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THE TAXONOMY OF THE SOUTHERN AFRICAN LEAF-TOED
GECKOS (SQUAMATA: GEKKONIDAE), WITH A REVIEW OF
OLD WORLD “*PHYLLODACTYLUS*” AND THE DESCRIPTION OF
FIVE NEW GENERA

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Despite the removal of several monophyletic groups of leaf-toed geckos, the gekkonid genus *Phyllodactylus* remains polyphyletic. An evaluation of morphological features and allozymes suggest that Old World species assigned to the genus *Phyllodactylus* are not closely related to New World taxa, to which this generic name applies. Further, Old World species as a unit do not form a demonstrably monophyletic group. Osteological and external characters are used to describe and diagnose five new genera of leaf-toed geckos, each corresponding to a clade supported by apomorphic characters: *Dixonius* (two species, southeast Asia), *Haemodracon* (two species, Socotra Island, Yemen), *Cryptactites* (monotypic, South Africa), *Goggia* (eight species, southern Africa), and *Afrogecko* (three species, southern Africa). In addition, the genus *Euleptes* Fitzinger 1843 is resurrected for a single species endemic to the Mediterranean region. Redescriptions and diagnoses are provided for two other currently recognized genera of leaf-toed geckos, *Christinus* from Australia and *Ebenavia* from Madagascar. *Phyllodactylus* is restricted to New World species only (although the monophyly of this group is not strongly established), with the Madagascan species *P. brevipes* remaining *incertae sedis*.

The recognition of monophyletic units of leaf-toed gekkonids is a necessary step towards the reconstruction of phylogeny, but available higher order analyses do not suggest appropriate outgroups. Regardless of whether other African gekkonids or other leaf-toed gekkonids are chosen as the outgroup, character analysis supports a partially resolved pattern of relationship within the southern African genus *Goggia*. The preferred phylogeny for this genus is: (*G. microlepidotus* (*G. gemmulus* (*G. lineatus* (*G. braacki*, *G. essexi*, *G. hewitti*, *G. hexaporus*, *G. rupicolus*))))). Speciation events associated with the evolution of taxa in the unresolved portion of the phylogeny were probably simultaneous and related to Late Tertiary climatic changes in temperate southern Africa. If this is true, the lack of resolution in the phylogeny is real (representative of the synchronous loss of continuity between several populations) rather than artifactual. Genetic distances between species pairs in this group reflect both isolation by geographic distance prior to speciation and post-speciation divergence.

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The genus *Phyllodactylus*, as presently construed, is a speciose and geographically widespread assemblage of small to moderate sized geckos, with representatives on five continents. All of the geckos assigned to this genus possess a terminal pair of enlarged "leaf-like" scansors on each digit, reflecting the traditional reliance of gekkonid systematists on digital morphology as the primary, and often sole, indicator of generic allocation (e.g., Boulenger 1885; Loveridge 1947). Digital structure, however, is notoriously prone to parallel evolution in this group of lizards (Russell 1979; Carillo de Espinoza et al. 1990) and there is no a priori reason to assume that digital similarity reflects phylogenetic affinity any more accurately than other characters. Although the digital similarities shared by members of some gekkonid genera have been corroborated by other characters (Russell 1972; Bauer 1990; Kluge and Nussbaum 1995), this is not the case in *Phyllodactylus*. Indeed, Kluge (1983) could find no features that served to unite all of the species then assigned to the genus into a diagnosable whole.

Although the distribution of *Phyllodactylus* was regarded as possibly relictual by some authors (Schmidt 1923; Russell 1972; King and Horner 1993), nearly all modern workers have recognized the probable polyphyly of the group (Dixon 1964; Dixon and Anderson 1973; Russell 1972; Rieppel and Schneider 1981; Cogger et al. 1983; King 1987; King and Horner 1993). Dixon (1964) stated the "studies of the osteology of Old and New World members of the genus reveals [sic] constant differences in such features as phalangeal formulae, scapulocoracoid element, shape of the prefrontals, number of presacral vertebrae, fusion of nasals, neoteny in union of parietals, all of which suggests that the Old and New World groups belong to separate genera." Russell (1972) indicated that differences between some Old World groups were as great as those between Old and New World taxa and believed that the Old World members of the group did not form "a coherent entity," and this has subsequently been echoed by other authors (e.g., Dixon and Kroll 1974; Kluge 1983; Haacke 1996).

Certain putatively monophyletic groups have been recognized within *Phyllodactylus* (*sensu lato*) and have been accorded generic status. Dixon (1964) reviewed the systematics of the

North and Central American members of the group, and Dixon and Huey (1970) reviewed the South American forms. Dixon and Anderson (1973) diagnosed and separated the southwest Asian taxa now referred to *Asaccus*, and Dixon and Kluge (1964) separated *Crenadactylus*, now referred to the family Diplodactylidae. Dixon and Kroll (1974) resurrected the older name *Paroedura* for the casque-headed Madagascan forms. Kluge (1983) regarded the remaining *Phyllodactylus* as polyphyletic and indicated that Dixon held similar views. Kluge (1983) further erected the genus *Urocotyledon* for those African and Seychellian forms exhibiting the derived conditions of the loss of the second ceratobranchial arch and the presence of caudal scansors. Most recently, Wells and Wellington (1984) erected the genus *Christinus* for the Australian geckos formerly assigned to *Phyllodactylus*, although their evidence for its diagnosis was unconvincing.

Even after the removal of these units, there is still no convincing evidence for the monophyly of *Phyllodactylus*. Kluge (1993) recognized 56 *Phyllodactylus* species. An additional five species have since been described and two others have been resurrected from synonymy, all from South Africa. Species currently retained in *Phyllodactylus* are chiefly distributed in the New World, with the greatest diversity in the arid regions of the Pacific coast of Mexico and South America, and in Venezuela. The remaining Old World *Phyllodactylus* include two species in Thailand, one in the Mediterranean region, two on the island of Socotra, one in Madagascar, and 13 (one undescribed) in southern Africa (Figs. 1, 2). This scattered distribution is difficult to explain and further suggests that the members of the genus do not form a single evolutionary unit. In this paper we present further evidence against the monophyly of *Phyllodactylus*, provide additional evidence for the monophyly of several of the Old World leaf-toed genera that have not been rigorously diagnosed (*Christinus* and *Ebenavia*), and provide evidence for the recognition of six additional monophyletic groups of Old World "*Phyllodactylus*."

Although higher order patterns of relationship within the Gekkonoidea are generally well established (Kluge 1987), relationships at the inter-generic level within the Gekkonidae remain obscure (Russell 1972; Bastinck 1981; Bauer

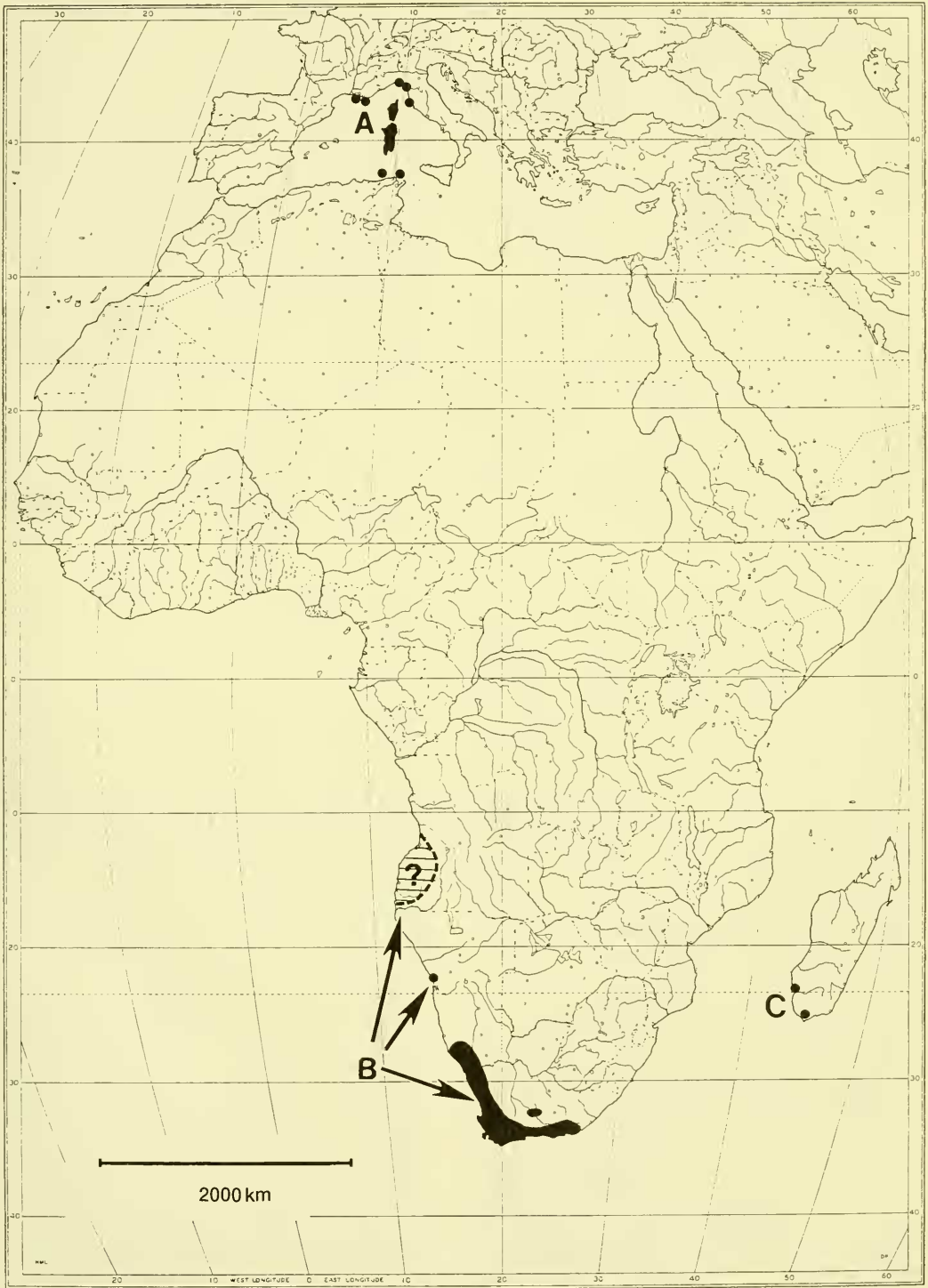


FIGURE 1. Distribution of *Phyllodactylus europaeus* in and around the central Mediterranean (A), the 12 species of southern African *Phyllodactylus* (B), and *P. brevipes* in Madagascar (C, after Glaw and Vences 1994).

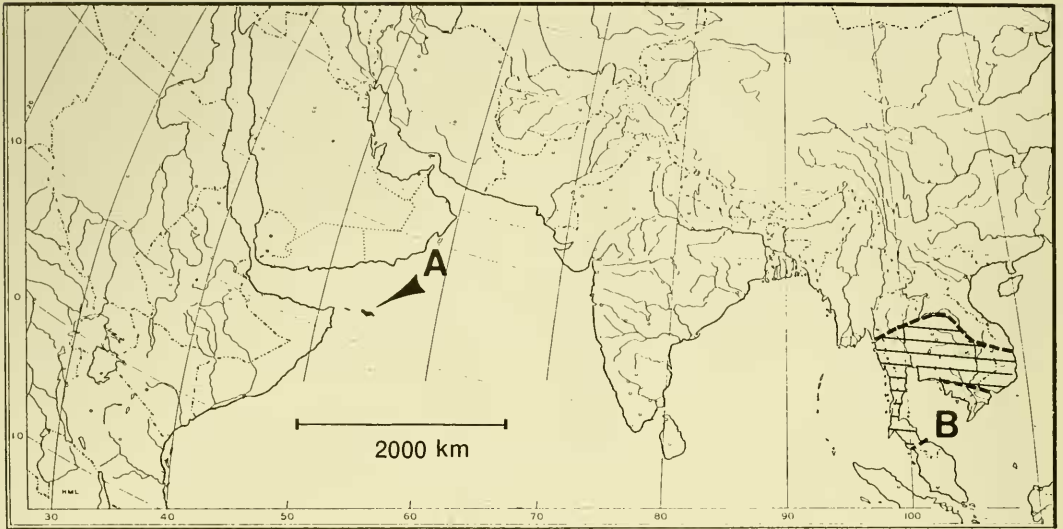


FIGURE 2. Distribution of *Phyllodactylus riebeckii* and *P. trachyrhinus* on Socotra Island, Yemen (A), and *P. siamensis* and *P. melanostictus* in Southeast Asia (B).

1990; Kluge 1983, 1987, 1995; Kluge and Nussbaum 1995). Phylogenetic analyses of single genera are thus hampered by a lack of knowledge of possible outgroup taxa, or outgroups must be defined so broadly as to make polarity assignments virtually impossible. Although we are unable to present a phylogenetic hypothesis for relationships among the various clades up to now included within *Phyllodactylus*, the recognition of such monophyletic subunits and their removal from the polyphyletic assemblage to which they are now assigned is a necessary step toward this goal. The new and resurrected genera recognized herein may be treated as monophyletic operational units in any subsequent attempts to reconstruct the phylogeny of gekkonids as a whole.

Relationships within each of the newly recognized clades of leaf-toed geckos are generally non-problematic, as most of these clades correspond to a single geographic region and all but one of these regions contains only one or two species. In the case of the *Phyllodactylus* of southern Africa, however, there are twelve recognized species in three apparently very distantly related clades (genera). Several hypotheses of higher order relationship exist for southern African gekkonids, but these are poorly resolved and partially conflicting. Nonetheless, there are sufficient data for us to present some phylogenetic

and biogeographic analysis of the most speciose of these clades.

MATERIALS AND METHODS

Specimens were examined externally using a binocular dissecting microscope or hand lens. Specimens of all Old World *Phyllodactylus* species (except *P. brevipes*) were examined, as were representative New World species and species referred to other leaf-toed gekkonid genera. The species lists of Kluge (1983, 1991, 1993, 1996) served as a guide to the recognized taxa. We follow Kluge (1987) for the naming of higher taxonomic units of gekkonids. The following species were examined externally: *Asaccus elisae*, *A. gallagheri*, *A. griseonotus*, *Christinus guentheri*, *C. marmoratus*, *Ebenavia inunguis*, *Phyllodactylus angelensis*, *P. angustidigitatus*, *P. ansorgii*, *P. bauri*, *P. braacki*, *P. bugastrolepis*, *P. clinatus*, *P. darwini*, *P. davisii*, *P. delcampi*, *P. dixonii*, *P. duellmani*, *P. essexi*, *P. europaeus*, *P. galapagensis*, *P. gemmulus*, *P. gerrhopygus*, *P. gilberti*, *P. heterurus*, *P. hewitti*, *P. hexaporus*, *P. homolepidurus*, *P. inaequalis*, *P. insularis*, *P. interandinus*, *P. julienni*, *P. lanei*, *P. leei*, *P. lepidopygus*, *P. lineatus*, *P. martini*, *P. melanostictus*, *P. microlepidotus*, *P. microphyllus*, *P. muralis*, *P. palmeus*, *P. partidus*, *P. pau-*

cituberculatus, *P. peringueyi*, *P. porphyreus*, *P. pulcher*, *P. pumilus*, *P. reissii*, *P. riebeckii*, *P. rupicolus*, *P. santacruzensis*, *P. sentosus*, *P. siamensis*, *P. swartbergensis*, *P. tinklei*, *P. trachyrhinus*, *P. tuberculosus*, *P. unctus*, *P. ventralis*, *P. wirshingi*, *P. xanti*, *Paroedura androyensis*, *P. bastardi*, *P. gracilis*, *P. guibeae*, *P. pictus*, *P. stumpffi*, *Urocotyledon inexpectata*, and *U. wolterstorffi*. Specimens were examined in or borrowed from the following collections: California Academy of Sciences (CAS), British Museum (Natural History) (BMNH), University of Kansas Museum of Natural History (KU), Academy of Natural Sciences of Philadelphia (ANSP), Louisiana State University Museum of Natural Sciences (LSUMZ), United States National Museum (USNM), Field Museum of Natural History (FMNH), Museum für Naturkunde der Humboldt Universität zu Berlin (ZMB), Port Elizabeth Museum (PEM and PEM-AM), American Museum of Natural History (AMNH), John Ellerman Museum, University of Stellenbosch (JEM), Transvaal Museum (TM), National Museum, Bloemfontein (NMB), Museo Zoologico de la Specola, Università di Firenze (MZUF), Zoologisches Forschungsinstitut und Museum A. Koenig (ZFMK), and the South African Museum (SAM). In addition, several specimens in the collection of the senior author (AMB) were also consulted. These specimens will be deposited in the CAS collection. Specimens of the following species were not examined, but were compared on the basis of published descriptions: *Phyllodactylus bordai*, *P. brevipes*, *P. rutteni*, *P. transversalis*, *Paroedura homolorhinus*, *P. masobe*, *P. oviceps*, and *Urocotyledon weileri*. For some of the taxa, represented by small samples in our study, observations were supplemented by literature information. These include *Christinus guentheri* (Cogger 1971; Cogger et al. 1983), *C. marmoratus* (Stephenson 1960), *Phyllodactylus ansorgii* (Boulenger 1907), *P. europaeus* (Wiedersheim 1876; Fürbringer 1922; Rieppel and Schneider 1981), and the Socotran *Phyllodactylus* (Loveridge 1947).

Osteological comparisons were made using cleared-and-stained specimens [prepared following the methods of Wassersug (1976) and Bauer (1986)], dry skeletal material, and radiographs prepared from intact museum specimens. Radiographs were prepared using a Faxitron cabinet

x-ray unit at 20–40 kV for 20–45 seconds. Images were exposed onto Polaroid type 55 positive/negative film and observations made with a Micron 775 microfiche reader. A complete list of osteological specimens and radiographic material is presented in Appendix A. As only representative New World species were examined in detail, we here rely on Dixon (1964; in litt.) for the generality of certain statements regarding the osteology of these taxa.

Protein electrophoresis was also used to examine phenetic and phylogenetic relationships among representative leaf-toed gekkonid taxa. Tissues from all southern African *Phyllodactylus* (except *P. ansorgii*), as well as from representative "leaf-toed" geckos from other regions (see Appendix B) were compared at 24 allozyme loci (Table 1). Most tissues were obtained by the authors in the field and have been deposited in the frozen tissue collection at the Museum of Natural Science, Louisiana State University (LSUMZ H-series). Additional material was obtained from the frozen tissue collections of the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ-FC) and Dr. S. Blair Hedges, Pennsylvania State University (SBH). Samples of liver tissue dissected from freshly killed specimens or obtained from frozen tissue collections were homogenized in deionized water, stored in liquid nitrogen or in an ultracold freezer, and subjected to horizontal starch gel electrophoresis using standard techniques (Selander et al. 1971; Harris and Hopkinson 1976; Hillis et al. 1996). In the phylogenetic analysis (applied only to African *Phyllodactylus*) loci were considered to be characters and alleles character states (Buth 1984). Polymorphisms were treated as recommended by Murphy (1993) and Mabee and Humphries (1993) and data were analyzed using PAUP 3.0 (Swofford 1990). In the phenetic analysis Nei (1978) genetic distances were calculated using the BIOSYS computer package (Swofford and Selander 1981).

RELATIONSHIPS AMONG LEAF-TOED GECKOS

The relationships of *Phyllodactylus* to other gekkonine genera have never been adequately reconstructed. This has been due, in part, to the fact that, aside from the leaf-like scensors of the toes, most *Phyllodactylus* are relatively conservative in morphology, retaining many plesio-

TABLE 1. Buffer systems and loci scored in the analysis of the Old World leaf-toed geckos.

Enzyme	Enzyme Commission No.	Locus	Buffer System
Aspartate aminotransferase (2 loci)	2.6.1.1	Aat-1,2	B
Aconitase (2 loci)	4.2.1.3	Acon-1,2	C
Adenylate kinase	2.7.4.3	Ak	A
Creatine kinase	2.7.3.2	Ck	A
Fumarase	4.2.1.2	Fum	A
Glucose dehydrogenase	1.1.1.47	Gdh	B
Glucose phosphate isomerase (2 loci)	5.3.1.9	Gpi-1,2	B
Isocitrate dehydrogenase (2 loci)	1.1.1.42	Icdh-1,2	C
L-lactate dehydrogenase (2 loci)	1.1.1.27	Ldh-1,2	B
Malate dehydrogenase (2 loci)	1.1.1.37	Mdh-1,2	B
Malic enzyme	1.1.1.40	Me	C
Dipeptidase (2 loci)	3.4.13.11	Pep-1,2	A
Tripeptide aminopeptidase	3.4.11.4	Pep-3	A
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh	C
Phosphoglucomutase (2 loci)	5.4.2.2	Pgm-1,2	B
Pyruvate kinase	2.7.1.40	Pk	A

morphic character states relative to other gekkonid taxa (Hamilton 1960; Kluge 1983).

Few authors have suggested explicit patterns of relationship among the various geographically delimited groups of "*Phyllodactylus*." Russell (1972) recognized a number of groups of gekkonid geckos on the basis of similarities in digital structure. He specified, however, that these represented morphological groupings only, rather than explicitly evolutionarily cohesive units. Russell's *Phyllodactylus* group included *Phyllodactylus*, *Ebenavia*, *Ptyodactylus* and *Uroplatus*, and the taxa now allocated to *Paroedura*, *Urocotyledon*, *Asaccus*, and *Christinus*. Although he did not initially regard these as necessarily forming a natural unit, Russell (1976) subsequently suggested that similarities between *Uroplatus*, *Ptyodactylus*, and *Phyllodactylus* might have phylogenetic significance. Nonetheless, he proposed no explicit hypothesis of relationship among these forms. Kluge (1983) subsequently presented evidence from hyoid morphology to argue for the non-monophyly of Russell's *Phyllodactylus* group.

