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Phylogenetic Relationships of southern African geckos in the *Pachydactylus* Group (Squamata: Gekkonidae)

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Abstract.—Pachydactylus and its close relatives (*Chondrodactylus*, *Colopus*, *Palmatogecko*) constitute the most species-rich component of the southern African gekkonid fauna. We conducted a phylogenetic analysis of mitochondrial (cyt*b*, 12S rRNA, 16S rRNA) and nuclear (RAG-1) gene sequences for these geckos. *Pachydactylus tetensis* + *P. tuberculosus* form the sister group to the remaining taxa, and we resurrect the genus *Elasmodactylus* to accommodate these two basal species. The *P. bibronii* group is sister to *Chondrodactylus angulifer*, and is here transferred to the latter genus. *Pachydactylus kochii* is the sister species of *Colopus wahlbergii* and is transferred to that genus. All remaining taxa - including the *P. namaquensis* group, the 'small-bodied' *Pachydactylus*, and *Palmatogecko* - form a well-supported monophyletic assemblage recognised herein as *Pachydactylus sensu stricto*. The major clades within *Pachydactylus* s.s. include the *capensis*, *serval/weberi*, *rangei*, *rugosus*, and *geitje* groups, as well as a diverse "northwestern group" that occurs chiefly in northern Namibia and southern Angola. The fine-scale regional endemism apparent among members of the southern African *Pachydactylus* Group probably reflects an interplay between substrate specialisation and vicariant events (both geologically and climatically associated) since at least the Miocene. Explicit phylogenies for *Pachydactylus*, cordylid lizards, scorpions, and other taxa provide a basis for the first fine-scaled analytical biogeographic analysis of southern Africa.

Key words.—Gekkonidae, *Pachydactylus*, *Chondrodactylus*, *Colopus*, *Elasmodactylus*, *Palmatogecko*, Phylogeny, Taxonomy, Biogeography.

The *Pachydactylus* Group of geckos constitutes the most speciose gekkonid assemblage in Africa (Bauer 1993, 1999). In addition to *Pachydactylus sensu stricto*, the assemblage, as currently construed includes *Rhoptropus*, *Chondrodactylus*, *Colopus*, and *Palmatogecko* (all limited to southern Africa) and *Tarentola*, a chiefly Mediterranean genus, with representatives in Macaronesia (Canary Islands, Cape Verde Islands, Selvages) and the Neotropics (Cuba, Bahamas, Jamaica). Two other genera, *Kaokogecko* and *Geckonia*, have recently been relegated to the synonymies of *Palmatogecko* and *Tarentola*, respectively (Kluge & Nussbaum 1995; Carranza *et al.* 2002). The monophyly of the *Pachydactylus* Group (we

herein use the convention of capitalising 'Group' in this context to distinguish it from the lower case 'group' used in reference to putatively monophyletic species clusters within *Pachydactylus sensu stricto*) is well-established, based on the hyperphalangeal condition of digit I of both the manus and pes (Haacke 1968, 1976d; Russell 1972, 1976). Hyperphalangy is otherwise unknown in gekkotan lizards except for a single species of Asian *Cnemaspis*, in which different digits are involved (Bauer & Das 1998). Several morphologically-based higher order phylogenetic analyses of gekkonids have borne out the monophyly of the *Pachydactylus* Group as a whole (Bauer 1990; Kluge & Nussbaum 1995),

and more recently, molecular phylogenetic studies have also suggested that the group is a natural unit (Lamb & Bauer 2001, 2002). Only the immunological study of Joger (1985) rejected the monophyly of the *Pachydactylus* Group, regarding *Tarentola* (and *Geckonia*) as unrelated to the southern African forms.

Mitochondrial and nuclear DNA sequence data have been used to reconstruct species level relationships within *Tarentola* (Carranza *et al.* 2002; 15 of 22 species included). With respect to the genera from southern Africa, monophyly of *Rhoptropus* (seven species) as well as its intra- and intergeneric relationships have also been established on the basis of corroborative morphological, allozyme, and mitochondrial DNA data (Bauer & Good 1996; Lamb & Bauer 2001, 2002). Relationships among the remaining taxa of *Pachydactylus* Group geckos are more incompletely resolved. Haacke (1976d) postulated close affinities between the burrowing genera *Chondrodactylus*, *Colopus*, and *Palmatogecko* (including *Kaokogecko*) and hypothesised that collectively they formed the sister group of *Pachydactylus*. In a phylogenetic study based on immunological distance data and selected morphological characters, Joger (1985) supported the union of *Chondrodactylus* and *Colopus* but regarded all three burrowing genera as having arisen within *Pachydactylus* proper (Fig. 1). Bauer (1990) and Kluge & Nussbaum (1995) accepted the close relationship of all three genera, also suggesting that one or more may have arisen within *Pachydactylus*.

Within *Pachydactylus sensu stricto* some putatively monophyletic species groups have been identified on the basis of external morphology, e.g., the *P. capensis* group (Broadley 1977), the *P. punctatus* group (Bauer & Branch 1995), and the *P. serval* and *P. weberi* groups (McLachlan & Spence 1966). Branch *et al.* (1996) identified a *P. namaquensis* group on the basis of morphology and allozymes. More recently, molec-

ular approaches have been employed to test the monophyly of some of these groups and to erect explicit hypotheses of relationship among their constituent taxa. Thus, the monophyly of the *P. capensis* group, the *P. rugosus* group, the *P. bibronii* group, and the *P. namaquensis* group have all been corroborated on the basis of mitochondrial DNA sequence data (Lamb & Bauer 2000, 2001, 2002; Bauer & Lamb 2002). This work, combined with revisionary studies (Bauer *et al.* 2002; Bauer & Lamb 2003; Broadley 2003), has identified a number of new species within the last decade (*P. kladaroderma*, *P. haackei*, *P. parascutatus*, *P. waterbergensis*) and has resulted in the elevation of several species from subspecific to specific status (*P. formosus*, *P. barnardi*, *P. angolensis*, *P. katanganus*) or from synonymy (*P. robertsi*). Most recently, Lamb & Bauer (2002) sampled broadly across *Pachydactylus sensu stricto* and presented a phylogeny (Fig. 2) suggesting that large body size was primitive within the group and that the small-bodied species constituted a monophyletic group. As part of a long-standing research program on the geckos of southern Africa, we here expand our sampling of members of the *Pachydactylus* Group of southern Africa and present a phylogeny including the majority of recognised species in the group. In so doing we 1) test the monophyly of the
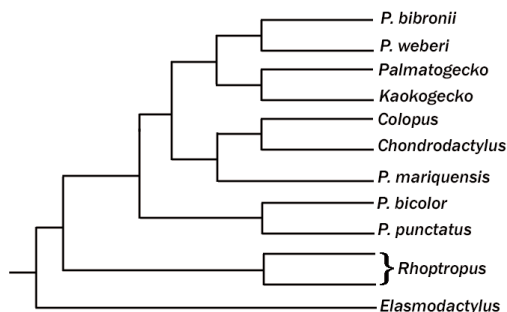

Figure 1. Hypothesis of relationships among selected taxa of the *Pachydactylus* Group based on a combination of immunological distance data and morphological characters. After fig. 3. from Joger (1985), but without the time scale originally included.
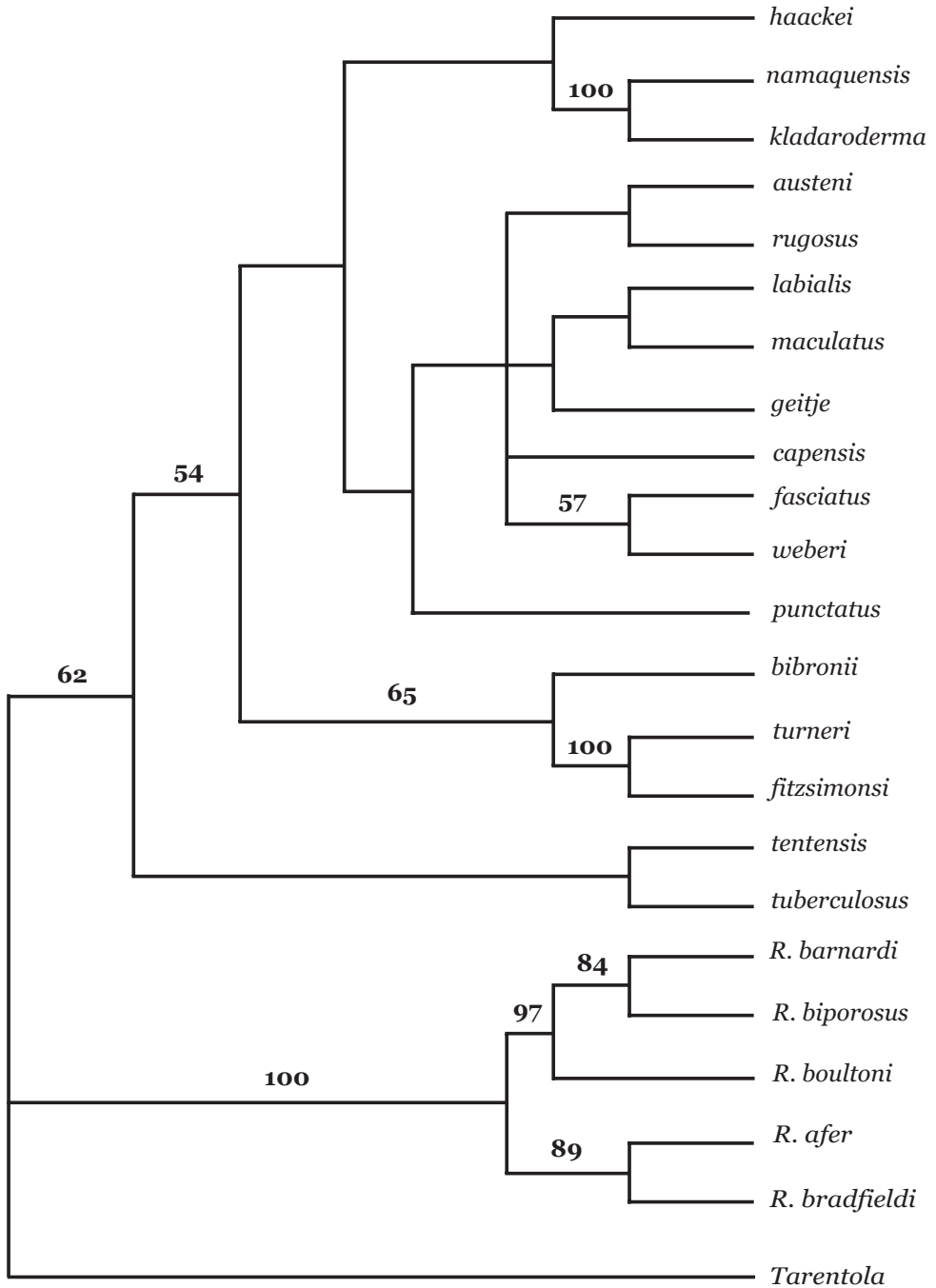
Figure 2. Hypothesis of relationships among a subset of southern African *Pachydactylus* Group taxa based on mitochondrial data (from Lamb & Bauer 2002).

