

# On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA sequence analysis of the African Gerrhosauridae

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The desert plated lizard (*Angolosaurus skoogi*), a ‘sand sea’ endemic of the northern Namib Desert, exhibits remarkable morphological convergence with other dune-dwelling lizards worldwide. This distinct ecomorphic condition sets *Angolosaurus* apart from the remaining genera in the family Gerrhosauridae. Indeed, a morphological phylogeny addressing generic relationships within the Cordyliformes (Cordylidae + Gerrhosauridae) identified *Angolosaurus* as the earliest diverging taxon among African gerrhosaurids. We re-evaluated the basal status of *Angolosaurus*, conducting a molecular phylogenetic analysis of the African and Madagascan gerrhosaurid genera. Our survey involved a comprehensive species-level comparison among the four nominal genera of mainland Africa (*Angolosaurus*, *Cordylolaurus*, *Tetradactylus* and *Gerrhosaurus*). Mitochondrial DNA sequence data from the cytochrome *b*, ND2, 12S and 16S rRNA genes were combined for analysis using both parsimony and maximum likelihood procedures. In contrast to the morphological hypothesis, our results do not depict *Angolosaurus* as the sister taxon to other African gerrhosaurids. Rather, the molecular analyses consistently place *Angolosaurus* within *Gerrhosaurus*, rendering the latter genus paraphyletic. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 78, 253–261.

ADDITIONAL KEYWORDS: convergent evolution – *Gerrhosaurus* – mitochondrial DNA – Namib Desert – ultrasammophile.

## INTRODUCTION

Many desert lizards exhibit broadly convergent features in morphology, and certain xeric environments have produced remarkably similar evolutionary outcomes (Mosauer, 1932; Pough, 1969; Luke, 1986; Arnold, 1995). Desert sand dunes represent an extreme environmental setting in which selective forces have apparently generated dune ‘ecomorphs’ (*sensu* Losos *et al.*, 1998) in six lizard families (Arnold, 1994, 1995). Convergent morphological features often shared among these dune specialists include modified digits, a countersunk lower jaw and tympanic shields.

The Namib Desert of southern Africa is renowned for its expansive ‘sand seas’ and ultrasammophilous (*sensu* Koch, 1961) endemics, including four species of lizards representing the families Gekkonidae, Gerrhosauridae and Lacertidae. As a reflection of their ecomorphic specialization to aeolian sands, each of these four species was described as (or reassigned to) a monotypic genus. Recently, the lacertid *Aporosaura anchietae* was synonymized with *Meroles* (Arnold, 1991; Harris, Arnold & Thomas, 1998), and the closely related gekkonids *Palmatogecko rangei* and *Kaokogecko vansyli* have been shown to fall within the species-rich genus *Pachydactylus* in both morphological and molecular analyses (Joger, 1985; T. Lamb & A. M. Bauer, unpubl. data).

The desert plated lizard (*Angolosaurus skoogi*) of the northern Namib sand sea also exhibits typical dune

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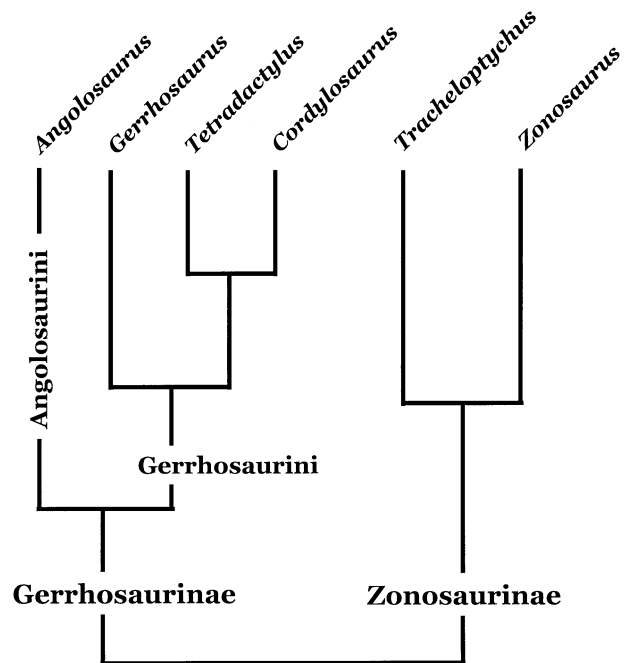


**Figure 1.** Profile of an adult male desert-plated lizard, illustrating such dune ecomorph characters as the countersunk-jaw, tympanic shield and cylindrical body.

ecomorph characters: a spade-like rostrum, lateral toe fringes and tympanic shields (Fig. 1). The lizard's modified snout and smooth-scaled cylindrical body allow it to 'dive' a metre or more beneath the dune surface (Mitchell *et al.*, 1987; Arnold, 1994, 1995). Moreover, *Angolosaurus* exhibits a suite of behavioural, ecological and physiological traits that reflects ultrapsammophilous adaptation (Hamilton & Coetzee, 1969; Pietruszka *et al.*, 1986; Pietruszka, 1987, 1988; Seely *et al.*, 1988; Nagy *et al.*, 1991).

