

Original article

## Molecular phylogenetics of Malagasy skinks (Squamata: Scincidae)

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**Abstract.**—Malagasy skinks are a poorly known group, and their relationships have not been critically evaluated previously. In this paper we present a phylogeny of Malagasy “scincine” lizards, based on quantitative phylogenetic analysis of data from seven molecular markers. Our analysis confirms the paraphyly of “*Amphiglossus*”, and supports *Madascincus* as a valid genus. *Pygomeles* is sister to three groups of “*Amphiglossus*” and *Voeltzkowia*, but relationships within this clade are tenuous. *Paracontias* is monophyletic, but the subgenera *Malacontias* and *Paracontias* are not supported. These data support the monophyly of all sampled Malagasy “scincines” as well as a southern African + Malagasy “scincine” clade. Despite their low vagility, these skinks appear to have reached Madagascar by dispersal over water, rather than as a result of vicariance.

**Key words.**—*Amphiglossus*,  $\alpha$ -Enolase, Gapdh, Madagascar, Phylogeny, Scincidae, Scincinae.

Knowledge of the herpetofauna of Madagascar is still in the discovery phase. Many species are known from a single specimen or location, and new information about distributions, behaviour, and basic biology is being published every year (Raxworthy & Nussbaum 1994; Glaw & Vences 1996; Andreone & Raxworthy 1998; Krüger 1999; Andreone *et al.* 2000; Andreone *et al.* 2001). With many nocturnal or burrowing species, the ten genera of skinks (Scincidae) are probably the most poorly studied group of reptiles in Madagascar (Glaw & Vences 1994), as shown by the description of nine new species of *Amphiglossus* (Raxworthy & Nussbaum 1993), two new *Pseudoacontias* (Nussbaum & Raxworthy 1995), three *Paracontias*, and one *Pseudoacontias* (Andreone & Greer 2002), and the new genus *Sirenoscincus yamagishii* (Sakata & Hikida 2003a). The two genera belonging to the subfamily Lygosominae (*Trachylepis* and *Cryptoblepharus*) are widespread and fully limbed, whereas the eight gen-

era from the subfamily “Scincinae” are all endemic to the Malagasy region, and all show limb reduction to some degree (Glaw & Vences 1994; note that Greer’s (1970a) subfamily Scincinae has been shown to be paraphyletic, but has yet to be formally revised (Whiting *et al.* 2003)).

*Amphiglossus* Duméril and Bibron 1839 was the first genus of Malagasy “scincines” described, with *Amphiglossus astrolabi* as the type species. Boulenger (1887) moved *A. astrolabi* to the limb-reduced genus *Scelotes*, distributed throughout southern Africa, where most limbed Malagasy “scincines” were placed from that time on (e.g., Angel 1942; de Witte & Laurent 1943). Greer (1970b) placed the Malagasy members of *Scelotes incertae cedis* within the subfamily Scincinae. In a series of 19 papers from 1979-1987, Brygoo resurrected *Amphiglossus*, moving the Malagasy species of *Scelotes* into that genus or *Androngo* Brygoo, 1982, depending on the number of presacral

vertebrae. Andreone & Greer (2002) moved three of the species of *Androngo* back to *Amphiglossus*, leaving the former monotypic, and revising *Amphiglossus* to include species showing digit reduction. Of all the scincid genera present in Madagascar, *Amphiglossus* is currently the largest with 37 species (35 endemic to Madagascar, one endemic to the Comoro Islands, and one endemic to the Glorioso Islands, northwest of Madagascar).

The two completely limbless Malagasy genera are *Cryptoscincus* Mocquard, 1894, which is monotypic and known only from the two type specimens, and *Paracontias* Mocquard, 1894, with eight species divided into three subgenera (Brygoo 1980b). *Voeltzkowia* Boettger, 1893 is composed of three completely limbless species (currently placed in the nominotypical subgenus), and two species with very rudimentary hindlimbs that were originally described in the genus (now subgenus) *Grandidierina* (Brygoo 1981b). The newly described monotypic *Sirenoscincus* Sakata & Hikida 2003b shows similarity in some scale characters to *Voeltzkowia* but is unique in having forelimbs with no hindlimbs (Sakata & Hikida 2003a).

*Pseudoacontias* Bocage, 1889 was originally described as completely limbless from a single type specimen of *P. madagascariensis*, which was destroyed by fire in 1978 (Brygoo 1980b). The status of the genus remained uncertain until 1995 when a second species (*P. angelorum*) was described with no forelimbs and "flaplike hindlimbs with no toes" (Nussbaum & Raxworthy 1995 pg. 94). In 2002 a third species was described (*P. menamainty*) with "a button like scale" representing each forelimb, and no hindlimbs (Andreone & Greer 2002 pg.161). Most recently *P. unicolor*, a completely limbless species was described from Nosy Be (Sakata & Hikida 2003b). Although the validity of the genus is no longer in question, *Pseudoacontias* remains enigmatic as all four described species are known from single specimens. *Pygomeles* A. Grandidier, 1867, also contains one limbless species (known from the

two types) and one species with rudimentary hindlimbs (Brygoo 1984c).

Despite much research effort (Angel 1942; de Witte & Laurent 1943; Brygoo 1979, 1980a, b, c, d, 1981a, b, c, d, 1983a, b, 1984a, b, c, d, e, 1985, 1986, 1987), relationships between Malagasy and African "scincines" and within the Malagasy group are unknown and have never been critically evaluated (Raselimanana & Rakotomalala 2003). In 1943 de Witte & Laurent presented a tree depicting phylogenetic relationships for all African and Madagascan skink genera showing limb reduction, but there is no explanation of how the tree was derived. De Witte & Laurent (1943) show Malagasy "scincines" as monophyletic, with *Proscelotes* and *Sepsina* described as the most primitive of the African genera and the most closely related to the Malagasy forms. Within Malagasy genera, *Amphiglossus* was considered primitive and described as giving rise to the Malagasy "Acontias" (*Pseudoacontias*, *Pseudoacontias*, and *Paracontias*), as well as the group of *Voeltzkowia*, *Pygomeles*, *Grandidierina* and *Cryptoscincus*.