remaining species groups, 2) provide a hypothesis of relationships for previously ungrouped species, and 3) establish the phylogenetic position of the burrowing genera previously regarded as either the sister group of, or embedded within, *Pachydactylus* (the functional implications of our findings are detailed elsewhere, Lamb & Bauer, in press). Finally, we address the taxonomic and biogeographic implications of our phylogenetic findings.

MATERIAL AND METHODS

Taxon sampling.—We sampled 36 recognised species of *Pachydactylus* (including representatives of all previously proposed species groups), both species of *Palmatogecko*, and the monotypic *Colopus* and *Chondrodactylus*. Certain taxa within the *P. serval* and *P. weberi* groups (*P. kobosensis*, *P. robertsi*, *P. waterbergensis*), currently undergoing revision (Bauer *et al.* submitted), were not included in the analysis. In addition, genetic material of *P. angolensis*, *P. amoenus*, and *P. katanganus* was unavailable and these taxa were excluded from the analysis. Likewise, we did not include representative subspecies of polytypic forms, some of which may warrant specific recognition. These issues will be addressed in a more comprehensive monograph of the entire *Pachydactylus* Group (unpubl. data). With the exception of *Pachydactylus tsodiloensis* and *Colopus wahlbergii*, we sequenced two or more specimens for each species. *Rhoptropus afer* and *R. boultoni*, representing respective major clades within their genus (Bauer & Good 1996), were also included; a species level phylogeny of this genus has been presented elsewhere (Lamb & Bauer 2001). The Mediterranean species *Tarentola mauritanica* and the North African *T. annularis* served as outgroups. Sampled taxa, together with collection localities and museum voucher numbers are presented in Appendix I. GenBank accession numbers are complied in Appendix II.

Sequence procurement and alignment.— Genomic DNA was extracted from preserved tissues (liver, muscle) or shed skin using the Qiagen QIAamp DNA Mini kit. Regions from three mitochondrial genes, 12S rRNA (12S; 350 bp), 16S rRNA (16S; ≅ 450 bp), and cytochrome *b* (cyt*b*; ≅ 700bp), were initially selected for phylogenetic analysis. Given the mutational saturation observed for cyt*b* among the large-bodied *Pachydactylus* (snout-vent length > 70 mm; Lamb & Bauer 2002), we also sequenced a more slowly evolving nuclear gene, RAG-1 (Groth & Barrowclough 1999). The 16S and cyt*b* fragments were amplified with primer pairs LGL 286 + LGL 381 (Bickham *et al.* 1996), and L14724 (Meyer *et al.* 1990) + H15560 (Palumbi *et al.* 1991), respectively, using a thermal cycling regime of 32 cycles at 92 °C for 45 sec, 50-52 °C for 35 sec, and 72 °C for 1 min. The RAG-1 gene fragment (≅ 800 bp) was amplified with the primers 5'-TAA AGA TGC CTT TYC TGT AAA CCA AAG -3' (this study) and R18 (Groth & Barrowclough 1999) for 40 cycles at 92 °C for 45 sec, 51 °C for 35 sec, and 72 °C for 1 min. Amplification products, purified over High Pure PCR Product columns (Roche Diagnostic Corp.), were sequenced on an Applied Biosystems 377 automated sequencer using dye-labeled terminators (BigDye™ Terminator kit, Applied Biosystems, Inc). Forward and reverse sequences were generated for each sample and their complementarity confirmed using the Sequence Navigator software (Applied Biosystems Inc.).

Sequences were aligned using CLUSTAL X 1.81, applying default settings (Thompson *et al.* 1997). Given the indel variation commonly observed among rRNA gene sequences, we examined 12S and 16S alignments in greater detail, exploring gap placements for a series of gap opening and extension costs. Regions of rRNA sequence for which nucleotide position homologies varied across gap parameters were

Table 1. Summary statistics for parsimony and Bayesian analyses.

Dataset	No. of sites	No. of informative sites		Model		MrBayes parameters	
		*Pachydactylus**	All taxa	hLRT	AIC	nst	rates
12S	288	122	131	GTR+I+G	GTR+I+G	6	Invgamma
16S	412	145	158	GTR+I+G	GTR+I+G	6	Invgamma
cyt*b*		662					
1st pos.		97	106	TVM+I+G	GTR+I+G	6	Invgamma
2nd pos.		51	57	TrN+I+G	TVM+I+G	2	Invgamma
3rd pos.		216	217	GTR+I+G	GTR+I+G	6	Invgamma
RAG -1	784						
1st pos.		29	41	HKY+G	K81uf+G	2	Gamma
2nd pos.		21	34	HKY+G	HKY+G	2	Gamma
3rd pos.		61	83	HKY+G	K81uf+G	2	Gamma
Total	1858						

*= *Pachydactylus sensu stricto*, *Chondrodactylus*, *Colopus*, and *Palmatogecko*

considered alignment-ambiguous and excluded from analysis.

Phylogenetic analysis.—Our phylogenetic reconstruction relies predominantly on Bayesian analytical methods. We used Modeltest 3.06 (Posada & Crandall 1998) to identify the most appropriate model of sequence evolution for the 12S and 16S genes as well as for each codon position within cyt*b* and RAG-1. Both hierarchical likelihood ratio tests (hLRTs) and the Akaike information criterion (AIC) were implemented to identify models of DNA substitution that provided the best fit to each data partition.

We used MrBayes 3.0b4 (Huelsenbeck & Ronquist 2001) to conduct a Bayesian analysis of the combined data, employing the gene partition substitution parameters identified by Modeltest. This approach allowed eight discrete DNA substitution/rate categories to be incorporated in the analysis, corresponding to the two ribosomal genes and each codon position within cyt*b* and RAG-1 (Table 1). The analysis was initiated with random starting trees and run for 1.0×10^6 generations, sampling Markov chains every 100 generations. We used the Metropolis-coupled Markov chain Monte Carlo algorithm, engaging four incre-mentally heated Markov chains. To ensure Markov chains did not become entrapped on local optima, we analyzed the combined data in three separate runs. Burn-in was determined graphically, plotting likelihood scores against generation time, and those trees generated prior to burn-in (generally, the first 500 trees) were discarded. We used the MrBayes 'sumt' com-mand to create a majority rule consensus tree showing all compatible partitions, generate an average likelihood score, calculate posterior clade probabilities (pP), and estimate average branch lengths across all post burn-in trees.

We also analyzed the sequence data using max-imum parsimony (MP) to allow comparisons to clades (and their support) identified by Bayesian inference. Prior to MP analysis, we conducted an incongruence length difference test (ILD), implemented in PAUP* 4.0 (Swofford 2002) as a partition homogeneity test, to detect possible incongruence among genes. This test (100 random addition sequences of taxa; 500 replicates) did not con-tradict the congruence of the four gene sequence partitions ($P = 0.97$), which were combined for MP analysis. Parsimony trees were generated using the heuristic search option in PAUP* 4.0, with tree bisection-recon-nection branch swapping, MULPARS, and ran-

dom addition of sequences (1000 replicates). Bootstrap analysis involving 1000 pseudoreplicates was executed to estimate nodal support for MP trees.

RESULTS

Upon exclusion of ambiguously aligned regions in the 12S and 16S sequences, the combined data comprised 1858 nucleotides. Sequence variation, substitution models, and Bayesian parameters for the gene partitions are summarised in Table 1.

The three independent Bayesian runs yielded statistically equivalent log-likelihood scores and identical consensus trees, providing support for the assumption that these analyses converged on a single optimum, which we present as our preferred hypothesis of relationships (Fig. 3). A total of 827 informative nucleotide sites were analyzed using MP, with 669 sites contributed by the mtDNA partition and 158 by RAG-1. These combined data yielded two equally parsimonious trees of 6333 steps (CI = 0.27; RI = 0.35), presented as a consensus tree that is entirely consistent with the Bayesian tree, although less well resolved (Fig. 4).

Certain nodes receiving strong pP support in the Bayesian analysis, particularly some of the deeper nodes, are less well supported by bootstrap analysis of the parsimony tree. We believe these discrepancies may stem from equal weighting employed in the parsimony analysis; as a result, bootstrap support has probably been attenuated by the effects of saturation for certain data partitions, e.g., 3rd position sites for cyt*b*. For example, node D (Fig. 3), which received a pP = 0.96 (BI) and a bootstrap value of 84% (MP), garnered a bootstrap value of 97% in a MP analysis of the more slowly evolving RAG-1 gene alone.

