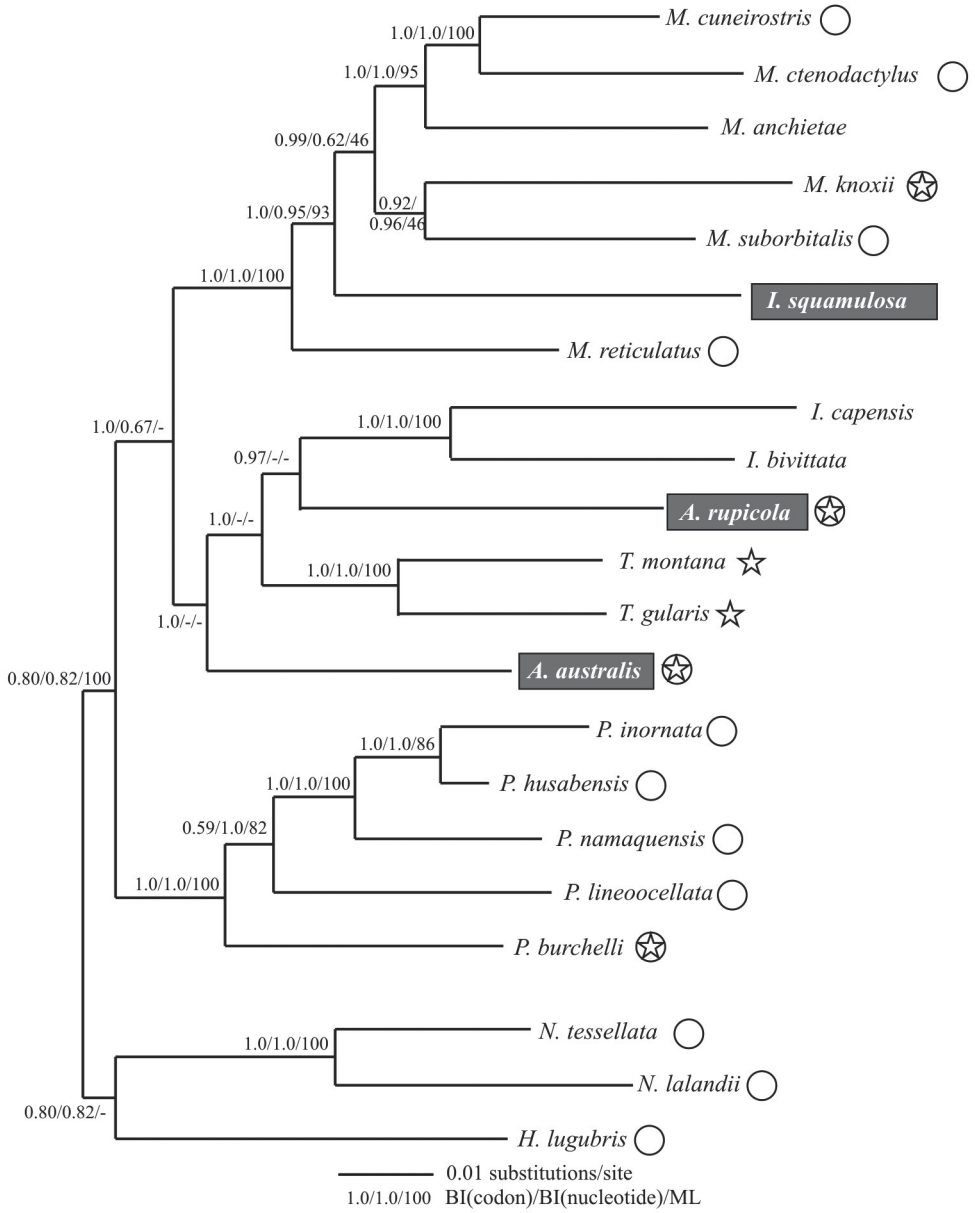

FIGURE 1. Phylogenetic relationships of the southern African clade of lacertid lizards (Lacertidae: Eremiadini) estimated from four mitochondrial and nuclear markers (Bayesian topology estimated using a nucleotide substitution model shown). Nodes that are supported using Bayesian inference (posterior probabilities > 0.95) using nucleotide substitution models and maximum likelihood (bootstrap values >75%) using GTR+I+G nucleotide substitution model are shown at nodes (post. prob. using nucleotide-substitution model/bootstrap value for ML). A dash indicates that the node was not supported for the particular analysis. Species highlighted in grey are those species which are reclassified in this study. Stars next to species names indicate presence of gular fold; circles indicate presence of collar and a star within a circle indicate the presence of both a gular fold and a collar.

TABLE 1. List of specimens used in the phylogenetic analyses with genus and species names, ID numbers, Museum accession ID numbers and EMBL accession numbers for each gene. All sequences listed here were used in Edwards *et al.* (2012), except for those highlighted in grey, which were additional individuals sequenced for this study.

Genus	Species	SANBI Herpbank Accession ID	Museum Accession ID*	EMBL accession (16S)	EMBL accession (ND4)	EMBL accession (RAG1)	EMBL accession (KIAA)
Australolacerta	*australis*	GW08	N/A	HF547772	HF547725	HF547691	HF547651
		MH0531	N/A	DQ871152$	HF547726	DQ871208$	HF547652