*Angolosaurus* is a member of the Cordyliformes, a sub-Saharan/Malagasy assemblage of scincomorph lizards whose monophyly is strongly supported on morphological (Böhme, 1988; Estes, de Queiroz & Gauthier, 1988; Lang, 1991), molecular (Frost *et al.*, 2001) and karyological (Olmo & Odierna, 1980; Odierna *et al.*, 2002) grounds. Generic-level comparisons within the Cordyliformes identify *Angolosaurus* as the sister taxon to the other three African gerrhosaurid genera (Lang, 1991; Fig. 2). Does the basal, monotypic status of *Angolosaurus* truly reflect African gerrhosaurid relationships, or does its distinct ecomorphic condition belie a more recent ancestry? Systematic reassessments of the Namib's other ultrapsammophilous lizards bring this question to the fore.

The phylogenetic position of *Angolosaurus* within Cordyliformes as a whole necessitates a brief overview of cordyliform relationships. Although the monophyly of this clade has never been questioned, a long-standing debate continues regarding the recognition of one (Cope, 1871; McDowell & Bogert, 1954; Romer, 1956; Odierna *et al.*, 2002) vs. two families (Boulenger, 1887; Loveridge, 1942; Harvey & Gutberlet, 1995; Mouton & van Wyk, 1997). Lang (1991), who con-



**Figure 2.** Lang's (1991) morphological hypothesis depicting generic, tribal and subfamilial relationships within the Gerrhosauridae.

ducted the only explicitly phylogenetic analysis of the order, recognized two families – Cordylidae and Gerrhosauridae – on the basis of morphology. He partitioned the latter into two subfamilies: (1) Gerrhosaurinae, an African assemblage comprising two tribes (Angolosaurini, Gerrhosaurini), and (2) Zonosaurinae, a Malagasy clade.

Lang's (1991) interpretation of *Angolosaurus* (and thus Angolosaurini) as being basal to the other gerrhosaurines is compromised in part by the numerous (seemingly) apomorphic characters that define *A. skoogi* (see References above). Further, Lang confined his analysis to accepted cordyliform genera, an approach that (1) cannot test the monophyly of polytypic genera; and (2) restricts the positions in which monotypic forms like *Angolosaurus* can be placed. Hence, any attempt to reassess the systematic status of *Angolosaurus* should entail extensive taxon sampling of Africa's other gerrhosaurids, using species as terminal taxa. Herein we present the first molecular phylogenetic survey of the Gerrhosaurinae. We employ mitochondrial DNA sequence data to (1) conduct a comprehensive analysis of species-level relationships within and among currently recognized genera; and (2) test Lang's hypothesis that *Angolosaurus* is the sister taxon of the remaining gerrhosaurines. In light of our results, we discuss the ecomorphic evolution of *Angolosaurus* as an ultrapsammophile and offer a revised taxonomy for the Gerrhosaurinae.

## MATERIAL AND METHODS

## TAXON SAMPLING

We examined 13 terminal taxa (species and subspecies) assigned to the four nominal genera of Gerrhosaurinae. These taxa included the two monotypic genera *Angolosaurus* and *Cordylusaurus*, all eight species (subspecies) of *Gerrhosaurus*, and three out of five species in the serpentiform genus *Tetradactylus*. Whenever possible, we processed two (or more) specimens per taxon, especially for those species with broad geographical ranges. We also examined one species each of the two Malagasy gerrhosaurid genera, *Tracheloptychus* and *Zonosaurus* (though a recent, preliminary analysis of sequence data for the 12S and 16S ribosomal genes depicts *Tracheloptychus* within a *Zonosaurus* clade (Odierna *et al.*, 2002)). Two cordylids, *Cordylus cataphractus* and *Platysaurus capensis*, served as outgroups. Sampled taxa, together with collection localities, museum voucher numbers and GenBank accession numbers are compiled in the Appendix.