Both analyses provided strong support for a monophyletic southern African group (clade A) with *Rhoptropus* as sister group to the remaining taxa, the latter with low parsimony bootstrap support (Fig. 3). The monophyly of the southern African taxa exclusive of *Rhoptropus* (clade B) is supported by a posterior probability of 1.00. Within *Pachydactylus* the basal clade (pP = 1.00) includes *P. tetensis* and *P. tuberculosus*, both relatively large, weak-skinned, chiefly arboreal forms from tropical east Africa, mainly found north of the Zambezi River. The remaining *Pachydactylus* and the burrowing genera *Colopus*, *Chondrodactylus*, and *Palmatogecko* (clade C) receive 84% bootstrap support and a posterior probability of 1.00. The two equally parsimonious alternative topologies differ in their relative placement of *Pachydactylus mariquensis* and the *P. namaquensis* group. The consensus parsimony tree includes six branches forming a polytomy (Fig. 4). Based on Bayesian inference, the most basal members of this group form a clade incorporating the *P. bibronii* group (*P. bibronii*, *P. turneri*, *P. fitzsimonsi*) with *Chondrodactylus angulifer* as its sister taxon. All four species are large bodied geckos with generally wide distributions, ranging from temperate areas of the Western Cape to Kenya and Rwanda (Spawls *et al.* 2002). This clade as a whole is well supported, as are all its internal relationships.

The remainder of the *Pachydactylus* Group (clade D) is associated with a posterior probability of 91%. Within this group, *Colopus wahlbergii* + *P. kochii* form the sister group to all remaining species. Under Bayesian inference this speciose clade (labeled as *Pachydactylus sensu stricto* in Fig. 3) is divided into two subclades (E and F), neither of which receives strong support. Clade E includes the *P. namaquensis* group, a clade of large-bodied, weak-skinned geckos, as the sister to a clade of small-bodied taxa confined chiefly to northern Namibia and southern Angola (northwestern group). This group
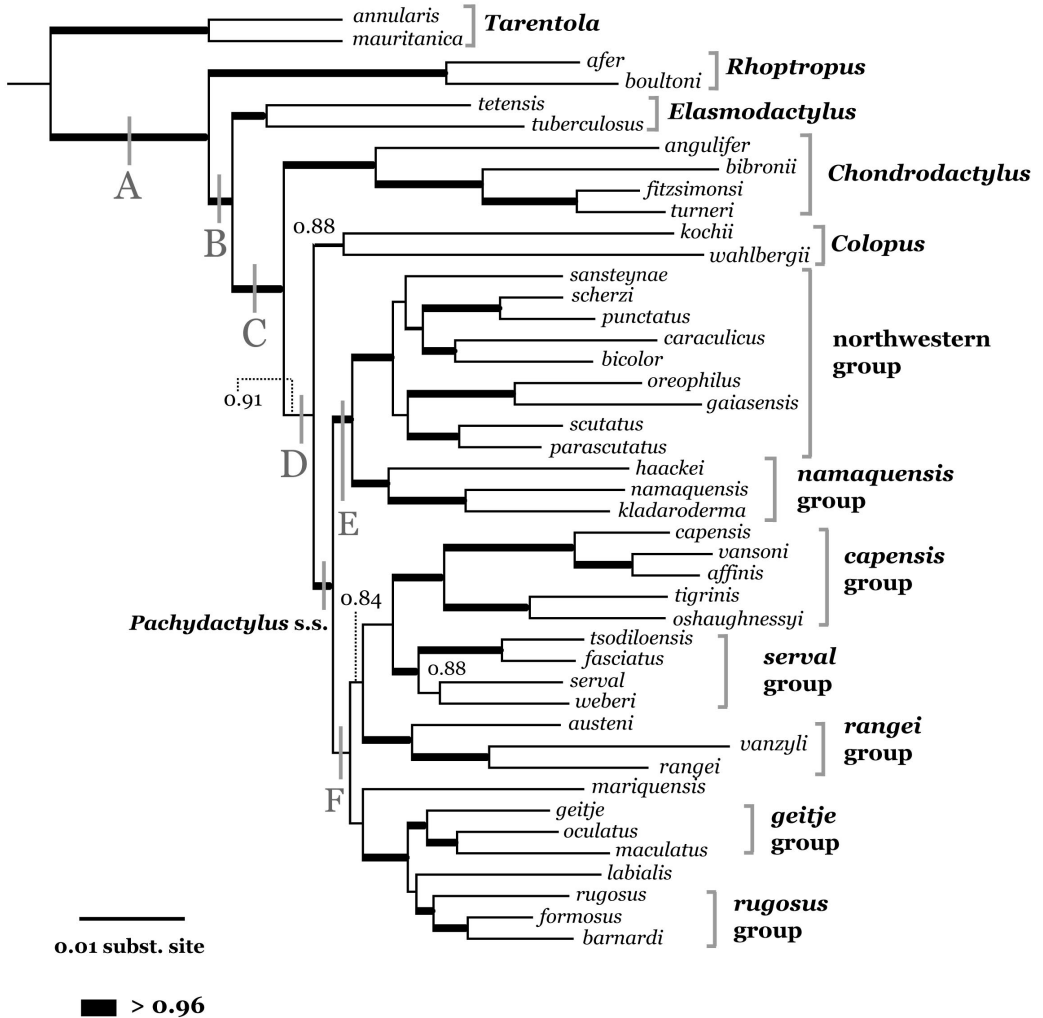
Figure 3. Bayesian inference phylogram for the southern *Pachydactylus* Group representing analysis of the combined sequence data for the 12S, 16S, cyt*b*, and RAG-1 genes (1858 bp). This topology is a majority rule consensus tree of all compatible partitions for trees sampled during three independent Bayesian analyses (incorporating model parameters in Table 1). Bold branches indicate posterior probabilities (pP) ≥ 0.96; exact values for pP between 0.80 and 0.95 are listed above branches. Letter designations (A-F) correspond to clades discussed in this paper. Group names indicated to the right of the figure correspond to monophyletic species groups within *Pachydactylus sensu stricto*. Generic assignments reflect the taxonomic conclusions of this paper (see Discussion).

includes the very widely distributed *P. punctatus* and its sister species *P. scherzi*, *P. scutatus* and the allied *P. parascutatus* (Bauer *et al.* 2002), *P. sansteynae* (see Michels & Bauer 2004 for the correct spelling of this name), originally described as part of the *P. serval* group (Steyn & Mitchell 1967), and a number of relatively poorly-known species (*P. caraculicus*, *P. bicolor*, *P. oreophilus*, and *P. gaiasensis*). Explicit relationships among these forms have not been proposed previously, although *P. bicolor* was initially described as a subspecies of *P. punctatus* based on superficial similarities (Hewitt 1926).

Clade F (pP = 0.84) is divided into two major subclades, one consisting of *P. geitje*, *P. oculatus*, *P. maculatus*, *P. labialis* and members of the *P. rugosus* group (P. *rugosus*, *P. formosus*, *P. barnardi*; Lamb & Bauer 2000) and the second including the *P. serval/weberi* group (*P. serval*, *P. weberi*, *P. fasciatus*, *P. tsodiloensis*) plus the *P. capensis* group (*P. capensis*, *P. affinis*, *P. vansoni*, *P. tigrinus*, *P. oshaughnessyi*; Bauer & Lamb 2002) as the sister group to *P. austeni* plus *Palmatogecko* (*P. rangei* and *P. vanzyli*). *Pachydactylus mariquensis* is weakly supported as a basal member of the clade including the *geitje* and *rugosus* groups in the Bayesian analysis and one of the MP trees. In the second MP tree, however, *P. mariquensis* is basal to the more inclusive clade including both the *capensis* and *rugosus* groups.

Alternative Topologies.—The resulting topology from Bayesian inference (Fig. 3) places
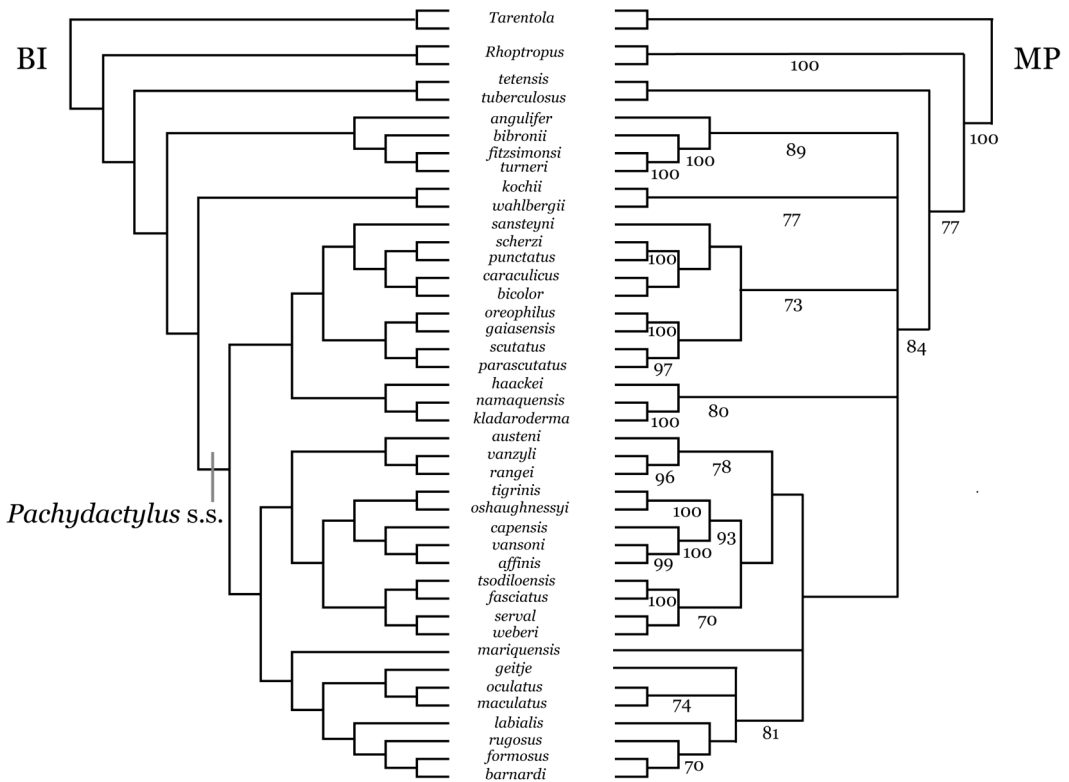

Figure 4. Comparison of Bayesian inference (BI; left) and maximum parsimony consensus (MP; right) trees derived from the combined sequence data. The MP tree is a consensus of two equally parsimonious trees. Bootstrap values > 50% are listed below branches of the MP tree.