Australolacerta	*rupicola*	MCZ38869	MCZ38869	HF547773	HF547727	HF547692	HF547653
		MCZ38874	MCZ38874	HF547774	HF547728	HF547693	HF547654
Heliobolus	*lugubris*	MCZ37870	MCZ37870	DQ871141$	HF547729	DQ871199$	—
		MCZ37894	MCZ37894	DQ871142$	HF547730	DQ871200$	HF547655
Ichnotropis	*bivittata*	KTH09-075	MBUR2074	HF547775	HF547731	HF547694	HF547656
Ichnotropis	*capensis*	AMB6001	N/A	DQ871148$	HF547732	DQ871206$	HF547657
		AMB6067	CAS209602	DQ871149$	HF547733	DQ871207$	HF547658
		WP031	N/A	—	HF547734	HF547695	HF547659
Ichnotropis	*squamulosa*	MB21340	N/A	—	—	HF547698	HF547661
		RSP373	N/A	HF547777	HF547737	HF547699	HF547662
		SVN362	N/A	HF547776	HF547736	HF547697	HF547660
		WP122	N/A	—	—	HF547700	HF547663
		WP125	N/A	HF547778	HF547738	HF547701	—
Meroles	*anchietae*	PEMR17286	PEMR17286	HF547779	—	—	—
		WP928	N/A	HF547781	HF547740	HF547703	—
		WC09-011	PEMR17931	HF547780	HF547739	HF547702	HF547664
Meroles	*ctenodactylus*	JM03609	N/A	HF547783	HF547741	HF547704	—
		JM03611	N/A	—	HF547742	HF547705	HF547665
		JM03613	N/A	HF547784	HF547743	HF547706	HF547666
Meroles	*cuneirostris*	WP921	N/A	HF547788	HF547747	HF547710	HF547670
		WP914	N/A	HF547787	HF547746	HF547709	HF547669
		MB20484	MB20484	HF547785	HF547744	—	HF547667
		MCZA38244	MCZA38244	HF547786	HF547745	HF547708	HF547668
Meroles	*knoxii*	H6179	H6179	HF547790	HF547750	HF547712	—
		AMB5629	CAS:HERP:206782	DQ871146$	HF547748	DQ871204$	HF547671
		ATTKMK2	N/A	HF547789	HF547749	HF547711	HF547672
		SER017	N/A	HF547791	HF547751	—	—
		SVN084	PEMR18357	HF547792	HF547752	HF547713	—