## SEQUENCE PROCUREMENT AND ALIGNMENT

Tissue samples were processed at field collection sites and preserved in a saturated salt–DMSO buffer. Genomic DNA was extracted from liver or muscle using the Qiagen QIAamp DNA Mini kit. Regions from four mitochondrial genes, including the two ribosomal genes (12S, 16S) and two protein-coding genes, cytochrome *b* (*cytb*) and subunit 2 of NADH dehydrogenase (ND2), were selected for phylogenetic analysis. Segments approximately 350 bp in length for 12S, 550 bp for 16S, 400 bp for *cytb* and 350 bp for ND2 were amplified for 32 cycles at 92°C for 45 s, 50–55°C for 35 s and 72°C for 1 min. Primer sequence sources are as follows: 12S, 16S (Bickham *et al.*, 1996); *cytb* [LGL765 (light strand) (Bickham, Wood & Patton, 1995) and H15149 (heavy strand) (Meyer *et al.*, 1990)]; ND2 [(Macey *et al.*, 1997) and Angol-ND2 (heavy strand) 5'-GGG GCT ART TTT TGT CAG GT-3' (this study)]. Amplification products, purified over Centrisep columns, served as templates in cycle-sequencing reactions employing dye-labelled terminators (PRISM kit, Applied Biosystems Inc.), followed by electrophoresis in an Applied Biosystems 377 automated DNA sequencer. Forward and reverse sequences were generated for each sample and their complementarity confirmed using the Sequence Navigator software (Applied Biosystems Inc.).

Sequences were initially aligned using the CLUSTAL X program, applying default settings (Thompson *et al.*, 1997). Given the indel variation commonly observed in rDNA sequences, we examined 12S and 16S alignments in greater detail, exploring

gap placements for a series of gap opening (= 5, 10, 15 and 20) and extension costs (= 0.10 and 5.0) with the Multiple Alignment Parameters option in CLUSTAL X. Regions of these ribosomal RNA sequences whose nucleotide position homologies varied across different gap parameters were considered alignment-ambiguous and therefore excluded from phylogenetic analysis.

## PHYLOGENETIC ANALYSIS

Substitution patterns and other features of animal mtDNA evolution can generate significant homoplasy, especially at higher levels of sequence divergence. Thus, phylogenetically informative variation in mtDNA sequence data may be confounded by transition biases, substitution saturation or, less frequently, base compositional bias. We used two approaches to assess levels of substitution saturation for the two protein-coding genes. First, pairwise differences for transitions (ts) and transversions (tv) were plotted against corrected pairwise divergences (HKY 85 model; Hasegawa, Kishino & Yano, 1985) for ingroup taxa (i.e. all gerrhosaurids). The *cytb* and ND2 data sets were partitioned by codon position, providing separate scatter plots for differences at first, second and third positions. We also compared uncorrected vs. corrected pairwise divergences for each of the three codon positions, as in Reed & Sperling (1999). In this second qualitative test, the degree to which scatter plot points deviate from the  $x = y$  line reflects saturation levels.

Phylogenetic inference was based on maximum parsimony (MP) and maximum likelihood (ML) analyses implemented in PAUP\* 4.0 (Swofford, 1999).

Given the distinct post-transcriptional functions of the four genes, we recognize the potential for incongruence among these sequence data and its potential impact on phylogenetic accuracy. To assess combinability of the data sets, we performed the incongruence length difference (ILD) test of Farris *et al.* (1994). ILD analysis involved 1000 replicates using the partition homogeneity test in PAUP\*; parsimony-uninformative characters were excluded from the respective data sets prior to analysis. Results of the ILD test showed no significant conflict among data sets ( $P = 0.2300$ ), which were combined for MP analysis (but see Darlu & Lecointre, 2002). Parsimony trees were generated using the heuristic search option, with tree bisection–reconnection branch rearrangement (TBR), MULPARS and random addition of sequences (1000 replicates).

Prior to ML analysis, we used the MODELTEST program (ver. 3.06; Posada & Crandall, 1998) to identify the substitution model most appropriate for the combined data. MODELTEST selects one of up to 56 models that best fit the DNA data, executing a hierarchical

series of likelihood ratio tests ( $\delta = -2 \log \Lambda$ ) to compare likelihood scores between increasingly complex models for a given user tree. We used the program's default settings to generate a neighbour-joining tree as a test tree and, subsequently, to compare substitution models ranging from simple (Jukes–Cantor) to increasingly parameter rich (general time-reversible). Upon securing appropriate model parameters for the combined data, we performed ML analysis in a manner similar to the MP search, using a series of heuristic searches (100 replicates) with random stepwise addition of sequences and TBR. Bootstrap analyses involving 1000 (MP) and 100 (ML) pseudoreplicates were conducted to estimate confidence limits for topological patterns revealed by these procedures.

