Footprints in the sand: independent reduction of subdigital lamellae in the Namib–Kalahari burrowing geckos

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Many desert organisms exhibit convergence, and certain physical factors such as windblown sands have generated remarkably similar ecomorphs across divergent lineages. The burrowing geckos *Colopus*, *Chondrodactylus* and *Palmatogecko* occupy dune ecosystems in the Namib and Kalahari deserts of southwest Africa. Considered closely related, they share several putative synapomorphies, including reduced subdigital pads (toe pads) and spinose digital scales. Though recognized as part of Africa's ecologically diverse *Pachydactylus* Group, the burrowing geckos' precise phylogenetic affinities remain elusive. Convergent pedal modification provides a tenable alternative explaining the geckos' derived terrestriality and adaptation to Namib and Kalahari sands. We generated a molecular phylogeny for the *Pachydactylus* Group to examine evolutionary relationships among the burrowing geckos and infer historical patterns of pedal character change. Bayesian and parsimony analyses revealed all three burrowing genera to be deeply nested within *Pachydactylus*, each genus belonging to a separate clade. Strong support for these distinct clades indicates ecomorphological adaptations for burrowing have evolved independently three times in the southern *Pachydactylus* Group. We argue that the physical properties of Namib and Kalahari sands played a principal role in selecting for pedal similarity.

Keywords: convergence; ecomorphology; Gekkonidae; phylogenetics; Namib; Kalahari

1. INTRODUCTION

To solve similar environmental problems, unrelated organisms may either evolve different traits or converge on similar solutions. Repeated morphological patterns observed in equivalent ecological settings often disclose convergence wrought by comparable selective forces. While such outcomes support the role of selection, its operational strength is perhaps better gauged by a pattern's frequency of recurrence. East Africa's lacustrine cichlids (Kocher *et al*. 1993; Allender *et al*. 2003), Caribbean *Anolis* lizards (Losos *et al*. 1998), coral reef wrasses (Westneat *et al*. 2005), and *Myotis* bats (Ruedi & Mayer 2001) all provide exemplary cases, in which particular ecomorphs have arisen multiple times under similar environmental conditions. The independent origins of traits documented in these studies provide important evidence for the role of ecological selection pressures in evolution.

Many desert lizards also exhibit broad convergence, and certain xeric environments—for example, the loose, windblown sand of dunes—have produced remarkably similar evolutionary outcomes in several divergent taxa (Pough 1969; Pianka 1986; Arnold 1995). One conspicuous pattern shared among sand-dwelling (psammophilous) lizards is pedal specialization, often involving the elaboration of lateral phalangeal scales into fringes that

facilitate running or 'swimming' in loose sand (Luke 1986). Dune-dwelling adaptation has taken different forms in geckos, including the evolution of toe fringes, though the six genera possessing such fringes are all primitively terrestrial forms (Bauer & Russell 1991). Within arboreal gecko lineages, the digits of psammophilous taxa have instead undergone morphological reduction, resulting in diminution or loss of the gekkotan subdigital pad—arguably one of nature's most complex pedal structures (Russell 2002).

In most geckos, climbing involves dry adhesion, a function of the subdigital pads (toe pads), whose millions of hair-like setae interact via van der Waals forces with substrate surfaces (Autumn *et al*. 2002; Huber *et al*. 2005). Adhesion requires proximity between setae and substrate, and geckos achieve this intimate contact by engaging adipose pads or vascular sinuses that subtend the setal-bearing plates (lamellae). Fine-tuned control governing the kinematics of setal attachment and detachment is accomplished by elaborate musculotendinous networks (Russell 2002). Remarkably, toe pads have evolved on multiple occasions in geckos, once in the Diplodactylidae and several times within the Gekkonidae (Russell 1979; Han *et al*. 2004). Conversely, taxa in both families have also lost this adhesive system, having undergone ecological shifts from arboreal to terrestrial adaptive zones (Bauer & Russell 1991).