In analyzing relationships within *Asaccus*, Arnold and Gardner (1994) used a range of leaf-toed geckos as the outgroup (*Paroedura stumffi*, *Phyllodactylus europaicus*, *P. galapagensis*, *P.*

riebeckii, *P. siamensis*, *P. trachyrhinus*). They regarded *Paroedura* as "apparently related" to other *Phyllodactylus* and by implication they accepted at least some level of close relationship among the remaining leaf-toed geckos in their outgroup. However, no explicit support for this assumption was provided.

The only hypothesis explicitly suggesting affinities between geographically separated groups of *Phyllodactylus* is that of Greer (1990). He suggested that the Australian leaf-toed geckos (genus *Christinus*) might have evolved from African *Phyllodactylus* stock, citing for his support the shared derived conditions of *Christinus* spp. and *Phyllodactylus porphyreus*. The fusion of the nasal bones is, however, the only derived feature mentioned by Greer that is shared by this pair of taxa (and several other leaf-toed gekkonids).

Thus, little or no evidence from morphology exists to corroborate *Phyllodactylus* monophyly. Likewise in our study we uncovered no putative synapomorphies for this genus as presently construed. Although it cannot be used to demonstrate monophyly, nor to falsify phylogenetic hypotheses, we used genetic distance data to examine the issue of similarity among leaf-toed geckos. The distribution of alleles among the 24 loci is presented in Table 2. A total of 185 alleles was

observed among the loci surveyed. Alleles per locus ranged from three in Gpi-2, Mdh-1, and Mdh-2 to 14 in Pep-3. The average number of alleles per locus was 7.7. Numbers of fixed allozyme differences and Nei (1978) genetic distances (D_N) were calculated among sixteen species of leaf-toed geckos (Table 3), including all southern African species (except *Phyllodactylus ansorgii*) as well as *Christinus marmoratus* (Australia), *Paroedura pictus* (Madagascar), *Phyllodactylus xanti* (western North America), *P. wirshingi* (Puerto Rico), and *P. siamensis* (southeast Asia). *Afroedura loveridgei* (Mozambique), a representative of a genus that may be among a cluster of African geckos forming the outgroup to southern African *Phyllodactylus* was also included. Pairwise differences between *Phyllodactylus* species and the other genera are large (Nei distances 1.10–2.08, mean 1.62; fixed allozyme differences 16–21, mean 19), and many approach or exceed the limit of resolution of allozyme electrophoresis. For example, any similarity between two taxa showing 21 fixed differences out of 24 loci (see Table 3) is more likely to be due to chance than to common ancestry.

Similarly high levels of differentiation exist between sets of *Phyllodactylus* species inhabiting different geographic regions (Table 4; Fig. 3). Indeed, some of the differences within "*Phyllodactylus*" are even greater than those between "*Phyllodactylus*" and the other leaf-toed genera. For example, there are 23 fixed differences between *Phyllodactylus porphyreus* and *P. siamensis*, *P. xanti*, and *P. wirshingi* ($D_N = 3.18$).

Even within geographic regions, huge genetic distances exist. *Phyllodactylus xanti* and *P. wirshingi*, both members of the *P. tuberculatus* group (Dixon 1960, 1964), are as distinct from one another (18 fixed differences, $D_N = 1.39$) as are many of the species on different continents. The same is true of some of the comparisons among southern African species. *Phyllodactylus peringueyi* is particularly distinct (20–22 fixed differences [$D_N = 1.79$ –2.49] from any other *Phyllodactylus* species, including the others in southern Africa). *Phyllodactylus porphyreus* and *P. swartbergensis* are slightly less distinct from the remaining African forms, but still very different (15–18 fixed differences from other species [$D_N = 0.98$ –1.38], 17 [$D_N = 1.23$] from each other). *Phyllodactylus microlepidotus* shows

13–15 fixed differences ($D_N = 0.78$ –0.98) from the *lineatus* group species, and within the *lineatus* group, fixed differences range from three to 11 ($D_N = 0.16$ –0.61).

Maximum recorded intrageneric Nei (1978) genetic distances in geckos are 1.19 for *Phelsuma* (Good and Bauer 1995), 1.04 for *Rhoptropus* (Bauer and Good 1996), 0.87 for *Pachydactylus* (Branch et al. 1996), and 0.68 for *Rhacodactylus* (Good et al. 1997). Most of the distances among *Phyllodactylus* species far exceed those levels, and in fact are equivalent to distances among the genera *Hemidactylus*, *Lygodactylus*, *Phelsuma*, *Rhoptropus*, *Pachydactylus*, *Palmatogecko*, and *Tarentola* ($D_N = 1.25$ –3.14; Good and Bauer unpubl.). The only distances in the present analysis that are consistently less than these intergeneric distances are within the *lineatus* complex of southern African *Phyllodactylus* and between this complex and *P. microlepidotus* (Fig. 3).

We use the evidence from this analysis, along with the absence of morphological characters supporting *Phyllodactylus* monophyly to justify the assumption that the genus consists of several unrelated, or distantly related clades that have been artificially grouped. This necessitates the further analysis of characters within "*Phyllodactylus*" in order to delineate putatively monophyletic subunits.

PREVIOUSLY RECOGNIZED MONOPHYLETIC GROUPS OF LEAF-TOED GECKOS

New World *Phyllodactylus*

In the New World *Phyllodactylus* occurs from Riverside County, California south along the west coast of North America to northwestern Panama, and in South America from southern Ecuador to northern Chile. It is also present along the coast of Colombia and Venezuela, on Barbados and Puerto Rico, in Belize and adjacent offshore islands, and in the Galapagos (Dixon 1962, 1964, 1968; Dixon and Huey 1970). Most authors have accepted the monophyly of New World *Phyllodactylus* as a whole (e.g. Dixon 1964; Vanzolini 1968; Carillo de Espinoza et al. 1990) although this has not been rigorously demonstrated. Dixon (1964) provided a diagnosis for the Neotropical (including North American) spe-

TABLE 2. Overall allele frequencies of African and other selected leaf-toed gekkonids. Abbreviations: BRA = *Phyllodactylus braacki*, ESS = *P. essexi*, GEM = *P. gemmulus*, HEW = *P. hewitti*, HEX = *P. hexaporus*, LIN = *P. lineatus*, MIC = *P. microlepidotus*, RUP = *P. rupicola*, SWA = *P. swartbergensis*, PER = *P. peringueyi*, SIA = *P. stamensis*, XAN = *P. xanti*, WIR = *P. wishingi*, AFR = *Afroedura loveridgei*, CRI = *Christinus marmoratus*, PAR = *Paroedura pictus*. *Afroedura loveridgei* has been included as a representative of the African gekkonid radiation. Lower case letters represent different allelic states of each locus. Unless multiple alleles and their frequencies are listed it may be assumed that all of the specimens examined for a given species (see Appendix B) are homozygous for the indicated allele.

Locus	Taxa/Alleles																
	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	PER	SIA	XAN	WIR	AFR	CRI	PAR
Aat-1	b	b	b	b	b	b	b	b	b	a	c	d	e	f	c	g	h
Aat-2	a	a	a	a	b(0.85)	a	a	a	a	a	b	c	c	d	b	b	b
Acom-1	b(0.25)	b	c	b	d(0.15)	e(0.95)	g	b	g	a	h	i	j	j	h	h	h
Acom-2	b	b	b	b	b	f(0.05)	c	b	b	a	d	e	f	g	h	i	j
Alk	a	a	a	a	a	a	b	a	b	a	c	d	e	f	g	h	i
Ck	b	b	c	b	b	c	e	c	d	a	f	g	h	i	j	k	l
Fium	b	b	b	b	b	b	b	b	c	a	c	d	e	d	f	g	h
Gdh	a	a	a	a	a	a	a	a	b	a	c	a	a	a	d	e	f
Gpi-1	c	b	e	c	c	d	f	c	a	a	g	d	h	i	j	k	c
Gpi-2	a(0.95)	a	c	a	a	a	a	a	c	a	a	a	a	a	a	a	c
	b(0.05)	b	b	b	b	b	b	b	a	a	a	c	e	g	h	i	j
Icdh-1	b	b	c	b	b	b(0.85)	d	b	a	a	a	e	g	g	h	i	j
	b	b	b	b	b	c(0.15)	a	b	c	a	a	d	e	f	a	a	g
Icdh-2	b	b	b	b	b	a	a	b	c	a	d	e	e	f	g	h	h
Ldh-1	b	b	b	b	b	b	b	b	c	a	a	a	a	a	c	d	a
Ldh-2	a	a	a	a	a	a	a	a	b	a	a	a	a	a	c	d	a
Mdh-1	b	b	b	b	b	b	b	b	c	a	b	b	b	b	b	b	b
Mdh-2	a	a	a	a	a	a	a	a	a	a	a	b	c	c	a	a	a
Me	a	b	a	a	a	a	a	a	b	a	c	a	a	a	a	a	a
Pep-1	d	b	c	c	c	e	e	c	c	a	f	g	h	i	j	j	k
Pep-2	b	a	b	b	b	c	c	a	a	a	d	e	e	e	a	a	a
Pep-3	c	a	g	b	d	e	i	f	h	a	j	k	l	m	n	a	m
Pgdh	b	b	b	b	b	b(0.95)	e	b	d	a	f	g	h	h	e	b	i
	b	b	d	b	b	c(0.05)	e	b	b	a	a	g	h	h	e	b	i
Pgm-1	b	b	d	b	b	c	e	b	b	a	f	g	h	i	j	k	k
Pgm-2	b	b	b	b	c	b	e	b	a	a	d	b	b	e	f	f	g
Pk	a	a	b	a	a	a	a	a	a	a	c	d	e	e	f	a	a

TABLE 3. Fixed differences (above diagonal) and Nei (1978) genetic distances (below diagonal) between species pairs of leaf-toed geckos. Abbreviations as for Table 2.

	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	PER	SIA	XAN	WIR	AFR	CRI	PAR
BRA	—	4	10	3	3	7	13	4	18	16	21	18	18	20	20	17	18
ESS	0.213	—	11	5	5	8	14	6	17	16	21	19	19	20	21	17	19
GEM	1.232	0.613	—	10	10	5	15	7	17	17	22	18	18	21	20	18	19
HEW	0.162	0.234	0.539	—	3	7	14	4	16	16	21	18	18	20	19	17	18
HEX	0.158	0.235	0.553	0.135	—	7	13	4	17	16	21	19	19	20	20	17	18
LIN	0.339	0.408	0.275	0.347	0.341	—	13	4	17	15	21	16	17	20	19	16	19
MIC	0.775	0.875	0.981	0.875	0.775	0.771	—	13	17	15	20	19	19	20	20	18	17
RUP	0.213	0.288	0.405	0.182	0.184	0.183	0.780	—	16	15	21	17	17	20	19	16	17
POR	1.376	1.232	1.232	1.099	1.227	1.223	1.232	1.099	—	17	22	23	23	23	21	21	20
SWA	1.095	1.099	1.232	1.099	1.093	0.981	0.981	0.981	1.232	—	20	19	19	21	19	16	20
PER	2.086	2.079	2.485	2.079	2.074	2.070	1.792	2.079	2.485	1.792	—	20	21	21	22	18	18
SIA	1.385	1.569	1.386	1.386	1.563	1.089	1.569	1.232	3.178	1.569	2.079	—	15	20	20	19	21
XAN	1.385	1.569	1.386	1.386	1.563	1.223	1.569	1.232	3.178	1.569	2.079	0.981	—	18	20	19	21
WIR	1.794	1.792	2.079	1.792	1.786	1.782	1.792	1.792	3.178	2.079	2.485	1.792	1.386	—	21	21	21
AFR	1.794	2.079	1.792	1.569	1.786	1.559	1.386	1.569	2.079	1.569	1.386	1.792	1.792	2.079	—	14	20
CRI	1.229	1.232	1.386	1.232	1.227	1.096	1.386	1.099	2.079	1.099	1.386	1.569	1.569	2.079	0.875	—	16
PAR	1.510	1.569	1.569	1.386	1.406	1.559	2.079	1.232	1.792	1.792	2.079	2.079	2.079	2.079	1.792	1.099	—

TABLE 4. Mean Nei genetic distances (below diagonal) and fixed alleles differences (above diagonal) of leaf-toed geckos by geographic region.

	Southern Africa	Southeast Asia	New World
Southern Africa	—	18.7	19.7
Southeast Asia	1.64	—	17.5
New World	1.84	1.39	—

cies of *Phyllodactylus*, which he assumed were monophyletic. These taxa were characterized by the absence of femoral or preanal pores, the presence of cloacal bones, phalangeal formulae of manus and pes 2-3-4-5-3, cruciform interclavicle, 26 presacral vertebrae, five pairs of sternal ribs, fused premaxillary bones, paired nasals, vomers, and parietals, lunate prefrontals projecting posteriorly, and an absence of a cartilaginous union between the precoracoid ray of the epicoracoid and the scapula.

Russell (1972), however, has demonstrated that the stated reduction in the phalangeal formula of the pes from 2-3-4-5-4 does not occur in any of the New World species of the genus. This removes one of the most convincing arguments for the monophyly of New World *Phyllodactylus* as most of the other features are primitive, or at least broadly distributed among gekkonids as a whole. However, the absence of preanal pores is derived within gekkonids, and the ligamentous union of the scapula and precoracoid ray of the epicoracoid occurs elsewhere among leaf-toed genera only in *Asaccus* and some of the southern African *Phyllodactylus*, and might also be apomorphic. The reduction to a single egg per clutch seen in most New World *Phyllodactylus* (Dixon and Huey 1970) is probably derived at the level of gekkonids (Kluge 1987) but the presence of two-egg clutches has also been recorded (e.g., Kushlan 1981), and this character's variability within the group needs to be assessed.

Dixon (1960, 1964) recognized three species groups of *Phyllodactylus* in North and Central America: *Phyllodactylus unctus* (to which he believed some South American forms were related), *P. delcampi*, and *P. tuberculosus*, in which he included species occurring from southern California through western Mexico, Central America, and South America, as well as the Galapagos and the Caribbean. Dixon (1964) re-

garded the *unctus* and *delcampi* groups as closely related. Although Murphy (1983) presented evidence to the contrary, Dixon's conclusions have been supported by most data (e.g., Murphy and Papenfuss 1980; Grismer 1994).

Dixon's three species groups have been accepted by subsequent workers (e.g., Vanzolini 1968), although the monophyly of these units has not been rigorously established. Within the *P. tuberculosus* group several putatively monophyletic subunits have been proposed, including groups in the West Indies (Dixon 1961), Central America (Dixon 1968), and South America (Dixon and Huey 1970; Kroll and Dixon 1972). The Galapagos species are closely related to one another (Van Denburgh 1912) and to the South American west coastal forms (Dixon and Huey 1970; Wright 1983, 1984), although more than one invasion of the islands has been proposed.

We have not examined all New World *Phyllodactylus* in detail, nor have we critically evaluated the monophyly of this group as a whole, or that of any of its subunits, as this would have expanded the scope of the analysis significantly and would have duplicated the efforts of other workers more intimately involved with relationships among American *Phyllodactylus*. Rather, we have constrained our focus to Old World leaf-toed geckos. For this purpose confirmation of the monophyly of American *Phyllodactylus* is not essential. It is only necessary to demonstrate that putatively monophyletic Old World groups do not share a preponderance of derived characters with some or all of the American forms. *Phyllodactylus* has as its type species a West Indian form, *P. pulcher*, currently considered as a member of the *P. tuberculosus* group. The identification of any clades of Old World leaf-toed geckos that can be diagnosed as monophyletic units distinct from New World forms



FIGURE 3. UPGMA phenogram illustrating Nei (1978) genetic distances among representative species of *Phyllodactylus* and other leaf-toed geckos. Note that only members of the *Phyllodactylus lineatus* complex of southern Africa cluster together closely, that *P. peringueyi*, also from southern Africa, is highly divergent from these forms, and that non-African *Phyllodactylus* do not cluster together.

therefore justifies the application of alternative (available or new) generic names.

Old World Leaf-toed Geckos

Asaccus Dixon and Anderson, 1973

The genus *Asaccus* was erected by Dixon and Anderson (1973) for two species of Middle Eastern leaf-toed geckos. The number of taxa now recognized is seven, distributed in eastern Arabia (Oman and the United Arab Emirates), Iraq, Iran, Syria and Turkey (Arnold and Gardner 1994; Rastegar-Pouyani 1996). This genus exhibits several derived features including a reduction in the phalangeal formula of the manus and pes to 2.3.4.4.3, a lack of preanal pores, loss of cloacal sacs and bones, and the loss of the left oviduct and associated reduction of clutch size to one (Arnold and Gardner 1994; Leptien 1994a, b, 1996). The reduction of phalangeal formula had been noted previously (Russell 1972). Arnold and Gardner (1994) reported that the reduced number of phalanges is a transient state in some species, and that three species eventually develop the normal phalangeal complement.

Urocotyledon Kluge, 1983

Kluge (1983) transferred the four species *inexpectata*, *wolterstorffi*, *palmata*, and *weileri* to the new genus *Urocotyledon*. The lack of the second ceratobranchial arch and possession of a well-formed scansorial pad on the ventral surface of the tail tip were used as apomorphic diagnostic characters for the genus. The insular species *U. inexpectata* occurs on the granitic Seychelles (Cheke 1984), whereas *U. wolterstorffi* is restricted to the eastern Usambara and Uluguru Mountains (Broadley and Howell 1991) and *U. weileri* and *U. palmata* occur in Cameroon and the adjacent Congo (Perret 1963).

Christinus Wells and Wellington, 1984

Australian "*Phyllodactylus*", including a complex of mainland forms involving several chromosome races (King 1981, 1987; King and Rofe 1976), were formally removed from *Phyllodactylus* by Wells and Wellington (1984) and placed in a new genus, *Christinus*. Wells and Wellington (1984) diagnosed *Christinus* on the basis of plesiomorphic or unpolarizable external features common to many leaf-toed geckos. Greer (1990)

provided a preliminary diagnosis for *Christinus* that included osteological features, among them the unquestionably derived elevated number (27–28) of presacral vertebrae. We here present a more complete characterization and diagnosis of the genus.

TYPE SPECIES. — *Diplodactylus marmoratus* Gray, 1845, by original designation.

CONTENT. — *Christinus marmoratus* (Gray, 1845), *C. guentheri* (Boulenger, 1885). *Christinus marmoratus* contains several unnamed chromosomal races (King and Rofe 1976), which should be recognized at the species level (Bauer and Henle 1994).

CHARACTERIZATION AND DIAGNOSIS. — *Christinus* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; granules on snout slightly larger than those on body dorsum; rostral scale without median cleft; first supralabial enters nostril; enlarged chinshields and lateral gulars; margins of pupil crenelate in preserved specimens; preanal pores absent; series of 3–4 cloacal spurs present, better developed in males; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with relatively rounded or pointed nasal projection of moderate length; frontal moderately broad, only slightly constricted over orbits, without maxillary contact; maxillary bone bearing approximately 30 teeth in adults; postfrontal bones with anterior and posterior projections subequal or with anterior longer than posterior, without pronounced lateral spine; stapes imperforate; coronoid bone strongly developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present; neural arches of atlas paired or fused; 27–28 presacral vertebrae, 1 lumbar vertebra; 4 cervical ribs, 2–3 sternal ribs, 2–3 mesosternal ribs; one pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); hypoischium bifurcate distally; cloacal sacs and a single pair of cloacal bones present. Clutch size variable (1–2 in

Christinus marmoratus, King 1977, How et al. 1987; 1–3 [mean of 1.3] in *C. guentheri*; Cogger et al. 1983).

Christinus may be diagnosed from all other leaf-toed geckos by the apomorphic increase in number (27–28) of presacral vertebrae (24–26 in all other taxa). In addition, the fusion of the nasals is a derived feature among gekkonids that distinguishes *Christinus* from all leaf-toed "ptyodactyline" forms except *Ebenavia*, the Socotran and some southern African *Phyllodactylus* and *P. brevipes*. *Christinus* differs from *Ebenavia*, *P. peringueyi* and *P. swartbergensis* in being atuberculate, and from the remaining forms in the presence of 4 (vs. 3) cervical ribs. The presence of cloacal sacs and bones further distinguishes it from the Socotran forms, whereas the absence of preanal pores and the imperforate condition of the stapes distinguishes it from *P. microlepidotus* and the *P. lineatus* complex, and the presence of more than two enlarged scales per cloacal spur and the presence of transverse projections on the interclavicle serve to diagnose it from the remaining southern African *Phyllodactylus*.

DISTRIBUTION. — *Christinus* occurs in temperate Australia from Shark Bay, Western Australia to northeastern New South Wales and in the Lord Howe and Norfolk Island groups in the Tasman Sea (Cogger 1992; Bauer and Henle 1994).

Paroedura Günther, 1879

Guibé (1956) reviewed the Madagascan leaf-toed geckos. The majority of the species he considered have since been removed to *Paroedura* by Dixon and Kroll (1974). Another species, *Phyllodactylus barbouri*, has been placed in the synonymy of *Diplodactylus granariensis*, an Australian species (Bauer and Henle 1994). Guibé also regarded *Phyllodactylus porphyreus* as occurring in Madagascar on the basis of his inclusion of Mocquard's (1900) *P. brevipes* in the synonymy of this species.

There are ten species in *Paroedura*, nine in Madagascar and one in the Comores. Relationships among the species remain unresolved (Nussbaum and Raxworthy 1994), but the monophyly of the group is well supported by a variety of osteological characters (Dixon and Kroll 1974; Nussbaum and Raxworthy 1994a) including: loss of the second ceratobranchial, paired atlas, imperforate stapes, cruciform interclavicle,

2–3 sternal ribs, 1–2 mesosternal ribs, and 3–4 cervical ribs.