……*continued on the next page*

TABLE 1. (Continued)

Genus	Species	SANBI Herpbank Accession ID	Museum Accession ID*	EMBL accession (16S)	EMBL accession (ND4)	EMBL accession (RAG1)	EMBL accession (KIAA)
Meroles	*reticulatus*	WP010	N/A	HF547795	HF547754	HF547715	HF547674
		WC09-005	PEMR17938	HF547794	HF547753	HF547714	HF547673
		WP011	N/A	HF547796	HF547755	—	HF547675
Meroles	*suborbitalis*	AJC638	N/A	HF547797	HF547756	HF547716	HF547676
		MB20609	PEMR16974	HF547798	HF547757	—	—
		MB21589	N/A	HF547799	HF547758	HF547717	HF547677
		SVN049	PEMR18376	HF547800	HF547759	HF547718	HF547678
Nucras	*lalandii*	HB124	N/A	HF951553	HF951532	HF951537	—
		HB037	N/A	HF951554	HF951533	HF951538	HF951548
		HZ246	N/A	HF951555	HF951534	HF951539	HF951549
Nucras	*tessellata*	MB20650	PEMR16873	HF951556	HF951535	HF951540	HF951550
		MB20687	PEMR16872	HF951557	HF951536	HF951541	HF951551
		MB21061	N/A	HF951558	—	HF951542	HF951552
		KTH08-069	N/A	HF951559	—	HF951543	—
Pedioplanis	*burchelli*	KTH137	N/A	DQ871122$	—	DQ871180$	—
		MH0334	N/A	DQ871120$	HF547761	DQ871178$	HF547679
Pedioplanis	*husabensis*	MCZFS37127	MCZ R184164	DQ871139$	—	DQ871197$	—
		ABE473	N/A	DQ871138$	—	DQ871196$	—
Pedioplanis	*inornata*	ABE-393-mu	NHMW 35340:9	DQ871137$	HF547762	DQ871195$	HF547680
		KTH595	N/A	DQ871140$	—	DQ871198$	—
Pedioplanis	*lineoocellatalineoocellata*	ABA-20-mu	NHMW 35360:1	DQ871106$	HF547763	DQ871164$	HF547681
Pedioplanis	*lineoocellata pulchella*	MH0336	N/A	DQ871107$	HF547764	DQ871165$	—
		SVN189	N/A	HF547802	HF547765	HF547719	HF547682
Pedioplanis	*namaquensis*	AMB4541	N/A	DQ871099$	HF547766	DQ871157$	HF547684
		AMB4558	CAS:HERP:200033	DQ871101$	HF547767	DQ871159$	HF547685
Tropidosaura	*gularis*	EL036	N/A	HF547803	—	HF547720	HF547686
		RSP200	N/A	HF547804	HF547768	HF547721	HF547687
Tropidosaura	*montanamontana*	HB082	N/A	HF547805	HF547769	HF547722	HF547688
Tropidosaura	*montanarangeri*	MBUR00544	N/A	HF547806	HF547770	HF547723	HF547689
		MBUR00552	N/A	HF547807	HF547771	HF547724	HF547690

* N/A = Individuals were measured alive in the field and released, no voucher specimen deposited in a museum; TM = Ditsong museum; PEM = Port Elizabeth Museum; MCZ = Museum of Comparative Zoology, Harvard University; CAS = Californian Academy of Science; H = Ellerman Collection of Stellenbosch University