Chondrodactylus + the *P. bibronii* complex and *Colopus* + *P. kochii* in separate clades outside *Pachydactylus sensu stricto*. To determine whether this departs significantly from phylogenies in which either clade falls within *Pachydactylus sensu stricto*, we examined differences between the Bayesian tree and *a posteriori* topological hypotheses in which these two clades were respectively constrained to occur within *Pachydactylus*. This was done by comparing the likelihoods of the alternative trees using the Shimodaria-Hasegawa test (Shimodaria & Hasegawa 1999). Each constrained topology was generated by heuristic parsimony searches in PAUP*, and its likelihood score was based on a substitution model (GTR + G +I) computed in Modeltest for the combined (all genes) dataset. Results for both tests significantly favoured the Bayesian topology (test i: -lnL 28634.48 vs. -lnL 28665.62, *P* = 0.004; test ii: -lnL 28634.48 vs. -lnL 28661.16, *P* = 0.009) and thereby support both *Chondrodactylus* and *Colopus* clades as distinct lineages relative to *Pachydactylus sensu stricto*.

DISCUSSION

Phylogeny.—Our results are largely consistent with a more limited phylogenetic analysis of *Pachydactylus* (17 taxa) based solely on mitochondrial sequence data (Lamb & Bauer 2002; Fig. 2). The retrieval of *P. tetensis* and *P. tuberculosus* as basal taxa is confirmed, as are the monophyly and near-basal position of the *P. bibronii* group. Also recovered are the monophyly and intra-group relationships for the *P. capensis*, *P. namaquensis* and *P. rugosus* groups, each of which has been identified previously on the basis of morphology and corroborated by mitochondrial gene sequence data (Lamb & Bauer 2000, 2002; Bauer & Lamb 2001). In addition, both the close affinities and specific distinctness of the *P. punctatus*/*P. scherzi* (Bauer & Branch 1995) and *P. scuta-*

tus/*P. parascutatus* species pairs (Bauer *et al.* 2002) are supported. While no explicit relationships among *P. geitje*, *P. oculatus* and *P. maculatus* have previously been proposed, *P. oculatus* was synonymised with *P. maculatus* by Loveridge (1947), and all three share similar body form and proportions. Indeed, all members of the more inclusive clade to which these species and the *P. rugosus* group belong are characterised by a relatively short snout and a partly, to fully pigmented, venter.

Higher order relationships among *Pachydactylus* are also largely congruent with those of the mitochondrial dataset of Lamb & Bauer (2002) but differ in the placement of the *P. namaquensis* group, which was previously identified as the sister group to all of the small-bodied members of the genus, albeit with weak support. This placement and other differences between the results of Lamb & Bauer (2002) and the topologies presented here are likely the result of a strong phylogenetic signal provided by the RAG-1 sequence data as well as the effects of denser taxon sampling, especially within the northwestern group.

The relationships of the burrowing geckos are not entirely unexpected. Although Haacke (1976d) provided a tree in which *Palmatogecko*, *Colopus* and *Chondrodactylus* formed a group outside of *Pachydactylus*, he noted that their specialisations might have evolved within *Pachydactylus*. Joger (1985) explicitly postulated that these forms had evolved within the genus and support for this interpretation has been given by Bauer (1990) and Kluge & Nussbaum (1995), although the generic level analyses of these authors were not suitable for testing this hypothesis. The affinities of *Palmatogecko* to *Pachydactylus austeni* are unsurprising to anyone who has seen these two taxa. Although *austeni* lacks the specialised pedal morphology of the other two species (Russell & Bauer 1990; Bauer & Russell 1991), it is similar in most other fea-

tures, including general morphology and to a lesser extent, colour pattern. Indeed, *austeni* replaces *rangei* south of the Holgat River, where Namib dunes give way to coastal dunes (Haacke 1976a). That *Chondrodactylus* should be allied to the large-bodied *Pachydactylus bibronii* group has not been previously proposed but is eminently plausible. In addition to large size, these geckos share a disproportionally wide head, dorsal skull surface ornamentation, and a pattern of prominent white spots in at least some individuals of all species. Perhaps most surprising is the fact that *Colopus* and *Chondrodactylus* are not closely related. Their affinities were supported by phalangeal loss superimposed on the ancestral hyperphalangic pattern (Haacke 1968, 1976d; Russell 1972, 1976; Joger 1985). However, the actual morphology of the digital loss is quite different (Lamb & Bauer 2005), and aside from this feature *Colopus* bears a much more striking resemblance to *P. kochii*, with which it shares a very similar external digital morphology (Haacke 1968, 1976b; Russell 1972).

Taxonomic Implications.—Lamb & Bauer (2002) outlined possible taxonomic implications of their preliminary phylogenetic analysis of *Pachydactylus*, but postponed taxonomic action pending a more comprehensive data set. The strong support for the inclusion of *Chondrodactylus*, *Colopus* and *Palmatogecko* within *Pachydactylus sensu lato* (Lamb & Bauer 2005; this paper) necessitates a reconsideration of the taxonomy of the southern African *Pachydactylus* Group as a whole, since *Pachydactylus* as previously construed is demonstrably paraphyletic. We favour a classification and taxonomic scheme that maintains only monophyletic generic and higher named groupings. Several options for achieving this result are available, ranging from the synonymisation of all names with *Pachydactylus* to the wholesale fragmentation of the group into ten or more genera should the existing content of the burrowing genera remain

unchanged. No solution will be entirely satisfying as each would result in changes in the application of long-established generic names and attendant disruption of the concepts associated with these names. Nonetheless, we believe that systematics is best served by the recognition of exclusively monophyletic groups, and we here apply names to achieve this goal with minimal disruption.

Only a few names are available in the generic synonymy of *Pachydactylus* (Wermuth 1965; Kluge 2001). *Pachydactylus* Wiegmann, 1834 has as its type species *Pachydactylus bergii* Wiegmann, 1834, which is a junior subjective synonym of *P. geitje* (Sparrman, 1778). *Colopobus* Fitzinger, 1843 is strictly synonymous with *Pachydactylus*, as its type species is *Anoplopus inunguis* (Wagler, 1830) [= *Gecko inunguis* Cuvier, 1817], another junior subjective synonym of *P. geitje* (Sparrman, 1778) (see Loveridge 1947 and Brygoo 1990 for comments). Two other synonyms of *Pachydactylus*, *Cantinia* Gray, 1845 (type species *P. elegans* Gray, 1845 [= *P. capensis* (Smith, 1845)]) and *Homodactylus* Gray, 1864 (type species *H. turneri* Gray, 1864 [= *P. turneri* (Gray, 1864)] are junior homonyms of older names in other taxonomic groups (a nomenclatural point not noted by Lamb & Bauer 2002). The only name currently in synonymy and actually available for use is *Elasmodactylus* Boulenger 1894, with its type species *E. tuberculosus* Boulenger by monotypy.

Based on the results presented herein and on the availability of the following existing names for use within *Pachydactylus sensu lato* - *Pachydactylus* Wiegmann, 1834, *Colopus* Peters, 1869, *Chondrodactylus* Peters, 1870, *Elasmodactylus* Boulenger, 1894; *Palmatogecko* Andersson, 1908, *Kaokogecko* Steyn & Haacke, 1966 - we propose an allocation of names that maintains only monophyletic generic groupings while minimising disruption of existing usages. As all these generic names are

masculine, reallocations among genera will not affect the form of the specific epithets of their constituent taxa (Table 2).

The group including the species *tuberculosus* and *tetensis* is assigned to the resurrected genus *Elasmodactylus*. *Elasmodactylus* has also been applied to *P. namaquensis* (Sclater, 1898), but neither this form nor its recently described relatives are closely related to *E. tuberculosus*. Joger (1985) suggested resurrecting the name *Elasmodactylus* because he believed that members of this group were basal to *Pachydactylus* plus *Rhoptropus*, citing their retention of precloacal pores as evidence for their plesiomorphic position. Most recently Broadley & Cotterill (2004) have used *Elasmodactylus* in a subgeneric context.

ELASMODACTYLUS BOULENGER

Elasmodactylus Boulenger, 1894, Proc. Zool. Soc. London 1894: 722. Type species: *Elasmodactylus tuberculosus* Boulenger, 1894, by monotypy.

Diagnosis.—*Elasmodactylus* may be diagnosed by the following suite of characteristics: body large, robust (adults > 75 mm SVL); skull surface smooth; digit I of manus and pes hyperphalangic (phalangeal formulae - 3-3-4-5-3 manus and 3-3-4-5-4 pes), digits broadly dilated, bearing 8-14 undivided subdigital lamellae beneath digit IV of pes, lacking paraphalanges and interdigital webbing; males with series of precloacal pores; tail depressed; dorsal skin tuberculate, fragile. Precloacal pores are primitively absent in the *Pachydactylus* Group as a whole, and independent reversals have occurred in *Elasmodactylus* and some *Rhoptropus* (Bauer & Good 1996). Fragile skin, which may be used in regional integumentary loss, a predator escape strategy (Bauer *et al.* 1989; Bauer *et al.* 1993), has apparently evolved independently in *Elasmodactylus* and the *P. namaquensis* group.

Content.—*Elasmodactylus tetensis* (Loveridge, 1953), **comb. nov.**; *E. tuberculosus* Boulenger, 1894.

Distribution.—Tropical southeastern Africa from the lower Zambezi Valley of Zambia, Zimbabwe and Mozambique to Tanzania and the southern Democratic Republic of Congo.