Hewitt (1929) also concluded that the Madagascan "Acontias" were derived from *Amphiglossus* and only distantly related to the African forms. In his review of the "scincinae" lizards of sub-Saharan Africa and the surrounding islands, Greer (1970b) did not attempt to discuss the Malagasy complex in detail, but did state that they were closest to the mainland *Proscelotes* and *Sepsina* based on a small interparietal that does not contact the supraoculars, and a well developed post orbital bone. The most complete treatment of Malagasy "scincines" was Brygoo's series of papers (1979-1987). Although he did make some statements about similarity of specific genera, he did not explicitly address the relationships among genera. Brygoo's most widely used character was the number of presacral vertebrae which he used to define the genus *Androngo* and the subgenera and groups of *Amphiglossus*, although some of these groups

overlap in their number of presacral vertebrae (Brygoo 1981d; 1984b, d, e, 1987). It has been suggested that a low number of presacral vertebrae is the primitive condition for skinks (Greer *et al.* 2000), but the usefulness of this character in diagnosing monophyletic groups has been questioned (Andreone & Greer 2002). Andreone & Greer (2002) also point out that *Amphiglossus* as currently defined, is composed of “the most generally primitive members” of Malagasy “scincines”, and is therefore “almost certainly a paraphyletic group” (pg.163).

In this study we use four nuclear and three mitochondrial gene regions to present a molecular phylogenetic hypothesis for many of the Malagasy “scincines”. We investigate the monophyly of Malagasy “scincines” and their relationship to southern African genera. We also test the monophyly of *Amphiglossus* and *Paracontias*, and look at the relationships among Malagasy “scincines”.

## MATERIALS AND METHODS

*Sampling.*—Taxon sampling included the Malagasy genera *Amphiglossus* (14/37 spp.), *Paracontias* (3/8 spp.), *Pygomeles* (1/2 sp.), and *Voeltzkowia* (1/5 sp.); representatives from the genera *Cryptoscincus*, *Androngo*, *Sirenoscincus* (all monotypic), and *Pseudoacontias* were not available for inclusion in this study (see Appendix 1 for specimen information). The southern African genera *Scelotes* (9 spp.), *Typhlacontias* (2 spp.), *Melanoseps* (1 sp.), *Proscelotes* (1 sp.), and *Sepsina* (1 sp.), were included to test previously hypothesised relationships between southern African and Malagasy genera. In order to place the Malagasy taxa within skinks as a whole, species from *Trachylepis* (formerly African *Mabuya*), *Sphenomorphus*, and *Tiliqua* (subfamily Lygosominae); *Feylinia* (subfamily Feylininae); and “*Eumeces*”, and *Scincus* (subfamily “Scincinae”) were included. Based on prior study (Whiting *et al.* 2003), the subfam-

ily Acontinae (represented here by *Acontias*, and *Typhlosaurus*) has been shown to be basal within skinks and was therefore used to root all analyses.

*Molecular data.*—DNA was extracted from liver or muscle tissue preserved in 95-100% ethanol using the Qiagen DNeasy kit (Valencia, CA). DNA templates and controls were amplified using standard PCR techniques in 50  $\mu$ l reactions, and products were visualised via 2% agarose gel electrophoresis. Primers and protocols for the amplification of 18S rDNA, 16S rDNA, 12S rDNA,  $\alpha$ -Enolase (Enol), C-mos, and cytochrome b (cyt *b*) are listed in Whiting *et al.* (2003). Glyceraldehyde-3-phosphate dehydrogenase (Gapdh) was amplified using the primers L890 and H950, which are designed to amplify intron XI and portions of exons 11 and 12 (Friesen *et al.* 1997), using AmpliTaq gold® (Perkin Elmer), 2.5% DMSO and the following cycling profile: 95°(12:00); 94°(0:30), 65°(0:30), 72°(1:00) x 35 cycles; 72°(5:00). Target products were purified using the Montage™ PCR<sub>96</sub> Filter Plate and Kit (Millipore Co.) and sequenced using the Perkin Elmer Big Dye® version 3 cycle sequencing kit. Sequencing reactions were purified using Sephadex® in MultiScreen™ Durapore PVDF plates (Millipore Co.). Purified sequencing reactions were analyzed on either an ABI 3100, or ABI 3730 automated sequencer. To insure the accuracy of sequences, negative controls were included, complementary strands were sequenced, and sequences were manually checked using the original chromatograph data in the program Sequencher® 4.0 (GeneCodes Co.).

*Alignment and tree reconstruction.*—Alignment was done using direct optimization (DO) in the program POY v.3.0 (Wheeler *et al.* 2003). Protein coding genes (C-mos and cyt *b*) were aligned, based on conservation of the amino acid reading frame using Sequencher 4.0 (GeneCodes Co.), and entered into POY as “prealigned data”. POY analyses were performed under the maximum likelihood criteri-

on with a 10 parameter model (s10). This model computes changes between each nucleotide and gaps as a separate parameter (for a total of 10), and is similar to a general time reversible model with gaps added. POY analysis was performed with all parameters estimated from the data, four gamma classes, 200 replicates, SPR and TBR branch swapping, tree drifting and fusing, and the parsimony ratchet. The implied alignment resulting from the optimal POY search was used for all further analyses.

The aligned data set was partitioned by gene region, and the hierarchical likelihood-ratio tests as implemented in Modeltest (Posada & Crandall 1998) were used to determine the appropriate model of sequence evolution for each gene region. Separate Bayesian analyses were performed for each gene region using the chosen models of evolution in MrBayes 3.0 (Huelsenbeck & Ronquist 2001). The mitochondrial and nuclear partitions as well as the combined dataset were analyzed using a partitioned Bayesian approach, with the appropriate models of evolution implemented for each gene, and all parameters allowed to vary between partitions. It is accepted that different genes evolve at different rates and under different constraints, and this is further shown by the divergence profiles of the genes used in this study. Partitioned Bayesian analysis was used in an attempt to model evolution within these data more accurately. All Bayesian analyses consisted of 2500 000 generations, four incrementally heated chains, and trees sampled every 1000 generations. Stationarity was determined as the point at which likelihood scores plateaued, and trees recorded prior to that point were discarded as the "burn in". Posterior probabilities (PP) were assessed as part of all Bayesian analyses, and nodes with probabilities from 0.90 - 1.0 were considered strongly supported (Wilcox *et al.* 2002).

For comparison, a maximum parsimony (MP) analysis was performed in PAUP\* (Swofford 2002) with gaps coded as missing data. A

heuristic search with 100 000 random additions was performed, and nodal support was estimated using a bootstrap analysis with 100 000 bootstrap replicates of two random additions each.