Chondrodactylus, *Colopus* and *Palmatogecko* are terrestrial gekkonids endemic to arid southwest Africa. Although their toe pads are greatly reduced or altogether absent (figure 1), myological characters supporting their
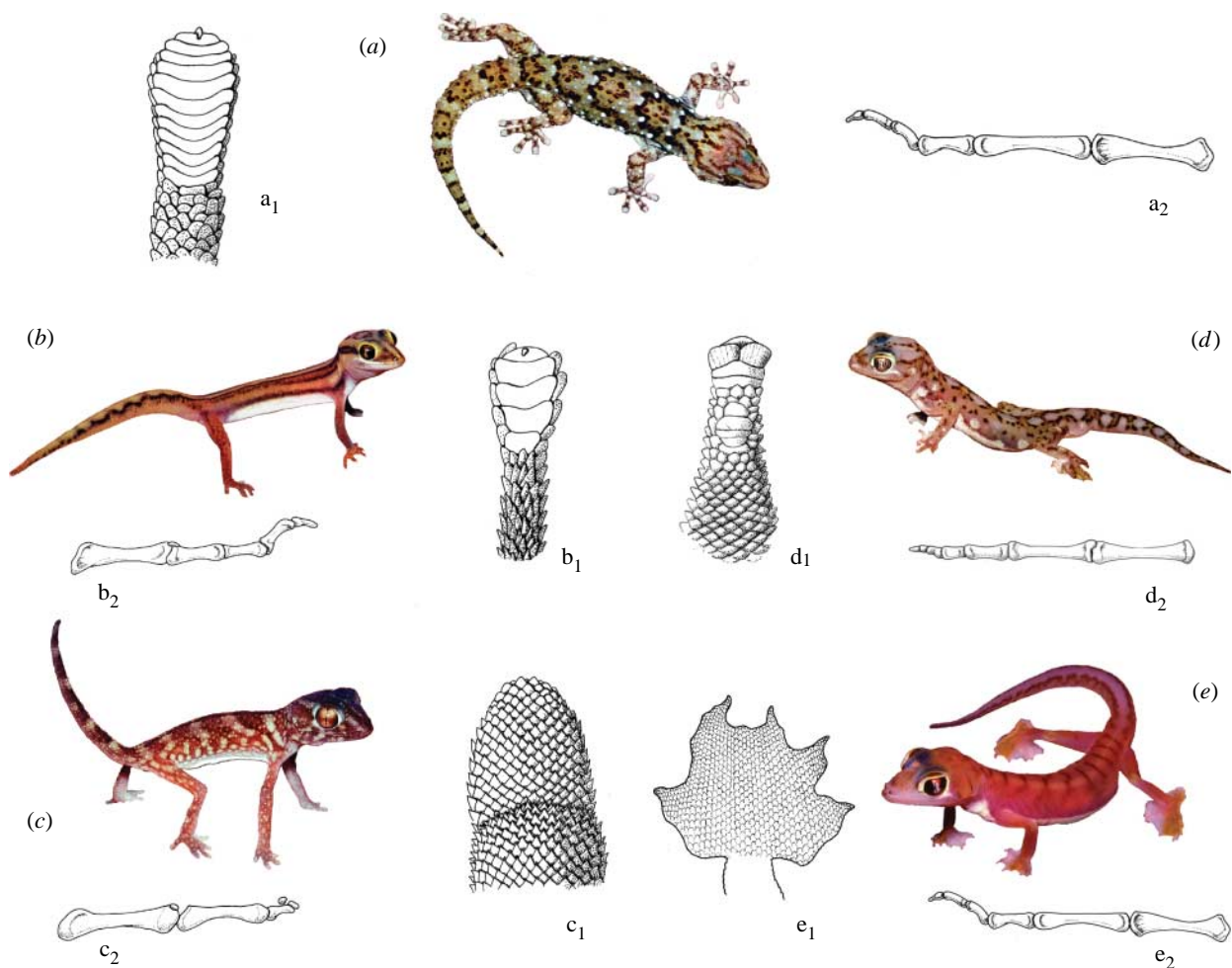
Figure 1. *Pachydactylus turneri* (*a*) representing the plesiomorphic (=climbing) subdigital condition for the *Pachydactylus* Group—and the four species of burrowing geckos, (*b*) *Colopus wahlbergii*, (*c*) *Chondrodactylus angulifer*, (*d*) *Palmatogecko vanzyli*, and (*e*) *Palmatogecko rangei*. Digital modifications in the burrowing genera are revealed in ventral surface (a_1, b_1, c_1, d_1) and phalangeal element (a_2, b_2, c_2, d_2, e_2) illustrations of digit IV of the manus. Ventral aspect of the entire manus (e_1) is shown for *Palmatogecko rangei*. Note the spinose scales (b_1, c_1, d_1) present on digits of the burrowing taxa.

arboreal ancestry persist (Russell & Bauer 1990; Bauer & Russell 1991). Distinctive spinose scales also cover relatively short digits and/or plantar surfaces of the feet (figure 1). These pedal modifications facilitate locomotion and burrowing in dune systems of the Namib and Kalahari deserts (Haacke 1976d; Bauer & Russell 1991). Speculation is mixed regarding the advent and evolution of pedal modification in these taxa. Key in resolving competing views on terrestrial origins is a clarification of phylogenetic relationships among the three genera—henceforth termed the burrowing geckos—and the lineage to which they belong, the *Pachydactylus* Group (sensu Russell 1972).

The *Pachydactylus* Group is a chiefly African assemblage comprising six genera and 73 nominal species. Spanning arboreal to ultrapsammophilous forms, this ecologically varied clade is united by an additional phalanx (hyperphalangy) in the first digit of both manus and pes (Russell 1972; Haacke 1976d). Hyperphalangy is otherwise rare in geckos; thus, monophyly of the *Pachydactylus* Group is widely accepted (Russell 1972; Haacke 1976d; Bauer 1990a; Kluge & Nussbaum 1995). Two subgroups are recognized: a northern, largely Mediterranean clade (Carranza *et al.* 2002) and a broadly distributed southern lineage (Bauer 1999). In contrast to the rather uniform northern clade (a single genus), the southern lineage exhibits extraordinary morphological variation and phyletic richness, attributed in part to the subcontinent's topographical diversity (Crowe 1990; Bauer 1999).

Pachydactylus is Africa's most species-rich gekkonid genus (40+spp.), occurring throughout the continent's southern sector (Bauer 1999). Its broad distribution encompasses the geographic ranges of *Chondrodactylus*, *Colopus*, *Palmatogecko* and *Rhoptropus*—all the remaining genera in the southern *Pachydactylus* Group. Haacke (1976d) postulated close systematic affinities among *Chondrodactylus*, *Colopus* and *Palmatogecko*, hypothesizing that they formed the sister group of *Pachydactylus*. Similarly, the burrowing geckos formed a monophyletic group that was sister to *Rhoptropus*+*Pachydactylus* in a cladistic analysis of African–Madagascan gekkonid genera (Kluge & Nussbaum 1995). Others (Joger 1985; Bauer 1990a) have suggested that the burrowing geckos may have arisen within *Pachydactylus*. Bauer & Good (1996) hypothesized that *Rhoptropus* is sister taxon to a monophyletic *Pachydactylus* sensu lato, i.e. *Pachydactylus*+ *Chondrodactylus*, *Colopus* and *Palmatogecko*. Clearly, a consensus on evolutionary relationships among these southern genera is yet to be established.