"Phyllodactylus" brevipes Mocquard, 1900

Nussbaum and Raxworthy (pers. comm.) have rediscovered *Phyllodactylus brevipes* and conclude that it is very dissimilar from *P. Porphyreus* (contra Guibé 1956). A large series of this species is presently being studied (Nussbaum and Raxworthy, in prep.), but was unavailable to us during the preparation of the present manuscript. Dixon and Kroll (1974) regarded *P. brevipes* as being allied to its African congeners, but did not elaborate. Kluge and Nussbaum (1995), however, noted that *Phyllodactylus brevipes* "belongs to another part of the history of Gekkonini" relative to the southern African taxa of leaf-toed geckos.

Ebenavia Boettger, 1878

The generic separation of *Ebenavia* from *Phyllodactylus* was based on the absence of claws, enlarged chinshields, and enlarged midventral caudal scales in the former (Boettger 1878; Boulenger 1885). Most workers (e.g., Boettger 1878; Russell 1972) have regarded the two genera as closely allied. Bastinck (1981) further suggested that *Ebenavia* is derived from within *Phyllodactylus* but did not base this assumption on any repeatable analytical method. Dixon and Kluge (1964) provided some osteological data for this genus. These were confirmed by our observations except for the phalangeal formula of the pes, which was found to be unreduced (2-3-4-5-3 according to Dixon and Kluge 1964). Our observations differ considerably, however, from those of Wellborn (1933). Because the initial generic diagnosis was brief and published in Latin, we here provide an expanded redescription and diagnosis, incorporating both external and osteological features.

TYPE SPECIES. — *Ebenavia inunguis* Boettger, 1878, by monotypy.

CONTENT. — *Ebenavia inunguis* Boettger, 1878. An undescribed species is known from dry coastal habitats in Madagascar (R. A. Nussbaum, in litt. February, 1996).

CHARACTERIZATION AND DIAGNOSIS. — *Ebenavia* may be distinguished from all other gekkonids by the following combination of char-

acteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation tuberculate, tubercles very high relative to width of base, keeled or mucronate; granules on snout mucronate, larger than those on dorsum of body; rostral scale without median cleft; first supralabial excluded from nostril; no enlarged chinshields; margins of pupil crenelate in preserved specimens; preanal pores absent; 1–2 enlarged scales on each cloacal spur, much more well developed in males; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with moderately long, triangular nasal projection; frontal relatively thin, only slightly constricted over orbits, without maxillary contact; total number of maxillary tooth positions (unilateral) in adults greater than 40; postfrontal bones with posterior projection much thicker than anterior, without pronounced lateral spine; stapes imperforate; coronoid bone weakly developed, only slightly raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present; neural arches of atlas fused; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 2 sternal ribs, 2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes), some or all digits clawless; hypischium not bifurcate; cloacal sacs and a single pair of cloacal bones present; clutch size usually two (Angel 1942; pers. observ.; but see Henkel and Schmidt 1991, 1995).

Ebenavia exhibits at least three derived diagnostic features relative to other leaf-toed geckos: the presence of amphicoelous vertebrae, a primitive condition for gekkonoids (Kluge 1967, 1987), but one that is most parsimoniously regarded as derived in gekkonoids, the absence of claws on all digits (at least in males), and the very large number of marginal teeth (Bauer 1990; Kluge and Nussbaum 1995). Further, some of the dorsal tubercles in this genus are mucronate or multicarinate rather than simply keeled, and the snout granules are also mucronate. These conditions are not found in other tuberculate leaf-toed geckos. In addition to these features, *Ebenavia* may be distinguished from the superficially similar *Phyllodactylus peringueyi* by its lack of sexual dichromatism, presence of one versus two

pairs of cloacal bones, 26 versus 24 presacral vertebrae, crenelate versus straight-edged pupil margins, and presence of transverse projections of the interclavicle. In all of these features, however, *Ebenavia* exhibits the apparently plesiomorphic conditions, and *P. peringueyi* the apomorphic ones. A more complete diagnosis and description of this genus will appear shortly (R. A. Nussbaum and C. Raxworthy, pers. comm.).

DISTRIBUTION. — The single described species of this genus occurs in Madagascar, the Comores, and Mauritius (Blanc 1971). It has also been reported from Pemba Island, off the coast of Tanzania (Loveridge 1957), although the validity of these records requires verification (Broadley and Howell 1991).

REMARKS. — Although *Ebenavia* possesses several uniquely derived characteristics among leaf-toed geckos (see diagnosis), its superficial similarity to *P. peringueyi* from littoral areas of the Eastern Cape, South Africa is striking (Branch and Bauer 1994). *Ebenavia inunguis* has been found in the littoral zone, as well as in forests at moderate to high elevation (Angel 1942; Raxworthy 1988; Andreone 1991). Certain aspects of the overall morphology of these forms is also reminiscent of some of the Peruvian species of *Phyllodactylus* that inhabit the arid littoral regions of the west coast (Huey 1979; Carillo de Espinoza et al. 1990). Such similarities appear to represent convergence towards activity on sand, soil or vegetation (as opposed to rock), rather than a real phylogenetic signal.

ADDITIONAL MONOPHYLETIC GROUPS OF LEAF-TOED GECKOS

The removal of *Asaccus*, *Paroedura*, *Urocytleon*, and *Christinus* from *Phyllodactylus* leaves 18 recognized species of Old World *Phyllodactylus*. As indicated by earlier workers (e.g., Dixon 1964; Russell 1972; Kluge 1983) and suggested by the genetic distance data presented herein, there seems to be no support for the retention of these taxa within *Phyllodactylus*. As the type species of the genus, *P. pulcher*, is from Barbados, the name clearly is applicable to some or all of the New World species and new or resurrected names may be applied to diagnosable units of "*Phyllodactylus*" from the Old World. Three currently unused generic names have been

proposed for leaf-toed geckos (Wermuth 1965; Kluge 1993, 1996). However, two of these, *Discodactylus* and *Gerrhopygus* are applicable to New World taxa and one of them (*Discodactylus* Fitzinger 1843) is preoccupied. The remaining available name, *Euleptes* Fitzinger 1843 has as its type species by original designation *Euleptes wagleri* Fitzinger 1843 (= *Phyllodactylus europaeus* Gené 1838). This name is therefore available for the Mediterranean species of leaf-toed gecko and is resurrected below.

Mediterranean Leaf-toed Geckos

Fitzinger's (1843) description of *Euleptes*, like those of many of the names proposed in *Systema Reptilium*, is brief and totally inadequate. We here provide a redescription and diagnosis of this monotypic genus.

Euleptes Fitzinger, 1843

TYPE SPECIES. — *Euleptes wagleri* Fitzinger, 1843 (= *Phyllodactylus europaeus* Gené, 1838), by original designation.

CONTENT. — *Euleptes europaea* (Gené, 1838).

CHARACTERIZATION AND DIAGNOSIS. — *Euleptes* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; granules on snout not larger than those on dorsum of body; no rostral crease or division; first supralabial enters nostril; no enlarged chinshields; a single large cloacal spur on each side of vent, especially well-developed in males; preanal pores absent; subcaudal scales not transversely enlarged, tail prehensile, but without well-developed terminal scansorial pad; margins of pupils crenellate in preserved specimens; no sexual dichromatism; nasal bones paired; parietals paired; premaxilla with relatively short, triangular nasal projection; frontal moderately broad, strongly constricted over orbits, without maxillary contact; approximately 25 maxillary tooth positions (unilateral) in adults; postfrontal bones with subequal anterior and posterior projections, or with thicker anterior projection, without pronounced lateral spine; stapes perforate; coronoid bone weakly developed, barely raised

above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process lacking, medial projection of hyoid cornu much reduced; neural arches of atlas fused, at least in adults; 26 presacral vertebrae, 2 lumbar vertebrae; 3 cervical ribs, 2 sternal ribs, 2 mesosternal ribs; 0–1 pair of clavicular fenestrae, clavicles not strongly dilated; interclavicle dagger-shaped, with small transverse processes; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); cloacal sacs and bones present, a second, irregular (second) set of cloacal bones is associated with the cloacal spur in males; clutch size two (Fretey 1975; Rieppel and Schneider 1981), or less frequently one (Wiedersheim 1876; Klingelhöffer 1957).

Euleptes may be distinguished from all other leaf-toed geckos except *Asaccus* and New World and southeast Asian *Phyllodactylus* by its perforate stapes. It may be differentiated from all of these by the absence of tubercular scales and the fusion of the atlantal arches. The presence of a second pair of cloacal ossifications, first noted by Wiedersheim (1876), is a derived condition appearing elsewhere among leaf-toed geckos only in *P. peringueyi* (Branch and Bauer 1994), in which it is variable, and in some *Paroedura* (contra Nussbaum and Raxworthy 1994). The prehensile tail of *Euleptes* has long been recognized (Fitzinger 1843; Wiedersheim 1876) and its superficial morphology has been investigated in some detail (van Eijsden 1983). *Urocotyledon* also has a prehensile tail, but Kluge (1983) considered the presence of a well-demarcated scansorial pad as synapomorphic for that genus only.

ETYMOLOGY. — From the Greek *eu-* (true or very) and *leptos* (small, thin, or delicate), apparently in reference to the overall shape and size of the type species, although this was not made explicit by Fitzinger (1843). The generic name is feminine.

DISTRIBUTION. — The single species of this genus occurs at several insular and near-coastal sites from the Gulf of Marseille in the west to coastal Tuscany in the east. It also occurs on Corsica and Sardinia and their satellite islands and on Cani Island and the Galite Archipelago just off the north coast of Tunisia (Fig. 1; Bruno 1980; Delaugerre and Dubois 1985).

REMARKS. — Although various aspects of population variation and distribution within the Mediterranean region have been discussed (e.g., Bruno 1980; Delaugerre and Dubois 1985; Delaugerre and Cheylan 1992), there have been no interpretations of the relationship of this form to other leaf-toed geckos.

Socotran Leaf-toed Geckos

The geographic isolation of the two Socotran *Phyllodactylus* from other members of the genus and their shared absence of cloacal sacs and bones has resulted in the general supposition that these two species are sister taxa, despite the fact that they differ from one another in size and in a number of obvious external characteristics. An analysis of both osteological and external characteristics supports the unity of the Socotran leaf-toed geckos and demonstrates that they can be separated from all other "*Phyllodactylus*" on the basis of apomorphic features. Consequently *Phyllodactylus riebeckii* and *P. trachyrhinus* are here removed from *Phyllodactylus* to a new genus.

Haemodracon, new genus

TYPE SPECIES. — *Diplodactylus riebeckii* Peters, 1882.

CONTENT. — *Haemodracon riebeckii* (Peters, 1882), *H. trachyrhinus* (Boulenger, 1899).

CHARACTERIZATION AND DIAGNOSIS. — *Haemodracon* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scancers; dorsal scalation atuberculate; scales on snout smaller than those on dorsum of body (enlarged co-ossified snout scales present in *H. trachyrhinus*); enlarged chinshields present; rostral entire or completely divided; first supralabial enters nostril; margins of pupil crenelate in preserved specimens; preanal pores absent; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with short triangular nasal projection; frontal broad, not strongly constricted over orbits, with extensive maxillary contact; 25–30 maxillary tooth loci in adults; postfrontal bones with longer

posterior than anterior projection, without pronounced lateral spine; stapes imperforate; coronoid bone raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present; neural arches of atlas paired; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 3 sternal ribs, 1–2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); cloacal sacs and bones absent.

The absence of cloacal sacs and bones is a derived character state (Kluge 1967, 1982, 1987, 1995; Kluge and Nussbaum 1995) unique to *Haemodracon* among leaf-toed geckos, except for members of the genus *Asaccus* (Dixon and Anderson 1973; Arnold and Gardner 1994). *Haemodracon* is distinguished from the six species in the latter genus by the retention of the plesiomorphic states with respect to phalangeal formula of the manus (reduced to 2.3.4.4.3 in all *Asaccus*, at least during some stage in ontogeny), and presence of two oviducts (left oviduct lacking in *Asaccus*) (Arnold and Gardner 1994). The fused nasals of *Haemodracon* represent a derived condition shared with *Paroedura*, *Christinus*, some *Urocotyledon*, and some African *Phyllodactylus*. *Haemodracon* also differs from *Asaccus* in being atuberculate and in possessing an imperforate stapes.

ETYMOLOGY. — From the Latinized Greek *haema-* (blood) and *dracon* (dragon) signifying dragon's blood, in reference to the fact that members of this genus are endemic to the island of Socotra, known for an agave, *Dracaena cinnabari*, that produces a deep red resin referred to as dragon's blood. Socotra itself is sometimes called the "Island of the Dragon's Blood" (Botting 1958). The International Code of Zoological Nomenclature (Appendix D, VI.29) recommends that in generic names formed from compound Greek nouns the attribute in such a name (in this case "dragon" [*draco*] – the type of blood) should precede the substantive. However, since the resulting name is not particularly euphonious, we have chosen to reverse the order of the nouns. *Haemodracon* is masculine.

DISTRIBUTION. — The two species of this genus are confined to Socotra Island (Republic of Yemen), in the Gulf of Aden (Fig. 2).

Southeast Asian Leaf-toed Geckos

Taylor (1962), in describing *Phyllodactylus melanostictus*, compared it to *P. siamensis*, the only other east Asian leaf-toed gecko, but made no claims regarding its affinities to this or other leaf-toed geckos. Although clearly specifically distinct, these two taxa share a large number of traits, some apomorphic, that are rare or unique among leaf-toed gekkonids. As there is no evidence for the monophyly of a unit including both these forms and the New World leaf-toed geckos to which the name *Phyllodactylus* is correctly applied, the southeast Asian taxa are here removed from *Phyllodactylus* and described and diagnosed as a new genus.

Dixonius, new genus

TYPE SPECIES. — *Phyllodactylus siamensis* Boulenger, 1898.

CONTENT. — *Dixonius siamensis* (Boulenger, 1898), *D. melanostictus* (Taylor, 1962).

CHARACTERIZATION AND DIAGNOSIS. — *Dixonius* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation tuberculate, tubercles keeled longitudinally; granules on snout larger than those on dorsum of body; rostral scale with median cleft; first supralabial enters nostril; enlarged chinshields and lateral gulars; margins of pupil crenellate in preserved specimens; preanal pores present; series of three to seven cloacal spurs present, better developed in males; midventral row of transversely enlarged caudal scales, tail without terminal scansorial pad; no sexual dichromatism; nasal bones paired; parietals paired with a dorsomedial extension forming a prominent posteriorly-directed triangle; premaxilla with moderately long, lanceolate nasal projection; frontal moderately broad, only slightly constricted over orbits, with extensive maxillary contact; approximately 35 maxillary tooth positions in adults; postfrontal bones with posterior projection much thicker than anterior, without pronounced lateral spine; stapes perforate; coronoid bone weakly developed, barely raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process lacking, but cerato-

hyal inflated in the region where this structure typically appears, medial process of hyoid cornu elongate; neural arches of atlas paired; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 3 sternal ribs, 1–2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes), but with phalanx 2 of digit IV of manus greatly reduced in length; ossifications present in the extensor tendons of digits II–V of manus and pes; hypoischium bifurcate proximally; cloacal sacs and a single pair of cloacal bones present.

The presence of preanal pores in this genus distinguishes it from all other leaf-toed geckos except the African *Phyllodactylus lineatus* complex. The tuberculate dorsum of *Dixonius* distinguishes it from *Christinus*, *Euleptes*, *Haemodracon*, "*Phyllodactylus*" *brevipes*, and all African *Phyllodactylus* except *P. swartbergensis* and *P. peringueyi*, which lack preanal pores. The reduction in length of phalanx 2 of digit IV of the manus, and the proximally bifurcate hypoischium are derived features that also serve to diagnose this genus from all other leaf-toed geckos.

ETYMOLOGY. — A patronym in honor of James R. Dixon of Texas A & M University, a long time student of the genus *Phyllodactylus* (*sensu lato*), a scholar, and a gentleman. Dr. Dixon has long expressed the belief that Old World *Phyllodactylus* were generically distinct from the New World taxa to which the name is correctly applied. The generic name is masculine.

DISTRIBUTION. — The two species of this genus occur in southeast Asia (Fig. 2). Although initially described from Thailand (Taylor 1963), both species have been recorded from elsewhere in the region. Both have been documented from southern Vietnam (Bobrov 1992, 1993, 1995), suggesting that their distribution also includes Cambodia (Kampuchea) and perhaps southern Laos. To the west, *D. siamensis* extends into Burma (Annandale 1905; Taylor 1963).

REMARKS. — Dixon (1964) erroneously stated that the Asian forms exhibited reduction in phalangeal formula of digit four of the manus. However, the second phalanx of this digit is extremely short, and the third is moderately so (Russell 1972). Russell (1972) considered that

this condition might be a forerunner of the phalangeal loss seen in *Asaccus*. Kluge and Nussbaum (1995) incorrectly indicated that a derived condition of fewer than five phalanges in digit IV of the manus occurs in *Dixonius* and possibly *Haemodracon*.

Southern African Leaf-toed Geckos

The remaining Old World "*Phyllodactylus*" are native to southern Africa. Unlike the other geckos removed from *Phyllodactylus*, this group is both relatively speciose and highly morphologically diverse. Although no demonstration of the monophyly of this group has ever been put forward, it has been included as an operational unit in two phylogenetic analyses of African gekkonids (Bauer 1990; Kluge and Nussbaum 1995). Recent descriptions and resurrections of taxa have brought the number of recognized taxa to 12, including seven representatives of the *Phyllodactylus lineatus* complex, a group of small, morphologically similar geckos distributed through much of South Africa's Cape Provinces (Branch et al. 1995; Bauer et al. 1996; Good et al. 1996).

In order to evaluate the possible monophyly of the southern African "*Phyllodactylus*," the characters used in diagnosing other leaf-toed genera were evaluated for all southern African taxa. Information for certain characters was lacking for *Phyllodactylus ansorgii*, for which the only osteological data are derived from radiographs of the two females types, and for Haacke's (1996) undescribed Angolan species, known to us only through his published partial data set.

Dorsal scalation. Among African *Phyllodactylus*, tubercles are present only in *P. swartbergensis* and *P. peringueyi*. Unlike all other leaf-toed geckos, the tubercles of the former are smooth and flattened. Those in the latter species are strongly keeled. We regard the smooth tubercles as autapomorphic for *P. swartbergensis* and thus of no phylogenetic value. The tubercles of *P. peringueyi* are similar to those seen in most tuberculate leaf-toed geckos. Dixon (1964) reported that dorsal tubercles are present in all New World *Phyllodactylus* except *P. unctus*, *P. leei*, and *P. gerrhopygus* and regarded this condition as derived within the New World taxa. However, the condition is variable among the gekkonids in

general and cannot be assigned polarity at the hierarchical level under consideration here.

Rostral cleft. A dorsal rostral cleft is present in *P. microlepidotus*, *P. lineatus*, *P. braacki*, *P. gemmulus*, *P. hewitti*, *P. hexaporus*, *P. essexi*, and *P. rupicolus* and absent from the remaining taxa. Rostral creases occur in *Dixonius*, and *Haemodracon trachyrhinus*.

Nostril. The first supralabial is excluded from the nostril in *P. peringueyi*, *P. porphyreus*, and *P. swartbergensis* and enters the nostril in all other southern African species. Supralabial contact with the rim of the nostril is the most common condition among other leaf-toed geckos. It is excluded only in *Ebenavia*, *Urocotyledon*, and some New World *Phyllodactylus*.

Chinshields. Enlarged chinshields are absent in *P. peringueyi*, *P. ansorgii*, *P. porphyreus*, and *P. microlepidotus*. In *P. swartbergensis* the enlarged scales cover all of the anterior throat. In *P. gemmulus* there is a single enlarged scale posterior to the mental and in all remaining species there is a pair of enlarged scales behind the mental. The presence of enlarged chinshields in other leaf-toed geckos is variable, occurring in all groups except *Ebenavia*, *Euleptes*, and *Urocotyledon*.

Pupil. The shape of the margin of the pupil has long been debated as a character in systematic analyses (e.g., Underwood 1951, 1954; Cogger 1964; Kluge 1967; Bauer 1986). All leaf-toed geckos examined, except *P. peringueyi*, have a crenelated edge to the pupil in preserved specimens. This is also evident in living animals exposed to bright light. In *P. peringueyi*, however, the pupil margin is straight-edged (Branch and Bauer 1994; Haacke 1996) both in life and in preserved specimens. The latter condition would appear to represent a derived state for *P. peringueyi*.

Preanal pores. The African *Phyllodactylus* are the only geographic unit of leaf-toed geckos in which preanal pores are variably present. All other leaf-toed genera except *Dixonius* lack pores (Bastinck 1981; Kluge and Nussbaum 1995). Although some authors (e.g., Maderson and Chiu 1970) have considered the presence or absence

of preanal glands and pores of little phylogenetic value, this is clearly dependent upon the hierarchical level being considered. On the basis of a composite leaf-toed outgroup, the presence of pores may be regarded as derived. However, using the broad African gekkonid outgroup of Kluge and Nussbaum (1995) the loss of pores is apomorphic. Pores are also absent in *Ptyodactylus* and *Uroplatus*, the "fan-toed" members of Russell's (1972) *Phyllodactylus* group.

Cloacal spurs. The cloacal spurs of all members of the *P. lineatus* complex, as well as *P. microlepidotus*, have 3–6 spinous scales in males, with 2–3 considerably smaller scales in females. In *P. peringueyi* there are two isolated spines on each spur, these being slightly larger in males. In both *P. porphyreus* and *P. swartbergensis* males possess a single enlarged, rounded scale on the spur. This is only slightly larger in males than in females and may be the same size in both sexes in the former species. *Euleptes europaica* males also have a single cloacal spur.

Sexual dichromatism. Sexual dichromatism is rare among nocturnal lizards, and is unique among African leaf-toed geckos in *P. peringueyi*. In this species females are primarily unicolored, whereas males are characterized by a lighter dorsal stripe (Branch and Bauer 1994). Dichromatism of the tail has been reported for some *Asaccus* (Arnold and Gardner 1994), but is a rare and derived condition within the Gekkonidae as a whole.