*Hypothesis testing.*—Specific hypotheses of relationships recovered in the combined analysis tree were tested using the Shimodaira Hasegawa test (SH test; Shimodaira & Hasegawa 1999) as implemented in PAUP\* (Swofford 2002). The anticonstrain command in PAUP\* was used to find the best tree not including the group of interest, and this tree was compared to the optimal tree under the GTR+I+G model (with all parameters estimated). The SH test was then performed using the Rell bootstrap with 10 000 replicates.

## RESULTS

*Molecular data.*—The molecular data used in this study include approximately 5600 bases across seven gene regions for 45 taxa. For all non-Madagascan lizards, sequences for 18S, 16S, 12S, C-mos, *cyt b*, and *Enol* are the same as those used in Whiting *et al.* (2003) and were taken from GenBank. GenBank accession numbers for the sequences newly generated for this paper are as follows: Gapdh: AY391229-391251, *Enol*: AY391212-391228, 18S: AY391195-391211 AY802765-6, C-mos: AY391178-391194 AY802767-8, 12S: AY391123-391141 AY802761-2, 16S: AY391142-391159 AY802763-4, and *cyt b*: AY391160-391177 AY802769-70. Uncorrected maximum pairwise sequence divergence across all taxa, within southern African + Malagasy "scincines", and within Malagasy "scincines" is shown for each gene in Table 1. These divergence profiles reflect the phylogenetic utility of individual markers at different taxonomic levels.

*Combined analyses.*—Modeltest analysis indicates that the appropriate models of nucleotide substitution are as follows: GTR+G+I for 12S,

Table 1: Uncorrected maximum pairwise sequence divergence based on POY implied alignment across all taxa, African and Malagasy “scincines” (clade D; Fig. 1), and Malagasy taxa, for each molecular marker used in this study.

Gene region	Sequence length (bp)	Parsimony informative sites	All taxa	African and Mal- agasy “scincines”	Malagasy “scincines”
Gapdh	400	144	35.6%	17.7%	15.1%
Enol	276	99	17.9%	13.1%	8.2%
18S	1803	49	1.5%	1.0%	0.11%
16S	659	224	15.9%	15.5%	13.7%
12S	1150	509	25.5%	24.4%	18.3%
Cyt <i>b</i>	732	344	26.8%	24.2%	23.7%
C-mos	594	126	10.8%	8.2%	4.9%

16S, and *cyt b*, TrN+I for 18S, HKY+G for *cmos* and *gapdh*, and K80+G for *Enol*. Stationarity was reached before 50 000 generations, and after discarding the first 50 trees (burn in), the 50% majority rule tree was obtained from the remaining 2450 data points (shown in Fig. 1). Malagasy “scincines” form a well supported monophyletic group with the genus *Amphiglossus* recovered in two distinct clades, while *Paracontias* is monophyletic. There is good support (PP = 0.88) for *Paracontias* + a clade of *Amphiglossus* consisting of *A. stumpffi*, *A. intermedius*, *A. igneocaudatus*, *A. mouroundavae*, and *A. melanopleura* (clade A). The remaining Malagasy taxa form a single clade with *Pygomeles* sister to a somewhat unresolved clade consisting of the remaining *Amphiglossus* species and *Voeltzkowia* (clade B). Within clade B, there are three well supported groups of *Amphiglossus* including *A. astrolabi* + *A. waterloti*, *A. melanurus* + *A. ornaticeps*, and *A. punctatus* + *A. sp.* + *A. macrocerus*. Relationships between these clades of *Amphiglossus*, as well as the placement of *A. mandokava*, *A. tsaratananensis*, and *Voeltzkowia* are unresolved or poorly supported.

The southern African genera *Sepsina*, *Scelotes* and *Proscelotes* are sister to Malagasy “scincines”, together forming clade C. Lygosomine species + *Scincus* and *Eumeces* form a single group (clade E) which is sister to a strongly supported southern African and Malagasy “scincine” clade (clade D). Posterior

probabilities are fairly high across the tree, except within clade B.

MP analysis was largely congruent with the Bayesian analysis with the exception of a few nodes within clade E (not shown). Therefore from this point on the combined analysis will refer to the partitioned Bayesian analysis. Bootstrap support from the MP analysis is shown in Fig. 1 for comparison with posterior probabilities.

*Gene trees and Hypothesis testing.*—We followed Wiens (1998) and analyzed gene regions individually to look for strongly supported conflict at nodes throughout the tree. Support for specific relationships found in individual gene trees, as well as mitochondrial and nuclear partitions, are summarised in Table 2. Results from individual gene trees showed very little conflict, but many relationships were unresolved or poorly supported. Enolase was the only gene showing strong conflict (PP = 0.90–1.0) at multiple nodes. The combination of all data resulted in an increase in posterior probabilities and emphasises the benefits of a total evidence approach (Kluge 1989; Eernisse & Kluge 1993; Kluge & Wolf 1993; Chippindale & Wiens 1994; Nixon & Carpenter 1996; Kluge 1998). In order to investigate the conflict of *Enol* further, it was removed and the remaining dataset was reanalysed. The topology resulting from the parsed analyses was identical to the total data tree, showing that the three conflicting nodes seen in the individual *Enol*

tree did not significantly influence the total analysis.

**DISCUSSION**

*Taxonomic implications.*—All Malagasy “scincines” sampled in this study form a strongly supported monophyletic group to the exclusion of all southern African taxa (SH test  $P = 0.0197$ ), confirming the removal of Malagasy species from *Scelotes*, and the hypotheses of Hewitt (1929) and deWitte and

Laurent (1943) of a Malagasy clade distinct from the African “scincines”. The placement of *Sepsina*, *Proscelotes* and *Scelotes* as sister group to the monophyletic Malagasy clade lends credence to statements by de Witte and Laurent (1943) and Greer (1970a) that *Proscelotes* and *Sepsina* are the closest African relatives to the Malagasy “scincines”.

The relationships within Malagasy “scincines” are much more complex than previously thought, with a paraphyletic “*Amphiglossus*” forming a minimum of two separate groups.