Members of the *P. bibronii* clade, now including *Chondrodactylus angulifer*, are highly morphologically distinctive with respect to the remaining members of the *Pachydactylus* Group. We propose the application of the name *Chondrodactylus* for all members of this clade. This is the most disruptive of the taxonomic changes we advocate, as the generic reassignment affects both the geographically most widespread member of the group, *P. turneri*, and one of the most often cited taxa (although often in error for *P. turneri*), *P. bibronii*. Nonetheless, we consider this solution to be preferable to the inclusion of this clade within a more broadly diagnosed and highly heterogeneous *Pachydactylus*.

CHONDRODACTYLUS PETERS

Homodactylus Gray, 1864, Proc. Zool. Soc. London 1864: 59 (non *Homodactylus* Fitzinger, 1843 = Gerrhosauridae). Type species: *Homodactylus turneri* Gray, 1864, by monotypy.
Chondrodactylus Peters, 1870, Mber. Akad. Wiss. Berlin 1870: 110. Type species: *Chondrodactylus angulifer* Peters, 1870, by monotypy.

Diagnosis.—Earlier diagnoses of *Chondrodactylus*, then incorporating only *C. angulifer*, emphasized the highly autapomorphic digital features of that species (FitzSimons 1943; Loveridge 1947; Haacke 1976c) and do not serve to distinguish the additional constituent taxa recognized here from other members of the *Pachydactylus* Group. We here re-diagnose *Chondrodactylus* on the basis of the following suite of characteristics: body large, robust (adults > 80 mm SVL); dorsal surface of skull rugose or sculptured; digit I of manus and pes

Table 2. New taxonomy of southern African *Pachydactylus* Group geckos based on this study. Species group names refer only to clades within *Pachydactylus sensu stricto* and correspond to those indicated in Fig. 3. Remarks include changes since Branch (1998), as well as references to recent phylogenetic, taxonomic and nomenclatural treatments. The status of subspecies within polytypic taxa will be discussed elsewhere (Bauer *et al*. in prep.).

Taxon	Author	Species group	Remarks
Pachydactylus	Wiegmann, 1834		
P. affinis	Boulenger, 1896	*capensis*	See Bauer & Lamb 2002.
P. amoenus	Werner, 1910	—	Not included in this study. Probably allied to *P. mariquensis*.
P. angolensis	Loveridge, 1944	northwestern	Not included in this study. Resurrected from synonymy of *P. scutatus* (Bauer *et al*. 2002).
P. austeni	Hewitt, 1923	*rangei*	
P. barnardi	FitzSimons, 1941	*rugosus*	Elevated from subspecific status within *P. rugosus* (Lamb & Bauer 2000).
P. bicolor	Hewitt, 1926	northwestern	
P. capensis	(Smith, 1846)	*capensis*	Includes *P. mentalis* Hewitt, 1926, regarded as valid by Kluge (2001). See Bauer & Lamb (2002).
P. caraculicus	FitzSimons, 1959	northwestern	
P. fasciatus	Boulenger, 1888	*serval/weberi*	
P. formosus	Smith, 1849	*rugosus*	Elevated from subspecific status within *P. rugosus* (Lamb & Bauer 2000).
P. gaiasensis	Steyn & Mitchell, 1967	northwestern	
P. geitje	(Sparrman, 1778)	*geitje*	
P. haackei	Branch et al., 1996	*namaquensis*	See Branch *et al*. (1996).
P. katanganus	de Witte, 1953	*capensis*	Not included in this study. Elevated from subspecific status within *P. oshaugnessyi* (Broadley 2003).
P. kladaroderma	Branch *et al*., 1996	*namaquensis*	See Branch *et al*. (1996).
P. kobosensis	FitzSimons, 1938	*serval/weberi*	Not included in this study. A valid Namibian endemic species (Bauer, Lamb & Branch, in prep), but not included by Branch (1998).
P. labialis	FitzSimons, 1938	*rugosus* ?	Probably most closely allied to *P. rugosus* group, but weakly supported.
P. maculatus	Gray, 1845	*geitje*	
P. mariquensis	Smith, 1849	—	Not obviously closely allied to any of the larger species groups.
P. namaquensis	(Sclater, 1898)	*namaquensis*	See Branch *et al*. (1996).
P. oculatus	Hewitt, 1927	*geitje*	
P. oreophilus	McLachlan & Spence, 1967	northwestern	
P. oshaughnessyi	Boulenger, 1885	*capensis*	See Bauer & Lamb (2002).
P. parascutatus	Bauer *et al*., 2002	northwestern	Recently described species endemic to NW Namibia (Bauer *et al*. 2002).
P. punctatus	Peters, 1854	northwestern	See Bauer & Branch (1995).
P. rangei	(Andersson, 1908) comb. nov.	*rangei*	*Palmatogecko* synonymised with *Pachydactylus* (this paper).
P. robertsi	FitzSimons, 1938	*serval/weberi*	Not included in this study. Resurrected from synonymy of *P. scutatus* and placed in *P. serval/weberi* group (Bauer *et al*. 2002).
P. rugosus	Smith, 1849	*rugosus*	See Lamb & Bauer (2000).
P. sansteynae	Steyn & Mitchell, 1967	northwestern	Specific epithet emended by Michels & Bauer (2004).
P. scherzi	Mertens, 1954	northwestern	See Bauer & Branch (1995).
P. scutatus	Hewitt, 1927	northwestern	See Bauer *et al*. (2002).
P. serval	Werner, 1910	*serval/weberi*	Under revision (Bauer, Lamb & Branch), includes several undescribed species.
P. tigrinus	Van Dam, 1921	*capensis*	See Bauer & Lamb (2002).
P. tsodiloensis	Haacke, 1966	*serval/weberi*	
P. vansoni	FitzSimons, 1933	*capensis*	See Bauer & Lamb (2002).
P. vanzyli	(Steyn & Haacke, 1966) comb. nov.	*rangei*	*Palmatogecko* synonymised with *Pachydactylus* (this paper).
P. waterbergensis	Bauer & Lamb, 2003	*serval/weberi*	Not included in this study. Recently described species endemic to the Waterberg, northern Namibia.
P. weberi	Roux, 1907	*serval/weberi*	Under revision (Bauer, Lamb & Branch), includes several undescribed species.

Table 2 continued...

Table 2. continued.

Taxon	Author	Species group	Remarks
Colopus	Peters, 1869		
C. kochii	(FitzSimons, 1959) comb. nov.	—	
C. wahlbergii	Peters, 1869	—	
Chondrodactylus	Peters, 1870		
C. angulifer	Peters, 1870	—	
C. bibronii	(Smith, 1846) comb. nov.	—	
C. fitzsimonsi	(Loveridge, 1947) comb. nov.	—	
C. turneri	(Gray, 1864) comb. nov.	—	
Elasmodactylus	Boulenger, 1894		Resurrected from synonymy of *Pachydactylus* (this paper).
E. tuberculosus	Boulenger, 1894	—	
E. tetensis	(Loveridge, 1953) comb. nov.	—	
Rhoptropus	Peters, 1869	—	
R. afer	Peters, 1869	—	See Lamb & Bauer (2001).
R. barnardi	Hewitt, 1926	—	See Lamb & Bauer (2001).
R. biporosus	FitzSimons, 1957	—	See Lamb & Bauer (2001).
R. boultoni	Schmidt, 1933	—	See Lamb & Bauer (2001).
R. bradfieldi	Hewitt, 1935	—	See Lamb & Bauer (2001).
R. diporus	Haacke, 1965	—	Elevated from subspecific status within *R. bradfieldi* (Bauer & Lamb 2001).
R. taeniostictus	Laurent, 1964	—	

hyperphalangic, with or without phalangeal loss in digit IV of manus (phalangeal formulae - 3-3-4-5-3 or 3-3-4-4-3 manus and 3-3-4-5-4 pes), digits with or without subdigital scansors (if present 8-12 beneath digit IV of pes), lacking paraphalanges and interdigital webbing; precloacal pores lacking; tail weakly to moderately depressed; dorsal skin tuberculate, not fragile.

Content.—*Chondrodactylus angulifer* Peters, 1870; C. *bibronii* (Smith, 1846), **comb. nov.**; C. *fitzsimonsi* (Loveridge, 1947), **comb. nov.**; C. *turneri* (Gray, 1864), **comb. nov.**

Distribution.—All of southern Africa exclusive of the extreme southern and southwestern Cape and portions of the Highveld and Drakensberg. Extending northwards into Angola in the west and Kenya in the east.

Molecular phylogenetic support for the clade including *Colopus* plus *P. kochii* is relatively weak. However, it is corroborated by morphological features, most notably the elongation of the trunk and the extreme reduction of the terminal subdigital scansors, although these derived features also occur in some species of *Pachydactylus sensu stricto* (e.g., *P. mariquensis*, *P. rangei*, *P. vanzyli*). Further evidence for the monophyly of *Colopus* will be presented in a more comprehensive revision of the *Pachydactylus* Group (Bauer *et al.,* in prep.). As *P. kochii* is a relatively recently described species (FitzSimons 1959) with a rather limited distribution in west central Namibia, the name has not been widely cited and its generic reallocation is unlikely to be disruptive.

COLOPUS PETERS

Colopus Peters, 1869, Mber. Akad. Wiss. Berlin 1869: 57. Type species: *Colopus wahlbergii* Peters, 1869, by monotypy.

Diagnosis.—*Colopus* was originally diagnosed by Peters (1869) on the basis of its granular subdigital scales and much reduced lamellae, and digital features have remained the crucial elements in subsequent diagnoses (FitzSimons 1943; Loveridge 1947; Haacke 1976b). We here re-diagnose *Colopus* on the basis of the following suite of characteristics: body small (adults < 65 mm SVL), slender, elongate; dorsal surface of skull smooth; digit I of manus

and pes hyperphalangic, with or without phalangeal loss in digit IV of manus (phalangeal formulae - 3-3-4-5-3 or 3-3-4-4-3 manus and 3-3-4-5-4 pes), lacking paraphalanges and interdigital webbing, subdigital surface granular, except distally, where there are 2-3 narrow subdigital lamellae beneath digit IV; precloacal pores lacking; tail cylindrical in cross section; dorsal skin smooth, not fragile.