We report DNA sequences for one nuclear and three mitochondrial loci, from which we derive a phylogenetic hypothesis for the southern *Pachydactylus* Group. We use
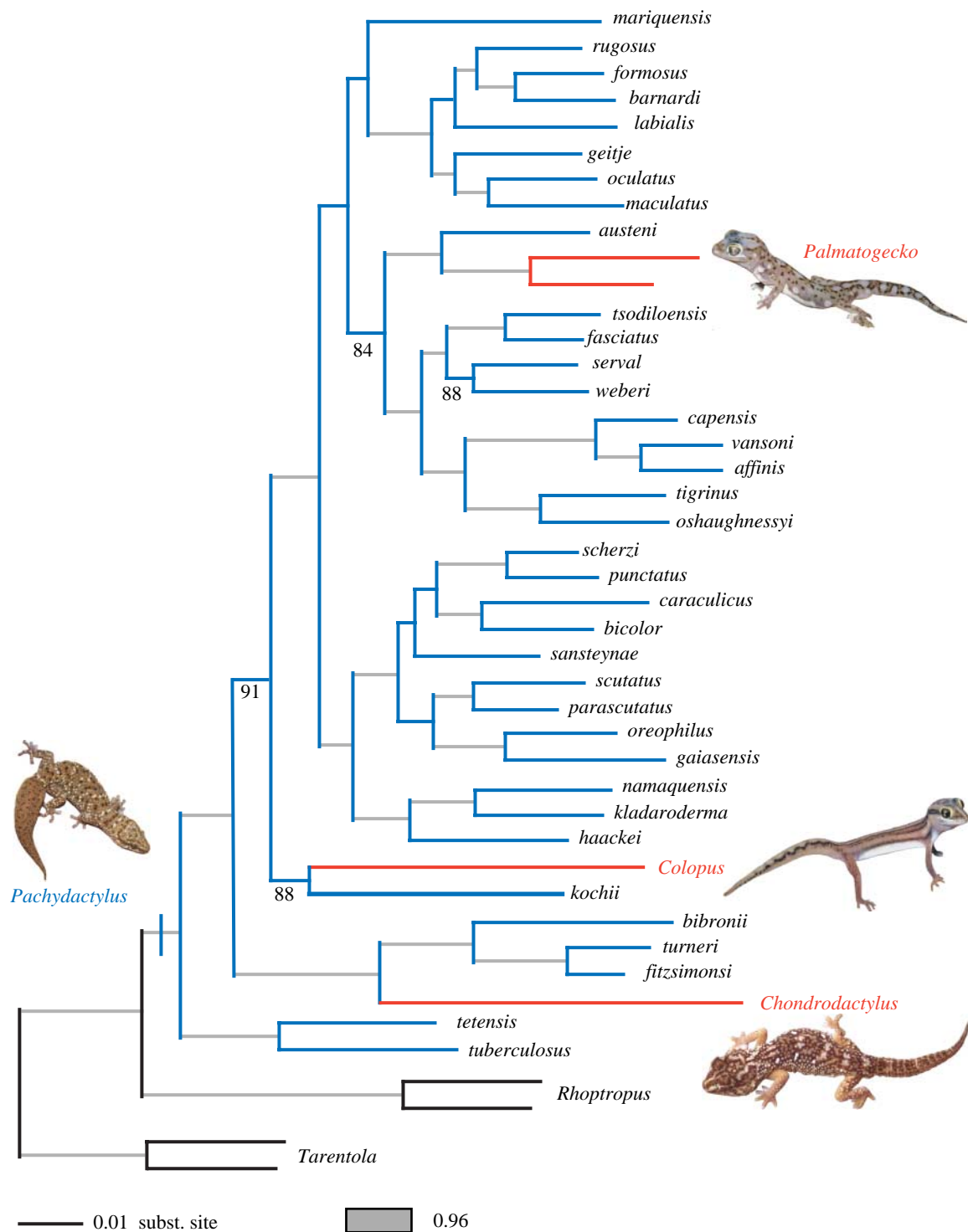
Figure 2. Bayesian inference phylogram for the southern *Pachydactylus* Group. Tree branches are coded blue for *Pachydactylus* and red for the burrowing genera (also illustrated). Specific epithets are those of *Pachydactylus*. Grey branches indicate posterior probabilities (pP)≥0.96; exact pP values between 0.80 and 0.95 are listed below branches.

this molecular phylogeny to establish the systematic status of *Chondrodactylus*, *Colopus* and *Palmatogecko* and address the question: does pedal modification in the burrowing geckos trace to a single origin, or did it arise independently and repeatedly through convergence?

2. MATERIAL AND METHODS

(a) *Taxon sampling*
In addition to the burrowing genera, our sampling regime for the southern *Pachydactylus* Group included 36 species of

Pachydactylus and two of *Rhoptropus* (*R. after* and *R. boultoni*, representing the two major clades within this genus; Lamb & Bauer 2001). Taxon sampling for *Pachydactylus* was effectively complete: only one new and a few undescribed species, all within the uncontested *weberi* group (Bauer & Lamb 2003; Bauer *et al.* in press), were not included in the analyses. The northern African species *Tarentola annularis* and *Tarentola mauritanica* served as outgroups. Sampled taxa, museum voucher numbers, locality data, and GenBank accession numbers are compiled in the electronic supplementary material.