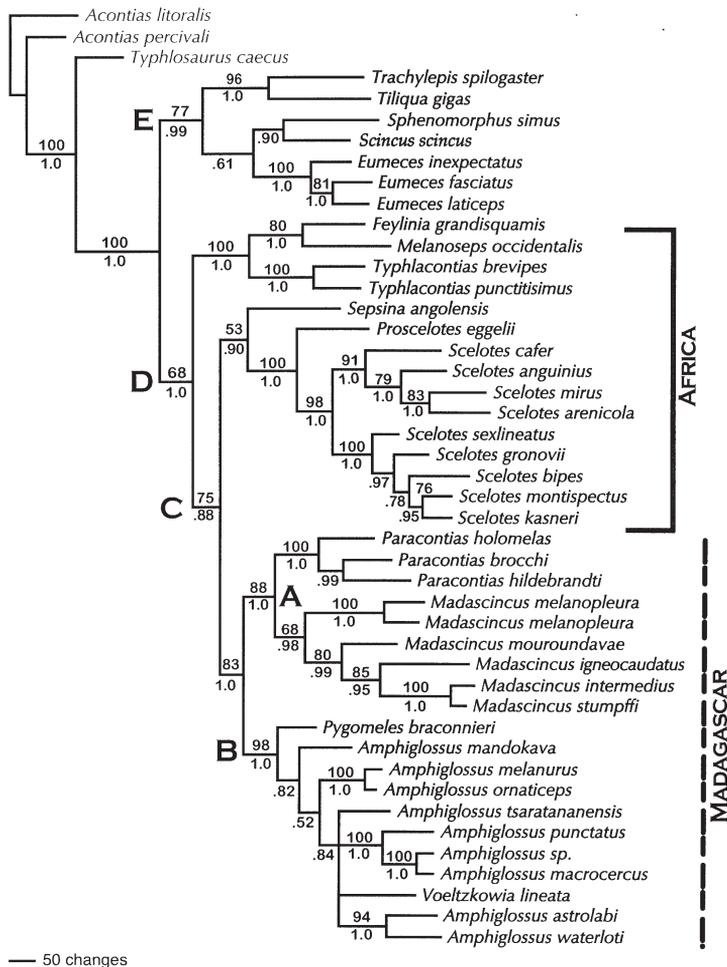


Figure 1: Bayesian analysis of the combined dataset. 50% majority rule of 2450 trees, with posterior probabilities listed below branches. Bootstrap support values from the MP analysis (> 50%) are shown above the branches. Capital letters denote major clades as discussed in the text.

Table 2: Specific relationships are listed in the leftmost column, along with support from the individual and combined data trees. Posterior probabilities (PP) from the combined Bayesian analysis are listed in the first column (converted to percentages). Results from individual gene tree are listed under the specific gene and denoted with the following symbols: + = the relationship is present with 0.90-1.00 posterior probability, - = the relationship is contradicted (0.90-1.00 posterior probability), U = the relationship is unresolved or poorly supported, and U+ = the relationship is present with 0.50-0.89 posterior probability.

Clade	PP	16S	12S	18S	Cyt <i>b</i>	C-mos	Gapdh	Enol	Mt DNA	Nuc DNA
<i>Madascincus</i> + <i>Paracontias</i> = Clade A	100	U	U+	U	-	+	+	U+	+	+
Clade B	100	+	+	U	+	+	+	+	+	+
Clade C	88	U+	U+	U	U	U	+	-	+	U
Southern African + Malagasy "scincines" = Clade D	100	U	+	U	U	+	NA	-	+	U+
Clade E	99	U	+	U	U	U	U+	-	+	U
Malagasy "scincines"	100	U	U+	U	U+	+	U+	U	+	U+
<i>Madascincus</i>	98	U+	+	U	U	+	U	U+	+	U

*Amphiglossus igneocaudatus*, *A. intermedius*, *A. mouroundavae*, *A. melanopleura* and *A. stumpffi* form the sister group to *Paracontias* (clade A, Fig. 1), and a clade sufficiently distinct to warrant generic status. When any member of this group is forced into the other clade of Malagasy species, the resulting tree is significantly less likely (SH test  $P = 0.0102$ ). This group includes representatives of the subgenus *Madascincus* Brygoo 1981d as well as members of the *igneocaudatus* group of *Amphiglossus* as defined by Brygoo (1984b). The former group (including *A. melanopleura* -type species, *A. mouroundavae* and *A. ankodabensis*) was diagnosed by Brygoo (1984b) as being pentadactyl, having the interparietal small or absent, a SVL of < 80 mm, and fewer than 35 presacral vertebrae. Two additional species, *A. punctatus* (recovered here in clade B, SH test  $P < 0.001$ ), and *A. minutus*, have subsequently been described and assigned to *Madascincus* (Raxworthy & Nussbaum 1993; Glaw & Vences 1994). The former, however, differs substantially from all other members of the group (Glaw & Vences 1994). Brygoo (1984d) described the *igneocaudatus* group of *Amphiglossus* (consisting of *A. igneocaudatus*, *A. intermedius*, *A. pollenii*, and *A. stumpffi*) based on the presence of a dark lateral band, 35-45 presacral vertebrae, and four well developed pentadactyl limbs. Aside from the ple-

siomorphic trait of unreduced digital complement, the two clusters share few obvious diagnostic features. Their grouping suggests that this lineage is morphologically diverse, with more robust-limbed, shorter-bodied basal members and more elongate, shorter-limbed derived members (the *igneocaudatus* group). With the inclusion of the *igneocaudatus* group, however, Brygoo's (1981d, 1984b) diagnosis of *Madascincus* requires revision. We here recognise *Madascincus* as a valid genus, which may be defined as those pentadactyl Malagasy skinks sharing a closer ancestry with *Paracontias*, than with other skinks.

All remaining sampled species of *Amphiglossus* are found within clade B (Fig. 1) along with *Pygomeles* and *Voeltzkowia*. Within this clade there are three well supported groups of *Amphiglossus* species, (*A. melanurus* + *A. ornaticeps*), ((*A. punctatus* + (*A. macrocercus* + *A. sp.*)), as well as (*A. astrolabi* + *A. waterloti*). The former two clades do not correspond to any previously hypothesised groups, and with the exception of *A. punctatus*, none of these species belong to either of Brygoo's designated subgenera. On the other hand, *A. astrolabi* and *A. waterloti*, which are recovered as well supported sister taxa in all analyses, correspond to Brygoo's subgenus *Amphiglossus*, defined by the presence of 37-38 presacral ver-

tebrae, 28-34 scale rows around midbody, and > 200 mm SVL (Brygoo 1981d). Both are found in aquatic or semiaquatic environments and have been observed foraging under water (Raxworthy & Nussbaum 1993). *Amphiglossus reticulatus* is only known from the type specimen, but appears to be closely allied with *A. waterloti*. The type was also collected in a swampy area (Brygoo 1980c) and is therefore most likely a member of this clade. One of the most distinctive synapomorphies of this group is the position of the nostril centrally above the first upper labial, which may be an adaptation to an aquatic lifestyle (Brygoo 1981d; Raxworthy & Nussbaum 1993). Given the weak support for the placement of both *Voeltzkowia*, *A. tsaratananensis* and *A. mandokava* within clade B we are unable to falsify the monophyly of clade B “*Amphiglossus*” and conservatively retain the existing generic allocations for all members of this group.