Color pattern variation in *P. porphyreus* may be extreme. Although most specimens are marbled or vaguely banded above, a vertebral stripe is sometimes present (Fig. 8a). FitzSimons (1957) noted a pale vertebral streak in a specimen from Hout Bay. This color morph is now known to be a common in many populations and we have examined specimens from Knysna and Port Elizabeth with bold white stripes. It is not related to sex.

Premaxilla. The nasal process of the premaxilla is short and rounded in *P. peringueyi*, *P. porphyreus*, and *P. swartbergensis*. In all other African *Phyllodactylus* it is moderately long and lanceolate in shape. The condition of this character could not be evaluated in *P. ansorgii*. Our observations are consistent with those of Haacke

(1996), who also reported that the elongate, lanceolate process was present in the undescribed Angolan species. Short, rounded or somewhat pointed nasal processes are found in *Urocotyledon* and *Haemodracon*. A somewhat intermediate character state is present in *Christinus*.

Nasals. The nasals are primitively paired in gekkonids (Kluge 1967, 1987) with the azygous condition occurring only in *Afroedura*, *Ailuronyx*, *Cnemaspis* (part), *Ebenavia*, *Hemiphyllocladactylus*, *Homopholis* (part), *Lepidodactylus*, *Lygodactylus*, *Microgecko*, *Nactus*, *Paroedura*, *Perochirus*, *Phelsuma*, *Pseudogekko*, *Uroplatus*, and some Old World *Phyllodactylus*, according to Kluge (1987). The azygous condition apparently also occurs in at least some *Urocotyledon* (J. R. Dixon, in litt., 1993). We found fused nasals in *Haemodracon* and *Christinus*, also in some African *Phyllodactylus*. The azygous condition occurs in *P. peringueyi*, *P. porphyreus*, and *P. swartbergensis*, and we tentatively record it as such in *P. ansorgii* as well, although this is not certain based on the radiographs available to us. Haacke (1996) recorded the fused condition in one of two individuals of *P. microlepidotus* he examined and in only one of six *P. porphyreus*, as well as in a single specimen of an undescribed Angolan species of leaf-toed gecko. Given our larger sample size for osteological observations we retain our assessment of character state distribution.

Although he rejected this character's utility at higher levels, Kluge (1987) suggested that it might be informative with respect to intergeneric relationships. Both Bauer (1990) and Kluge and Nussbaum (1995) interpreted the azygous condition as derived for African gekkonids.

Fronto-maxillary contact. The frontal is excluded from the maxillary bone by the prefrontal in *P. swartbergensis* and is excluded or meets at a single point in *P. porphyreus*. The remaining species exhibit extensive contact. The condition in *P. ansorgii* could not be evaluated. There is generally no contact in *Christinus*, *Euleptes* or *Ebenavia*, but other leaf-toed geckos exhibit extensive contact.

Postfrontal. Postfrontal shape varies considerably among leaf-toed geckos. In all African species the anterior and posterior projections of

the postfrontal are subequal in length and width. This is in contrast to the conditions seen in New World *Phyllodactylus* and *Dixonius*, in which the posterior projection is much inflated and often somewhat longer than the anterior, and the condition seen in *Ebenavia* and *Christinus*, in which the anterior projection is larger. *Phyllodactylus peringueyi* is unique among African species in possessing a laterally projecting "spine" at the angle of the postfrontal. The entire bone, while still symmetrical, is often reduced to a thin crescent in the *P. lineatus* species complex.

Parietal. Kluge (1987) regarded the paired state of the parietals seen in most gekkonids as derived for gekkonoids. Thus the presence of the azygous condition within the Gekkonidae is a secondary derivation and apomorphic at this level. Among species of African *Phyllodactylus* the partial fusion of the parietals is autapomorphic for *P. swartbergensis*. Haacke (1996) noted difficulty in determining the condition of this character in this species. His observation of a single parietal or even a fused fronto-parietal plate in juveniles of other species is not supported by any of our observations and if correct would appear to suggest a unique pattern of skull development in these forms.

Stapedial foramen. Kluge (1987) reported the imperforate condition in *Ailuroonyx*, *Cnemaspis*, *Ebenavia*, *Geckonia*, *Gehyra*, *Gekko*, *Hemiphyllodactylus*, *Homonota*, *Lepidodactylus*, *Perochirus*, *Ptenopus*, *Ptychozoon*, *Ptyodactylus*, *Thecadactylus*, *Urocotyledon*, *Uroplatus* and the perforate condition in *Afroedura*, *Aristelliger*, *Bunopus*, *Calodactylodes*, *Chondrodactylus*, *Cosymbotus*, *Cyrtopodion*, *Geckolepis*, *Gonydactylus*, *Hemidactylus*, *Heteronotia*, *Homopholis*, *Lygodactylus*, *Pachydactylus*, *Palmatogecko*, *Phelsuma*, *Pristurus*, *Quedenfeldtia*, *Rhoptropus*, *Saurodactylus*, *Stenodactylus*, *Tarentola*, *Teratoscincus*, and *Tropiocolotes*. Only in *Phyllodactylus* did he record both conditions as occurring.

Although the presence of a stapedial foramen is a derived feature at the level of the Squamata (Underwood 1971; Greer 1976), Bauer (1990) and Kluge and Nussbaum (1995) regarded the imperforate condition as derived within the southern African gekkonines. The stapes is imperforate in *P. peringueyi*, *P. swartbergensis*,

and *P. porphyreus*. According to Haacke (1996) the stapes is also imperforate in the undescribed Angolan species. We were unable to score the condition of this character in *P. ansorgii*, and despite Kluge and Nussbaum's claim that the stapedial foramen is present in this species, we treat the condition as unknown. All remaining African *Phyllodactylus* have a stapedial foramen.

Hyoid. All of the southern African leaf-toed geckos retain the second ceratobranchial arch and thus exhibit the "ptyodactyline" condition (Kluge 1983). Joger (1985) criticized Kluge's tribal division based on variation in this character and proposed a hypothesis of relationship among Afro-Malagasy gekkonids that conflicted with Kluge's tribal assignments, but did not include any "*Phyllodactylus*" among his taxa. Bauer (1990) likewise criticized the accordance of special weight to the ceratobranchial character, but incorporated it into a broader data set. Kluge and Nussbaum (1995) themselves demonstrated that in light of a more complete data set the ceratobranchial arch character must have involved several independent evolutionary events. Thus the Gekkonini and Ptyodactylini previously hypothesized cannot be accepted as proven evolutionary entities.

The African species vary, however, with respect to the presence of the inner proximal ceratohyal process and the development of the medial process of the hyoid cornu. In *P. porphyreus*, *P. swartbergensis*, and *P. peringueyi* the former is present and the latter is elongate; in the remaining species the former is absent and the medial process of the hyoid cornu is only weakly to moderately developed. The condition in *P. ansorgii* could not be determined on the basis of available material. Prominent development of both processes is also typical of New World *Phyllodactylus* and *Christinus*, whereas both are poorly developed in *Euleptes*. In *Dixonius* the inner proximal ceratohyal process is lacking, but the associated region of the ceratohyal shaft is inflated, whereas in *Paroedura* this process is well-formed, but the hyoid cornu possesses only a short medial process. As noted by Fürbringer (1922) and Wellborn (1933), many attributes of the hyoid are intragenerically, or even intraspecifically variable. Nonetheless these features appear to be relatively stable in the taxa considered here.

Atlas. Bauer (1990) and Kluge and Nussbaum (1995) considered the paired condition of the atlas to be primitive among padded African gekkonids. Among African species of *Phyllodactylus* this state characterizes *P. ansorgii* (fide Kluge and Nussbaum 1995), *P. swartbergensis*, and *P. microlepidotus*. Some individuals of the *P. lineatus* species group also exhibit the paired condition, although the atlantal arches are generally fused in adults. Among other leaf-toed geckos, the derived condition is present in *Ebenavia*, *Urocotyledon*, *Euleptes*, and *Christinus* (may be variable in this genus). Haacke (1996) reported fused atlantal arches in *P. swartbergensis*, one *P. porphyreus*, one *P. lineatus*, and in the single specimen of an undescribed species from Angola. As this character is unambiguously scorable on cleared and stained material, we here ignore Haacke's observations in favor of our own based on larger samples.

Presacral vertebrae. The number of presacral vertebrae varies from 23 to 29 among fully-limbed gekkonoids (Wellborn 1933; Hoffstetter and Gasc 1969), although the majority of taxa possess 26. This would appear to be the primitive condition for gekkonids. *Phyllodactylus peringueyi* possesses 24 presacral vertebrae (Branch and Bauer 1994). All other species of African *Phyllodactylus* examined possess the primitive condition of 26 presacral vertebrae, except of 1 of 56 *P. lineatus* (25) and 4 of 39 *P. porphyreus* (1–25, 3–27). These exceptions are not regarded as phylogenetically significant. Haacke (1996) recorded 25 presacral vertebrae in an undescribed Angolan species. An elevated number of presacrals (27–28) is seen in *Christinus*, but all other leaf toed geckos have 26 presacrals, as do most African gekkonids in general.

The number of lumbar vertebrae is highly variable among the African species. One was recorded in *P. peringueyi*, *P. ansorgii*, *P. swartbergensis*, *P. microlepidotus* and some *P. porphyreus*. Two were recorded in the majority of *P. porphyreus* and all of the *P. lineatus* group geckos except *P. gemmulus*, which has three lumbar. Wellborn (1933) recorded a single lumbar as the most common condition among gekkonoids.

Ribs. The number of sternal vs. mesosternal ribs varies among African leaf-toed geckos. The

most commonly encountered state in *P. ansorgii* and *P. porphyreus* is two sternal and two mesosternal ribs. Haacke (1996) reported the same condition in *P. swartbergensis* and an undescribed Angolan species. We also observed specimens of the former with one and two, and two and one sternal and mesosternal ribs, respectively. The *P. peringueyi* examined have two sternal and either one or two mesosternal ribs. In *P. microlepidotus* the most common condition was three sternal and two mesosternal ribs. All remaining species had either two sternal and two mesosternal or three sternal and two mesosternal ribs, with variation due primarily to the length of the mesosternal extension. The conditions are highly variable among extralimital leaf-toed taxa. Kluge and Nussbaum (1995) considered the primitive condition for African gekkonids to be 5–6 pairs of attached sternal and xiphisternal (= mesosternal) ribs, with reductions to totals of four and three pairs representing successive derived reductions.

Cervical rib number among most gekkonids, and most leaf-toed geckos is three. This number characterizes *P. porphyreus*, *P. swartbergensis*, *P. microlepidotus* and some specimens of the *P. lineatus* species group. Other individuals have four cervical ribs, a condition also seen in *Christinus*, some *Urocotyledon*, and some *Paroedura*. In *P. peringueyi* there are typically only two well-developed cervical ribs. An asymmetrical third rib was found anterior to the other two in a single specimen.

Clavicle. The shape of the clavicle and the presence of clavicular fenestrae is variable among African *Phyllodactylus*. As in most other leaf-toed geckos there is usually a single large fenestra occupying much of the dilated portion of each clavicle. However, at least some *P. porphyreus*, *P. swartbergensis*, and *P. lineatus* lack the fenestra entirely, although the clavicle is clearly very thin in the region where the fenestra would typically occur. In *P. swartbergensis* and, to a lesser extent, *P. porphyreus* the clavicle itself is not as strongly dilated as in other species. Among other leaf-toed geckos, fenestrae are sometimes absent in *Euleptes europaea*, which also exhibits relatively weak dilation of the clavicle. Two pairs of clavicular fenestrae, or bilateral asymmetry (two fenestrae on one side, one on the other) were observed in a small number of *P. peringueyi* and

P. porphyreus, and in some species of *Paroedura* and New World *Phyllodactylus*. Kluge (1995) considered one or more fenestrae to be primitive for sphaerodactyls, with the absence of fenestrae representing an apomorphic condition.

Interclavicle. Kluge and Nussbaum (1995) evaluated variation in interclavicle shape among African gekkonids and divided it into two character states, based on the retention (primitive) or reduction (derived) of lateral arms. According to them, *Euleptes* is intermediate and among African *Phyllodactylus* species *lineatus* shows the primitive condition and *porphyreus* the derived. While noting variability in the African "*Phyllodactylus*" they scored the genus as a whole as derived for the character. Within African species, a cruciform interclavicle with well-developed lateral processes is present in *P. microlepidotus* and all members of the *P. lineatus* group. The interclavicles of *P. peringueyi* and *P. swartbergensis* are without lateral projections, whereas that of *P. porphyreus* is somewhat intermediate. We agree with Kluge and Nussbaum, however, in scoring the splintlike condition in this species as derived. Radiographs suggest that the condition in *P. ansorgii* approximates that of *P. porphyreus* and Haacke (1996) indicated that an undescribed Angolan species has a similar structure.

Scapular-precoracoid connection. The nature of the union of these two pectoral elements was generally determined on the basis of Alcian blue stain uptake in cleared-and-stained specimens but could be inferred from radiographs based on the presence or absence of a tissue "shadow" (indicating cartilage) at the junction of the scapula and precoracoid. *Phyllodactylus microlepidotus* and all members of the *P. lineatus* group possess a ligamentous connection between these elements, whereas a cartilaginous connection is found in *P. peringueyi*, *P. swartbergensis* and *P. porphyreus*. The condition in *P. ansorgii* could not be determined on the basis of the radiographs of the types. Among other leaf-toed gekkonids a ligamentous connection is found only in *Asaccus* and New World *Phyllodactylus*. The condition is variable among potential African outgroup taxa.

Extraphalangeal digital ossifications. Russell and Bauer (1988) recorded paraphalanges as present only in *Uroplatus* among members of the *Phyllodactylus* group of Russell (1972). Among other African genera they were recorded in *Homopholis*, *Lygodactylus* and *Palmatogecko*. In each case the pattern of these elements is different and is assumed to have evolved independently. As Kluge and Nussbaum (1995) noted, the appendix in Bauer (1990) presented the distribution of character states for this character incorrectly. The data were, however, entered correctly in Bauer's (1990) original analysis based on the data reported by Russell and Bauer (1988), accounting in part for the discrepancy in Bauer's cladogram and that derived by Kluge and Nussbaum (1995) by rerunning the data as incorrectly listed in the appendix.

Small, nodular ossifications were noted in the digits of *P. swartbergensis* and *P. microlepidotus*. In both they are associated with digits II–V of both manus and pes. In general form these elements resemble the paraphalanges reported in *Lygodactylus* and *Calodactylodes* by Russell and Bauer (1988); however, in the African taxa (and in *Dixonius*), such elements are dorsally, rather than laterally situated and are not associated with the scansorial apparatus and appear rather to be ossifications in the extensor tendons of the digits. We do not accept the presence of these elements as evidence of shared ancestry as their presence in the only two large African species of *Phyllodactylus* suggests that their ossification may be attributable to size alone.

Hypoischium. Kroll and Dixon (1972) reported that the distal end of the hypoischium is forked in members of the *P. gerrhopygus* group that possess abdominal plaques. We found a pronounced distal bifurcation in *P. swartbergensis* and a weakly developed bifurcation in one specimen of *P. lineatus*. In most non-African leaf-toed geckos the hypoischium is undivided, although in *Dixonius* there is a proximal rather than distal bifurcation.

Cloacal bones. The occurrence of these structures has been reviewed on several occasions (Smith 1933; Kluge 1967, 1982; Rieppel 1976; Russell 1977; Kluge and Nussbaum 1995). Typically a single pair of elements is present in gekkonids. The presence of an irregular second

pair of ossifications associated with the cloacal spurs is unique to *P. peringueyi* among the African leaf-toed geckos and occurs elsewhere among former *Phyllodactylus* only in the genus *Euleptes*. In the latter genus the second ossification is usually conspicuous, whereas in *P. peringueyi* it is small or even absent in some specimens.

Chromosomes. Karyological data have been published for a variety of leaf-toed geckos outside of Africa (King, 1981, 1987; King and Rofe 1976 for *Christinus*; McBee et al. 1984; Navarro et al. 1981 for Neotropical forms). Four South African taxa have been investigated by Gordon (unpublished). *Phyllodactylus porphyreus* and *P. swartbergensis* have a diploid number of 34 with one large pair of submetacentric elements, one medium-sized pair with short p-arms, one pair of small metacentric elements and 14 pairs of acrocentric or subtelocentric elements. For *P. microlepidotus* $2N = 36$, the karyotype differing by the presence of one additional intermediate-sized biarmed pair. Gordon examined three specimens of *P. lineatus*. These also had a diploid number of 36, but an additional two or three pairs of small elements are biarmed and pair 2 exhibits female sex-correlated heteromorphism.

Comparing the African *Phyllodactylus* to two members of the *Pachydactylus* clade (*Pachydactylus capensis* and *Rhoptropus afer*) Gordon concluded that the four leaf-toed geckos he examined were relatively similar and probably monophyletic. Following Joger (1985), Gordon accepted $2N = 36$ as a derived condition of a monophyletic Southern African gekkonine group. He regarded the $2N = 34$ condition of *P. porphyreus* and *P. swartbergensis* as a synapomorphy uniting these two taxa. Further, he regarded the loss of biarmed chromosome pair four as synapomorphic of this species pair. However, in light of the more recent phylogeny of Kluge and Nussbaum (1995), the claim for polarizing the diploid number is called into question. Indeed, there appear to be numerous exceptions to $2N = 36$, even among the southern African clade as defined by Joger (1985). Since the position of *Phyllodactylus* relative to other African or extralimital geckos remains unclear, there is no basis at present for assigning polarity to this character. One or the other, or perhaps both states may be apomorphic relative to an appropriate

outgroup. The sex chromosome heteromorphism recorded in *lineatus* was regarded as autapomorphic by Gordon, but might apply at a higher level, and could be a synapomorphy of the *lineatus* complex of seven species. Similar ZZ/ZW heteromorphisms have been demonstrated in *P. lanei* (King 1981) and *Christinus marmoratus* (King and Rofe 1976).

A review of the characters presented here reveals that there are no demonstrably apomorphic features that unite all of the southern African leaf-toed geckos. Indeed, these geckos are variable in character state for a variety of features (such as stapedial perforation, presacral vertebral count, and interclavicle shape) that are generally invariant in other gekkonid genera (Bauer 1990; Kluge 1995; Kluge and Nussbaum 1995). Although this in itself is not evidence for the para- or polyphyly of the group, it clearly provides no support for monophyly. Further, the genetic distance data presented here and previously (Bauer et al. 1996) demonstrate that distances within the *P. lineatus* group, and between members of this group and *P. microlepidotus*, are small relative to those between these species and other African *Phyllodactylus*. Indeed, distances to *P. peringueyi* are as large as those to any "*Phyllodactylus*" elsewhere in the world, or even to representatives of other genera. Character state distributions among southern African "*Phyllodactylus*" support the recognition of three monophyletic units of uncertain affinity to one another. Because no names are available for these taxa we here present descriptions and diagnoses for three new genera.

Cryptactites, new genus

TYPE SPECIES. — *Phyllodactylus peringueyi* Boulenger, 1910.

CONTENT. — *Cryptactites peringueyi* (Boulenger, 1910) (Fig. 4a).

CHARACTERIZATION AND DIAGNOSIS. — *Cryptactites* may be distinguished from all other gekkonids by the following combination of characteristics: body size minute; digits bearing a single pair of enlarged ("leaf-toed") terminal scancers; dorsal scalation tuberculate, tubercles keeled longitudinally, granules on snout larger than those on dorsum of body; median rostral cleft; enlarged chinshields and gulars absent; no

midrostral crease or division; first supralabial excluded from nostril; margins of pupil straight-edged in preserved specimens; preanal pores absent; cloacal spurs with two enlarged spinous scales, larger in males than females; midventral caudal scales not transversely enlarged, tail without terminal scansorial pad; sexually dichromatic; nasals fused; parietals paired; premaxilla with moderately short, broad, spatulate nasal projection; frontal moderately broad, only slightly constricted over orbits, with maxillary contact at only a single point; approximately 25–28 maxillary tooth loci; postfrontal bones with posterior projection somewhat thicker than anterior, with pronounced lateral spine; stapes imperforate; coronoid bone moderately well developed, raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present, medial process of hyoid cornu elongate; neural arches of atlas fused; 24 presacral vertebrae, 1 lumbar vertebra; 2–3 cervical ribs, 2 sternal ribs, 1–2 mesosternal ribs; 1–2 pairs of clavicular fenestrae; interclavicle splintlike without lateral processes; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); hypoischium without terminal bifurcations; cloacal sacs and bones present, a second cloacal ossification is present in association with the cloacal spur in males (apparently individually variable); clutch size two.

The reduction to 24 presacral vertebrae is unique among leaf-toed geckos, and rare among gekkonids in general (Hoffstetter and Gasc 1969). The presence of a second pair of cloacal bones is derived and occurs elsewhere among leaf-toed geckos only in *Euleptes* and at least some *Paroedura*. *Cryptactites* differs from *Euleptes* in the presence of dorsal tubercles, fused nasals, and imperforate stapes. Branch and Bauer (1994) reviewed those osteological features that differentiated this genus from *Asaccus*, *Paroedura*, *Christinus*, *Urocotyledon* and *Haemodracon*. Significant differences with respect to *Ebenavia* are discussed in the redescription of that genus.

ETYMOLOGY. — From the Latinized Greek *crypto-* (hidden) and *actites* (shore dweller) in reference to the habitat of this inconspicuous gecko, which was “lost” to science for more than

80 years (Branch and Bauer 1994). The generic name is masculine.

DISTRIBUTION. — The single species in the genus is confined to coastal and riverine habitats (Fig. 4b) along the Kromme River estuary (Branch and Bauer 1994) and near Port Elizabeth (Willows, Schoenmakerskop, Chelsea Point; Branch 1996) in the Eastern Cape Province of South Africa (Fig. 5). The single record from “Namaqualand” is almost certainly in error.