Table 1. Summary statistics for parsimony and Bayesian analyses.

| dataset | no. of sites | no. of informative sites | | AIC model | MRBAYES parameters | |
		Pachydactylus[a]	all		Nst	rates
12S	288	122	131	GTR+I+G	6	invgamma
16S	412		158	GTR+I+G	6	invgamma
Cyt*b*	662					
first pos.		97	106	GTR+I+G	6	invgamma
second pos.		51	57	TVM+I+G	2	invgamma
third pos.		216	217	GTR+I+G	6	invgamma
RAG-1	784					
first pos.		29	41	K81uf+G	2	gamma
second pos.		21	34	HKY+G	2	gamma
third pos.		61	83	K81uf+G	2	gamma
total	1858					

[a] *Pachydactylus*, *Chondrodactylus*, *Colopus* and *Palmatogecko*.

(b) Sequence procurement and alignment

Genomic DNA was extracted from liver, muscle or shed skin using the Qiagen QIAamp DNA Mini kit. Regions from three mitochondrial genes, 12S rRNA ($\cong$ 350 bp), 16S rRNA ($\cong$ 450 bp) and cytochrome b (cyt*b*; $\cong$ 700 bp), were initially selected for phylogenetic analysis. These genes were amplified under a thermal cycling regime of 32 cycles at 92 °C for 45 s, 50–52 °C for 35 s, and 72 °C for 1 min using primers from Bickham *et al.* (1996) for the 12S and 16S fragments and the primer pair L14724 (Meyer *et al.* 1990)+ H15560 (Palumbi *et al.* 1991) for cyt*b*. Given the substitutional saturation observed for a shorter cyt*b* segment among the large-bodied *Pachydactylus* (eight spp. with snout-vent lengths greater than 70 mm; Lamb & Bauer 2002), we also sequenced a more slowly evolving nuclear gene, RAG-1 (Groth & Barrowclough 1999). An 800 bp fragment of RAG-1 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 s, 51 °C for 35 s, 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-labelled terminators (BigDye Terminator kit, Applied Biosystems, Inc).

Sequences were aligned using CLUSTAL X 1.81 (Thompson *et al.* 1997), and 12S and 16S alignments were examined in detail with regard to indel variation, exploring gap placements for a series of gap opening and extension costs. Regions of rRNA sequence for which inferred nucleotide position homologies varied across gap parameters were considered alignment-ambiguous and excluded from further analysis.

(c) Phylogenetic analysis

Our phylogenetic reconstruction relies predominantly on partitioned Bayesian analysis. We used MRMODELTEST 2.0 (Nylander 2004) to identify appropriate models of sequence evolution for the 12S and 16S genes, and for each codon position within cyt*b* and RAG-1, based on the Akaike information criterion (AIC). We used MRBAYES 3.0b4 (Huelsenbeck & Ronquist 2001) to conduct a Bayesian analysis, incorporating eight discrete substitution parameters 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 trees every 100 generations. We used

the Metropolis-coupled Markov chain Monte Carlo algorithm, engaging four incrementally heated Markov chains. To ensure Markov chains did not become entrapped on local optima, we analysed the combined data in three separate runs. Burn-in was determined graphically; trees generated prior to burn-in (generally, the first 500 trees) were discarded. We used the MRBAYES *sumt* command to create a majority rule consensus tree (*all compat*), generate an average likelihood score, calculate posterior clade probabilities (pP), and estimate average branch lengths across post burn-in trees.

We also analysed the sequence data using maximum parsimony (MP), allowing comparisons to clades (and their support) identified by Bayesian inference. Prior to MP analysis, we conducted an incongruence length difference test, 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 contradict the congruence of the four gene sequence partitions ($P=0.970$), which were combined for MP analysis. Parsimony trees were generated by a heuristic search in PAUP*, with tree bisection-reconnection branch swapping, MULPARS (save all equally most parsimonious trees) and random addition of sequences (1000 replicates). Nodal support for MP trees was estimated by a bootstrap analysis involving 1000 pseudoreplicates.

3. RESULTS

(a) Phylogenetic reconstruction

Upon exclusion of ambiguously aligned regions in the 12S and16S sequences, the combined data comprised 1858 nucleotides. Sequence variation, substitution models, and Bayesian parameters for the gene partitions are summarized in table 1.