In this study *Voeltzkowia* is recovered as nested within *Amphiglossus* of clade B, and appears to be a distinct lineage (as shown by the long branch length in Fig. 1), but this relationship is weakly supported and the inclusion of additional species from the genus would be needed to test this hypothesis. The genus *Cryptoscincus* is known from only the two type specimens, and morphologically seems to be very closely related to *Voeltzkowia* (Brygoo 1981b; Glaw & Vences 1994) and would presumably group with that genus within clade B. *Androngo* was recently reduced to a single species (Andreone & Greer 2002), with affinities to *Pygomeles* or “*Amphiglossus*”. We cannot comment on the composition or placement of *Androngo* as none of the relevant species were included in this study.

*Paracontias* is recovered as a strongly supported clade, but the subgenera *Malacontias* (composed of *P. holomelas* and *P. hildebrandti*) and *Paracontias* (*P. brocchi*) are not supported as *P. brocchi* and *P. hildebrandti* are sister taxa relative to *P. holomelas*.

The primitive number of presacral vertebrae for Malagasy “scincines” is assumed to be 26 (Glaw & Vences 1994; Andreone & Greer 2002), with more derived species evolving greater numbers of vertebrae. When the number of presacral vertebrae for each species is considered in light of phylogeny, no clear pattern of vertebral increase emerges. Therefore, these data support the idea that a high number of presacral vertebrae have evolved multiple times and therefore this character should be used with caution for phylogenetic inference (Andreone & Greer 2002).

Outside of the Malagasy skinks, clade D and E are very similar to the results found in previous studies (Whiting *et al.* 2003). Clade E is not statistically supported (SH test  $P = 0.3517$ ) by these data, while the monophyly of an Afro-Malagasy “scincine” clade (Clade D - SH test  $P = 0.0223$ ) is strongly confirmed. Relationships of the Malagasy “scincines” to other “scincine” genera in the Seychelles (*Pamela-scincus*, *Janetaescincus*), Mauritius (*Gongylo-morphus*), India (*Barkudia*), and Sri Lanka (*Sepsophis*, *Nessia*, *Chalcidoseps*) remain unexamined and are a priority for future research.

*Biogeography*.—Our results suggest a mainland African origin for the Afro-Malagasy “scincine” clade as a whole, with subsequent derivation of the Malagasy clade. This is consistent with patterns derived from many vertebrate groups including hyperoliine frogs (Vences *et al.* 2003) and cordyliform lizards (Odierna *et al.* 2002; Lamb *et al.* 2003), but contrasts with that obtained in chameleons, in which a Madagascan origin, with subsequent multiple invasions of Africa have been proposed (Raxworthy *et al.* 2002). Although we have not applied a molecular clock in our analysis, even the most basal divergences within the Afro-Malagasy clade are not compatible with the presumed separation of Africa from Madagascar (plus the Seychelles and India), which has been dated at 165-121 million years before present (Rabinowitz *et al.* 1983).

Despite the apparent low vagility of these skinks, many of which are fossorial, it seems likely that the Malagasy clade originated by dispersal over water from Africa. Thus “scincine” skinks may be added to a growing list of Afro-Malagasy lineages, including mammals (Yoder *et al.* 1996; Jansa *et al.* 1999), reptiles (Caccone *et al.* 1999; Mausfeld *et al.* 2000; Raxworthy *et al.* 2002; Townsend & Larson 2002; Nagy *et al.* 2003), and frogs (Vences *et al.* 2003), that appear to have achieved their current distributions via transoceanic dispersal. We anticipate that biogeographic patterns within the Malagasy “scincine” clade will be more reflective of vicariance patterns, but such an analysis must await greater taxon sampling and a more comprehensive knowledge of distribution patterns within Madagascar.

### ACKNOWLEDGEMENTS

We thank Ronald Nussbaum, Greg Schneider, Robert C. Drewes, Jens Vindum, Franco Andreone, Angelo Lambiris, and Nate Kley for providing tissue samples. We also thank the following people for translation, input or suggestions in the writing of this paper: Katharina Dittmar de la Cruz, Keith Crandall, and Seth Bybee. This research was supported by a National Science Foundation graduate research fellowship, a BYU graduate fellowship, and a Society of Systematic Biologists award for graduate student research to ASW, by NSF grants DEB-97-07568 to AMB, DEB-01-32227 to JWS, Jr., and a NSF DDIG (DEB 02-00362) to JWS, Jr. and ASW.

### LITERATURE CITED

- ANDREONE, F. & A. E. GREER. 2002. Malagasy scincid lizards: descriptions of nine new species, with notes on the morphology, reproduction and taxonomy of some previously described species (Reptilia, Squamata: Scincidae). *J. Zool.*, London 258: 139-181.
- ANDREONE, F. & C. J. RAXWORTHY. 1998. The colubrid snake *Brygophis coulangesi* (Domergue 1988) rediscovered in northeastern Madagascar. *Trop. Zool.* 11: 249-257.
- ANDREONE, F., J. E. RANDRIANIRINA, P. D. JENKINS & G. APREA. 2000. Species diversity of Amphibia, Reptilia and Liotyphla (Mammalia) at Ambolokopatrika, a rainforest between the Anjanaharibe-Sud and Marojejy massifs NE Madagascar. *Biodiv. Conserv.* 9: 1587-1622.
- ANDREONE, F., M. VENCES & J. E. RANDRIANIRINA. 2001. Patterns of reptile diversity at Berara Forest (Sahamalaza Peninsula), NW Madagascar. *Ital. J. Zool.* 68: 235-241.
- ANGEL, F. 1942. Les Lézards de Madagascar. *Mém. l'Acad. Malgache* 36: 1-194. pls. 1-22.
- BOULENGER, G. A. 1887. Catalogue of the Lizards from the British Museum (Natural History), Vol. III. Taylor and Francis, London.
- BRYGOO, E. R. 1979. Systématique des Lézards Scincidés de la région malgache. I. *Scelotes trivittatus* (Boulenger, 1896) nov. comb. synonyme de *Scelotes trilineatus* (Angel, 1949). *Bull. Mus. natn. Hist. nat., Paris*, 4A 1: 1115-1120.
- BRYGOO, E. R. 1980a. Systématique des Lézards Scincidés de la région malgache. II. *Amphiglossus astrolabi* Duméril et Bibron, 18Boettger, 1882; et *Scelotes waterlotti* Angel, 1930. *Bull. Mus. natn. Hist. nat., Paris*, 4A 2: 525-539.
- BRYGOO, E. R. 1980b. Systématique des Lézards Scincidés de la région malgache. III. Les “*Acontias*” de Madagascar. *Bull. Mus. natn. Hist. nat., Paris*, 4A 2: 905-915.
- BRYGOO, E. R. 1980c. Systématique des Lézards Scincidés de la région malgache. IV. *Amphiglossus reticulatus* (Kaudern, 1922) nov. comb., troisième espèce du genre; ses rapports avec *Amphiglossus waterlotti* (Angel, 1920). *Bull. Mus. natn. Hist. nat., Paris*, 4A 2: 916-918.
- BRYGOO, E. R. 1980d. Systématique des Lézards Scincidés de la région malgache. V. *Scelotes praeornatus* Angel, 1938, synonyme de *Scelotes s.l. frontoparietalis* (Boulenger, 1889). *Bull. Mus. natn. Hist. nat., Paris*, 4A 2: 1155-1160.
- Brygoo, E. R. 1981a. Systématique des Lézards Scincidés de la région malgache. VI. Deux Scincidae nouveaux. *Bull. Mus. natn. Hist. nat., Paris*, 4A 3: 261-268.
- BRYGOO, E. R. 1981b. Systématique des Lézards Scincidés de la région malgache. VII. Révision des genres Voeltzkowia Boettger, 1893, Grandidierina Mocquard, 1894, et Cryptoscincus Mocquard, 1894. *Bull. Mus. natn. Hist. nat., Paris*, 4A 3: 675-688.
- BRYGOO, E. R. 1981c. Systématique des Lézards Scincidés de la région malgache. VIII. Les *Mabuya*