REMARKS. — The diagnosis above reflects several corrections relative to the previously published redescription of *C. peringueyi* by Branch and Bauer (1994). The initial observations were based on radiographs of the two poorly-preserved types only, whereas the present information is derived from radiographs of specimens in better condition and a single cleared and stained specimen. Branch and Bauer (1994) indicated a paired condition for the nasal bones and tentatively regarded the stapes as perforate. In adult specimens examined the nasals are at least partially fused, but this condition may be individually variable. The stapes is always imperforate.

Goggia, new genus

TYPE SPECIES. — *Phyllodactylus lineatus* Gray, 1838.

CONTENT. — *Goggia braacki* (Good, Bauer, and Branch, 1996), *G. essexi* (Hewitt, 1925) (Fig. 6b), *G. gemmula* (Bauer, Branch, and Good, 1996), *G. hewitti* (Branch, Bauer, and Good, 1995), *G. hexapora* (Branch, Bauer, and Good, 1995), *G. lineata* (Gray, 1838) (Fig. 6a), *G. microlepidota* (FitzSimons, 1939), *G. rupicola* (FitzSimons, 1938) (Fig. 6c).

CHARACTERIZATION AND DIAGNOSIS. — *Goggia* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged (“leaf-toed”) terminal scansors; dorsal scalation atuberculate; granules on snout larger than those of dorsum of body; enlarged chinshields present or absent; rostral partially divided; first supralabial enters nostril; margins of pupil crenelate in preserved specimens; cloacal spurs consisting of 3–7 enlarged scales, better developed in males; preanal pores present; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism;

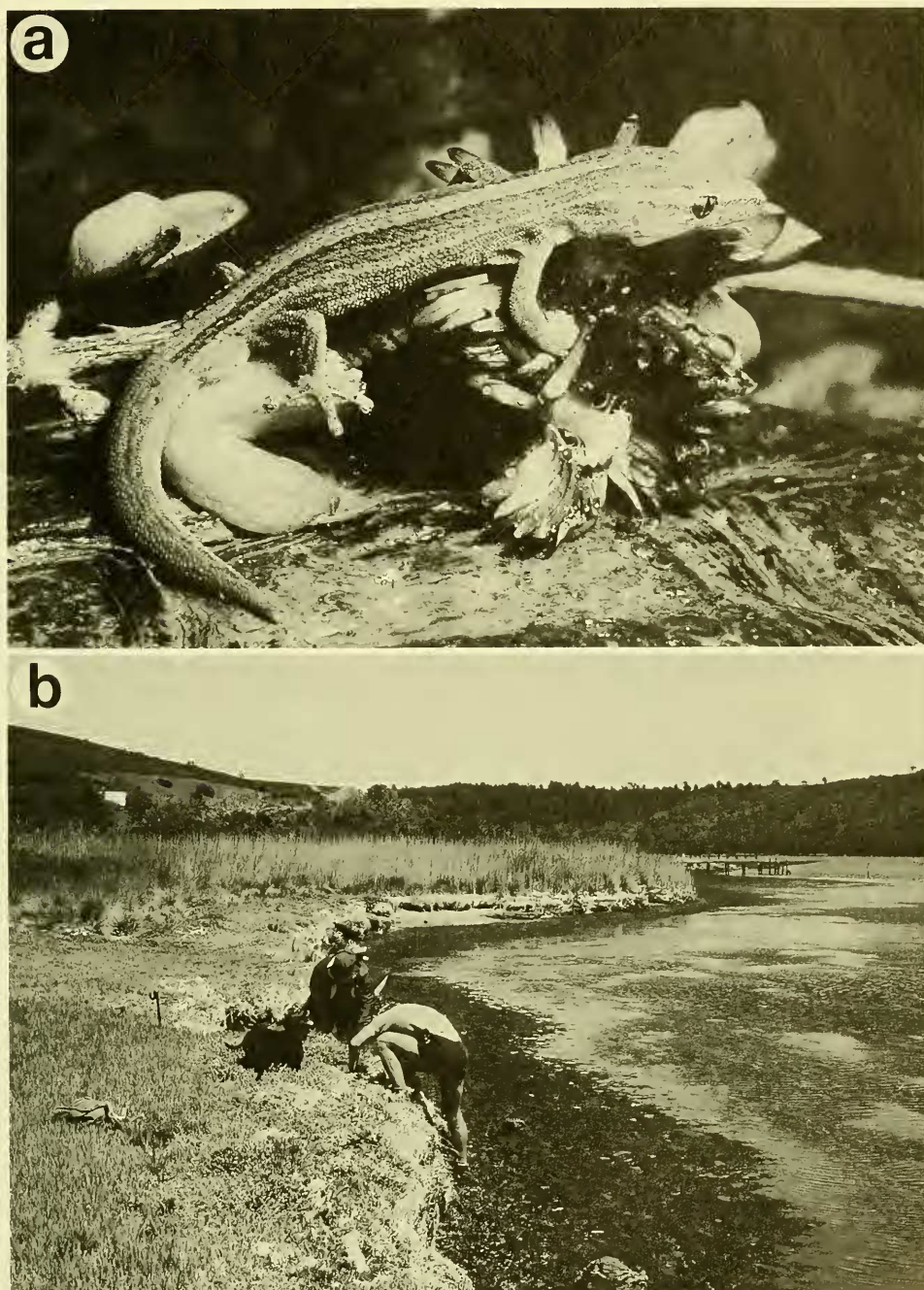


FIGURE 4. a) *Cryptactites peringueyi* (maximum SVL 29 mm) from Kromme River, Eastern Cape Province, South Africa. This specimen illustrates the straight-edged pupil and keeled dorsal tubercles that distinguish this genus from *Goggia* and *Afrogecko*. Note the striped dorsal pattern typical of males. Females have a unicolored dorsum. b) Habitat of *C. peringueyi* along the Kromme River Estuary. The species has so far been found only along the lower reaches of the Kromme and near Port Elizabeth.

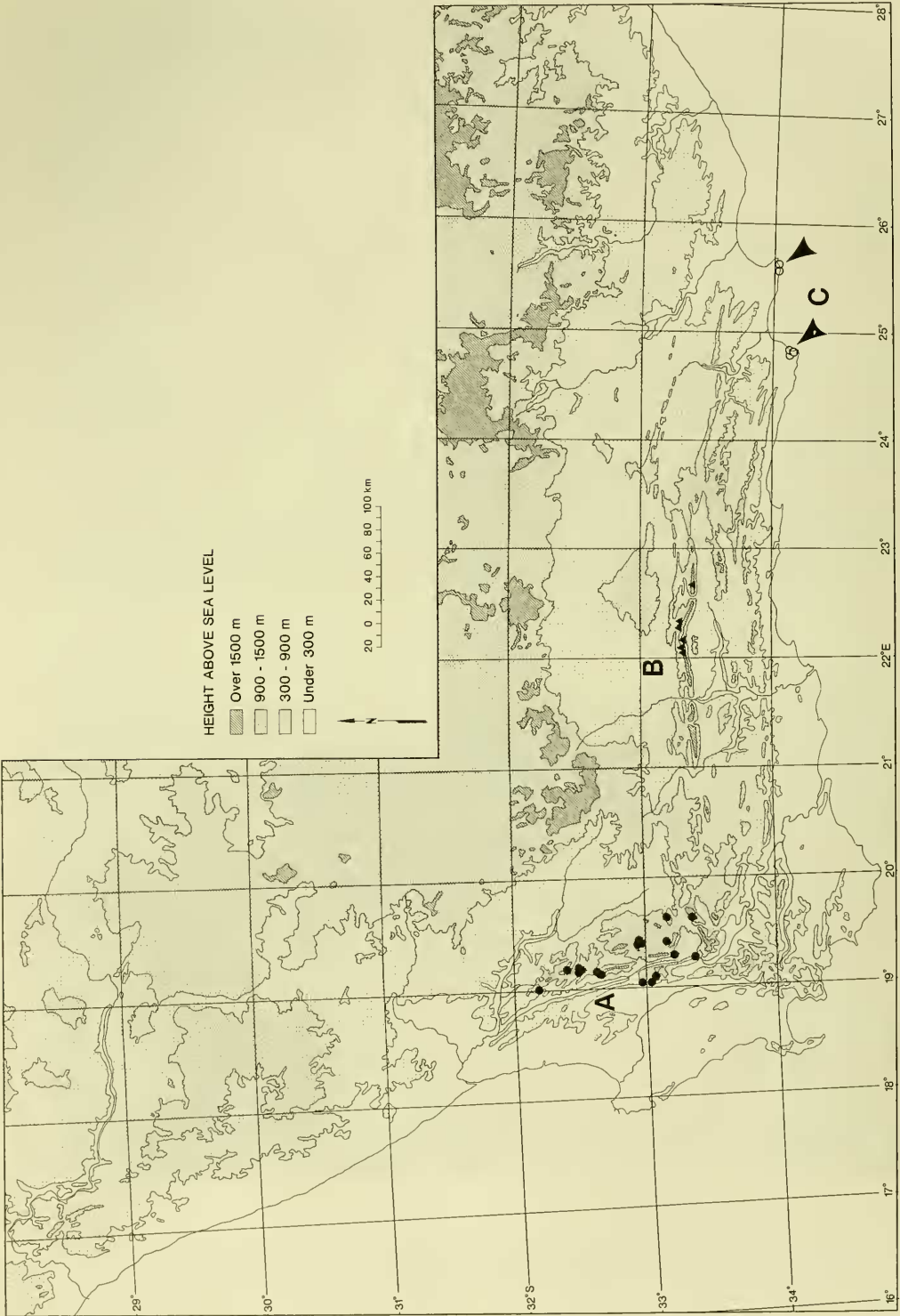


FIGURE 5. Distribution of African leaf-toed geckos. A = *Goggia microlepidota* (solid circles), B = *Afrogecko swartbergensis* (solid triangles), and C = *Cryptactites peringueyi* (open circles with arrows) in South Africa. See Appendix A for a complete list of localities.

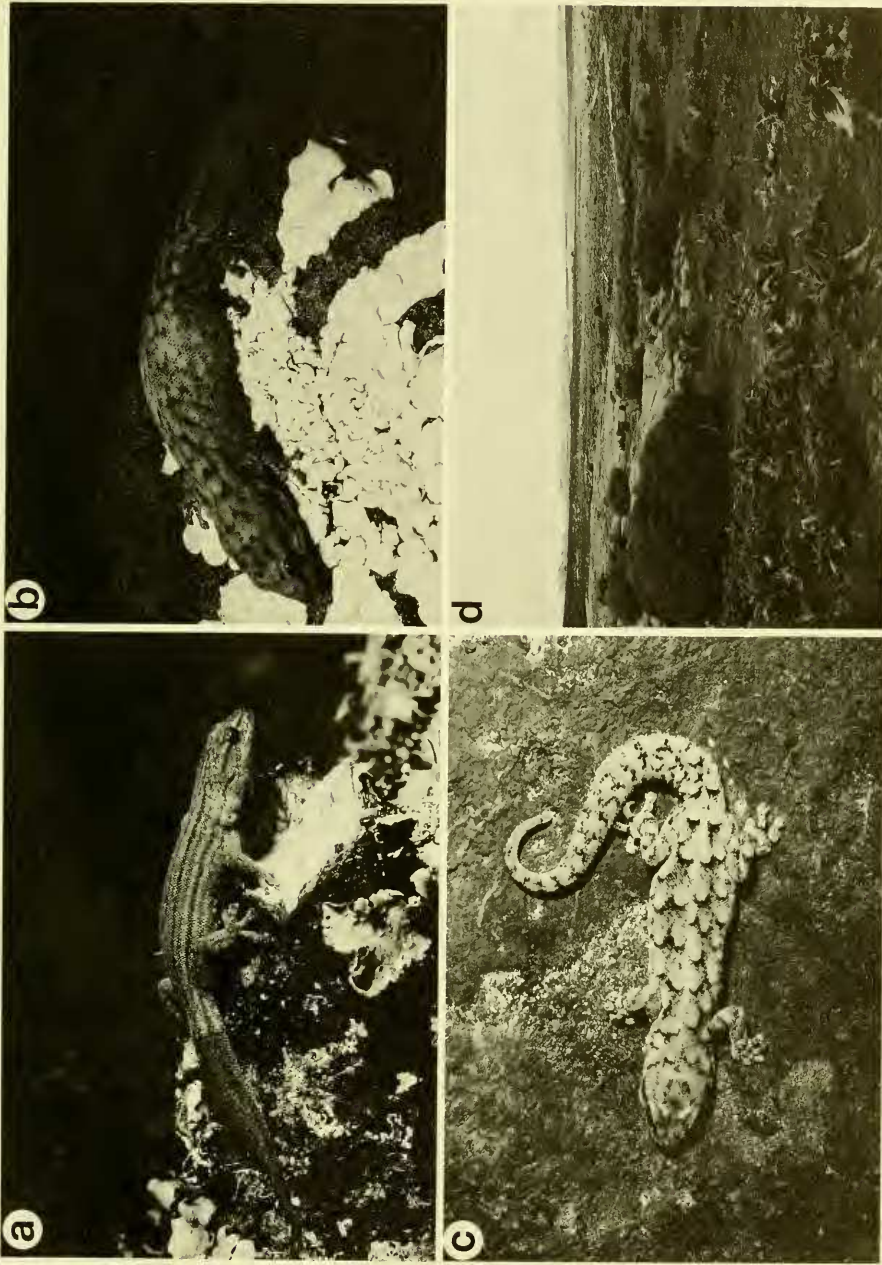


FIGURE 6. Representative members of the genus *Goggia*. a) *G. lineata* (maximum SVL 32 mm) from Warmwaterberg, Little Karoo, Western Cape Province, South Africa. This is the most widespread species in the genus and does not exhibit the depressed body form of most of its congeners. The striped pattern is not always present in this species but representatives of no other *Goggia* ever exhibit such a pattern. b) Topotypical *G. essexi* (maximum SVL 29 mm SVL) from Farm Hounslow, Eastern Cape Province, South Africa (gravid female). This species is restricted to the Stuurberg and adjacent rocky areas in valley bushveld vegetation. c) *G. ruficola* (maximum SVL 32 mm) from near Steinkopf, Northern Cape Province, South Africa. The relatively bright (usually orange) markings of the dorsum are typical of this species, which lives under flakes of exfoliating granite on exposed domes in areas of succulent Karoo vegetation (d).

nasal bones paired; parietals paired; premaxilla with moderately long, lanceolate nasal projection; frontal moderately broad, moderately strongly constricted over orbits, with extensive maxillary contact; 25–32 maxillary tooth loci in adults; postfrontal bones with anterior and posterior projections subequal, without pronounced lateral spine; stapedia foramen present; coronoid bone moderately well-developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hypoid present, inner proximal ceratohyal process absent, medial process of hyoid cornu short to moderate in length; neural arches of atlas fused or paired; 26 presacral vertebrae, 1–3 lumbar vertebrae; 3 (or rarely 4) cervical ribs, 2–3 sternal ribs, 1–2 mesosternal ribs; clavicular fenestrae variable, usually one pair of large fenestrae; interclavicle cruciform, with prominent lateral projections; union of scapula and precoracoid ray of epicoracoid ligamentous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); ossifications in digital extensor tendons usually absent (present in *G. microlepidota*); hypoischium not, or only weakly bifurcate distally; cloacal sacs and a single pair of bones present; clutch size two.

The presence of preanal pores in male *Goggia* is shared with only *Dixonius* among the leaf-toed geckos. These genera differ in many aspects of scalation (tuberculation, subcaudal scales) and osteology (scapular-precoracoid union, coronoid height, hypoischial shape, postfrontal shape, maxillary tooth loci). The reduction of both the inner proximal ceratohyal process and medial process of the hyoid cornu occurs only in *Goggia* and *Euleptes*. The midrostral crease occurs only in *Goggia*, *Dixonius*, and *Haemodracon trachyrhinus*. *Goggia* differs from *Cryptactites* and the remaining southern African "*Phyllodactylus*" in possessing a rostral crease, preanal pores, cloacal spurs consisting of three or more enlarged scales, ligamentous rather than cartilaginous scapular-precoracoid connection, a perforate vs. imperforate stapes, paired vs. fused nasal bones, elongate lanceolate nasal process of the premaxilla, extensive fronto-maxillary contact, prominent transverse processes of the interclavicle, and reduced processes of the hyoid cornu and ceratohyal. It is further differentiated from *Cryptactites* by its atuberculate scales, crenellate pupil margin, unreduced presacral

vertebral count, postfrontal shape, and lack of sexual dichromatism.

ETYMOLOGY. — The name is derived from the Afrikaans word "gogga" meaning a "creepy-crawly," usually an arthropod or reptile. In recent years the word has taken on connotations of endearment. The word has a Khoisan derivation and may have also given rise to the Xhosa term "rho-rho" meaning something to be feared. Because the modification of the noun "gogga" to form *Goggia* yields a feminine Latin ending to the word, we treat *Goggia* as feminine. The specific epithets of the constituent species have been modified accordingly. Note that in Afrikaans the letter "g" is guttural and is always pronounced like the "ch" in the Scottish word "loch."

DISTRIBUTION. — The genus as a whole is distributed in southwestern Africa, including extreme southern Namibia and parts of the Northern, Western and Eastern Cape Provinces of South Africa (Figs. 5, 7). The distribution of *Goggia* is essentially congruent with the winter rainfall area of South Africa (Haacke 1996). *Goggia lineata* is by far the most widespread species, ranging from southern Namibia (Arusberg Mountains and Karas District) south to the level of Mamre and Tulbagh, Western Cape Province, South Africa. This species is primarily found at elevations of less than 300 m, although there are records as high as at least 745 m. It is chiefly associated with plant debris, but may also be found under stones or bark (Branch and Braack 1989; Branch and Bauer 1995; Branch et al. 1995).

The large species *G. microlepidota* occurs in the sandstones of the Cedarberg (Visser 1979; Mouton and van Wyk 1981; Mouton et al. 1987; Branch and Bauer 1997) from Pakhuis Pass south to Ceres (Fig. 5). It is sympatric with *Goggia hexapora*, which occupies the Cedarberg and adjacent ranges, including the isolated Piketberg (Branch et al. 1995). A northern extension of this species range since its description is Farm Kliprivier, near Nieuwoudtville, represented by a single specimen in the National Museum, Bloemfontein (NMB 7169). All remaining species are allopatric (Fig. 7). *Goggia hewitti* occurs in the quartzitic sandstones of the southern Cape Fold Mountains, *G. essexi* in the Suurberg near Grahamstown, and *G. rupicola* is limited to isolated granite koppies in succulent Karoo vegetation in upland areas of Little Namaqualand (Fig.

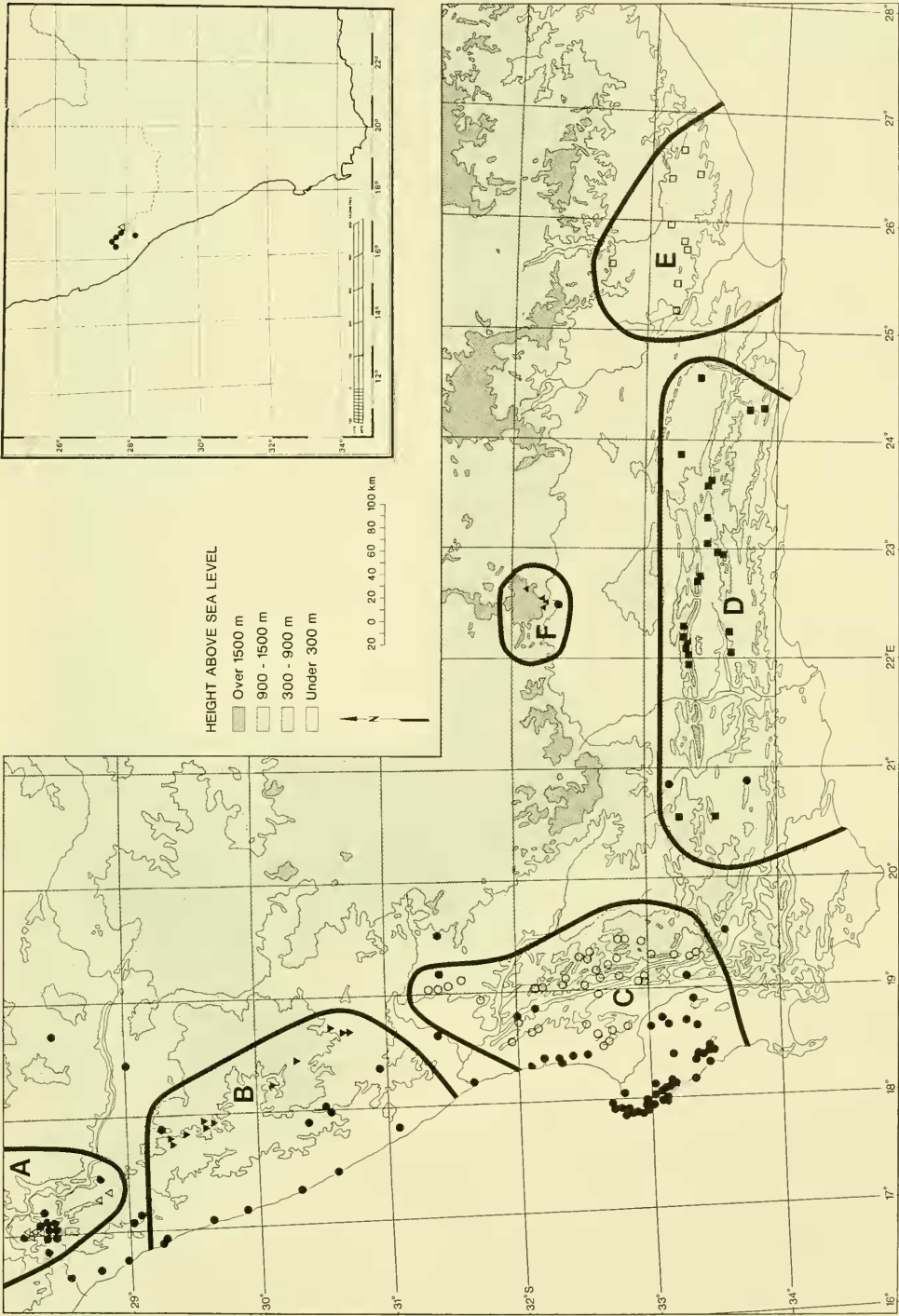


FIGURE 7. Distribution of the *Goggia lineata* complex in southern Africa. A = *G. gemmula* (open triangles), B = *G. rupicola* (inverted solid triangles), C = *G. hexapora* (open circles), D = *G. hewitii* (solid squares), E = *G. braacki* (solid squares), F = *G. essexi* (open squares). Remaining (mostly coastal) localities = *G. lineata* (solid circles). Inset map shows the southern Namibian localities for *G. lineatus* and *G. gemmulus*. See Branch et al. (1995), Bauer et al. (1996), and Good et al. (1996) for complete list of localities.