Content.—*Colopus kochii* (FitzSimons, 1959), **comb. nov.**; *C. wahlbergii* Peters, 1869.

Distribution.—Throughout the Kalahari, including most of Botswana, eastern portions of Namibia, western Zimbabwe, northern portions of the Northern Cape and Northwest Province, and isolated localities in Limpopo Province. Also in west central Namibia.

All remaining taxa, constituting the large group of small-bodied *Pachydactylus*, as well as the members of the *P. namaquensis* group (*sensu* Branch *et al.* 1996), form a monophyletic group with a high level of support under Bayesian inference. This group includes *P. geitje*, the type species of *Pachydactylus*, and we apply this generic name to all members of this speciose clade. This action results in a change only in the status of the two species of *Palmatogecko*, which now become *Pachydactylus rangei* and *Pachydactylus vanzyli*. The latter species was first described (Steyn & Haacke 1966) in a new genus, *Kaokogecko*, but has been rarely cited in the literature. *Kaokogecko*, which had generally been accepted as the sister group of *Palmatogecko sensu stricto* (Haacke 1976d; Joger 1985; Bauer 1990), was sunk into the synonymy of the older name by Kluge & Nussbaum (1995). *Palmatogecko rangei*, however, has been of particular biological interest because of its locomotor specialisations (see Russell & Bauer 1990) and has been cited frequently in both the technical and popular literature. Nonetheless, the unequivocal demonstration that the derived

features of *Palmatogecko* have evolved deep within the phylogeny of small-bodied *Pachydactylus* (Lamb & Bauer, in press) clearly necessitate its generic reallocation. Alternative strategies to maintain monophyletic groups while retaining *Palmatogecko* as valid (either inclusive or exclusive of *P. austeni*) would minimally necessitate the erection of a new genus for clade E and require either the erection of a new genus to accommodate the *capensis* and *serval/weberi* clades or their reallocation to *Palmatogecko*. Either scenario is unambiguously more disruptive to existing usage than that proposed by us.

Pachydactylus Wiegmann, 1834, Herpetol. Mexic.: 19 (non *Pachydactylus* Menge, 1868 = Arachnomorpha). Type species: *Pachydactylus bergii* Wiegmann, 1834 [= *Pachydactylus geitje* (Sparrman, 1778)], by monotypy.

Colobopus Fitzinger, 1843, Syst. Rept.: 19. Type species: *Anoplopus innunguis*, Wagler, 1830 (= *Gecko inunguis* Cuvier, 1817) [= *Pachydactylus geitje* (Sparrman, 1778)], by original designation.

Cantinia Gray, 1845, Cat. Spec. Liz. Coll. Brit. Mus.: 167 (non *Cantinia* Rye = *Coleoptera*). Type species: *Pachydactylus elegans* Gray, 1845 [= *Pachydactylus capensis* (A. Smith, 1845)], by original designation.

Diagnosis.—*Pachydactylus*, which includes species exhibiting a great diversity of body forms, is difficult to diagnose with respect to other members of the larger clade of which it is a member. There are presently no derived morphological features characterising all *Pachydactylus* exclusive of *Colopus*, although such features will be presented in a more detailed monograph and revision of the *Pachydactylus* Group (Bauer *et al.,* in prep.). However, the following combination of features may be used to diagnose the genus: body usually small (adults < 65 mm SVL, except for *P. namaquensis* group - to 85 mm SVL), short and stout to slender and moderately elongate; dorsal surface of skull smooth; digit I of manus and pes hyperphalangic (phalangeal formulae - 3-3-4-5-3 manus and 3-3-4-5-4 pes), with or without

paraphalanges and interdigital webbing, sub-digital surfaces granular (without scansors) or bearing 2-11 subdigital lamellae beneath digit IV; precloacal pores lacking; tail cylindrical to depressed in cross section; dorsal skin smooth to tuberculate, fragile or not.

Content.—*Pachydactylus affinis* Boulenger, 1896; *P. amoenus* Werner, 1910; *P. angolensis* Loveridge, 1944; *P. austeni* Hewitt, 1923; *P. barnardi* FitzSimons, 1941; *P. bicolor* Hewitt, 1926; *P. capensis* (A. Smith, 1846); *P. caraculicus* FitzSimons, 1859; *P. fasciatus* Boulenger, 1888; *P. formosus* Smith, 1849; *P. gaiasensis* Steyn & Mitchell, 1967; *P. geitje* (Sparrman, 1778); *P. haackei* Branch, Bauer & Good, 1996; *P. katanganus* de Witte, 1953; *P. kladaroderma* Branch, Bauer & Good, 1996; *P. kobosensis* FitzSimons, 1938; *P. labialis* FitzSimons, 1938; *P. maculatus* Gray, 1845; *P. mariquensis* (Sclater, 1898); *P. oculatus* Hewitt, 1927; *P. oreophilus* McLachlan & Spence 1967; *P. oshaughnessyi* Boulenger, 1885; *P. parascutatus* Bauer, Lamb & Branch 2002; *P. punctatus* Peters, 1854; *P. rangei* (Andersson, 1908), **comb. nov.**; *P. robertsi* FitzSimons, 1938; *P. rugosus* A. Smith, 1849; *P. sansteynae* Steyn & Mitchell, 1967; *P. scherzi* Mertens, 1954; *P. scutatus* Hewitt, 1927; *P. serval* Werner, 1910; *P. tigrinus* Van Dam, 1921; *P. tsodiloensis* Haacke, 1966; *P. vansoni* FitzSimons, 1933; *P. vanzyli* (Steyn & Haacke, 1966), **comb. nov.**; *P. waterbergensis* Bauer & Lamb, 2003; *P. weberi* Roux, 1907.

Distribution.—All of southern Africa except higher elevations of the Drakensberg, extending northward into Angola, the southern Democratic Republic of Congo, northern Malawi and northern Mozambique.

Biogeography.—The basal division in the southern African *Pachydactylus* Group is between diurnal geckos of the genus *Rhoptropus* and all remaining taxa. *Rhoptropus* is restricted to arid to hyperarid regions of Namibia and southern Angola, occupying the Namib and Pronamib and extending inland in places to approximately the 300 mm rainfall isohyet (Bauer *et al.* 1993; Bauer & Good 1996). Within the remaining groups, *Elasmodactylus* may be regarded as a truly tropical genus, with *E. tuberculosus* occurring in Tanzania, northern Zambia, and the southern Democratic Republic of Congo (DRC) and *E. tetensis* distributed in northeastern Zimbabwe, throughout northern Mozambique and southern Malawi north to Tanzania.

Chondrodactylus has the widest distribution of any of the clades. The range of *C. turneri* extends from South Africa well into Kenya and at least as far as central Angola (Benyr 1995), and that of *C. angulifer* spans more than 15° of latitude in the arid and semi-arid western part of the subcontinent. *Chondrodactylus bibronii* is more limited to temperate areas of South Africa, whereas *C. fitzsimonsi* has a relatively restricted range in northwestern Namibia and adjacent Angola. *Colopus* is essentially an exclusively arid zone genus, with *C. kochii* being restricted to the gravel plains of central and northern Namibia and *C. wahlbergii* being the only member of the *Pachydactylus* Group that qualifies as a Kalahari endemic (Haacke 1976b, 1984).

Within *Pachydactylus* (as newly construed) most of the larger clades are geographically coherent. The northwestern group has its greatest species richness along the Northern Namibian Escarpment (*sensu* Irish 2002) in an area that is largely coincident with the Kaokoveld centre of Floral Endemism (Volk 1966; van Wyk & Smith 2001). The one exception is *P. punctatus*, which has a vast distribution from lowland Mozambique to the Pronamib, and from south of the Orange River to northern Malawi and the southern DRC, with minimal morphological variation across the range (Bauer & Branch 1995). Based on Bayesian inference, the sister group of the

northwestern group is the *P. namaquensis* group, with its three recognised species distributed in the semiarid to arid zones of the Western and Northern Cape provinces of South Africa and in southwestern Namibia. All remaining *Pachydactylus* may be divided into a mostly southern and western group (the *P. geitje* and *P. rugosus* groups) and a group including the *capensis* group (mostly central and eastern), the *serval/weberi* group (mostly western and northwestern) and the *rangei* group (coastal Namib and adjacent regions).

Carranza *et al.* (2002) estimated the divergence between *Pachydactylus* and *Tarentola* at 14-24 MY based on the nonparametric rate smoothing method with two geologically estimated calibration points. A much older scenario was proposed by Joger (1985) based on immunological distance data, who postulated that basal divergences in the southern African *Pachydactylus* Group extend back to the earliest Tertiary. We have not estimated dates on our tree, but the divergences among major clades within the *Pachydactylus* Group are quite deep, certainly corresponding to at least Miocene cladogenesis. For example, divergence levels (Kimura two-parameter) for cyt*b* average 34 % among pairwise comparisons between *Elasmodactylus* versus *Pachydactylus* s.s., and mean distance of 26% within the small-bodied *Pachydactylus* is remarkably high. Indeed, the observed levels of cyt*b* divergence greatly exceed comparisons for other lizard congeners as well as most congeneric and confamilial distances for vertebrates in general (Johns & Avise 1998). Uncorrected sequence divergences for RAG-1 are similarly substantial; an average value of 6.2% between the distantly related *Gekko gecko* (AY662625) and members the southern *Pachydactylus* Group provides perspective for the 5.2% mean divergence observed for *Elasmodactylus* versus *Pachydactylus* s.s.