## RESULTS

### SEQUENCE VARIATION, DIVERGENCE, AND SUBSTITUTIONAL VARIATION

Upon exclusion of ambiguously aligned regions in the 12S and 16S sequences, the combined mtDNA data set comprised 1530 nucleotides (nts), of which 710 were variable and 565 were parsimony informative. Sequence variation and levels of divergence observed across the four mitochondrial genes are summarized in Table 1. Scatterplots of substitution patterns revealed saturation at higher divergence levels within the Gerrhosauridae at 3rd position ts for *cytb* and ND2 (not illustrated). These trends were reflected in the second qualitative test for saturation (uncorrected vs. corrected divergences) in which 3rd positions for both genes again exhibited some degree of saturation (Fig. 3).

### PHYLOGENETIC ANALYSIS

Given evidence suggesting 3rd position saturation in

the protein-coding genes, we examined the combined data with heuristic searches employing different levels of character weighting. These analytical permutations for MP included: (1) equal weighting, all characters; (2) weighting transversions 2.0 times transitions for all substitutions (based on ratio estimates); and (3) eliminating 3rd position transitions for *cytb* and ND2 codons. Our results centre on those well-supported clades common to all three MP analyses.

Figure 4 depicts a strict consensus of the two shortest trees obtained with equal weighting analysis. The monophyly of Zonosaurinae as well as Gerrhosauridae as a whole is affirmed. Support for a monophyletic Gerrhosaurinae was not provided, though several well-supported clades were retrieved, including: *Cordylosaurus* + *Tetradactylus* (bootstrap (BS) value of 95%) and (*G. nigrolineatus*, *G. auritus*) + *Gerrhosaurus flavigularis* (BS = 100%). Moreover, equal-weighting MP places *Angolosaurus* as the sister taxon to *G. typicus* (BS = 98%), a pairing nested well within a clade of *Gerrhosaurus* spp.

The tv 2× ts MP analysis generated a single most-parsimonious tree (Fig. 5), which also retrieved a well-supported Gerrhosauridae and Zonosaurinae. Gerrhosaurinae was recovered as well but with weak support (BS = 54%). Within the Gerrhosaurinae, two large, weakly supported clades were identified, the first depicting *Cordylosaurus* + *Tetradactylus* (itself a well-defined clade) as sister group to *Gerrhosaurus major* ssp. In the second major clade, *G. validus* ssp. were recovered as sister group to the remaining gerrhosaurines. Within the second clade (1) *G. flavigularis* was again strongly supported as sister taxon to *G. nigrolineatus* + *G. auritus*, and (2) *Angolosaurus skoogi* and *G. typicus* received comparable support as sister species.

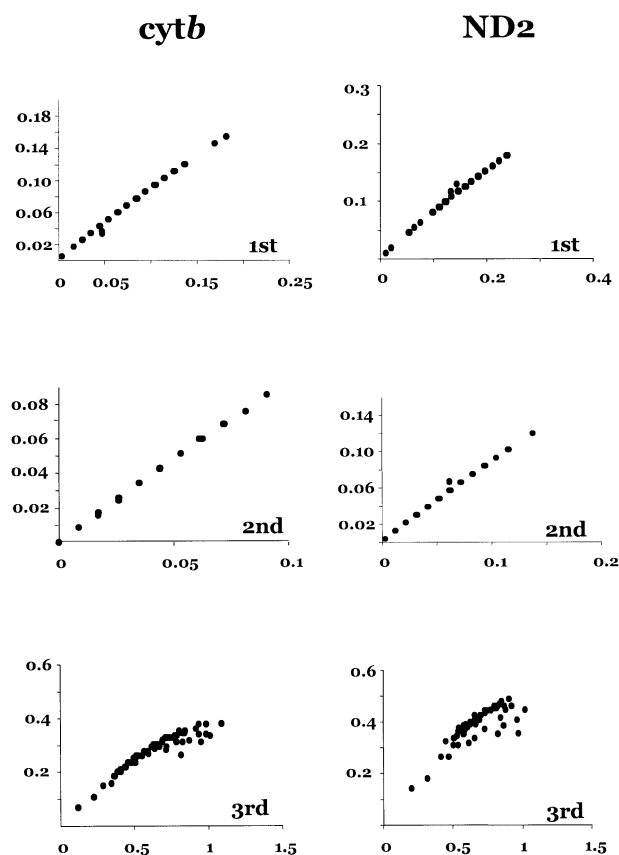
Results of the third parsimony analysis (eliminating 3rd position transitions for *cytb* and ND2) yielded two