6d) including the Kamiesberg and Komaggas Hills (Branch et al. 1995). *Goggia gemmula* occurs on granite boulders in the Richtersveld and adjacent southern Namibia (known in Namibia only from Macmillan's Pass near Rosh Pinah, Karas District; Bauer et al. 1996). Only *G. braacki* inhabits the inland escarpment of southern Africa, being found on dolerite outcrops in the Nuweveldberg near Beaufort West (Good et al. 1996).

Afrogecko, new genus

TYPE SPECIES. — *Gecko porphyreus* Daudin, 1802.

CONTENT. — *Afrogecko porphyreus* (Daudin, 1802) (Fig. 8a), *A. ansorgii* (Boulenger, 1907), *A. swartbergensis* (Haacke, 1996) (Fig. 8b). Haacke's (1996) undescribed Angolan species is tentatively referred to this genus, although the data he presented do not permit this to be done with confidence.

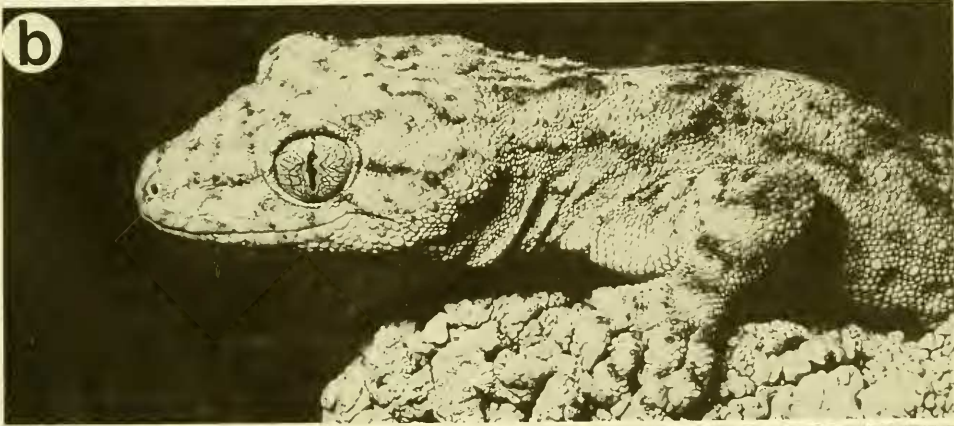
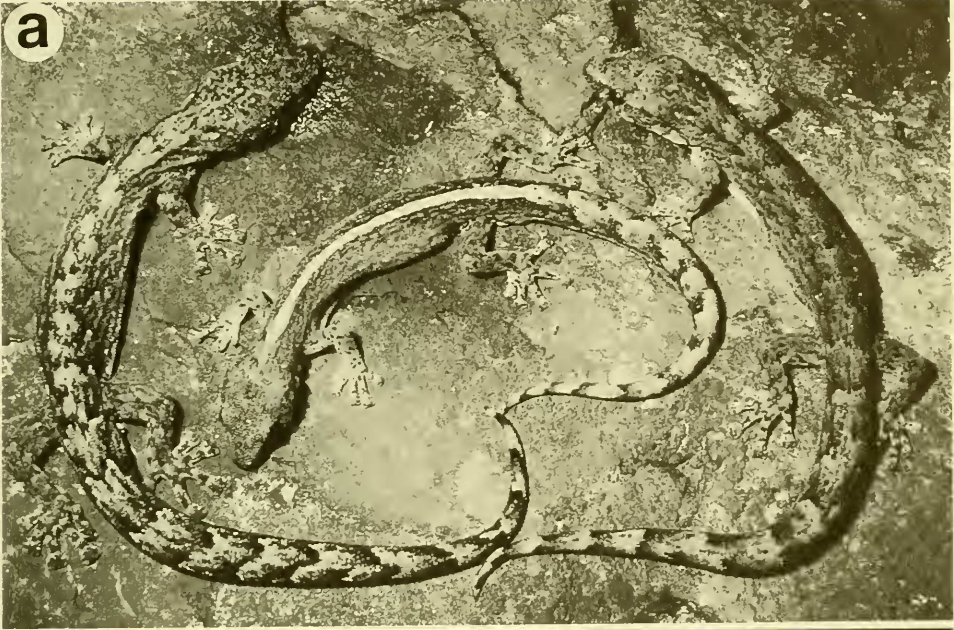
CHARACTERIZATION AND DIAGNOSIS. — *Afrogecko* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate or with low, rounded tubercles; granules on snout larger than those on dorsum of body; enlarged chinshields present or absent; rostral entire; first supralabial excluded from nostril (enters nostril in *A. ansorgii*); margins of pupil crenellate in preserved specimens; cloacal spurs consisting of a single enlarged scale (sometimes flanked by much smaller scales that are somewhat larger than adjacent body granules), more well-developed in males; preanal pores absent; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired (partially fused in *A. swartbergensis*); premaxilla with short rounded nasal projection; frontal moderately broad, only slightly con-

stricted over orbits, with maxillary contact absent or reduced to a single point; 26–36 maxillary tooth loci in adults; postfrontal bones with anterior and posterior projections subequal, without pronounced lateral spine; stapedial foramen absent; coronoid bone moderately well-developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present, medial process of hyoid cornu elongate; neural arches of atlas paired or fused; 26 presacral vertebrae (rare individual variation from 25–27 occurs), 1–2 lumbar vertebrae; 3 cervical ribs, 1–3 (usually 2 sternal ribs, 1–2 (usually 2) mesosternal ribs; clavicular fenestrae variable, may be absent or consist of one or two pairs of fenestrae; interclavicle without prominent lateral projections (character with high individual variability); mesoscapula-precoracoid union cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); ossifications present (*A. swartbergensis*) or absent in digital extensor tendons; hypoischium bifurcate distally or not; cloacal sacs and a single pair of cloacal bones present; clutch size two.

Afrogecko differs from all other leaf-toed geckos except *Cryptactites* (and some specimens of *Euleptes*) in the absence of prominent transverse processes of the interclavicle. The short, broad nasal process of the maxilla is found elsewhere only in *Cryptactites* and *Urocoyledon*. Although numerous features are shared with *Cryptactites*, *Afrogecko* differs from this form in possessing smooth dorsal scales or rounded tubercles (vs. keeled tubercles), a crenellate pupil margin, 26 presacral vertebrae, no postfrontal spine, and no sexual dichromatism. All species of *Afrogecko* are also much larger than *Cryptactites peringueyi*, with even hatchlings of the former approaching or surpassing maximal adult sizes of the latter.

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FIGURE 8. Representatives of the genus *Afrogecko*. a) Three specimens of *A. porphyreus* (maximum SVL 56 mm) from Walmer, Port Elizabeth, Eastern Cape Province, South Africa illustrating variation in dorsal pattern within a single population. b) *A. swartbergensis* (maximum SVL 75 mm) from the Groot Swartberge, Western Cape Province, South Africa. Note the smooth, enlarged, rounded tubercles unique to this species. The crenellated pupil margin is typical of all southern African leaf-toed geckos except *Cryptactites peringueyi*. c) Typical habitat of *A. swartbergensis* in the north-facing slopes of the Groot Swartberge. This habitat is also typical of *Goggia hewitti*, although the latter species typically occupies smaller rock cracks and crevices.



ETYMOLOGY. — The name refers to the restriction of this genus to the African continent and is masculine.

DISTRIBUTION. — The distribution of the genus is disjunct in southwestern Africa. *Afrogecko ansorgii* and an undescribed species (Haacke 1996) occur in southern Angola (Fig. 9) and the remaining species occur in the temperate regions of the Western and Eastern Cape Provinces of South Africa. *Afrogecko ansorgii* is known only from the types obtained from “Maconjo, Benguella” (= Maconge, Mocamedes Province, 15°01’S 13°12’E, 700 m), Angola. *Afrogecko swartbergensis* described from the Swartberg Pass, is now known to have a wider distribution in the Groot Swartberge, Cape Fold Mountains, Western Cape Province (Branch and Bauer 1997) (Figs. 5, 8c).

Afrogecko porphyreus is widespread in the southern and southwestern portions of the Cape (Fig. 9) chiefly in association with mesic mountain fynbos (De Kock, undated). The South African distribution of this species was previously mapped at the quarter degree square level by Visser (1984). The species is commensal under some conditions and has expanded its range with human assistance. Within South Africa the range has expanded to the east. Branch and Hanekom (1987) recorded the easternmost locality for the species in the Tsitsikamma National Park, but populations are now well-established in Port Elizabeth (pers. observ.). This species is also known from a number of islands off of the west coast of South Africa (Robben Id., Jutten Id., Dassen Id., Meeuw Id., Marcus Id., Malgas Id., and Schappen Id.; Branch 1991). It has also been recorded from St. Helena (FitzSimons 1943), although these specimens represent an introduction. Madagascan records (Angel 1942; Guibé 1956; Blanc 1971) are in error as they refer to *Phyllodactylus brevipes*, a distinctive, and probably endemic Malagasy species (Dixon and Kroll 1974; Glaw and Vences 1994; R. A. Nussbaum, pers. comm.).

The absence of *Afrogecko* from the Northern Cape and Namibia (except as introduced populations) is probably real, although additional collecting may reveal its presence in the southern Northern Cape and/or extreme northern Namibia.

REMARKS. — In addition to the nominate form, two subspecies of *Afrogecko porphyreus*

have been described, *A. p. cronwrighti* (Hewitt 1937), and *A. p. namaquensis* (Hewitt 1935). Loveridge (1947) questioned the validity of the former, and recent reviews (e.g., Branch 1988) have not recognized either form. Both forms were described from the periphery of the species’ distribution. *Afrogecko p. cronwrighti* was described from Cape St. Francis and probably represents the easternmost non-human-assisted limit of the range of the species. The Bitterfontein type locality of *A. p. namaquensis*, is also peripheral. Records from north 32°30’S are very scarce and the only records north of Bitterfontein are Werner’s (1910) record from Warmbad, a record from Swakopmund, and an old record from Damaraland (Boulenger 1885). The literature record for Warmbad has since been regarded as referring to *Goggia lineata* (Mertens 1955; Branch et al. 1995), and the Damaraland record is considered a locality error. The Swakopmund record probably represents an introduction. The validity of the two subspecies of *Afrogecko porphyreus* will be examined in more detail elsewhere (Branch and Bauer 1997), but neither form is here accorded specific or subspecific rank.

KEY TO LEAF-TOED GECKOS OF SOUTHERN AFRICA

Earlier reviewers (FitzSimons 1943; Loveridge 1947) published keys to the southern African *Phyllodactylus* then recognized. However, five additional species have since been described and additional material has become available for all species except *Afrogecko ansorgii*. Although a key to a subset of the *Goggia lineatus* complex species has been published recently (Branch et al. 1995), no comprehensive key for all southern African leaf-toed geckos exists. With the new generic allocations of the 12 recognized southern African species, we take this opportunity to present such a key, based primarily on easily determined external characters.

- 1a. Dorsal scalation homogeneous 3
- b. Dorsal scalation heterogeneous, with enlarged tubercles 2
- 2a. Dorsal tubercles keeled, body size small *Cryptactites peringueyi*
- b. Dorsal tubercles flattened and smooth, body size large *Afrogecko swartbergensis*

- 3a. Rostral scale entire, preanal pores absent in males 4
 b. Rostral scale with dorsal midline crease, preanal pores present in males 5
- 4a. Preanal scales enlarged, first supralabial . . . enters nostril. *Afrogecko ansorgii*
 b. Preanal scales not enlarged, first supralabial excluded from nostril.
 *Afrogecko porphyreus*
- 5a. No enlarged chinshields, body size large, midbody scale rows >95.
 *Goggia microlepidota*
 b. 1-2 enlarged postmental scales, body size small, midbody scale rows <90 6
- 6a. Midbody scale rows usually fewer than 80 7
 b. Midbody scale rows usually more than 80 8
- 7a. Usually 5 preanal pores in males; usually fewer than 10 granules between nostril and anterior border of orbit; body rounded, head deep *Goggia lineata*
 b. Usually 4 preanal pores in males; usually more than 10 granules between nostril and anterior border of orbit; head and body depressed *Goggia gemmula*
- 8a. Six preanal pores in males (Kouebokkeveld and Cedarberg region)
 *Goggia hexapora*
 b. Four preanal pores in males 9
- 9a. Nasorostrals usually 2; maximum SVL rarely more than 30 mm. 10
 b. Nasorostrals usually 1 (rarely 0 or 2); maximum SVL 37 mm 11
- 10a. Nasorostrals 2-3 (rarely 1); granules around midbody about 85 (80-90); dorsum usually with bright orange spots (Namaqualand) *Goggia rupicola*
 b. Nasorostrals 1-2 (rarely 3); granules around midbody usually about 80 (78-84); dorsum without bright markings (Eastern Cape) *Goggia essxi*
- 11a. Southern Cape Fold Mountains*
 *Goggia hewitti*
 b. Nuweveldberg. *Goggia braacki*

**G. hewitti* and *G. braacki* are not distinguishable on the basis of discrete morphological characters, but may be separated on the basis of several fixed allelic differences (Good et al. 1996). Because the taxa are entirely allopatric,

their distributions have been substituted in lieu of key morphological characters.

RELATIONSHIPS AMONG AFRICAN LEAF-TOED GECKOS

Until recently the only statements regarding relationships among the southern African leaf-toed geckos were limited to subjective interpretations of external morphology. For example, Werner (1910) considered *Afrogecko ansorgii* and *A. porphyreus* to be closely related and FitzSimons (1939) regarded *Goggia microlepidota* as most closely allied to *G. lineata*. *Cryptactites peringueyi*, because of its radically different morphology and uncertain provenance (see Branch and Bauer 1994) attracted particular attention. Hewitt (1937) and subsequent authors (FitzSimons 1943; Loveridge 1947; MacLachlan 1978) questioned the validity of the taxon and doubted that it was indigenous to southern Africa. The African origin of this genus is still questioned by some workers (see Haacke 1996).

Gordon (unpublished), using karyological data supplemented by morphological data from other sources, investigated relationships among four species of South African "*Phyllodactylus*." His data suggested the pattern (*lineatus (microlepidotus (porphyreus, swartbergensis)*)). Affinities of *P. porphyreus* with *P. brevipes* were also suggested, although not investigated. Gordon, however, warned of limitations in the karyological data set and considered data insufficient to examine broader patterns of relationship. This analysis was weakened by the absence of an appropriate outgroup, an a priori assumption on ingroup monophyly, and the use of the criterion of commonality to assign polarity.

Most systematic work has focused on the species now assigned to *Goggia*, particularly those small species constituting the *G. lineatus* group. Following suggestions that *Goggia lineata* was probably a composite species (Branch and Braack 1989; Oelofsen et al. 1987) Branch, Bauer and Good (1995) reviewed the status of this taxon on the basis of both morphological and allozyme characters. They resurrected *G. rupicola* and *G. essxi* to specific status, described two additional species, *G. hewitti* and *G. hexapora*, and concluded that the *G. lineata* complex was a natural unit and provided a diagnosis for this species group. Subsequent analysis of the *G.*

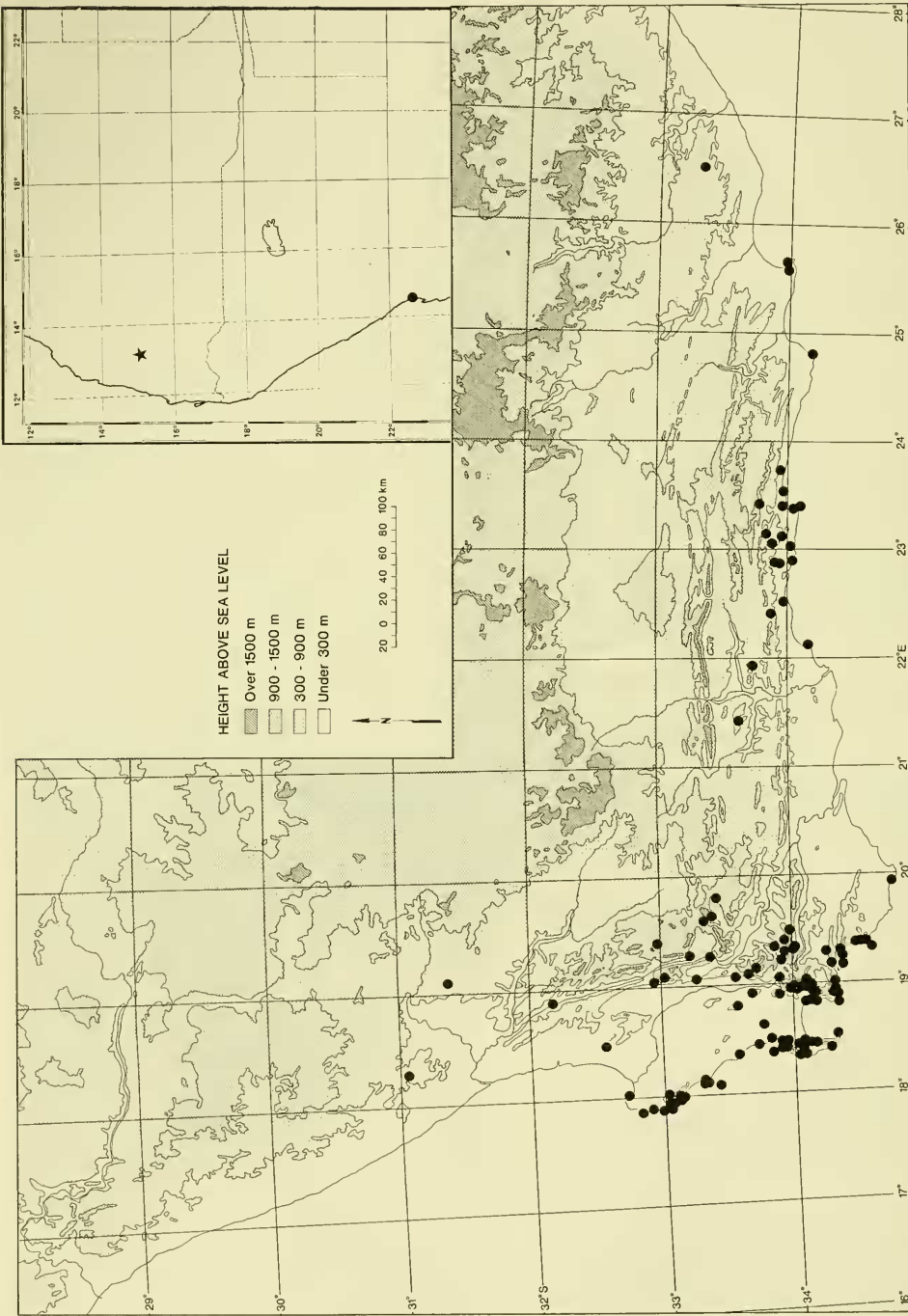


FIGURE 9. Distribution of *Afrogelco porphyreus* (solid circles) in South Africa. Inset map shows an introduced population in Swakopmund, Namibia and the only known locality of *Afrogelco aisorgii* (star) in southern Angola. See Appendix A for a complete list of localities for *A. porphyreus*.

lineata group has revealed two additional species, *G. gemmula* (Bauer et al. 1996), and *G. braacki* (Good et al. 1996). The latter species is morphologically indistinguishable from *G. hewitti* and differs from *G. hexapora* only in the number of preanal pores in males, although fixed allozyme differences unambiguously support its specific recognition.

Any attempt at reconstructing the phylogeny of the African leaf-toed geckos is hindered by the lack of an identified suitable outgroup, or series of outgroups. Among African gekkonid genera, only the monophyly of the *Pachydactylus* clade, first identified by Underwood (1954) and modified by Russell (1972), has been supported by subsequent analysis (Haacke 1976; Joger 1985; Bauer 1990; Kluge and Nussbaum 1995; Bauer and Good 1996). Another group of African gekkonid genera, including *Pristurus*, *Narudasia*, *Quedenfeldtia*, and *Saurodactylus* has been allied with the New World sphaerodactyline genera (Kluge 1995; Kluge and Nussbaum 1995), although relationships among the Old World genera remain unclear (Kluge 1995).

Bauer (1990) presented a phylogeny of Afro-Malagasy gekkonines that he characterized as preliminary and non-comprehensive. In this preliminary analysis he excluded a number of genera (*Gehyra*, *Lepidodactylus*, *Nactus*, *Tarentola*, *Geckonia*, *Saurodactylus*, *Tropicolotes*, *Quedenfeldtia*, *Pristurus*, *Hemidactylus*) that are peripheral or extralimital to southern Africa, but which occur in the greater Afro-Malagasy region. These taxa were explicitly excluded, not because he regarded them as irrelevant or outside the southern African and Malagasy radiations (as assumed by Nussbaum and Raxworthy 1994b), but because the analysis was preliminary and operationally so constrained. Bauer (1990:277) noted that the assumptions of the monophyly of the group as a whole and the monophyly of the constituent genera were likely not to be valid.