Candidate vicariant events in this time frame include the uplift of the great Western Escarpment about 18 MY (Moon & Dardis 1988) and the initiation of hyperarid conditions in the Namib by the establishment of the Benguela upwelling along the Namibian coast in the Late Miocene (Siesser 1980). This latter event has been implicated in cladogenesis and the evolution of dune-dwelling adaptations of both gerrhosaurid lizards (Lamb *et al.* 2003) and lacertid sand lizards (Arnold 1991; Lamb & Bauer 2003) and may have played a role in the origin and/or speciation of the *P. rangei* group. River courses are another category of putative agents of cladogenesis. Although regarded by some (e.g., Gascon *et al.* 2000; Matthee & Flemming 2002) as relatively unimportant for terrestrial species, rivers have been identified as possible agents in lineage splitting in the cordylid genus *Platysaurus* (Scott *et al.* 2004). Bauer (1999) suggested a role for the Orange River in the history of the *Pachydactylus serval* group and Bauer & Lamb (2002) hypothesised that the Zambezi and Limpopo rivers were associated with cladogenesis in the *P. capensis* group.

Climate change has also been postulated to have been important in the diversification of the southern African biota. In particular, Plio-Pleistocene temperature fluctuations, pluvial cycles and their associated vegetational changes are believed to have been significant drivers of faunal change in the subcontinent (Deacon & Lancaster 1988; deMenocal 2004), and have been regarded as likely agents in promoting population isolation and speciation in several squamate groups (e.g., Matthee & Flemming 2002; Tolley *et al.* 2004). Older divergences in other lizard groups (e.g., Daniels *et al.* 2002, 2004; Matthee *et al.* 2004) have been associated with Miocene climatic events, such as cooling associated with the development of the south polar ice cap (Woodruff *et al.* 1981) and the initiation of the cold Benguela current system along the west coast (Siesser 1978, 1980) or cooling and drying caused by the northward rift of the African

continent and the closure of the Tethys seaway (Axelrod & Raven 1978; Tyson 1986). Modelling studies have demonstrated that many southern African organisms, including reptiles, are highly vulnerable to the effects of climate change (Erasmus *et al.* 2002; Midgley *et al.* 2003), supporting the idea that climate change may be an important factor in range fragmentation and potentially in cladogenesis.

On the whole, the *Pachydactylus* Group exhibits extensive regional endemism throughout southern Africa, but this is especially so in the arid western part of the subcontinent corresponding to the Nama-Karoo and Desert biomes (Jürgens 1991; Irish 1994). Species richness in *Pachydactylus* is greatest in northwestern Namibia, a pattern typical of many lizard groups (Crowe 1990). As for many other organisms in this region, endemism is particularly high along the Western Escarpment and in the area to the west, particularly in association with rocky substrates (Barnard *et al.* 1998; Maggs *et al.* 1998; Simmons *et al.* 1998).

Bauer (1999) emphasised substrate specificity as an important factor in the promotion of cladogenesis in the *Pachydactylus* Group. The interplay of sand and rock substrates has resulted in the isolation of psammophilous forms because of their inability to colonise or even traverse rocky substrates intervening between sand accumulations. Predominantly arid conditions have existed in the Namib since the Late Cretaceous (Ward *et al.* 1983; Ward & Corbett 1990) and suggest that such isolating mechanisms could have been at play throughout the Tertiary in at least parts of the subcontinent. A variety of such "shifting sand" scenarios have been proposed as mechanisms promoting cladogenesis in a diversity of animals, including reptiles (Gordon & Griffin 1989; Simmons *et al.* 1998) and might also explain divergence within the *P. rangei* clade (Bauer 1999). Likewise the presence of isolated populations of *P. punctatus* and of the endemic *P. katan-*

ganus in southeast Katanga, DRC may have been the result of the "entrapment" of these taxa on remnant Kalahari "sand islands" within extensive savannah (Dapper 1988; Stokes *et al.* 1997; Broadley & Cotterill 2004).

The same scenarios have been invoked to account for isolation and subsequent speciation of obligate rupicolous species on inselbergs isolated by sandy substrates (Haacke 1982; Bauer 1993). For example, Bauer (1999) considered shifts in the Namib sand seas as causative in the diversification of *Rhoptropus*, whereas changes in the extent of the Kalahari sands have been implicated in speciation of strictly rupicolous *Platysaurus* (Broadley 1978; Jacobsen 1994).

Concordant areas of endemism may be expected among groups of organisms that respond similarly to historical and/or ecological conditions. Among lizards, both cordylids and geckos include many species that are highly substrate specific in microhabitat, resulting in low vagility and often narrowly circumscribed distributional ranges (Mouton & van Wyk 1994; Bauer 1999). Scorpions are another group that share similar constraints and exhibit high species richness in the arid southwest zone (Griffin 1998; Prendini 2000, 2001b, 2003, 2004; Prendini *et al.* 2003). In an argument paralleling that of Bauer (1999) for geckos, Prendini (2001b) argued that substrate specificity in scorpions, as well as other arthropod groups, has promoted vicariance and resulted in higher rates of speciation and greater species richness for stenotopic taxa.

Although the objective definition and delimitation of areas of endemism remains a challenge in biogeographic studies (Linder 2001), the identification of multiple groups sharing similar distributions sets the stage for a proper analysis. Until recently, the absence of robust species-level phylogenies for virtually all southern African biota has precluded the appli-

cation of analytical biogeographic approaches, such as cladistic biogeography (Humphries & Parenti 1999; Cotterill 2004). While narrative approaches comparing geological and climatic data with single phylogenies may be used to identify possible vicariance scenarios, they are inappropriate for testing biogeographic hypotheses. Fortunately, phylogenies adequate for inclusion in a cladistic biogeographic analysis of southern Africa are now available for a number of groups of organisms. *Pachydactylus* Group geckos are particularly appropriate in this regard as they occur in most areas of the subcontinent and exhibit endemism on a relatively fine scale. Other groups that share these features, and for which phylogenetic hypotheses exist include lacertids (Arnold 1991; Harris *et al.* 1998; Lamb & Bauer 2003), some scincids (Daniels *et al.* 2002; Whiting *et al.* 2003), cordylids (Frost *et al.* 2001; Scott *et al.* 2004), and especially scorpions (Prendini 2001a; Prendini *et al.* 2003). The combined analysis of phylogenetic patterns across these groups, as well as others, will allow the erection of the first fine-scaled hypothesis of southern African area relationships.

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APPENDIX I

Locality data for specimens sequenced. Collection acronyms: AMB = Aaron M. Bauer field series [specimens to be deposited in NMWN or CAS], CAS = California Academy of Sciences, GJC = Gregory Watkins-Colwell (Yale University, New Haven, USA) private collection, LSUMZ = Louisiana State University, MB = Mirko Barts private collection (Berlin, Germany), NMZB = National Museum of Zimbabwe, PEM = Bayworld (Port Elizabeth Museum), NMWN (formerly SMW) = National Museum of Namibia. Acronyms in square brackets indicate ultimate repository for specimens not yet accessioned into public museum collections.

CHONDRODACTYLUS

C. angulifer: AMB 5873 [NMWN], Farm Daweb, 2 km S Maltahöhe, Namibia; CAS 193829, 40.5 km W Orupembe, Namibia. **C. bibronii**: CAS 206821, 44 km S Port Nolloth on Kleinsee Road, Northern Cape, South Africa; CAS 214457, Farm Avondschijn, Northern Cape, South Africa (26° 52' 26" S, 21° 07' 29" E); CAS 197920, 24 km S Jansenville, Eastern Cape, South Africa (33° 04' 16" S, 24° 51' 57" E); CAS 200002, 10 km S Steinkopf, Northern Cape, South Africa (29°20'16"S, 17°47'31"E). **C. fitzsimonsi**: AMB 5995 [NMWN], CAS 206981, 34.3 km S Epupa Falls, Kunene Region, Namibia. **C. turneri**: LSUMZ 57335, Richtersveld National Park, Northern Cape, South Africa (28° 09' 57" S, 17° 01' 5" E); AMB 6132 [CAS], Aventura Eco Camp, Tshipise, Limpopo Province, South Africa (22° 36' 22" S, 30° 10' 35" E).

COLOPUS

C. kochii: CAS 214533, 20.1 km N Swakopmund, Namibia (22° 30' 14" S, 14° 29' 16" E); CAS 214557, 12 km N Swakopmund, Namibia (22° 34' 05" S, 14° 31' 16" E) . **C. wahlbergii**: MB, no number, no data.

ELASMODACTYLUS

E. tetensis: AMB 5759 [CAS], "Tanzania" (captive specimen); AMB 6180 [CAS], N bank Ruenya River, Mashonaland East, Zimbabwe (17° 15' 19" S, 33° 00' 12" E). **E. tuberculosus**: GJC 311, "Tanzania" (captive specimen).