$ Makokha JS, et al. (2007) Mol. Phylogenet. Evol. 44 (2), 622-633

Harris DJ, Batista V, Carretero MA (2004) Amphibia-Reptilia 25: 227-232

Harris,DJ, Arnold, EN Thomas, RH (1998) Mol. Phylogenet. Evol. 10 (1), 37-48

** Mayer W, Pavlicev M (2007) Mol. Phylogenet. Evol. 44 (3): 1155-1163

The members of *Pedioplanis* formed a well-supported monophyletic clade, as was expected (Edwards *et al*. 2012). The genera *Ichnotropis, Australolacerta* and *Tropidosaura* formed a well-supported clade (using the codon substitution model), within which *Australolacerta* was polyphyletic. Divergence between the two *Australolacerta* species was high compared to other inter-specific divergence levels within this study (16S: 9.55±2.08%; ND4: 22.69±1.60%; RAG1: 3.74±0.76%; KIAA: 1.90±0.47%), although a monophyletic *Australolacerta* could not be rejected using the SH and AU tests. *Meroles* formed a well-supported clade, within which the sand-diving, psammophilic species (*M. anchietae, M. cuneirostris, M. ctenodactylus*) formed a well-supported subclade. As was found previously (Edwards *et al.* 2012), *I. squamulosa* grouped with *Meroles* with strong support, and inclusion of this species within a monophyletic *Ichnotropis* can be rejected by the SH and AU tests ($P<0.01$, $P<0.001$, respectively).

Discussion

The phylogenetic analyses in this study shows that the two *Australolacerta* species are not monophyletic and that *Ichnotropis squamulosa* is placed within *Meroles*. The re-analysis using a codon-substitution model, instead of nucleotide-substitution model of evolution, also increased support for some nodes at the generic-level between the southern African lacertid lizards.

Codon-based models (such as GY94; Goldman & Yang 1994; Muse & Gaut 1994) may be the most biologically realistic models of coding sequence evolution as they explicitly incorporate information about the genetic code (Shapiro *et al.* 2006). However, the use of codon-substitution models in phylogenetic analyses is not as wide-spread as the use of nucleotide-substitution models, due to commonly used model selection programs, such as jModeltest (Posada & Crandall 1998), which do not include the codon-substitution models. Here, we found that the employment of a codon-substitution model produced the most resolved and best supported tree, clearly showing the paraphyly of *Australolacerta* and the placement of *I. squamulosa* within *Meroles*.

Monophyly of *Australolacerta*

The two species of *Australolacerta* are endemic to South Africa (Branch 1998), and both were originally placed within *Lacerta*, creating a zoogeographic paradox as most congeners were restricted to Eurasia (Arnold 1989). Arnold (1989), when describing *Australolacerta*, gave only a minimal diagnosis, noting that "… the South African species share a number of features with other Ethiopian lacertids which are not found in the apparent closest Palaearctic relatives, namely *Lacerta jayakari* etc.". The latter, now transferred to *Omanosaura*, was initially considered to form a basal lineage within the Eremiadini (Harris *et al.* 1998), although fuller taxon sampling of African lacertids (Arnold *et al.* 2007; Hipsley *et al.* 2009; Kapli *et al.* 2011) shows it to cluster with a suite of mainly north African genera (e.g. *Acanthodactylus, Mesalina, Ophisops*), with *Atlantolacerta* basal within the Eremiadini (Arnold *et al.* 2007). The sister relationship of *Australolacerta* and *Tropidosaura* proposed by Salvi *et al.* (2011) and Kapli *et al.* (2011) was based on the inclusion only of *A. australis*, and the inclusion of *A. rupicola* (Edwards *et al.* 2012; Engleder *et al.* 2013; this study) revealed the paraphyly of *Australolacerta* and the basal position of *A. australis* in a subclade including *Ichnotropis*, *Tropidosaura* and *A. rupicola.*

Both species are rupicolous and Kirchhof and Richter (2009) and Kirchhof *et al.* (2010a,b; 2012) give details of the species' biology. They are morphologically similar, albeit that many of these similarities are plesiomorphic within lacertids (Arnold 1989). Due to their high-altitude and small ranges (Branch 1998), the two species have been difficult to collect and therefore little morphological data exists for either species. Recent morphological analyses (Edwards *et al.* 2012) confirm the similarity between the two species. Yet, important features of hemipenial ornamentation and everted hemipenis structure remain unknown. Whether these similar morphologies reflect adaptive convergence to rupicoly or the retention of plesiomorphic features remains unknown.