**Table 1.** Sequence variation and levels of sequence divergence (% pairwise distances, derived from GTR model) observed for the mitochondrial genes used in this survey

Data partition	<i>cytb</i>	ND2	12S	16S
No. of nucleotides	368	350	382*	430*
No. of variable sites	180	210	184	136
No. of informative sites	148	170	147	100
No. of informative sites 1st codon position	32	53	–	–
No. of informative sites 2nd codon position	13	25	–	–
No. of informative sites 3rd codon position	103	92	–	–
Interspecific pairwise divergence values within Gerrhosaurinae	14.9–34.9	11.8–34.8	6.8–23.9	5.6–13.6
Divergence between <i>skoogi</i> / <i>typicus</i>	16.3	19.8	10.8	6.7
Divergence between <i>Meroles anchietae</i> and its sister clade†	17.8	21.1	8.6	6.0

\*No. of nucleotides after excluding ambiguous regions from the alignment.

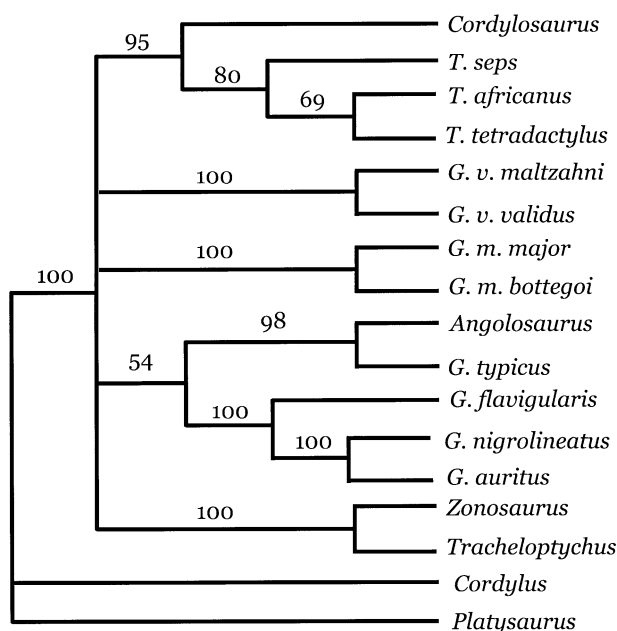
†T. Lamb & A. M. Bauer, unpubl. data.



**Figure 3.** Scatter plots of uncorrected pairwise divergences (y-axes) vs. corrected divergences (x-axes) for 1st, 2nd and 3rd position partitions for *cytb* and ND2. Deviation of points from an  $x = y$  line reflects the degree of saturation.

equally parsimonious trees (TL = 1653; CI = 0.50; RI = 0.51), one of which was identical to Fig. 5. The second tree (not illustrated) differed only in the placement of *Tetradactylus seps* within the *Cordylus*/*Tetradactylus* clade. Bootstrap support for this analysis, shown in Fig. 5, corroborates that of the other two MP trees.

Results of the MODELTEST identified the general time-reversible substitution model (Rodríguez *et al.*, 1990) with some sites assumed to be invariable (I) and variable sites assumed to follow a gamma distribution ( $\Gamma$ ) as the best fit for the combined data set. Parameter estimates for ML were as follows: (1) base frequencies – freq A = 0.3112, freq C = 0.277, freq G = 0.1617, and freq T = 0.2498; (2) rate matrix – [A-C] = 2.1642, [A-G] = 3.8048, [A-T] = 1.8490, [C-G] = 0.2334, [C-T] = 7.4971, and [G-T] = 1.0000; (3) I = 0.3484; and (4)  $\Gamma$  = 0.7339. ML recovered a topology similar to those of the two weighted parsimony analyses, corroborating (1) the sister species status for *Angolosaurus* and *G. typicus*; (2) a well-defined *Cordylus*/*Tetradactylus* clade; and (3) paraphyly of *Gerrhosaurus* with respect