In Bauer's (1990) analysis *Phyllodactylus* formed a trichotomy with *Afroedura* and the group including *Phelsuma*, *Lygodactylus*, *Urocotyledon*, *Ailuroonyx*, *Homopholis*, *Geckolepis*, *Ebenavia*, *Paroedura*, and *Uroplatus*. The trichotomy was supported by the presence of fused nasals, and fused atlantal arches. These characters are variable within the African "*Phyllodactylus*" and do not provide strong support for even this most general grouping of genera.

Kluge and Nussbaum's (1995) reanalysis of Bauer's (1990) data yielded a somewhat different pattern of relationship, but one that still provided no resolution of the affinities of *Phyllodactylus*. They retrieved the pattern (*Afroedura*, *Phyllodactylus*, (*Phelsuma*, *Rhotropella*), (*Lygodactylus*, *Urocotyledon*), (*Ailuroonyx*, *Homopholis*), *Geckolepis*, (*Ebenavia*, *Paroedura*, *Uroplatus*)). Using their own data set, the same authors presented a consensus cladogram for the endemic Ethiopian region ingroup taxa. According to this, *Phyllodactylus* forms a trichotomy with (*Lygodactylus* + *Rhotropella* + *Phelsuma*), and a group containing *Afroedura*, *Paragehyra*, *Ailuroonyx*, *Blaesodactylus*, *Paroedura*, *Ebenavia*, *Uroplatus*, and *Urocotyledon*. The inclusion of the extralimital ingroup taxa *Gehyra*, *Gekko*, and *Hemidactylus* yielded a consensus cladogram in which *Phyllodactylus* was the sister group of *Paragehyra*, with this pair forming an unresolved trichotomy with *Afroedura* and a group including all of the scansor-bearing geckos in the analysis except *Paroedura* and *Ptyodactylus*, which were sequentially more distant sister taxa of the trichotomy. Kluge and Nussbaum (1995) admitted, however, that their initial first run results were poorly resolved and that fewer than half of the clades in their final results are supported by two or more synapomorphies. Further, as they indicated, the coding of polymorphic data as missing (Platnick et al. 1991) ignores the independent evolution of certain character states and makes the data appear more robust than they actually are.

We agree with Kluge and Nussbaum (1995) that much more research on the higher classification of the Gekkonidae is required. On the basis of either Bauer's (1990) or Kluge and Nussbaum's (1995) results, an outgroup including nearly all African gekkonids with padded digits (perhaps excluding *Ptyodactylus*, which the latter authors found to be outside of all other padded genera) would have to be employed in any analysis of relationships among southern African leaf-toed geckos. This, of course, assumes the monophyly of the Ethiopian region gekkonids (a dubious assumption at best). Alternatively, an approach like that of Arnold and Gardner (1994), using other leaf-toed geckos as the outgroup could be employed. There is, however, no reason to assume the monophyly of these units or to

hypothesize some structured pattern of relationships among them. Recognizing these difficulties we present below the results of analyses using a number of different combinations of in- and outgroup taxa. We reiterate that there is no strong support for accepting the appropriateness of these outgroups. Rather we employ them because they are the only outgroups that have been suggested (Bauer 1990; Kluge and Nussbaum 1995), or assumed (Arnold and Gardner 1994) by previous phylogenetic analysis, or because they are suggested (albeit weakly) by the phenetic analysis of leaf-toed geckos presented herein. Further, it should be noted that the uniformity of the *Goggia lineata* group with respect to the morphological characters included in the analysis dictates that analyses employing only morphological data cannot yield resolution within this clade. This fact also necessarily yields multiple output trees of identical topology.

For the two polytypic genera *Goggia* and *Afrogecko* there are a number of intragenerically variable characters. Of the six variable morphological characters in *Afrogecko* for which character states could be determined in all three described species (condition of chinshields, dorsal scalation, and extraphalangeal ossifications, number of lumbar vertebrae, atlantal fusion, and circumnarial scalation) each pair of species share a common state for two. Polarity for most of these characters cannot be established using either *Goggia* or *Goggia* + *Cryptactites* as the outgroup. Likewise, using all leaf-toed gekkonids, or all African gekkonids does not clarify matters. The only character for which polarity has been established in the context of African gekkonids (atlantal arch fusion; see Kluge and Nussbaum 1995) exhibits the derived state in only *A. porphyreus*. Likewise, the presence of more than one lumbar vertebra, which, on the basis of general distribution in leaf-toed geckos, if not gekkonids as a whole (Wellborn 1933), may also be derived, is unique to *A. porphyreus* among *Afrogecko*. The large size, enlarged chinshields, and tuberculate dorsum of *A. swartbergensis* make this species the most distinctly different in the genus, but whether this reflects an early division from an *A. porphyreus* + *A. ansorgii* clade, or merely the accumulation of autapomorphies remains unclear. The phenetic analysis of allozyme data (Fig. 3) suggests that *A. porphyreus* and *A. swartbergensis* are rather dissimilar, but until addi-

tional material becomes available for *A. ansorgii* no phylogenetic resolution within the genus is possible.

Relationships within *Goggia* are more tractable as data, both morphological and allozyme, are available for all eight species. Only five of the morphological characters scored for all leaf-toed geckos were variable within *Goggia* (atlantal arch fusion, chinshield presence, number of mesosternal and sternal ribs, number of lumbar vertebrae, and presence of extraphalangeal ossifications). Using *Afrogecko* as the outgroup (weakly suggested by the phenetic allozyme analysis, Fig. 3) suggests only that *G. microlepidota* possesses a derived condition in having a total of five versus four ribs connecting to the sternum either directly or via the mesosternal extension. Using all leaf-toed geckos as the outgroup suggests that the presence of extraphalangeal ossifications in *G. microlepidota* is derived and that all remaining taxa share the apomorphic condition of and increased number (2–3) of lumbar vertebrae. If African gekkonids are chosen as the outgroup the fusion of the atlas and reduction to four sternal and mesosternal pairs of ribs seen in the *G. lineata* group would be interpreted as derived.

If all southern African leaf-toed geckos (excluding *Cryptactites*) are regarded as part of a single clade (suggested in the context of the phenetic allozyme analysis of leaf-toed gekkonids only, but unsupported by morphological data) thirteen allozyme loci (Table 5) provide possible evidence of relationships. All others were either monomorphic or could be mapped onto any phylogenetic hypothesis equally parsimoniously. The single phylogenetic hypothesis resulting from these data, with all other leaf-toed geckos (Appendix B), including *Cryptactites*, as outgroups, yielded five most parsimonious trees (35 steps, c.i. 0.857) all of which placed the group (*A. swartbergensis* (*A. porphyreus*, *G. microlepidota*)) as the sister group of the remaining species of *Goggia* (the *G. lineata* complex). In this analysis the monophyly of the *G. lineata* group is suggested by the presence of three allele combinations (Ck-b/c, Icdh1-b/c, and Icdh2-b) among its species that are unique among leaf-toed geckos. This is also reflected in the much smaller genetic distances within this group relative to other distances among leaf-toed geckos (Table 3; Fig. 3). The species pair *G. lineata* + *G. gemmula*

TABLE 5. Distribution of allozyme character states among the southern African leaf-toed geckos.

Locus	Taxa										Out
	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	
Acon-1	0	0	2	0	0	2	3	0	3	1	0
Ak	0	0	0	0	0	0	1	0	1	0	-
Ck	1	1	2	1	1	2	4	2	3	0	-
Fum	2	2	2	2	2	2	2	2	0	1	0
Gpi-1	0	2	4	0	0	3	5	0	1	1	0
Gpi-2	0	0	1	0	0	0	0	0	1	0	0/1
Icdh-1	1	1	1	1	1	1	2	1	0	0	0
Icdh-2	1	1	1	1	1	1	0	1	2	0	0
Ldh-1	2	2	2	0	2	2	2	2	0	1	0
Me	0	1	0	0	0	0	0	0	1	0	0
Pep-2	1	1	0	1	1	0	2	0	0	0	0
Pgdh	2	2	2	2	2	2	0	2	3	1	0
Pgm-2	0	0	0	0	2	0	1	0	1	1	0

is also retrieved in all five trees, but there is no further resolution among the *G. lineata* complex.

Employing only *Afrogecko* species as an outgroup to *Goggia* reduces the number of potentially informative allozyme characters to twelve, as only one allele is present at the Fum locus in all *Goggia*. This analysis yields 24 most parsimonious trees (length 14, c.i. 0.658). The strict consensus of these trees is largely unresolved, although the clade (*lineata* (*gemmula*, *microlepidota*)) is always retrieved.

Using only the five morphological characters that are not monomorphic among *Goggia* and assigning *Afrogecko* as the outgroup it is not possible to produce a tree which maintains the monophyly of the ingroup. The expansion of the morphological data set to 18 characters (Appendix C) that vary within the group *Afrogecko* plus *Goggia*, however, yields a single most parsimonious tree (length 22, c.i. 0.864) when *G. braacki*, *G. essexi*, *G. hewitti*, *G. hexapora*, *G. lineata*, and *G. rupicola*, which are identical for all characters scored, are treated as a single taxon. *Goggia microlepidota* is the sister species of the unresolved clade containing all of its congeners.

Examining only morphological data but expanding the outgroup to include all of the leaf-toed geckos yielded 225 equally most parsimonious trees each with a length of 40 and

a consistency index of 0.500. In the resulting strict consensus cladogram the monophyly of *Goggia* was not corroborated, as there is an unresolved trichotomy involving the *Goggia lineata* complex, *G. microlepidota*, and *Dixonius*. *Afrogecko*, *Cryptactites*, *Euleptes*, *Urotyledon*, and *Ebenavia* formed another, distantly related clade.

The incorporation of both allozyme and morphological data (30 characters) for *Goggia* and *Afrogecko* produced 102 trees of 60 steps and a consistency index of 0.700. The strict consensus of these trees collapsed most of the *lineata* complex species into a polychotomy but retrieved *lineata* and *rupicola* as sister taxa and *microlepidota* as the sister species of the entire *lineata* complex. Expanding the analysis of the full data set to include all of the leaf-toed geckos as outgroups yielded 45 most parsimonious trees (length 184, c.i. 0.880). A single strict consensus tree yielded the pattern (*microlepidota* ((*gemmula*, *lineata*), *rupicola*, (*braacki*, *essexi*, *hewitti*, *hexapora*))) (Fig. 10).

These results are largely consistent with the results of analyses performed by Good, Bauer, and Branch (1996). In their study *Goggia hewitti*, *G. hexapora*, *G. braacki* and *G. essexi* cluster together both phylogenetically and phenetically. In the phenetic analysis this group was next most

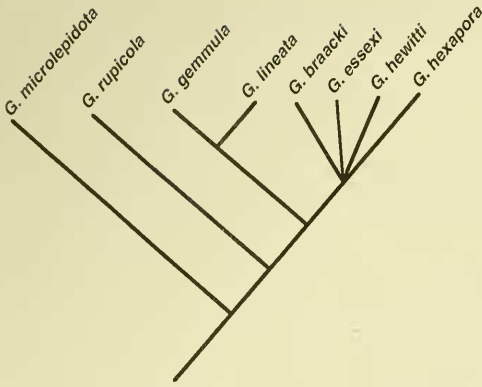


FIGURE 10. Consensus cladogram of relationships within the genus *Goggia* produced from the complete data set of allozyme and morphological characters. Note that there is no strong evidence that the outgroup taxa employed in this analysis (all other leaf-toed geckos) are monophyletic, or even paraphyletic.

similar to the group *G. lineata* + *G. rupicola*, with *G. gemmula* being the most dissimilar. The phylogenetic analysis yielded no resolution within the clade *essexi* + *hewitti* + *hexapora* + *braacki*, but placed *G. rupicola*, *G. lineata*, and *G. gemmula* as sequentially more distant sister taxa to this group. Using a technique developed by Good and Wake (1992, 1993), and de Queiroz and Good (1997), Good, Bauer, and Branch (1996) further analyzed the geographic patterns of geographic distance and demonstrated that at least some of the genetic distance that had accumulated between species reflected initial genetic divergence with geographic distance within the ancestral species prior to vicariance and subsequent speciation. Thus, the genetic distance of 0.288 between *G. essexi* and *G. rupicola* reflects an initial within species divergence of 0.25 Nei (1978) genetic distance units per 1000 km plus the accumulation of a post-vicariance genetic distance of approximately 0.13 genetic distance units. The distance between *G. essexi* and the geographically closer *G. braacki* (0.213) is less because of the lower initial geographic distance between populations in the ancestral form, not because of a difference in time of divergence. Taking this information into account their preferred phylogeny was (*gemmula* (*lineata* (*braacki*, *essexi*, *hewitti*, *rupicola*))) (Fig. 11).

The five species of the *Goggia lineata* complex that Good, Bauer, and Branch (1996) believed to

have separated from each other essentially simultaneously are each endemic to a single montane or upland rocky region. Based on minimum and maximum calibrations of 8.9 and 26 MY per Nei genetic distance unit (see Branch et al. 1995 for a review of the literature on this topic in the context of African gekkonids), this divergence probably took place 1.2–3.4 MYA. The calibration of 18 MY per unit first proposed by Brody et al. (1993) for cordylids in southern Africa yields an estimate of 2.3 MYA for the divergence. The divergence of the ancestor of these five taxa from *G. lineata* may be similarly calculated at 3.2 MYA (1.6–4.7 MYA), and that of *G. gemmula* from all remaining *lineata* complex species at 5.8 MYA (2.9–8.3 MYA). Because of the broad range of possible calibration values and the questionable validity of dating cladogenic events on the basis of distance data, we do not intend to attempt to tie these divergence estimates to particular candidate vicariant events in southern Africa. However, these results are broadly suggestive that events spanning from the Miocene to Pleistocene may have produced the observed patterns of diversity in *Goggia*. The Late Miocene cooling of the Atlantic Ocean and development of the Benguela Current produced increasing aridity in the region and resulted in the

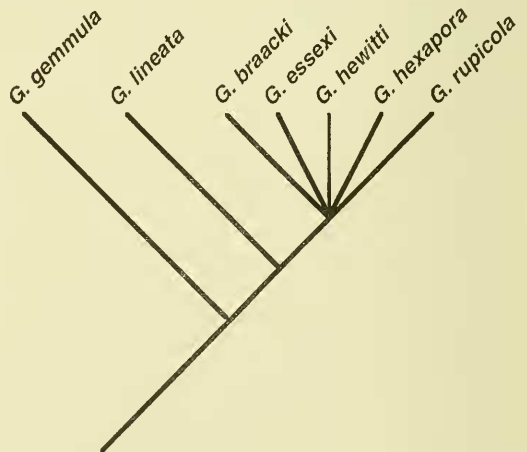


FIGURE 11. Preferred pattern of relationships among the *Goggia lineata* complex of species based on a combination of phylogenetic results and the analysis of genetic distance in relation to geographic distance (see Good et al. 1996). Under this hypothesis the group of five small *G. lineata* complex species cannot be resolved because they diverged simultaneously as a result of climatic changes affecting the entire range of the ancestral form.

cooler, more xeric southern African climate of the early Pliocene (Tyson 1986). Floral extinctions during this period yielded the contraction and fragmentation of formerly continuous habitat types that may have isolated ancestral populations of members of the *G. lineata* complex.

The much larger genetic distances between *Goggia microlepidota* and its congeners, as well as its overall morphological distinctness, suggest that the initial cladogenic event in the *Goggia* lineage took place well before the Late Miocene. Candidate events include secondary orogenic activity in the Cape Fold Mountains or earlier climatic changes.

Divergence distance between the two species of *Afrogecko* for which allozymes were examined is greater still (Fig. 3). Further, the highly disjunct distribution of this genus as a whole and the morphological disparity among species suggest that diversification within this group took place earlier in the Tertiary than that of *Goggia*. The origin of both genera, however, remains obscure and there are no obvious candidates for the immediate sister group of either.

Both *Afrogecko* and *Goggia* have radiated in southern Africa and include species endemic to remote montane areas, suggesting a long history in the region. The known distribution of *Cryptactites*, however, includes only two small areas of littoral and estuarine habitat near prominent headlands in the Eastern Cape. This pattern of distribution, as well as the fact that only a single species appears to occur in Africa, has raised the possibility that *Cryptactites peringueyi* may have arrived on the Eastern Cape by recent overwater dispersal (McLachlan 1988). A coastal headland distribution pattern is seen elsewhere in southern African lizards only in *Cryptobelpharus boutonii africanus*, apparently a relatively recent derivative of a widespread Indo-Pacific lineage known for overwater dispersal capabilities (Branch 1988; Haacke 1989). Very recent arrival appears unlikely for *C. peringueyi* because the species is clearly not conspecific with gekkonids from anywhere else in the world. Further, we have demonstrated that it differs significantly, both in allozyme and morphological characters from all other groups of leaf-toed geckos. Nonetheless, its affinities may lie with Madagascan or Asian groups rather than with other African gekkonids. It is interesting to note in this regard that the Port Elizabeth area, specifically the type locality of *C.*

peringueyi, received a large influx of floating pumice and associated organic debris following eruption of Krakatau in 1883 (Simkin and Fiske 1983; Oelofsen et al. 1986) and might be expected to receive propagules originating from Asia or the southern Indian Ocean.

Because the goal of this study was not to resolve relationships among leaf-toed geckos, but to delineate probable monophyletic groups among the Old World "*Phyllodactylus*," we cannot propose a reconstruction of the evolutionary history of each of these groups. However, the large genetic and morphological gaps separating each of the generic level taxa, diagnosed herein, from one another strongly suggest that the leaf-toed morphology has evolved on many occasions in many parts of the world, and that each clade of leaf-toed geckos may have had a long history independent of other superficially similar groups. We believe that the break-up of suspect polyphyletic groups, such as *Phyllodactylus*, into monophyletic units is a necessary first step in resolving relationships within higher order taxa. The future use of the monophyletic units *Eulepites*, *Haemodracon*, *Dixonius*, *Afrogecko*, *Cryptactites*, and *Goggia* should thus facilitate the resolution of patterns of affinity within the Gekkonidae.

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Appendix A

SPECIMENS EXAMINED. — Except for the southern African leaf-toed geckos, only skeletal specimens examined are listed. Specimens examined osteologically by means of radiographs are indicated by an asterisk (*), dry skeletal specimens are indicated by (sk) and cleared and stained specimens by (c&s). Locality data are provided for those southern African species that have not been recently revised. Named localities as well as quarter degree square coordinated are provided (see Leistner and Morris [1976] for an explanation of the quarter degree notation). A complete list of specimens examined for *Goggia lineata*, *G. rupicola*, *G. essexi*, *G. hewitti*, and *G. hexapora* was provided in Branch et al. (1995). Specimens examined for *G. gemmula* were given by Bauer et al. (1996) and those for *G. braacki* were listed by Good et al. (1996).