The two species are allopatric and geographically separated from one another by a distance of approximately 1700km. Few other genera in southern Africa are known to show such large geographical disjunctions between congeners, and analysis of previous examples has often revealed deep genetic divergence best reflected in generic re-assignment. Examples include: the erection of the genera *Kinyongia* and *Nadzikambia* for non-South African

dwarf chameleons previously included in *Bradypodion* (Tilbury *et al.* 2006), and *Inyokia* for the problematic Swazi rock snake that was shown to be sister to the tropical forest snake *Homonotus modestus* (Kelly *et al.* 2011). In one of the few exceptions of congeneric range disjunctions within the subcontinent, cordylid flat lizards of the *Platysaurus capensis* complex are separated geographically from other *Platysaurus* by approximately 850km (Branch & Whiting 1997). Other described lacertid species are also separated from congeners by large distances, for example *Heliobolus lugubris* is separated from its congeners (*H. spekii,* and *H. nitidus*) by >2000km and *Ichnotropis chapini* is separated from other *Ichnotropis* by approximately 2000km (Branch, 1998; Spawls *et al*. 2002). However, the Central African region is undersampled and it is possible that with increased sample collection new species may be discovered or that ranges of described species may increase, lessening the geographic gap between congeners.

Although there were no significant differences between the obtained trees and the constrained trees in the SH or AU test when the topology was constrained to monophyly for *Australolacerta* sequence divergence estimates and the long branch lengths in the phylogenetic analyses (Figure 1) all other evidence strongly suggests that the two *Australolacerta* species do not share a recent evolutionary history (Edwards *et al.* 2012).To provide consistency between taxonomic divisions in the Eremiadini, we propose that the two species of *Australolacerta* should be placed in separate genera. The type species of *Australolacerta* is *Lacerta australis* (Arnold 1989), and we therefore erect a new genus for the remaining species *Lacerta rupicola*, based on morphology and genetic divergence.

Vhembelacerta Edwards, Herrel, Vanhooydonck, Measey, Tolley& Branch, gen. nov.

Type species. *Lacerta rupicola* FitzSimons 1933

Content. *Vhembelacerta rupicola* (FitzSimons 1933)

Characterization and diagnosis. The monophyly of the monotypic genus *Vhembelacerta* is established on the basis of a suite of mitochondrial and nuclear markers (Edwards *et al.* 2012; this study). Morphologically similar to *Australolacerta* (differences noted in brackets below), it can be distinguished from all other lacertids by the following combination of characteristics (FitzSimons 1943; Jacobsen 1989; Branch 1998;Kirchhof& Richter 2009): size small, (SVL ~52mm), maximum snout-vent length (SVL) 70mm, tail somewhat depressed basally, cylindrical distally, nearly 1.5x SVL (up to 2x SVL); upper head shields smooth; nostril pierced between a supranasal, 2 postnasals and narrowly separated from first upper labial (in contact with first upper labial); supranasals in contact behind rostral; frontonasal much broader than long; prefrontals in contact; frontal hexagonal; supraoculars 4, 1st smallest and separated from frontal; parietals in contact with 4thsupraocular; shallow parietal foramen present (absent); rostral not entering nostril; 5 (4) upper labials anterior to subocular, whose lower border is not distinctly narrowed (lower border much shorter than upper) and only feebly keeled; lower eyelid scaly but with a about 3 enlarged and elongate scales in the middle (no enlarged scales in lower eyelid); elongate tympanic shield on upper anterior border of large, exposed ear-opening; five pairs of chin shields, first smallest, first 3 in contact in midline; gular fold distinct (present, but not strongly marked); collar present, straight, free, composed of 7–8 scales; dorsal scales flat, hexagonal, faintly keeled posteriorly and in 34–43 rows across midbody (small, granular, non-keeled and about 68 across midbody); ventral plates quadrangular, feebly imbricate and in 6 longitudinal and about 26 (28) transverse rows; a very large preanal plate, bordered by smaller plates (enlarged preanal preceded by two smaller ones); femoral pores 15–19; subdigital lamellae smooth, about 26 below 4th toe (23–25); and the adpressed hindlimb reaches the armpit (to collar).