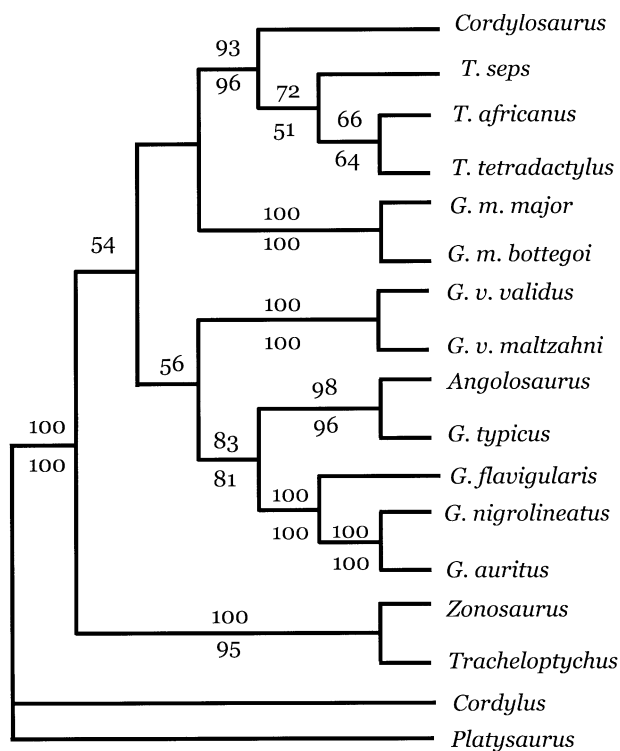
**Figure 4.** Strict consensus of two equally parsimonious trees (TL = 2153, CI = 0.50, RI = 0.47) generated from equal weighting parsimony analysis. Bootstrap values >50% are shown above branches.

to the other African genera (Fig. 6). However, ML differed relative to MP in offering moderate bootstrap support (74%) for the Gerrhosaurinae and placing *G. major* as the sister taxon to the other mainland African taxa.

To examine the strength of our molecular phylogenetic hypothesis relative to Lang's (1991) morphological interpretation, we conducted a parsimony analysis in which *Angolosaurus* was constrained basally to the other African gerrhosaurids. The resulting tree (TL = 2187; CI = 0.495; RI = 0.449) required 34 additional steps and was significantly longer than the equal-weighting tree (Wilcoxon signed-ranks test [ $P < 0.0001$ : Tempelton, 1983] and Kishino–Hasegawa test [ $P < 0.0001$ : Kishino & Hasegawa (1989)]). Constraining *Angolosaurus* similarly in an ML analysis produced a significantly lower likelihood score (difference in  $-\ln L = 86.39$ ,  $P < 0.0005$ : Kishino–Hasegawa test;  $P < 0.003$ : Shimodaira–Hasegawa [1999] test).

## DISCUSSION

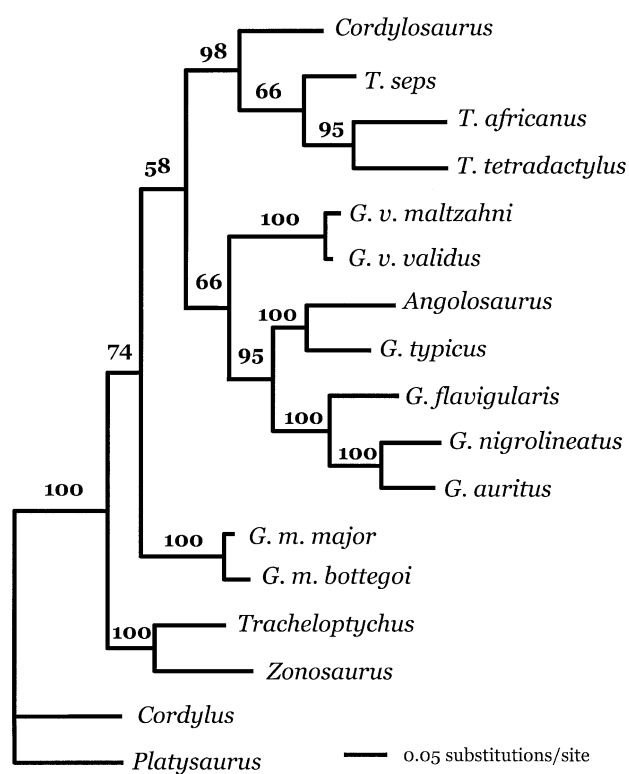
The molecular phylogenetic placement of *Angolosaurus* within Gerrhosaurinae differs not only from Lang's (1991) morphological hypothesis, but from prior taxonomic interpretations as well. Andersson (1916), who originally described the desert-plated lizard as *Gerrhosaurus skoogi*, inferred its close affinities



**Figure 5.** Single most-parsimonious tree (TL = 3058, CI = 0.49; RI = 0.48) generated from parsimony analysis weighting tv 2× ts. Bootstrap values (>50%) above branches are for the tv 2× ts analysis; values below branches are for the parsimony analysis eliminating 3rd position ts.