Afrogecko ansorgii: BMNH 1946.8.24.52-53*.
Afrogecko porphyreus: Namibia: Swakopmund (2214Da) AMNH 47898; South Africa, Northern Cape Province: Nieuwoudtville (3119Ae) SAM 3078; Western Cape Province: Bitterfontein (3118Ab) PEM-AM 6943; Jacobsbaai (3217Dd) CAS 167586-7*, 167589-90*, 173911*, 173912, 143913*, 175286-7*, 175408*, 176041, 176044, 176051*; Hoedklip, 32°49'45"S 17°51'07"E, 20 m (3217Dd) JEM FB 511; Maritzbaai, 32°58'37"S 17°52'50"E, <20 m (3217Dd) JEM FB 527; Clanwilliam (3218Bb) SAM 18564; Klein Tafelberg, 32°33'08"S 18°27'50"E, 320 m (3218Cb) JEM FB 837; Helenabaai, 32°45'52"S 18°01'48"E, 30 m (3218Cc) JEM FB 617; Kouebokkeveld Mts. (3219Cc) SAM 2408; Dasklip Pass, 13 km NE of Porterville (3219Cc) CAS 175319; Farm Excelsior, 32°57'26"S 19°25'23"E (3219Cd) AMB H8585 (c&s); Hoedjies Point, Saldanha (3317Bb)

SAM 45138-40; Saldanha, 33°01'15"S 17°56'57"E, >20 m (3317Bb) JEM FB 23-4; Marcuseiland, 33°02'32"S 17°58'11"E, <20 m (3317Bb) JEM FB 291-5, SAM 44776-7; Malgaseiland, 33°03'09"S 17°55'35"E, <20 m (3317Bb) JEM FB 333-4; Juteneiland, 33°04'57"S 17°57'19"E, <20 m (3317Bb) JEM FB 323-5, SAM 19431 (2 specimens), 19432, 44827-9; Plankiesbaai, 33°07'54"S 17°58'22"E, <15 m (3317Bb) JEM FB 255-6; Vondelingeiland, 33°09'08"S 17°58'00"E, <20 m (3317Bb) JEM FB 310-3; Meeuw Island (3318Aa) SAM 44770-1; Schaapen Island (3318Aa) JEM FB 125-6, PEM 1572-3, 1575-8, 1580, 1588-89; Boomgat, 33°01'42"S 17°57'37"E, <20 m (3317Bb) JEM FB 297; Leentjiesklip, 33°02'44"S 18°02'31"E, <20 m (3318Aa) JEM FB 286; Leentjiesklip, 33°04'09"S 18°02'25"E, <20 m (3318Aa) JEM FB 289-90; Konstabelberg 33°07'53"S 18°01'16"E, 120 m (3318Aa) JEM FB 269; Yzerfontein (3318Ac) SAM 44998-9; Dassen Island, 33°25'18"S 18°05'02"E, <20 m (3318Ac) JEM FB 862-3, PEM 4607-23, SAM 44830, 44833-4; Matroosbaai, 33°36'09"S 18°22'13"E, <20 m (3318Cb) JEM FB 450; Blouberg, 33°44'57"S 18°27'47"E, 188 m (3318Cb) JEM FB 192-3; Robben Island (3318Cd) PEM 10682, SAM 42979-80; Platteklip Gorge, Table Mountain (3318Cd) SAM 144; Table Mountain (3318Cd), AMNH 47899-900, SAM 2053-4; Range Cottage nr. Cape Town (3318Cd) MCZ 20980; Cape Town (3318Cd) AMNH 47901-6, MCZ 11930-1, PEM 10579-86, SAM 1174-6, 13588, 17679, 18856, 45496, ZMB 44028; Mowbray (3318Cd) SAM 43536; Cape Town, 33°49'06"S 18°22'22"E (3318Cd) SAM 47797-8; Betel, 33°34'24"S 18°48'35"E, 520 m (3318Db) JEM FB 146-7; Paarlberg, 33°42'47"S 18°55'30"E, 580 m (3318Db) JEM FB 196-7; Meerendal, 33°47'07"S 18°37'00"E, 380 m (3318Dc) JEM FB 100-1; Milnerton (3318Dd) SAM 43999; Jonkershoek (3318Dd) CAS 167605, PEM 4985, 5012; Simonsberg, 33°53'05"S 18°55'33"E, 1300 m (3318Dd) JEM FB 501; Groot-Winterhok, 33°03'50"S 19°05'40"E, 660 m (3319 Aa) JEM FB 1052; Slagboom, 33°14'21"S 19°17'09"E, 960 m (3319Ab) JEM FB 960-3; Obiekwa, 33°15'58"S 19°04'07"E, 420 m (3319Ac) JEM FB 965; Skurweberg, 33°21'48"S 19°16'35"E, 580 m (3319Ad) JEM FB 986; Lakenvleiland, 33°22'17"S 19°34'40"E, 1000 m (3319Bc) JEM FB 603; De Doorns, 33°22'30"S 19°39'53"E (3319Bd) PEM 663, SAM 47795-6; Matroosberg, slopes between ski huts and "conical peak" (3319Bd) PEM 3602-8; Du Toitskloof (3319Ca) SAM 43877-8; Eerste Tol Bainskloof, 33°37'31"S 19°06'13"E, 675 m (3319Ca) JEM FB 1048-9; Hawekwaberge, 33°41'05"S 19°05'42"E, 1140 m (3319Ca) JEM FB 920-1; 300 ft below Franshoek Pass on road to Fishhoek (3319Cc) CM 64516; Hottentotsholland Nature Reserve, 8 km E of Franschoek (3319Cc) CAS 175317; La Motte, 33°52'16"S 19°04'33"E, 400 m (3319Cc) JEM FB 484-5; Mont Rochelle, 33°53'35"S 19°09'17"E, 1120 m (3319Cc) JEM FB 1533-6; Stettyn, 33°52'31"S 19°20'25"E, 540 m (3319Cd) JEM FB 1547; Elandskloofdam, 33°57'11"S 19°17'33"E, 760 m (3319Cd) JEM FB 1260; Kleinfontein, 33°57'11"S 19°24'19"E, 880 m (3319Cd) JEM FB 1263-4; Jonaskop, 33°58'S 19°30'E, 1640 m (3319Dc) JEM FB 877-8; Baileys Peak, Rooiberg, 33°38'11"S, 21°26'04"E (3321Cb) PEM 8569, 8672-3; Bailey's Peak, Rooiberg, Little Karoo, 33°38'15"S, 21°26'22"E (3321Cb) 1166 m, CAS 195398; Gamka Mountain Reserve, 33°44'S, 21°56'E (3321Db) PEM 6746-8; Montagu Pass, Outeniquaberg (3322Cd) PEM1057; Saasveld Forest Station (3322Dc) PEM 3678; Goukamma Nature Reserve, Groenvlei, Knysna District (3422Bb) PEM 1038, 1045, 1056; Karatara (3322Dd) PEM-AM 5922; Leisure Island, Knysna, 33°48'S, 23°03'E (3323Cc) PEM 11788; Knysna, 33°57'00"S, 23°06'30"s (3323Cc) PEM 10124; Prince Alfreds Pass (3323Cc) PEM 1454; Formosa Conservation Area, 33°47'19"S, 23°23'58"E (3323Cd) PEM 9326; Steenoondrug, Grootrivier Pass, 33°57'50"S, 23°33'30"E (3323Dc) PEM 1928; Wynberg (3418Ab) SAM 1968; St. James (3418Ab) PEM 10597; Bergvliet, Cape Town (3418Ab) PEM 1554; Hout Bay (3418Ab) SAM 6096, ZFMK 20729-30; Simonstown (3418Ab) ZMB 23562 (2 specimens); Fischeok (3418Ab) PEM 1574, 1579, 1581-2, 1584-7; Cape Peninsula (3418Ab) CAS 111943*, PEM 10587-9; Constantia Nek (3418Ab) SAM 17969 (2 specimens); Cape Peninsula, Noordhoek (3418Ab) CAS 106039*, USNM 159123-4; Kalk Bay (3418Ab) PEM 10594-6; Cape of Good Hope (3418Ad) AMNH 47907, ZMB 408 (2 specimens); Olifantsbosch, Cape Point (3418Ad) SAM 44368-9; 1.4 km N of Steenbrasrivier on Rt. 44 (3418Bb) CAS 193647-49; S side of Steenbrasrivier at Rt. 44 (3418Bb) CAS 193650-1; Hottentots Holland above Sir Lowry's (3418Bb) SAM 3939; Somerset West (3418Bb) PEM 660, 666, 1436 [3 specimens]; Jonkershoek, 34°00'06"S 18°59'38"E, 1640 m (3418Bb) JEM FB 902; Rooskraal, 34°04'37"S 18°58'31"E, 680 m (3418Bb) JEM FB 1019-20; Strand, 34°06'08"S

- 18°49'13"E, 20 m (3418Bb) JEM FB 869, 913; Verkykerskop, 34°06'08"S 18°58'04"E, 1200 m (3418Bb) JEM FB 996-7; Verkykerskop, 34°06'08"S 18°58'21"E, 880 m (3418Bb) JEM FB 1015-6; Gandoupas, 34°07'52"S 18°56'60"E, 560 m (3418Bb) JEM FB 1024-5; Kogelberg, 34°10'40"S 18°55'52"E, 500 m (3418Bb) JEM FB 1034-5; Kogelberg, 34°12'14"S 18°55'48"E, 800 m (3418Bb) JEM FB 1031-2; Cape Point (3418bC) CAS 85909-10*, SAM 43234, 44604; Die Mond (3418Bd), MCZ 45471-9; Cape Hangklip (3418Bd) AMB 2140 (c&s), 2144 (c&s), 2146 (c&s), H8523 (c&s), H8530 (c&s), CAS 167591-603*, 167605*, 175299-300, 175301-12*, 200120-24, LSUMZ 57239-43, SAM 44025; Mountain Rose, 34°19'39"S 18°58'27"E, 140 m (3418Bd) JEM FB 1454-5; Rooielsrivier, 34°17'47"S 18°51'06"E, 220 m (3418Bd) JEM FB 1460; Cape Flats (3418Dc) SAM 428, ZMB 22898 (7 specimens); Boskloof, 34°00'24"S 19°20'56"E, 1000 m (3419Ab) JEM FB 1550-1; Boskloof, 34°01'48"S 19°21'38"E, 760 m (3419Ab) JEM FB 1549; Onrust, on beach (3419Ac) SAM 44800; Perdekloof, 34°17'45"S 19°13'38"E, 180 m (3419Ac) JEM FB 1530; Kleinmond, 34°20'37"S 19°16'33"E, 250 m (3419Ad) JEM FB 1516-8; Platberg, 34°22'16"S 19°16'21"E, 520 m (3419Ad) JEM FB 1321-2; Riviersonderend Mts. (3419Ba) SAM 18009, 18340; just W Cape Agulhas (3419Bd) SAM 44788; Die Kelders, Hermanus (3419Cb) SAM 18352; Franskraal, 34°35'27"S 19°23'25"E, 110 m (3419Cb) JEM FB 1419; Danger Point, 34°37'29"S 19°19'37"E, 20 m (3419Cb) JEM FB 1415-6; Wydgele, 34°29'25"S 20°25'48"E, De Hoop Nature Reserve (3420Ad) SAM 47794; Plettenberg Bay (3421Ac) PEM 1567-71, 7892; Mossel Bay (3422Aa) PEM 10590-3; Groenvlei, Sedgefield (3422Bb) PEM 1515; Goukamma Nature Reserve (3422Bb) PEM 6529; Knysna (3423Aa) SAM 13583 (2 specimens), 13585; 14329 (2 specimens); Robberg Nature Reserve (3423Ab) PEM3134-8; Eastern Cape Province: Coldstreams (3323Dc) PEM 1583; Walmer, Port Elizabeth (3325Cd) CAS 199986-8, LSUMZ 57244-6, PEM 7052-3, 8058, 8076-9; Humeewood Road, Port Elizabeth (3325Dc) PEM 2686; Grahamstown, 33°18'55"S, 26°31'50"E (3326Bc) PEM 6531, 7743; Cape St. Francis (3424Bb) PEM-AM 7649, 7791; Imprecise or untraceable localities: Tygerberg and Hout Bay ZFMK 21921-3; Langekuil near Don R., Clanwilliam SAM 2856-7; Meyverhouts Kraal, Clanwilliam SAM 3392; Riversdale Mts., 4000-4500 ft. SAM 17654 (2 specimens); Cape Province, ZMB 25045 (2 specimens); Namaqualand SAM 778; Cape SAM 545, 547, 1365; no locality, PEM 1929. Africa AMNH 6. *Afrogecko swartbergen-sis*: [all localities in Western Cape Province, Republic of South Africa] Gouekranshut, 33°19'16"S, 22°14'32"E (3322Ac) PEM 6876, 6879, 7834; 1.6 km along Summit track, Groot Swartberg, 33°21'S 22°03'E (3322Ac) PEM 6754, 6756, 6876; Head of Mooikloof, Groot Swartberg, 33°20'S, 22°18'E (3322Ad) CAS 180418*, 180419 (c&s), PEM 6877; Blesberg radio mast, 33°24'55"S, 22°41'34"E (3322Ad) PEM 7843. *Assaccus elisae*: BMNH 1961.15.01*, CAS 86525-7*, 86528 (sk), 86529*. *Assaccus gallagheri*: BMNH 1973.1847-9*, 1973.2894-5*. *Assaccus griseonotus*: CAS 170817-8*. *Christinus marmoratus*: CAS 74995*, 75029*, 83512-58, 83560-69, CAS 83570 (sk). *Cryptacites peringueyi*: [all records in Eastern Cape Province, Republic of South Africa] Kromme River Estuary (3424Bb) CAS 186374-5*; Kaia da Balaia, upper Kromme River, 34°07'S, 24°47'E (33424Bb) PEM 6886*, 6887, 6916*, 7210; bridge at Kromme River mouth, 34°08'S, 24°48'E (3424Bb) PEM 10875-6, 11334; 50 m NW kromme River Bridge, 34°08'S, 24°48'E (3424Bb) CAS 186383*, PEM 6910, 6911 (c&s), 6912-15*; 200 m W of Kromme River Bridge, 34°08'S, 24°48'E (3424Bb) PEM 6908, 6909; west bank of Kromme River mouth, 34°09'S, 24°49'E (3424Bb) PEM 8068; Willows, Port Elizabeth, 34°03'S, 25°37'E (3425Ba) PEM 12207-8; Chelsea Point, 34°03'S, 25°38'E (3425Ba) PEM 12206, SAM 8628* [paralectotype]; Schoenmakerskop, 34°04'S, 25°35'E (3425Ba) PEM 12209; Imprecise locality [in error]: Little Namaqualand (no specific locality) SAM 777* [lectotype]. *Dixonius melanostictus*: FMNH 178232*. *Dixonius siamensis*: BMNH 1946.8.24.51*, 1946.8.24.40-41*, 1931.10.13.3-4*, 1931.10.13.6, CAS 95254-5*, 95256 (sk), 95257*, FMNH 177696*, 177730 (c&s), 177732*, 177735*, 177766 (c&s). *Ebenavia inunguis*: CAS 66195-6*, ZMB 19007* (4 specimens), 19008* (2 specimens), 19009*, 19200* (4 specimens), 19460* (3 specimens), 19461* (8 specimens), 19462* (11 specimens), 19521* (11 specimens), 22598* (5 specimens), 30631* (6 specimens). *Euleptes europaea*: MZUF 19119-19139*, 19721*, USNM 014861(2 specimens), 037216. *Goggia braacki*: CAS 199989-91*, PEM R3270*, 4323*. *Goggia essexi*: CAS 186376-7*, PEM R664 (c&s), PEM R665*. *Goggia gemmula*: CAS 186352*, 200080*, 200090 (c&s), 200095*. *Goggia hewitti*: CAS 167607*, 175273*, 180353*, 180354 (c&s), 180357 (c&s), 180358*, 180369*, 180371-2*, PEM R 3623*. *Goggia hexapora*: CAS 113537*, 167606*, 167608 (c&s), 167609*, 175420*, 157421 (c&s), 200114*. *Goggia lineata*:

AMB H8611 (c&s), CAS 85926-7*, 167578-85*, 167588*, 173899*, 157288-99*, 157319*, 154415-9*, 176042-50*, 186319-21*, 200013*, 200015-6*, 200027*, 200068*, 200106*, 5 specimens (no number, c&s); PEM R3609*, 4588*. *Goggia microlepidota*: [all records in Western Cape Province, Republic of South Africa] Pakhuis Pass (3219Aa) - SAM 20531 (holotype), 45494-5; Engelmansklouf Gorge (3219Ac) PEM 6399; Waboomskloof, 32°24'00"S 19°12'30"E, 1370 m (3219Ac) JEM FB 687; Hoogvertoon, 32°29'11"S 19°09'35"E, 1260 m (3219Ac) JEM FB 606, 611; Sneeuwerghut, 32°29'13"S 19°10'30"E, 1340 m (3219Ac) JEM FB 938; Bokveldskloof, 32°29'40"S 19°09'50"E, 1465 m (3219Ac) JEM FB 688; Skurweberg 3, 33°22'11"S 19°16'27"E, 780 m (3319Ad) JEM FB 994; Buf-felsberg, 32°36'52"S 19°11'07"E, 820 m (3219Ca) JEM FB 1393-4; Middelbergpas, 32°37'53"S 19°09'06"E, 1100 m (3219Ca) AMB 2438 (c&s), CAS 167637*, 176035*, 180430-2*, JEM FB 1174-6; Zuurvlaakte, 32°58'08"S 19°03'04"E, 1030 m (3219Cc) JEM FB 598; Skurweberg, 32°56'37"S 19°23'42"E, 1125 m (3219Cd) JEM FB 1608-9; Skurweberg, 32°57'S 19°24'E, (3219Cd) JEM 1780; Excelsior, 32°57'26"S 19°25'23"E, 1020 m (3219Cd) JEM FB 1076-7; Op-den-berg, 32°58'05"S 19°24'35"E, 960 m (3219Cd) JEM FB 631; Louws Legplek, 32°02'40"S 19°03'29"E, 940 m (3319Aa) JEM FB 1056-8, 1072; Groot-Winterhoek, 33°03'50"S 19°05'40"E, 660 m (3319Aa) JEM FB 1050-1; Slagboom 33°14'21"S 19°17'09"E, 960 m (3319Ab) JEM FB 957-8; 33°11'29"S 19°37'42"E (3319Bc) JEM FB 1939; Grootvlakte, 33°21'13"S 19°37'14"E (3319Bc) JEM FB 2227; Imprecise locality: Cedarberg, SAM 43746. *Goggia rupicola*: CAS 19331-6*, 200003 (c&s). *Haemodracon riebeckii*: BMNH 1953.1.7.95 (c&s), ZMB 10109*. *Haemodracon trachyrhinus*: BMNH 1946.819.81*, 1967.496-7. *Paroedura guibaeae*: FMNH 73051*, 73059-60*. *Paroedura pictus*: ZMB 18983 (3 specimens). *Paroedura stumpfi*: CAS 156898-9*. *Phyllodactylus galapagensis*: CAS 10357 (sk). *Phyllodactylus ger-rhopygus*: CAS 84761*, 84763*, 84765 (sk). *Phyllo-dactylus gilberti*: CAS 12676*, 12679 (sk), 12681*.

Phyllodactylus homolepidurus nolascoensis: CAS 98534 (sk). *Phyllodactylus leei*: CAS 10062 (sk), 11053*, 11993*. *Phyllodactylus pumilus*: FMNH 197831*. *Phyllodactylus tuberculosus saxatilis*: CAS 58953 (sk). *Phyllodactylus unctus*: CAS 91343 (SK), 91352*, 91355*, 147376 (c&s). *Phyllodactylus ventralis*: FMNH 165833-5*. *Phyllodactylus wirshingii*: CAS 175498 (c&s), 175500*. *Phyllodac-tylus xanti xanti*: CAS 98509 (sk), 98510*, 98514*, 147377 (c&s). *Urocotyledon inexpectatus*: ZMB 9381* (3 specimens) - skulls examined by superficial dissection.

Appendix B

Tissue samples used in phenetic and phyloge-netic allozyme analysis of leaf-toed geckos. Fro-zen tissue collection numbers (if different from corresponding whole specimen numbers) are listed parenthetically. Collection abbreviations are detailed in the Materials and Methods section except GVH (= Gerald V. Haagner field series, to be deposited in PEM).

Afroedura loveridgei (n = 1) GVH 3969; *Afro-gecko porphyreus* (n = 5) CAS 193647-50, 195398 (LSUMZ H2800-4); *Afrogecko swartbergensis* (n = 1) CAS 180419 (LSUMZ H1508); *Christinus mar-moratus* (n = 1) unnumbered; *Cryptactites peringueyi* (n = 2) CAS 186374-5 (LSUMZ H1666-7); *Dixonius siamensis* (n = 1) MVZ uncatalogued; *Goggia braacki* (n = 10) CAS 199989-91, LZUMZ 57330-2, PEM R11890, 11922, 12379-80; *Goggia essexi* (n = 2) CAS 186376-7 (LSUMZ H1655-56); *Goggia gem-mula* (n = 5) CAS 186352 (LSUMZ H1658), 193364-5, 193641-2; *Goggia hewitti* (n = 7) CAS 180353-4, 180356-7, 180360, 180371-2 (LSUMZ H1501-7); *Goggia hexapora* (n = 4) CAS 200114, LSUMZ 57360, PEM R 12381-2; *Goggia lineata* (n = 5) CAS 193254, 193351-4 (LSUMZ H2794-8); *Goggia mi-crolepidota* (n = 1) CAS 180432 (LSUMZ H2799); *Goggia rupicola* (n = 5) CAS 193341-6 (LSUMZ H2805-9); *Paroedura picta* (n = 1) AMB 4176; *Phyl-lo-dactylus wirshingi* (n = 1) SBH 101730; *Phyllo-dactylus xanti* (n = 2) MVZ FC 13226-7.

Appendix C

Morphological characters used in analyses of the phylogeny of the genus *Goggia*. Character states for outgroup taxa, except *Afrogecko* spp. are based on composites for the entire genus.

Taxon	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>G. braacki</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. essexi</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. gemmula</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	2	1	0	1	0
<i>G. hewitti</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. hexapora</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. lineata</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. rupicola</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
<i>G. microlepidota</i>	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1
<i>A. porphyreus</i>	0	1	1	1	0	0	1	1	0	0	1	1	0	9	1	1	0	0
<i>A. swartbergensis</i>	1	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1
<i>A. ansorgii</i>	0	1	0	1	0	0	1	1	0	0	1	1	1	0	1	1	0	0
<i>Phyllodactylus</i>	2	1	9	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0
<i>Asaccus</i>	2	1	0	0	0	0	0	0	0	0	0	9	1	9	0	0	1	0
<i>Dixonius</i>	2	0	0	0	1	1	0	0	1	0	0	0	1	0	9	0	0	1
<i>Cryptactites</i>	2	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
<i>Haemodracon</i>	0	9	0	0	0	9	1	1	1	0	1	9	1	0	9	0	0	0
<i>Ebenavia</i>	2	1	1	1	0	0	0	1	0	0	1	9	0	0	1	0	0	0
<i>Christinus</i>	0	1	0	0	0	1	9	1	0	0	1	1	9	0	0	0	0	0
<i>Euleptes</i>	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0
<i>Urocotyledon</i>	0	1	1	1	0	0	1	9	1	0	1	9	0	0	1	0	0	0
<i>Paroedura</i>	0	1	0	0	0	0	0	1	1	0	1	1	1	9	0	0	0	0

Note that characters states were arbitrarily assigned numerical values and that polarity was established on the basis of choice of outgroup (see text).

1. Dorsal body scales atuberculate (0), tuberculate - smooth (1), or tuberculate - keeled (2).
2. Rostral cleft present (0), or absent (1).
3. First supralabial enters nostril (0), or excluded from nostril (1).
4. Enlarged chinshields present (0), or absent (1).
5. Preanal pores absent (0), or present (1).
6. Cloacal spurs consisting of 1-2 enlarged scales (0), or a comb of 3-7 scales (1).
7. Nasal process of premaxilla long and lanceolate (0), or short and broad (1).
8. Nasal bones paired (0), or fused (1).
9. Frontal bone not or barely contacting maxilla (0), or broad fronto-maxillary contact (1).
10. Parietal bones paired (0), or fused (1).
11. Stapes perforate (0), or imperforate (1).
12. Inner proximal ceratohyal process absent (0), or present (1).
13. Atlantal arches fused (0), or paired (1).
14. Lumbar vertebrae 1 (0), 2 (1), or 3 (2).
15. 5 or more (0), or 4 or fewer (1) pairs of sternal + mesosternal ribs.
16. Interclavicle with (0), or without (1) well-developed lateral processes.
17. Precoracoid-mesoscapular connection cartilaginous (0), or ligamentous (1).
18. Extraphalangeal digital ossifications absent (0), or present (1).