The three Bayesian runs yielded statistically equivalent log-likelihood scores and identical consensus trees, supporting their convergence. Figure 2 depicts this consensus phylogram in which *Rhoptropus* is sister to the other southern group species (pP =1.0), and all three burrowing genera lie embedded within *Pachydactylus* (pP =1.0). The basal clade of *Pachydactylus* contains the two tropical African species, *Pachydactylus tetensis* and *Pachydactylus tuberculosus*. The remaining species of *Pachydactylus*, together with the three burrowing genera, form an assemblage (pP =1.0) with a largely arid zone distribution across southern Africa. Moreover, each
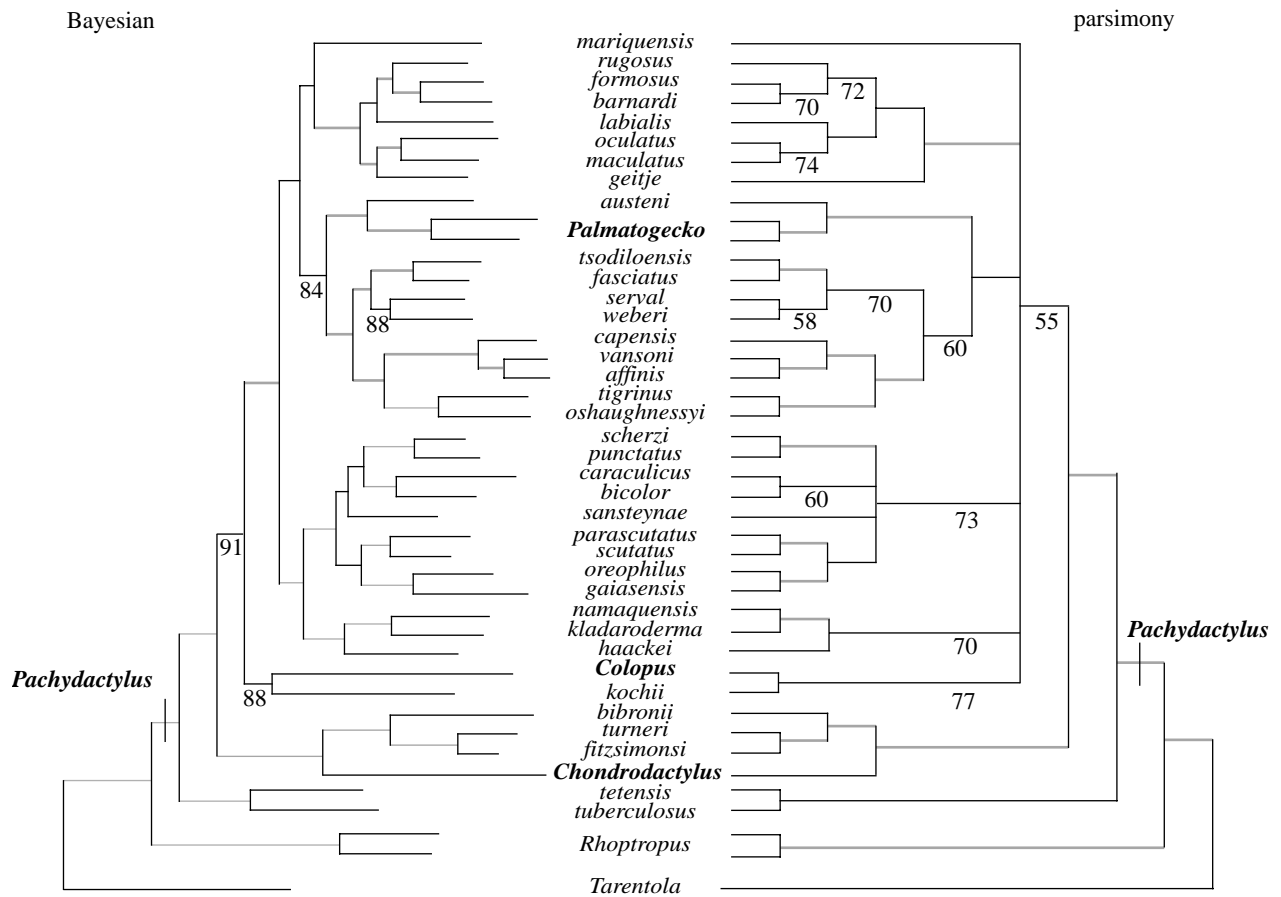
Figure 3. Comparison of Bayesian and MP trees, the latter a strict consensus of two equally parsimonious trees. Specific epithets are those of *Pachydactylus*; burrowing genera are listed in bold. Grey branches indicate posterior probabilities (pP) ≥ 0.96 and bootstrap values greater than or equal to 80% for the Bayesian and MP trees, respectively.

burrowing genus is placed in a separate clade, revealing three distinct lineage associations within the southern *Pachydactylus* radiation (figure 2). *Chondrodactylus* is sister taxon (pP = 1.0) to the *bibronii* complex, a group of three large-bodied species with well-developed toe pads. Within the remaining clade of *Pachydactylus*, *Palmatogecko* receives strong support (pP = 1.0) as sister taxon to *Pachydactylus austeni* and, elsewhere, *Colopus* is less well supported (pP = 0.88) as sister species to *Pachydactylus kochii*.

MP analysis of 827 informative nucleotides, with 669 sites contributed by the mtDNA partition and 158 by RAG-1, yielded two equally parsimonious trees (TL = 6333; CI = 0.273; RI = 0.351). The MP consensus tree is largely congruent with the Bayesian tree (figure 3). Bootstrap support for the clade of southern African *Pachydactylus* + *Chondrodactylus*, *Colopus* and *Palmatogecko* is reasonably strong (84%; 97%, based solely on the RAG-1 partition), and each burrowing genus falls within the respective clades of *Pachydactylus* recovered by Bayesian inference. Several other well-supported clades identified in both analyses corroborate previously recognized alpha-level groups in *Pachydactylus*, the taxonomic implications of, which will be detailed elsewhere (Bauer & Lamb 2005).

(b) *Hypothesis testing using alternative topologies*
The hypothesis suggesting a single origin for pedal modification in the burrowing geckos is by extension a phylogenetic hypothesis for their monophyly. To assess whether our molecular phylogeny (depicting multiple origins) differs significantly from topologies supporting a single origin, we compared the Bayesian tree with *a posteriori* hypotheses using the Shimodaira–Hasegawa (SH) test (Shimodaira & Hasegawa 1999). We compared the likelihoods of our Bayesian tree to five alternative topologies, constraining the following taxa to be monophyletic: (i) *Chondrodactylus* + *Colopus* + *Palmatogecko*; (ii) *Chondrodactylus* + *Colopus*; (iii) *Chondrodactylus* + *Palmatogecko*; (iv) *Colopus* + *Palmatogecko*; and (v) all species of *Pachydactylus* (exclusive of the burrowing taxa). Each constrained topology was generated by a heuristic parsimony search in PAUP*; its likelihood score was based on a substitution model (GTR+G+I) computed in MRMODELTEST for the combined dataset. Results for all SH tests were highly significant in favour of the Bayesian tree (table 2).