- des îles de l'océan Indien occidental: Comores, Europa, Séchelles. Bull. Mus. natn. Hist. nat., Paris, 4A 3: 911-930.
- BRYGOO, E. R. 1981d. Systématique des Lézards Scincidés de la région malgache. IX. Nouvelles unités taxonomiques pour les *Scelotes* s.l. Bull. Mus. natn. Hist. nat., Paris, 4A 3: 1193-1204.
- BRYGOO, E. R. 1983a. Systématique des Lézards Scincidés de la région malgache. X. Rapports de *Gongylus johannae* Günther, 1880, des Comores et de *Sepsina valhallae* Boulenger, 1909, des Glorieuses, avec les espèces malgaches. Bull. Mus. natn. Hist. nat., Paris, 4A 5: 651-660.
- BRYGOO, E. R. 1983b. Systématique des Lézards Scincidés de la région malgache. XI. Les *Mabuya* des Madagascar. Bull. Mus. natn. Hist. nat., Paris, 4A 5: 1079-1108.
- BRYGOO, E. R. 1984a. Systématique des Lézards Scincidés de la région malgache. XII. Le groupe d'espèces *Gongylus melanurus* Günther, 1877, *G. gastrostictus* O'Shaunessy, 1879, et *G. macrocercus* Günther, 1882. Bull. Mus. natn. Hist. nat., Paris, 4A 6: 131-148.
- BRYGOO, E. R. 1984b. Systématique des Lézards Scincidés de la région malgache. XIII. Les *Amphiglossus* du sous-genre *Madascincus*. Bull. Mus. natn. Hist. nat., Paris, 4A 6: 527-536.
- BRYGOO, E. R. 1984c. Systématique des Lézards Scincidés de la région malgache. XIV. Le genre *Pygomeles* A. Grandidier, 1867. Bull. Mus. natn. Hist. nat., Paris, 4A 6: 769-777.
- BRYGOO, E. R. 1984d. Systématique des Lézards Scincidés de la région malgache. XV. *Gongylus igneocaudatus* A. Grandidier, 1867, et *Scelotes intermedius* Boettger, 1913. Les *Amphiglossus* du groupe *igneocaudatus*. Bull. Mus. natn. Hist. nat., Paris, 4A 6: 779-789.
- BRYGOO, E. R. 1984e. Systématique des Lézards Scincidés de la région malgache. XVI. Les *Amphiglossus* du groupe *ornaticeps*. Bull. Mus. natn. Hist. nat., Paris, 4A 6: 1153-1160.
- BRYGOO, E. R. 1985. Systématique des Lézards Scincidés de la région malgache. XVII. *Gongylus splendidus* A. Grandidier, 1872, *Scelotes macrolepis* Boulenger, 1888, et *Scelotes decaryi* Angel, 1930. Bull. Mus. natn. Hist. nat., Paris, 4A 7: 235-247.
- BRYGOO, E. R. 1986. Systématique des Lézards Scincidés de la région malgache. XVIII. Les *Cryptoblepharus*. Bull. Mus. natn. Hist. nat., Paris, 4A 8: 643-690.
- BRYGOO, E. R. 1987. Systématique des Lézards Scincidés de la région malgache. XIX. Données nouvelles sur le genre *Androngo*. Bull. Mus. natn. Hist. nat., Paris, 4A 9: 255-263.
- CACCONE, A., G. AMATO, O. C. GRATRY, J. BEHLER & J. R. POWELL. 1999. A molecular phylogeny of four endangered Madagascar tortoises based on mtDNA sequences. Mol. Phylogenet. Evol. 12: 1-9.
- CHIPPINDALE, P. T. & J. J. WIENS. 1994. Weighting, partitioning and combining characters in phylogenetic analysis. Syst. Biol. 43: 278-287.
- EERNISSE, D. J. & A. G. KLUGE. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. Mol. Biol. Evol. 10: 1170-1195.
- FRIESEN, V. L., B. C. CONGDON, H. E. WALSH & T. P. BIRT. 1997. Intron variation in marbled murrelets detected using analyses of single-stranded conformational polymorphisms. Mol. Ecol. 6: 1047-1058.
- GLAW, F. & M. VENCES. 1994. A Fieldguide to the Amphibians and Reptiles of Madagascar. M. Vences & F. Glaw Verlags GbR, Köln, Germany.
- GLAW, F. & M. VENCES. 1996. Bemerkungen zur Fortpflanzung des Walkskins *Amphiglossus melanopleura* aus Madagaskar (Saria: Scincidae), mit einer übersicht über die Fortpflanzungsperioden madagassischer Reptilien. Salamandra 32: 211-216.
- GREER, A. E. 1970a. A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. 139: 151-183.
- GREER, A. E. 1970b. The systematics and evolution of the subsaharan Africa, Seychelles, and Mauritius scincine scincid lizards. Bull. Mus. Comp. Zool. 140: 1-23.
- GREER, A. E., C. ARNOLD & E. N. ARNOLD. 2000. The systematic significance of the number of presacral vertebrae in the scincid lizard genus *Mabuya*. Amphib.-Reptil. 21: 121-126.
- HEWITT, J. 1929. On some Scincidae from South Africa, Madagascar and Ceylon. Ann. Trans. Mus. 13: 1-8.
- HUELSENBECK, J. P. & F. R. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754-755.
- JANSA, S. A., S. M. GOODMAN & P. K. TUCKER. 1999. Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyinae): a test of the single-origin hypothesis. Cladistics 15: 253-270.
- KLUGE, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38: 7-25.
- KLUGE, A. G. 1998. Total evidence or taxonomic congruence: cladistics or consensus classification. Cladistics 14: 151-158.
- KLUGE, A. G. & A. J. WOLF. 1993. Cladistics: what's in a word. Cladistics 9: 183-199.
- KRÜGER, J. 1999. Neue Erkenntnisse zur Faunistik einiger Reptilien Madagaskars. Salamandra 35: 65-76.