Coloration: top of head and dorsum dark brown, back with paired narrow reddish brown vertebral stripes, and a white dorsolateral stripe that extends from the eye to the tail base (head and dorsum olive-green, body with numerous spots that are yellow dorsally and white on flanks, demarcated by a dorsolateral series of orange spots).

Distribution. Endemic to the Soutpansberg mountain range in Limpopo Province, South Africa (Branch 1998).

Etymology. The species is endemic to the Vhembe region of Limpopo Province, South Africa, after which the genus name is partially constructed. The second part of the name "lacerta' (L. lizard) also retains the historical link to the genus *Lacerta* to which the single species was originally referred.

Australolacerta Arnold 1989

Type species. *Lacerta australis* Hewitt 1926

Content. *Australolacerta australis* (Hewitt 1926)

Characterization and diagnosis. With the transfer of *Lacerta rupicola* to *Vhembelacerta,* a re-diagnosis of *Australolacerta* is required. The monophyly of the monotypic genus *Australolacerta* is established on the basis of a suite of nuclear and mitochondrial markers (Edwards *et al.* 2012). Morphologically closest to *Vhembelacerta*, it can be distinguished from all other lacertids by the following combination of characteristics (FitzSimons 1943; Branch 1998): head moderately depressed, body feebly so; SVL 50–65mm, maximum 70mm; adpressed hindlimb reaches collar; tail cylindrical; head shields normal with upper head shields smooth, occipital region flat; snout pointed, shorter than postocular part of head; nostril pierced between the nasal and one or two postnasals, and 1st upper labial, with nasals in contact with one another behind rostral; frontoparietals paired in contact; parietals in contact with the 4th of four supraoculars and separated from the postoculars; parietal foramen absent; interparietal about twice as long as broad, in good contact with occipital; a series of 9 granules between supraoculars and supraciliaries; 4 upper labials anterior to subocular, which has a strongly-marked keel along upper border and a lower border that is much shorter than upper; elongate temporal shield posterior to the subocular, followed by 3 smaller rounded ones; temporal scales small and granular, similar to dorsal scales; ear-opening large, exposed, bordered anteriorly by an elongate tympanic shield and with no auricular denticulation; lower eyelid scaly, lacking vertically-enlarged scales in the middle; 6 lower labials and five pairs of enlarged chin-shields, 1st smallest, 4th largest, and 1st three pairs in median contact with one another; gular fold present, but not strongly marked; collar composed of 8 plates, straight, free, and even-edged; dorsal scales small, granular, smooth, similar to laterals and about 68 across midbody; ventral plates quadrangular, feebly imbricate, in 6 longitudinal and 28 transverse series; preanal plate enlarged, preceded by two smaller scales; Forelimb with small granular scales on upper surface of forearm and a series of strongly enlarged, smooth and imbricate plates along anterior surface of humerus; hindlimb with granular scales on upper surface of tibia; a series of much enlarged and vertically elongate plates run along anterior surface of thigh and on the lower surface of tibia;. 16–19 femoral pores; sub-digital lamellae smooth; scales on tail enlarged, quadrangular, elongate; more or less smooth dorsally, becoming keeled distally, and below scales smooth basally, more strongly keeled and bluntly mucronate distally.