4. DISCUSSION
Geckos have experienced incontestable evolutionary success in xeric ecosystems, forming one of the more significant components of desert vertebrate fauna worldwide (Pianka 1986). The majority possesses toe pads and are rock outcrop (rupicolous) specialists; relatively few desert-dwelling geckos are truly terrestrial, of which fewer still represent pad-bearing lineages (Bauer & Russell 1991). The rarity of such transformation, in conjunction with systematic inferences for the monophyly of *Colopus*, *Chondrodactylus* and *Palmatogecko* (Haacke 1976d; Kluge & Nussbaum 1995), is consistent with interpretations that

Table 2. Results of SH tests comparing the Bayesian inference tree with alternative topologies. ($\varDelta - \ln L$ is the difference in ln-likelihood between the alternative topology as stated and the Bayesian tree depicted in figure 2. Each SH test involved 10 000 RELL optimizations.)

topology	$- \ln L$	$\varDelta - \ln L$	p
Chondrodactylus + Colopus + Palmatogecko monophyly	28 713.92	79.26	0.000
Chondrodactylus + Colopus monophyly	28 681.46	46.97	0.001
Chondrodactylus + Palmatogecko monophyly	28 714.85	80.19	0.000
Colopus + Palmatogecko monophyly	28 688.11	53.62	0.001
Pachydactylus monophyly	28 731.23	96.57	0.000
Bayesian tree	28 634.66	—	—

their digital modifications for burrowing were derived but once from a climbing ancestor. Using multi-genic sequence data and effectively complete taxon sampling, we have generated the first explicit phylogenetic hypothesis for the southern *Pachydactylus* Group. Highlights of this robust phylogeny include: (i) the unequivocal incorporation of *Chondrodactylus*, *Colopus* and *Palmatogecko* within *Pachydactylus*, and (ii) their placements in distinct, separate clades. From these findings, we argue that subdigital transformations observed among the burrowing geckos evolved independently. In effect, the convergence on a pedal design for locomotion and burrowing in sand reflects repeated divergence in function within lower-level clades of *Pachydactylus*.

(a) Secondary terrestriality in historical context

We also used our phylogeny of the *Pachydactylus* Group to explore character changes associated with the evolution of secondary terrestriality, providing an historical context that is essential for interpreting morphological adaptation (Wainwright & Reilly 1994; Pagel 1997, 1999). Species were categorized by habitat/substrate preferences, employing the following behavioural character states: (i) climbing generalist (arboreal); (ii) rupicolous (rock climbing specialist); (iii) terrestrial (mixed substrates); (iv) terrestrial (sandy substrates); and (v) burrowing. We reconstructed the evolution of habitat/substrate preferences by mapping character states onto the Bayesian topology in MacClade 4.0 (Maddison & Maddison 2000). To examine pedal modification in finer detail, we superimposed counts of subdigital lamellae onto the character tree to disclose possible patterns of lamellar change.

The reconstruction of character evolution in *Pachydactylus* revealed a major shift from general to strictly rupicolous climbing (figure 4), with the more basal members of the genus being arboreal opportunists (i.e. using both trees and rocky surfaces). Most *Pachydactylus* are indeed rupicolous, yet within this rock-specialist assemblage, the transition from climbing to terrestrial forms has occurred a minimum of eight times (figure 4). Interestingly, five of the eight terrestrial lineages occupy sandy substrates. A trend revealing lower lamellar counts among the more derived lineages must be interpreted with caution, given correlation between body size and number of lamellae in geckos (Bauer 1990b). This caveat notwithstanding, lamellar counts for terrestrial species represent the lowest numbers throughout the phylogeny. Such is the case for the sister species to *Palmatogecko* (*Pachydactylus austeni*; $n = 3$–4) and *Colopus* (*P. kochii*; $n = 3$). Further, both *P. kochii* and *P. austeni* qualify as

psammophiles, the latter species essentially replacing *Palmatogecko* on Namib dunes south of the Holgat River (Haacke 1976a).

In addition to lower lamellar counts, the terrestrial species of arid southwest regions (*P. austeni*, *P. kochii*, *Pachydactylus labialis*, *Pachydactylus mariquensis*, *Pachydactylus punctatus*, *Pachydactylus sherzi*) show concomitant reductions in: (i) pad area; (ii) size of the distal phalanges; and (iii) size of the dorsal interossei muscles, which permit digital hyperextension (Russell 1976). During hyperextension, the mechanism responsible for setal disengagement, the digits are peeled from the substrate distally to proximally, detaching setal fields to release the pad and foot. This elaborate mechanism remains operational in terrestrial *Pachydactylus*, but with a different purpose: their reduced subdigital pads are held hyperextended during locomotion on sand to prevent clogging of the setal fields (Bauer & Russell 1991).

The burrowing geckos carry this morphotypic trend further: *Colopus* and *Palmatogecko vanzyli* show nearly complete pad loss, and *Chondrodactylus* and *Palmatogecko rangei* are entirely padless (figure 1). As in terrestrial *Pachydactylus*, both *Colopus* and *Palmatogecko vanzyli* employ hyperextension to hold their reduced digital pads perpendicular to sandy substrates during locomotion (Haacke 1976a, 1976b). The distal phalanges of *Chondrodactylus* are extremely reduced (figure $1c_2$) and permanently hyperextended (Russell 1976). Thus, the burrowing geckos culminate the morphotypic series towards pad loss in secondary terrestriality among independent lineages of the southern *Pachydactylus* Group.