- LAMB, T., A. M. MEEKER, A. M. BAUER & W. R. BRANCH. 2003. On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA sequence analysis of the African Gerrhosauridae. *Biol. J. Linn. Soc.* 78: 253-261.
- LEVINTON, A. E., R. H. GIBBS, E. HEAL & C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985: 802-832.
- MAUSFELD, P., M. VENCES, A. SCHMITZ & M. VEITH. 2000. First data on the molecular phylogeography of scincid lizards of the genus *Mabuya*. *Mol. Phylogenet. Evol.* 17: 11-14.
- NAGY, Z. T., U. JOGER, M. WINK, F. GLAW & M. VENCES. 2003. Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. *Proc. R. Soc. Lond. B* 270: 2613-2621.
- NIXON, K. C. & J. M. CARPENTER. 1996. On simultaneous analysis. *Cladistics* 12: 221-241.
- NUSSBAUM, R. A. & C. J. RAXWORTHY. 1995. Review of the Scincine genus *Pseudoacontias* Barboza du Bocage (Reptilia: Squamata: Scincidae) of Madagascar. *Herpetologica* 51: 91-99.
- ODIERNA, G., A. CANAPA, F. ANDREONE, G. APREA, M. BARUCCA, T. CAPRIGLIONE & E. OLMO. 2002. A phylogenetic analysis of Cordyliformes (Reptilia: Squamata): comparison of molecular and karyological data. *Mol. Phylogenet. Evol.* 23: 37-42.
- POSADA, D. & K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.
- RABINOWITZ, P. D., M. F. COFFIN & D. FALVEY. 1983. The separation of Madagascar and Africa. *Science* 220: 67-69.
- RASELIMANANA, A. T. & D. RAKOTOMALALA. 2003. Scincidae, Skink. Pp. 986-993. *In* Goodman, S. M. & J. P. Benstead (Eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, USA.
- RAXWORTHY, C. J. & R. A. NUSSBAUM. 1993. Four new species of *Amphiglossus* from Madagascar (Squamata: Scincidae). *Herpetologica* 49: 326-341.
- RAXWORTHY, C. J. & R. A. NUSSBAUM. 1994. A rainforest survey of Amphibians, reptiles and small Mammals at Montagne D'Ambre Madagascar. *Biol. Conserv.* 69: 65-73.
- RAXWORTHY, C. J., M. R. J. FORSTNER & R. A. NUSSBAUM. 2002. Chameleon radiation by oceanic dispersal. *Nature* 415: 784-787.
- SAKATA, S. & T. HIKIDA. 2003a. A new fossorial scincine lizard of the genus *Pseudoacontias* (Reptilia: Squamata: Scincidae) from Nosy Be, Madagascar. *Amphib. Reptil.* 24: 57-64.
- SAKATA, S. & T. HIKIDA. 2003b. A fossorial lizard with forelimbs only: description of a new genus and species of Malagasy skink (Reptilia: Squamata: Scincidae). *Curr. Herpetol.* 22: 9-15.
- SHIMODAIRA, H. & M. HASEGAWA. 1999. Multiple comparison of log-likelihoods with applications to phylogenetic inference. *Mol. Biol. Evol.* 16: 1114-1116.
- SWOFFORD, D. L. 2002. PAUP\* Phylogenetic analysis using parsimony (\*and other methods), 4.0. Sinauer Associates, Sunderland, MA.
- TOWNSEND, T. & A. LARSON. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). *Mol. Phylogenet. Evol.* 23: 22-36.
- VENCES, M., J. KOSUCH, F. GLAW, W. BÖHME & M. VEITH. 2003. Molecular phylogeny of hyperoliid treefrogs: biogeographic origin of Malagasy and Seychellean taxa and re-analysis of familial paraphyly. *J. Zool. Syst. Evol. Research* 41: 205-215.
- WHEELER, W. C., D. S. GLADSTEIN & J. DE LAET. 2003. POY: Phylogeny reconstruction via direct optimization of DNA and other data, 3.0.11. American Museum of Natural History, New York, NY.
- WHITING, A. S., A. M. BAUER & J. W. SITES JR. 2003. Phylogenetic relationships and limb loss in southern African scincine lizards (Squamata: Scincidae). *Mol. Phylogenet. Evol.* 29: 582-598.
- WIENS, J. J. 1998. Combining data sets with different phylogenetic histories. *Syst. Biol.* 47: 568-581.
- WILCOX, T. P., D. J. ZWICKL, T. A. HEATH & D. M. HILLIS. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Mol. Phylogenet. Evol.* 25: 361-371.
- WITTE, DE G. F. & R. LAURENT. 1943. Contribution à la systématique des formes dégradées de la famille des Scincidae apparentées au genre *Scelotes* Fitzinger. *Mém. Mus. Roy. Hist. Nat. Belg* 26: 1-44.
- YODER, A. D., M. CARTMILL, M. RUVOLO, K. SMITH & R. VILGALYS. 1996. Ancient single origin for Malagasy primates. *Proc. Natl. Acad. Sci. USA* 93: 5122-5126.

Received: 22 June 2004;

Final acceptance: 8 November 2004.