Coloration: head and dorsum dark brown to olive, with numerous pale spots arranged in more or less regular longitudinal series that are yellow on back, white on flanks, and separated by a dorsolateral series of orange spots; upper surface head with pale green to yellow vermiculations; distinct pale vertical stripes on temporal region; indistinct pale spots on tail; venter bluish green; labials, chin-shields and throat pale greenish, with small black spots and mottling.

Distribution. Found in the southwestern Cape Fold Mountains in Western Cape Province, South Africa (Branch 1998).

Taxonomic position of *Ichnotropis squamulosa* Peters, 1854

Both the present phylogenetic analysis (Figure 1) and that of Edwards *et al.* (2012) clearly place *I. squamulosa* within *Meroles* with strong support, and with genus-level sequence divergences between *I. squamulosa* and *Ichnotropis*. There was a significant difference between the Bayesian topology and that in which *I. squamulosa* was constrained within *Ichnotropis* (SH and AU test: $P < 0.01$) supporting the conclusion that *I. squamulosa* should be moved to *Meroles*. A relationship between *I. squamulosa* and *Meroles* was found previously using nuclear markers (Mayer & Pavlicev 2007) and combined mitochondrial and nuclear datasets (Harris *et al.* 1998; Kapli *et al.* 2011). However, the taxonomic significance was not previously appreciated due to the incomplete taxon sampling for *Ichnotropis* in those analyses.

Confusion of *I. squamulosa* with members of the genus *Ichnotropis* is understandable as they are very similar morphologically, and cluster together when body dimensions, head measurements and limbs measurements are investigated (Edwards *et al*. 2012). The species possess a more slender body than most *Meroles*, and in addition displays characters not possessed by other *Meroles* (e.g. strongly keeled, imbricate body scalation and rugose head shields). The geographic range and habitat of *I. squamulosa* overlaps with that of a number of *Ichnotropis*, but not

that of other *Meroles* (Branch 1998; Spawls *et al.* 2002). An overlapping niche may explain the morphological similarities between *I. squamulosa* and other *Ichnotropis*, where limb dimensions reflect adaptation to substrate, and similar head shape are adaptation to similar diets. The absence of a nuchal collar is also unusual within *Meroles*, but also occurs in *M. anchietae* as well as in other lacertids (e.g. *Tropidosaura*) and its loss may be secondary and not indicative of shared ancestry. Both *Meroles* and *Ichnotropis* have symmetrical armatured hemipenes (Arnold 1986). However, due to intra-generic variation in hemipenial morphology in both *Ichnotropis* and *Meroles* (Arnold 1986), the hemipenis of *I. squamulosa* gives no insight to its generic placement. Indeed, the phylogenetic placement of *M. suborbitalis* (Figure 1) indicates that even the hemipenial armature in this species has been secondarily lost. Thus, we conclude that the similarity in body plan between *I. squamulosa* and *Ichnotropis* is a result of convergence and not shared ancestry (Edwards *et al.* 2012), and in light of genetic monophyly (Figure 1) we therefore transfer this species to the genus *Meroles*.

Meroles Gray 1838

Type species. *Meroles knoxii* (Milne-Edwards 1829)

Content. *Meroles anchietae* (Bocage 1867), *Meroles ctenodactylus* (Smith 1838), *Meroles cuneirostris* (Strauch 1867), *Meroles knoxii* (Milne-Edwards 1829), *Meroles micropholidotus* Mertens 1938, *Meroles reticulatus* (Bocage 1867), *Meroles squamulosus* (Peters 1854), *Meroles suborbitalis* (Peters 1869)

Characterization and diagnosis. The inclusion of *M. squamulosus* requires the genus to be redefined. Head shields normal and usually smooth (rugose in *squamulosus*), but occipital often very small or absent; nostril pierced between three nasals and widely separated from 1st upper labial; subocular not bordering mouth; lower eyelid scaly, without window; collar distinct (absent in *squamulosus*); gular fold absent; dorsal scales granular, juxtaposed or subimbricate, (but rhombic, strongly keeled and imbricate in *squamulosus*); ventral plates smooth, not or feebly imbricate, posterior borders straight; digits subcylindrical, compressed or depressed (feebly compressed in *squamulosus*), laterally serrated, denticulated or fringed (except in *squamulosus*); subdigital lamellae smooth or keeled (pluricarinate and spinolose in *squamulosus*), femoral pores present; parietal foramen present (absent or feebly marked in *squamulosus*); and tail long and cylindrical (in *knoxii, suborbitalis* and *squamulosus*) or depressed basally and feebly compressed distally.