Pachydactylus is an old (17–21 Myr ago) gekkonid lineage (Lamb & Bauer 2002; Carranza *et al.* 2002), and opportunities for ecological shifts from arboreal to terrestrial adaptive zones in southern Africa date to the Middle Miocene (Tyson & Partridge 2000). The subcontinent's mesic woodlands of the Lower Miocene (Bamford 2000) experienced substantive climatic change with the inception of the Benguela Current, which has drastically reduced precipitation along southwest Africa since the Middle Miocene (Siesser 1980). The marked reduction in Atlantic moisture also promoted aridity across central southern Africa, particularly in the Kalahari (Stokes *et al.* 1997). Attenuation of woodland habitat under increasingly xeric conditions may account for the prevalence of rupicoly in *Pachydactylus*.

Initial formations of the Namib and Kalahari dunes were contemporaneous with the subcontinent's palaeoclimatic change. Kalahari sands date from the Middle Miocene to Pleistocene (Stokes *et al.* 1997), and deposits
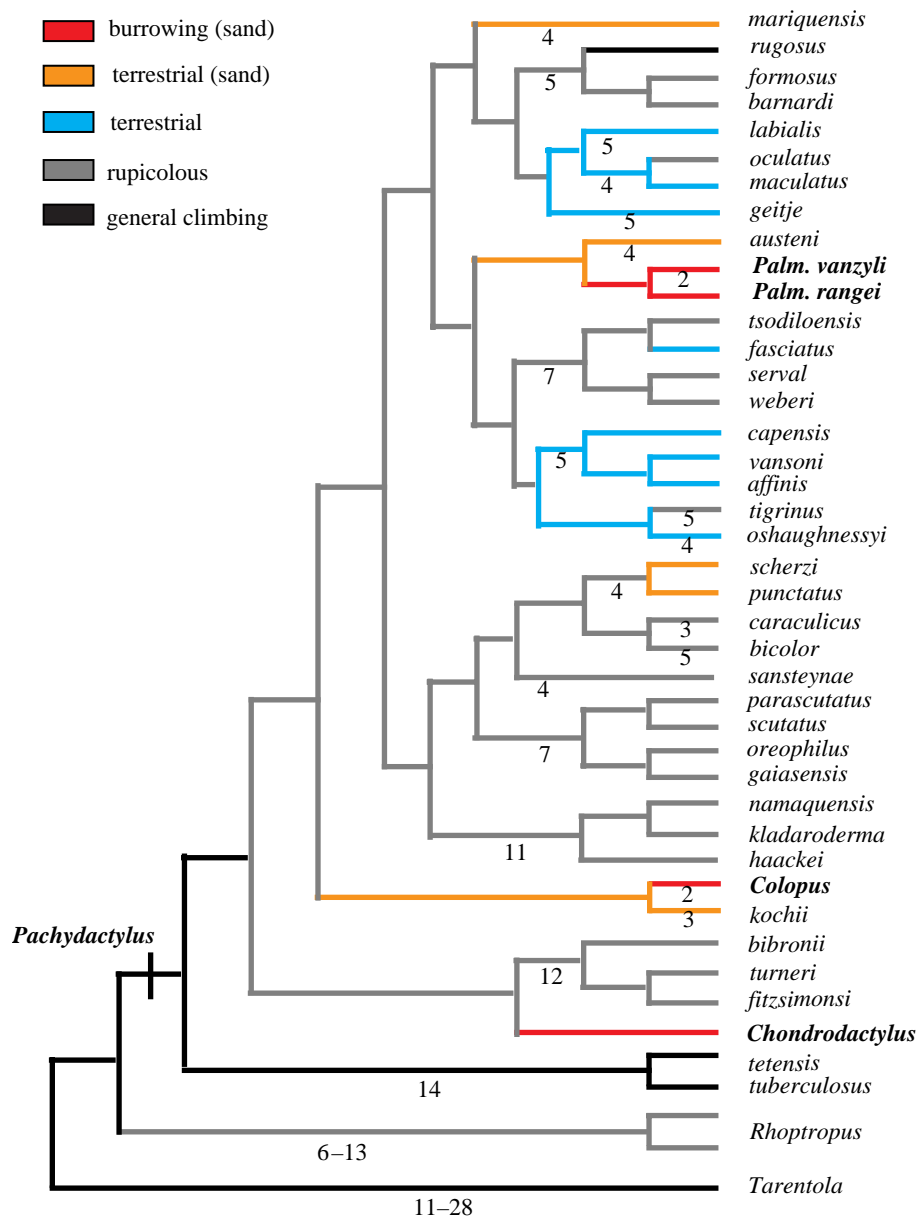
Figure 4. Reconstruction of the evolution of substrate preferences and digital lamellar counts on the Bayesian tree for the southern *Pachydactylus* Group.

underlying modern dune systems in the Namib represent episodic accumulations since the Miocene (Pickford *et al.* 1995; Lancaster 2000). Protracted aridity and recurrent dune formation are considered key selective agents in the evolution of Namib psammophilous taxa (Robinson & Seely 1980; Seely & Griffin 1986), including endemic lacertid and gerrhosaurid lizards (Lamb & Bauer 2003; Lamb *et al.* 2003). Southwest Africa's palaeoaridity apparently provided novel opportunities for *Pachydactylus* as well, allowing ancestral climbing lineages to exploit progressively extreme desert habitats.