with *G. validus*. Further, Loveridge (1942) actually relegated *skoogi* to subspecific status within *G. validus*. Although Loveridge never examined *skoogi*, then known only from a unique type, he nonetheless dismissed the specimen as being deformed through artefacts of preservation. Upon securing additional material, Fitzsimons (1953) erected the genus *Angolosaurus* to emphasize the species' distinctive morphology. Steyn (1963) rejected the proposed close affinities between *G. validus* and *A. skoogi*, noting instead the latter's superficial similarities to *G. auritus*. These earlier interpretations may have been influenced somewhat by biogeographical considerations: both *G. validus* and *G. auritus* occur in close proximity to *A. skoogi*. Conversely, an ≈ 1000-km gap separates *G. typicus* (Northern Cape Province, South Africa) from the Namib's northern sand sea.

Our molecular phylogenetic results have direct implications for the classification and taxonomy of the Gerrhosaurinae (*sensu* Lang, 1991). Clearly, *Angolosaurus* should be transferred to *Gerrhosaurus*, resurrecting the original name, *Gerrhosaurus skoogi* Andersson 1916. As a result of this nomenclatural change, the tribe Angolosaurini ceases to exist and



**Figure 6.** Phylogram recovered by maximum likelihood analysis under the GTR +  $\Gamma$  + I model of nucleotide substitution, with a  $-\ln L$  score of 11 140.52. Bootstrap values >50% are shown above branches.

Gerrhosaurini becomes redundant with respect to Gerrhosaurinae. Our results also point to possible generic reallocations for *Cordylosaurus* and *Tetradactylus*, although these cases are more problematic. Both MP and ML hypotheses indicate these small-bodied, attenuate forms appear to have arisen within *Gerrhosaurus*, but this grouping receives only marginal bootstrap support (Fig. 6). Of interest is a similar phylogenetic pattern recovered for the serpentiform cordylid *Chamaesaura*, which lies nested within *Cordylus* (Frost *et al.*, 2001).

To preserve existing usage while still reflecting phylogenetic relationships, we continue to recognize the genera *Cordylosaurus* Gray, 1865 and *Tetradactylus* Merrem, 1820. We consider the clade including *Gerrhosaurus flavigularis* Wiegmann, 1828 (type species for the genus) and all other gerrhosaurids except *G. major* to constitute *Gerrhosaurus sensu stricto*. Pending a combined analysis of our molecular data with comparable morphological data – a set in which gerrhosaurid species, as opposed to genera, serve as terminal taxa, e.g. Lockett (2002) – we regard *G. major* as *incertae sedis* within the Gerrhosaurinae.

The distinctive traits of *Gerrhosaurus skoogi*

(Fitzsimons, 1953; Steyn, 1963; Pietruszka *et al.*, 1986; Mitchell *et al.*, 1987) are best considered autapomorphies, which presumably evolved in association with the species' ultrapsammophilous habit. Although the Namib has experienced semi-arid to arid conditions for  $\approx 80$  Myr (Ward, Seely & Lancaster, 1983; Ward & Corbett, 1990), current hyperaridity traces to the Late Miocene, with the inception of the Benguela Current (Siesser, 1980). The Benguela upwelling, superimposed on a progressively arid climatic trend, helped create the Namib's latest hyperarid regime – the Namib Desert phase (Ward & Corbett, 1990). This setting, in conjunction with extensive sand deposition from regional rivers (primarily the Orange River [Rogers, 1977]), gave rise to the Namib's present sand seas (Lancaster, 1990; Ward & Corbett, 1990).

In the absence of lineage-specific substitution rates for gerrhosaurid lizards (see Bromham, 2002), we refrain from dating the haplotypic divergences observed among taxa. Nonetheless, the levels of sequence divergence between *Angolosaurus skoogi* and *Gerrhosaurus typicus* are among the lower pairwise distances observed across all gerrhosaurid comparisons (Table 1). Moreover, the *cytb* pairwise distance between these two species (15.7%; recalculated using Kimura's (1980) two-parameter model for comparative purposes) fall within mean *cytb* values for other lizard congeners (Johns & Avise, 1998). Were *Angolosaurus* indeed sister taxon to the remaining gerrhosaurines, one would anticipate the opposite trend in divergence levels (Table 1).