## APPENDIX

List of all specimen identification numbers and localities. Museum abbreviations follow (Levinton *et al.* 1985) with the following exceptions: AJL-FN = Angelo J. Lambiris field number, AMB = Aaron M. Bauer field number (specimens to be deposited in AMS), FA = Franco Andreone field number, NJK = Nathan J. Kley field number, No Voucher = no voucher specimen taken, (the lizard was identified, nondestructively sampled and released), RAN = Ronald Nussbaum field number (specimens to be deposited in UMMZ). Mad = Madagascar; SA = South Africa; TZ = Tanzania; Nam = Namibia

Species	Specimen ID #	Locality
<i>Acontias litoralis</i>	CAS 206800	SA: N Cape Province; vic..McDougall Bay water tank
<i>Acontias percivali</i>	YPM 12687	Unknown
<i>Amphiglossus astrolabi</i>	UMMZ 208804	Mad: Antsiranana; Antalaha, 2 km E. of Antanandavehely
<i>Amphiglossus igneocaudatus</i>	UMMZ 217449	Mad: Antananarivo; Antsirabe, Ibity
<i>Amphiglossus intermedius</i>	RAN 42624	Mad: Antsiranana; Antalaha, Ankavanana river
<i>Amphiglossus macrocerus</i>	UMMZ 208645	Mad: Fianarantsoa; Ivohibe, Andringitra, Iatara river
<i>Amphiglossus mandokava</i>	UMMZ 208654	Mad: Antsiranana; Sambava, Marojejy Reserve, Manantenina river
<i>Amphiglossus melanurus</i>	UMMZ 208708	Mad: Fianarantsoa; Ivohibe, Andringitra, Iatara river
<i>Amphiglossus melanopleura</i>	FA 1863	Mad:Manarikoba-Antsahamanara
<i>Amphiglossus melanopleura</i>	FA 1859	Mad: Andasin'I Governera
<i>Amphiglossus mouroundavae</i>	UMMZ 208738	Mad: Antsiranana; Sambava, Marojejy Reserve, Manantenina river
<i>Amphiglossus ornaticeps</i>	UMMZ 208743	Mad: Antsiranana; Sambava, Marojejy Reserve, Manantenina river
<i>Amphiglossus punctatus</i>	UMMZ 208787	Mad: Fianarantsoa; Ivohibe, Andringitra, Sahavatoy river
<i>Amphiglossus</i> sp.	UMMZ 208848	Mad: Fianarantsoa; Ivohibe, Andringitra, Kimora river
<i>Amphiglossus stumppfi</i>	UMMZ 208797	Mad: Antsiranana; Nosy Be, Lokobe Reserve, Ampasindava
<i>Amphiglossus tsaratananensis</i>	UMMZ 208798	Mad: Mahajanga; Bealanana, Tsaratanana, Matsabory
<i>Amphiglossus waterloti</i>	UMMZ 201597	Mad: Antsiranana; Ambanja, Manongarivo Reserve, Ambalafary
<i>Eumeces laticeps</i>	BYU 47336	Florida; Duval Co., Little Talbot Island
<i>Eumeces inexpectatus</i>	BYU 46699	Florida; Duval Co., Little Talbot Island
<i>Eumeces fasciatus</i>	BYU 46698	Florida; Holmes Co., Ponce de Leon Springs
<i>Feylinia grandisquamis</i>	NJK 0069	Unknown
<i>Melanoseps occidentalis</i>	CAS 207873	Equatorial Guinea: Bioko Id.; coast road ca. 5 km S. of Luba.
<i>Paracontias brocchi</i>	UMMZ 209153	Mad: Antsiranana; Montagne D'ambre, Antomboka river
<i>Paracontias hildebrandti</i>	UMMZ 209166	Mad: Antsiranana, Montagne D'ambre, Antomboka river
<i>Paracontias holomelas</i>	UMMZ 201644	Mad: Antsiranana; Sambava, Marojejy Reserve, Manantenina river
<i>Proscelotes eggeli</i>	CAS 168959	TZ: Tanga; Lushoto Dist.; W Usambara Mts., Mazumbai Forest
<i>Pygomeles braconnierei</i>	UMMZ 197125	Mad: Toliara; Amboasary, Beraketa
<i>Scelotes anguineus</i>	AJL-FN 452	SA: E Cape Prov.; Port Elizabeth
<i>Scelotes arenicola</i>	CAS 209635	SA: KZN Prov.; Kosi Bay Nature Reserve, NW corner of L. Nhlangwe
<i>Scelotes bipes</i>	CAS 224005	SA: W Cape Prov.; ~4.6 km N of Grootbaai, Bloubergstrand on Melkbos rd
<i>Scelotes caffer</i>	CAS 206859	SA: N Cape Prov.; Brandberg, Farms Kourootje and Kap Vley, De Beers
<i>Scelotes gronovii</i>	CAS 206990	SA: W Cape Prov.; 18.5 km N of jct rd R365 on R27 towards Lambertsbaai
<i>Scelotes kasneri</i>	CAS 206991	SA: W Cape Prov.; 18.5 km N of jct rd R365 on R27 towards Lambertsbaai
<i>Scelotes mirus</i>	No Voucher	Swaziland: Malolotja Reserve.
<i>Scelotes sexlineatus</i>	CAS206819	SA: N Cape Prov.; McDougall Bay.
<i>Scelotes montispectus</i>	CAS223934	SA: W Cape Prov.; ~4.6 km N Grootbaai, Bloubergstrand on Melkbos rd.
<i>Scincus scincus</i>	YPM 12686	Unknown
<i>Sepsina angolensis</i>	SMW 6694	Namibia: Kunene Reg.; Kamanjab District
<i>Sphenomorphus simus</i>	BYU 47016	Papua New Guinea: Gulf Prov.; Ivimka Research St., Lakekamu Basin
<i>Tiliqua gigas</i>	BYU 46821	Papua New Guinea: Gulf Province; Kakoro Village, Lakekamu Basin
<i>Trachylepis spilogaster</i>	CAS 206938	Nam: Karibib Dist.; Usakos-Hentiesbaai rd., 10 km E. of Spitzkopf turnoff
<i>Typhlacontias brevipes</i>	CAS 206947	Nam: Walvis Bay Dist.; S. bank of Kuiseb rv. Near Rooibank rd
<i>Typhlacontias punctatissimus</i>	CAS 223980	Nam: Kunene Reg; ~1.1 km N of Munutum rv, E bound Skeleton Coast P
<i>Typhlosaurus caecus</i>	AMB 6817	SA: N Cape Prov.; 9.9 Km S. of Lambertsbaai.
<i>Voeltzkowia lineata</i>	RAN 34923	Mad: Toliara; Betsioky