(b) *Ecomorphic status of the burrowing geckos*
When phylogenetic analysis demonstrates independent origins for morphological similarity, the repeated association of character function with particular environmental settings suggests adaptive significance of form. Ecomorphological analyses explore possible ties between organismal structure and environmental features that have presumably imposed selection (Losos & Miles 1994). Support for ecomorphological adaptation requires a

broadly based appraisal that not only confirms multiple origins of the focal characters but distinguishes those environmental features relevant to character form and function (Hibbits & Fitzgerald 2005). Having revealed eight terrestrial forays in an otherwise climbing lineage of geckos (figure 4), we turn attention to morphological similarities among the burrowing forms and ask whether these features indeed represent responses to comparable ecological challenges.

Identifying the environmental ties of a certain morphological feature is not always straightforward, as relevant parameters may include biotic variables, abiotic variables, or combinations thereof. *Colopus*, *Chondrodactylus* and *Palmatogecko* all inhabit desert sands, where the interaction between a particular, harsh physical environment and locomotor performance is readily apparent. Gekkotan toepad design is such that setae are passively self-cleaning with respect to small particles (Hansen & Autumn 2005), but mean sand grain size in the Namib, Kalahari and other deserts far exceeds this practical upper size limit (Bauer & Russell 1991). As noted previously,

sand's clogging effect on setal fields provides a cogent mechanistic explanation for both lamellar reduction and sustained digital hyperextension during locomotion. The loss of toe pad function notwithstanding, independent gains of digital form in sand dune environments may more persuasively convey convergence. To wit, all four burrowing geckos possess spinose scales on the ventral aspect of the digits and/or plantar surfaces of the feet (figure 1); these scales are short, erect structures, 'thereby acquiring appearance of a pyramid with a hexagonal base' (Haacke 1976*d*). This peculiar scale condition does not occur in the other terrestrial *Pachydactylus*, including respective sister species to *Colopus* and *Palmatogecko*.

The spinose scales play a functional role in burrowing as well as locomotion and are best understood in the context of the geckos' microhabitat preferences. None of the burrowing geckos are dune slipface specialists (though *Palmatogecko rangei* can readily traverse slipfaces). They tend to use other microhabitats: *Palmatogecko rangei* frequents windward sides of dunes; *Palmatogecko vanzyli* (formerly *Kaokogecko vanzyli*) occupies dry river courses and sandy gravel plains adjacent dunes; *Chondrodactylus angulifer* and *Colopus wahlbergii* prefer sandy flats or interdune valleys (Haacke 1976*a–c*). The substrate is generally more compact in these microhabitats, and the spinose ventral scales function as wedges to loosen consolidated sand during excavation (Haacke 1976*a–c*; Bauer & Russell 1991). The digging kinematics in *Palmatogecko rangei*—despite the presence of spinose plantar scales—is an altogether different approach involving interdigital webbing. The contour of the webbing's edge acts as a spade to break the sand surface while the webbing itself forms an efficient scoop (Russell & Bauer 1990).

Russell (1979) argued that the spinose scales also serve to exclude sand grains, and measurements of interspine distances for the burrowing geckos are sufficiently narrow to exclude sand grains of local modal size (Bauer & Russell 1991). Experimental evidence suggests that such exclusion prevents clogging of the plantar surfaces, particularly in moist sand (Bauer & Russell 1991). Nocturnal advective fogs routinely moisten the Namib (Robinson & Seely 1980) and are coincident with activity periods of the burrowing geckos (Haacke 1976*d*).

Reduced toe pads and spinose digital scales characterize two other psammophilous geckos: *Tarentola chazaliae* (formerly the monotypic *Geckonia*), in the northern *Pachydactylus* Group (Carranza *et al.* 2002), and *Diplodactylus damaeus*, an Australian diplodactylid (Russell 1979). Subdigital spinose scales have also evolved in primitively padless psammophilous geckos inhabiting coastal deserts with predictable precipitation (Bauer & Russell 1991).

The burrowing geckos share additional characters with other terrestrial geckos, including a cylindrical body, long slender limbs, elevated posture and restriction of autotomy to the tail base (Werner & Broza 1969; Haacke 1976*d*; Bauer & Russell 1995). All of these traits are largely uncoupled from phylogenetic history, both within the *Pachydactylus* Group and among geckos in general. Thus, their repeated evolution (pedal traits, particularly) in similar dune environments corroborates selection's role in shaping observed morphological similarities. Further, the straightforward nature of the presumed selective

agent, i.e. physical attributes of sandy substrates, provides a clear, direct association with pedal performance and, we argue, ecomorphological convergence among the burrowing geckos.

The ultimate goal of ecomorphological assessment involves recovering the precise evolutionary path that confers parallelism or convergence. Remarkably, recent population genetic studies have identified alleles at specific loci responsible for parallel character evolution in fruit flies (Gompel & Carroll 2003; Sucena *et al.* 2003) and stickleback fish (Colosimo *et al.* 2005), both model organisms whose genomic databases allow mapping such genes. Comparable genomic data are currently unavailable for geckos. Nonetheless, it is worth noting that the multiple origins of gekkotan subdigital pads trace to a common developmental transition of the outer epidermal (Oberhaütchen) layer, whose minute rugosities aid in skin shedding (Maderson 1970; Russell 2002). This layer is distinctly elaborate in geckos, bearing numerous sculpted spinules (Maderson 1970), and setae have been determined to be homologous Oberhaütchen outgrowths, exapted for the novel role of adhesion (Russell 2002). As such, lamellar formation likely entails a common developmental pathway that, if under regulatory control of one or few genes, may be readily, repeatedly reversed.

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