Remark. As the gender of *Meroles* is masculine the specific ending of *squamulosa* must be adjusted accordingly to *squamulosus*.

Ichnotropis Peters 1854.

Type species. *Ichnotropis macrolepidota* (Peters 1854); = *I. capensis* (Smith 1838)

Content. Uetz (2012) recognizes six species (excluding *squamulosus*): *Ichnotropis bivittata* Bocage 1866*, Ichnotropis capensis* (A. Smith 1838)*, Ichnotropis chapini* Schmidt 1919*, Ichnotropis grandiceps* Broadley 1967*, Ichnotropis microlepidota* Marx 1956*, Ichnotropis tanganicana* Boulenger 1917.

Characterization and diagnosis. The monophyly of the genus *Ichnotropis* remains to be established with complete taxon sampling of the referred species. The removal of *M. squamulosus*from *Ichnotropis* does not significantly alter the diagnosis for the genus given in FitzSimons (1943), as morphological variation within the remaining species still incorporates that of *M. squamulosus*.

Remark. No modern revision of the genus has been undertaken, and the status of a number of taxa remains equivocal, e.g. *Ichnotropis bivittata pallida* Laurent 1964; *Ichnotropis capensis nigrescens* Laurent 1952; *Ichnotropis microlepidota* Marx 1956, and the generic assignment of many requires molecular confirmation.

Revised key to genera of Southern African Lacertidae

1 Tail cylindrical, without a lateral fringe; rock-living or terrestrial 2
- Tail flattened, with a lateral fringe of large, flat scales; arboreal . . . . . *Holaspis* (Blue-tailed tree lizard)
2 Smooth or tubercular lamellae beneath toes 3

	Keeled lamellae beneath the toes	6
3	A distinct collar present; dorsal scales small, granular or flattened and not overlapping	4
-	No distinct collar; dorsal scales large, strongly keeled and overlapping	*Tropidosaura* (Mountain lizards)
4	Nostril pierced between 2–4 nasals; temporal scale elongate; rock-living	5
-	Nostril pierced between 2–3 nasals and well separated from first upper labial; temporal scale rounded; terrestrial	*Nucras* (Sandveld lizards)
5	Nostril in contact with first upper labial; four upper labials anterior to subocular, whose lower border is much shorter than upper; dorsal scales small, granular, non-keeled and about 68 across midbody	*Australolacerta* (Southern rock lizard)
-	Nostril narrowly separated from first upper labial; five upper labials anterior to subocular, whose lower border is not distinctly narrowed; dorsal scales flat, hexagonal, faintly keeled posteriorly and in 34–43 rows across midbody	*Vhembelacerta* (Soutpansberg rock lizard)
6	Belly plates in 10 or more long rows	7
-	Belly plates in 6 long rows	*Heliobolus* (Bushveld lizards)
7	Dorsal scales large, keeled and overlapping; head shields striated and keeled	8
-	Dorsal scales small or granular; head shields smooth or slightly rough	9
8	Subocular borders lip	*Ichnotropis* (Rough-scaled lizards)
-	Subocular does not border lip	*Meroles squamulosus* (Rough-scaled Desert Lizard)
9	Toes without a serrated or fringed edge: subocular bordering lip	*Pedioplanis* (Sand lizards)
	Toes with a serrated or fringed edge; subocular not bordering lip	*Meroles* (Desert lizards) part.

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