Interestingly, the levels of divergence observed between *Angolosaurus skoogi* and *Gerrhosaurus typicus* are quite similar those for the Namib's other ultrapsammophilous lizard, *Meroles anchietae*, and its sister clade of three congeners (Table 1). Comparable genetic differences in nucleotide sequence suggest temporal parallels in the independent evolution of a dune ecotomorph for each of these two saurian lineages. Ecological invasion of the Namib sand seas, with the attendant functional problems posed by loose, wind-blown sand, probably account for the observed character convergence, which entails keeled digits, tympanic shields, spatulate rostrum, sand-diving and subsand breathing. Thus, we dismiss Lang's (1991) hypothesis that *Angolosaurus* is a basal form among Africa's gerrhosaurids. It seems more likely – as Harris *et al.* (1998) noted for *M. anchietae* – that *Angolosaurus* is a product of rapid morphological adaptation to the Namib's geologically recent and environmentally extreme aeolian dunes.

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## APPENDIX

TISSUE SAMPLE VOUCHER SPECIMENS AND  
GENBANK ACCESSION NUMBERS

Collection acronyms are: AMB = Aaron M. Bauer field series, CAS = California Academy of Sciences, PEM = Port Elizabeth Museum, NMZB = National Museum of Natural History, Zimbabwe, UMMZ = University of Michigan Museum of Zoology, USEC = University of Stellenbosch Ecology Collection. GenBank accession numbers are listed for 12S, 16S, *cytb* and *ND2* genes, respectively.

*Angolosaurus skoogi* (CAS 206978, 214817 – Ondonduingo River, Namibia, 17°51'09'S, 12°06'51'E; AY167347, AY167364, AY167381, AY167398), *Cordylus subteselatus* (AMB 5960 – Opuho Road, Namibia, 18°27'11'S, 13°48'09'E; CAS 214798 – South of Karibib, Namibia, 22°16'13'S, 15°34'29'E; AY167342, AY167359, AY167376, AY167393), *Cordylus cataphractus* (CAS 206834 – Brandberg, Northern Cape, South Africa, 29°49'52'S, 17°22'35'E; AY167357, AY167374, AY167391, AY167408), *Gerrhosaurus auritus* (NMZB 16027 – Ndau School, Western Province, Zambia; AY167351, AY167368, AY167385, AY167402), *G. flavigularis* (NMZB 16481 – Marivalle Ranch, Kweke, Zimbabwe; PEM R14985 – Bazaruto Island, Mozambique; AY167349, AY167366, AY167383, AY167400), *G. major major* (PEM R5410 – Nagonha River, Zambezi Province, N Mozambique, 16°57'17'S, 38°42'37'E; NMZB 16199 – Chituripasi, Chipise, C.

L. Zimbabwe; AY167345, AY167362, AY167379, AY167396), *G. m. bottegoid* (Atakpame, Togo, West Africa; AY167346, AY167363, AY167380, AY167397), *G. nigrolineatus* (TM 80959 – Moebase Village, Mozambique, 16°58'58'S, 38°43'43'E; AY167350, AY167367, AY167384, AY167401), *G. typicus* (USEC-H3504; AY167348, AY167365, AY167382, AY167399), *G. validus maltzahni* (CAS 206935 – Usakos-Hentiesbaai Road, Namibia, 21°57'08'S, 15°16'48'E; AY167343, AY167360, AY167377, AY167394), *G. v. validus* (CAS 209608 – Farm Harmony, Northern Province, South Africa, 24°18'23'S, 30°50'36'E; NMZB 16268 – Chikwakwara, Chipise, C. L. Zimbabwe; AY167344, AY167361, AY167378, AY167395), *Platysaurus capensis* (AMB 4639, CAS 200057 – Tierhoek, Northern Cape Province, South Africa, 28°37'57'S, 17°00'43'E; AY167358, AY167375, AY167392, U71329), *Tetradactylus africanus fitzsimonsi* (PEM R14913–500 m NE Billson St., Kareedouw District, Eastern Cape Province, South Africa; AY167353, AY167370, AY167387, AY167404), *T. seps* (USEC-H3505; AY167352, AY167369, AY167386, AY167403), *T. tetradactylus* (not catalogued; Eensemeid Nature Reserve, Western Cape Province, South Africa; AY167354, AY167371, AY167388, AY167405), *Tracheloptychus petersi* (UMMZ 207157–8 km Ntolaria on RN6, just N of Fitheranana R., Madagascar; AY167356, AY167373, AY167390, AY167407), *Zonosaurus laticaudatus* (UMMZ [RAN 55301]–7.5 km ENE of Hazofotsy, Madagascar 24 49.0S 46 36.6 E; AY167355, AY167372, AY167389, AY167406).