PACHYDACTYLUS

P. affinis: AMB 6157-58 [CAS], vic. Verona, Mpumalanga, South Africa. **P. austeni**: CAS 206885, 1.5 km S Buffels River Mouth, Kleinsee, Northern Cape, South Africa (29° 42' 15" S, 17° 03' 42" E); CAS 186318, McDougall Bay, Northern Cape, South Africa. **P. barnardi**: CAS 206722, Groenriviermond, Northern Cape, South Africa; CAS 206831, Farm Kourootje, Northern Cape, South Africa. **P. bicolor**: CAS 214681-82, 68 km W Kamanjab on Torr Bay Road, Namibia (19° 43' 00" S, 14° 18' 40" E). **P. caraculicus**: CAS 206980, 41.9 km N Okanguati on Epupa Falls Road, Namibia; CAS 193804, 44.3 km N Okanguati, Namibia. **P. capensis**: AMB 6057a [embryo], 32 km south Jamestown, Eastern Cape, South Africa (31° 21' 51" S, 26° 43' 19" E); CAS 214501, Farm Avondschijn, Northern Cape, South Africa (29° 20' 16" S, 17° 47' 31" E). **P. fasciatus**: CAS 193681, 59.3 km W Kamanjab, Kunene Region, Namibia (19° 39' 06" S, 14° 21' 20" E); CAS 206936, 10 km E of Spitzkop turnoff on Usakos-Hentiesbaai Rd., Namibia (21° 57' 08" S 15° 16' 48" E). **P. formosus**: CAS 193250, Olifants River, Western Cape, South Africa; CAS 206715, Pakhuispas, Western Cape, South Africa. **P. gaiasensis**: CAS 214626-27, vic. Gai-As, Namibia (20° 47' 18" S, 14° 06' 44" E). **P. geitje**: CAS 175414, CAS 206687, Jacobsbaai, Western Cape, South Africa. **P. haackei**: PEM R11899, Richtersveld National Park, Northern Cape, South Africa (28° 07' 59" S 16° 59' 20" E); PEM R12523, Farm Kinderzitt, Namibia (28° 39' 34" S, 18° 41' 47" E). **P. kladaroderma**: PEM R11195, Molteno Pass, Western Cape, South Africa (32° 15' 09" S, 22° 34' 07" E); CAS 198301, 25 km NE Sutherland, Western Cape, South Africa (32° 22' 17" S, 20° 56' 12" E). **P. labialis**: CAS 193594, SE Gate, Richtersveld National Park, Northern Cape, South Africa; CAS 206865, Farm Vaalkol, Northern Cape, South Africa (29° 48' 29" S, 17° 21' 21" E). **P. maculatus**: AMB 6056 [CAS], 2 km S. Sundays River Bridge on Port Elizabeth-Addo Rd., Eastern Cape Province, South Africa (33° 34' 51" S, 25° 37' 40" E); PEM R15011, Swartkops, Port Elizabeth, Eastern Cape, South Africa. **P. mariquensis**: CAS 200076, 5.5 km N Kuboes on Kuboes Fountain Road, Northern Cape, South Africa (28° 25' 23" S, 17° 00' 40" E); PEM R15832, Springbok, Northern Cape, South Africa. **P. namaquensis**: PEM R11867, Skilpad Nature Reserve, nr. Kamieskroon, Northern Cape, South Africa; CAS 206923, 11 km S Steinkopf, Northern Cape, South Africa (29° 20' S, 17° 48' E). **P. oculatus**: CAS 198304, SE Sutherland, Northern Cape, South Africa (32° 39' 17" S, 20° 45' 55" E); PEM FN

1253 [PEM], NW Molteno Pass, Western Cape, South Africa (32° 03' 56" S, 22° 27' 01" E). *P. oreophilus*: CAS 214736, 214754, Para Camp, 2 km N Sesfontein, Namibia (19° 07' 28" S, 13° 35' 29" E). *P. oshaughnessyi*: NMZB 16431,16432, Marivalle Ranch, Kwekwe, Zimbabwe. **P. parascutatus**: CAS 214735, NMWN R 9454, vic. Para Camp, 2 km N Sesfontein, Namibia (19° 07' 28" S, 13° 35' 29" E); CAS 214749, Purros Rd., ca. 27 km W of Sesfontein, Namibia (19° 03' 16" S, 13° 30' 08" E); CAS 214750, Purros Rd., ca. 8 km W Sesfontein, Namibia (19° 10' 05" S, 13° 34' 03" E). *P. punctatus*: PEM R12537, Witputs Annex, approx. 50 km N Rosh Pinah, Namibia (27° 39' 33" S, 16° 47' 38" E); CAS 193670, 30.5 km W Kamanjab, Namibia (19° 34' 34" S, 14° 35' 56" E). *P. rangei*: CAS 214577, Rooibank, Namibia (23° 11' 21" S, 14° 38' 30" E); CAS 214780, Rooibank, Namibia (23° 11' 53" S, 14° 39' 29" E). *P. rugosus*: CAS 206958, 24 km W of C 35 jct. on Hentiesbaai-Uis Rd., Namibia (21° 18' 17" S, 14° 35' 14" E); CAS 201905, Sendelingsdrif Dump, Richtersveld National Park, Northern Cape Province, South Africa (28° 05' 02" S 16° 56' 30" E). *P. sansteynae*: CAS 214589, Skeleton Coast National Park, ca. 1 km S of Huab River Bridge, Namibia (20° 54' 03" S, 13° 32' 01" E); CAS 214767, Skeleton Coast National Park, N bank of Huab River at Huab River Bridge, Namibia (20° 54' 04" S, 13° 31' 30" E). *P. scherzi*: CAS 206956, 22.7 km N. of Ugab River crossing on rd. from Brandberg West Mine, Namibia (20° 47' 17" S, 14° 06' 41" E; CAS 193817, 37.0 km W Orupembe, Namibia *P. scutatus*: AMB 5943, Sesfontein Rd., 25.3 km N Palmwag, Namibia; CAS 193673, Kamanjab-Torrabaai Rd., Namibia (19° 37' 27" S, 14° 43' 19" E). *P. serval*: CAS 176252, 7 km N Grabwasser, Namibia; AMB 5013 [NMWN], Witputs Annex, approx. 50 km N Rosh Pinah, Namibia (27° 39' 33" S, 16° 47' 38" E). *P. tigrinus*: AMB 6163 [CAS], Dora Communal Land, Mutare, Zimbabwe; AMB 6188 [CAS], vic. Elim Mission, Nyanga District, Zimbabwe. *P. tsodiloensis*: MB, no number, Tsodilo Hills, Botswana. *P. vansoni*: CAS 195392, Lebombo foothills, KwaZulu/Natal, South Africa; AMB 6071 [CAS], 19 km SE Ingwavuma, KwaZulu-Natal, South Africa. *P. vanzyli*: CAS 193830, 40.5 km W Orupembe, Namibia); AMB 5979 [NMWN], Ondonduiengo Riverbed, Namibia (17° 50' 54" S, 12° 07' 28" E). *P. weberi*: CAS 206754, Kleinsee, Northern Cape Province, South Africa (29° 38' 49" S, 17° 05' 02" E); CAS 206902, 11 km S Steinkopf, Northern Cape, South Africa (29° 20' S, 17° 48' E).

RHOPTROPUS

R. afer: CAS 206949, 17.3 km E Hentiesbaai on Usakos Rd., Namibia (22° 03' 04" S, 14° 26' 29" E); CAS 193868, 30 km N Swakopmund on Hentiesbaai Rd., Namibia. *R. boultoni*: CAS 193661, 62.1 km E Kamanjab on Outjo Rd., Namibia; CAS 206975, E border of Skeleton Coast National Park, Namibia (17° 49' S, 12° 08' E).

TARENTOLA

T. mauritanica: AMB no number, vic. Gerona, Spain. *T. annularis*: 2 specimens, no data.

APPENDIX II

GenBank accession numbers for gene sequences used in this study.

Species	cyt*b*	12S rRNA	16S rRNA	RAG-1
Chondrodactylus angulifer	AY123394	DQ275403	AY123372	DQ275447
Chondrodactylus bibronii	AY026927	DQ275406	AY026935	DQ275450
Chondrodactylus fitzsimonsi	AF449125	DQ275404	AF449109	DQ275448
Chondrodactylus turneri	AF449124	DQ275405	AF449108	DQ275449
Colopus kochii	AY123398	DQ275374	AY123376	DQ275418
Colopus wahlbergii	AY123395	DQ275375	AY123373	DQ275419
Elasmodactylus tetensis	AY026926	DQ275407	AY026934	DQ275451
Elasmodactylus tuberculosus	AF449734	DQ275408	AF449119	DQ275452
Pachydactylus affinis	AY123414	DQ275389	AY123393	DQ275433
Pachydactylus austeni	AF449126	DQ275371	AF449110	DQ275415
Pachydactylus barnardi	AY123410	DQ275378	AY123388	DQ275422
Pachydactylus bicolor	AY123400	DQ275394	AY123378	DQ275438
Pachydactylus caraculicus	AY123399	DQ275393	AY123377	DQ275437
Pachydactylus capensis	AF449133	DQ275387	AF449117	DQ275431
Pachydactylus fasciatus	AF449128	DQ275384	AF449112	DQ275428
Pachydactylus formosus	AY123411	DQ275377	AY123389	DQ275421
Pachydactylus gaiasensis	AY123407	DQ275399	AY123385	DQ275443
Pachydactylus geitje	AF449132	DQ275380	AF449116	DQ275424
Pachydactylus haackei	AF449121	DQ275402	AF449105	DQ275446
Pachydactylus kladaroderma	AF449722	DQ275401	AF449106	DQ275445
Pachydactylus labialis	AF449130	DQ275379	AF449114	DQ275423
Pachydactylus maculatus	AF449127	DQ275382	AF449111	DQ275426
Pachydactylus mariquensis	DQ278601	DQ275370	DQ278599	DQ275414
Pachydactylus namaquensis	AF449123	DQ275400	AF449107	DQ275444
Pachydactylus oculatus	AY123402	DQ275381	AY123380	DQ275425
Pachydactylus oreophilus	AY123406	DQ275398	AY123384	DQ275442
Pachydactylus oshaughnessyi	AY123413	DQ275391	AY123391	DQ275435
Pachydactylus parascutatus	AY123405	DQ275397	AY123383	DQ275441
Pachydactylus punctatus	AF449135	DQ275411	AF449120	DQ275455
Pachydactylus rangei	AY123397	DQ275373	AY123375	DQ275417
Pachydactylus rugosus	AF449129	DQ275376	AF449113	DQ275420
Pachydactylus sansteynae	AY123404	DQ275396	AY123382	DQ275440
Pachydactylus scherzi	AY123401	DQ275392	AY123379	DQ275436
Pachydactylus scutatus	AY123403	DQ275395	AY123381	DQ275439
Pachydactylus serval	AY123409	DQ275385	AY123386	DQ275429
Pachydactylus tigrinus	AY123412	DQ275390	AY123390	DQ275434
Pachydactylus tsodiloensis	AY123408	DQ275383	AY123387	DQ275427
Pachydactylus vansoni	AY123415	DQ275388	AY123393	DQ275432
Pachydactylus vanzyli	AY123396	DQ275372	DQ278600	DQ275416
Pachydactylus weberi	AF449131	DQ275386	AF449115	DQ275430
Rhoptropus afer	AY026923	DQ275409	AY026931	DQ275453
Rhoptropus boultoni	AY026922	DQ275410	AY026930	DQ275454
Tarentola mauritanica	AF364327	DQ275413	AY828499	DQ275456
Tarentola annularis	AF364322	DQ275412	AF363571	DQ275456