

Cryptic speciation in the New Caledonian lizard genus *Nannoscincus* (Reptilia: Scincidae) including the description of a new species and recognition of *Nannoscincus fuscus* Günther

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ABSTRACT

The relationships of species within *Nannoscincus*, a genus of diminutive fossorial skinks from New Caledonia in the southwest Pacific, are presented based on genetic information derived from the mitochondrial ND2 gene. The genetic study strongly supports the monophyly of the genus. It also supports the monophyly of a group of three taxa (*N. gracilis*, *N. sleveni* and *N. garrulus*) previously identified as the ‘*gracilis* group’, thus supporting earlier inferences of relationships between these taxa based on morphological characters. However, the taxonomy of the species included in the ‘*gracilis* group’ is confounded by the unexpected high level of genetic differentiation between regionally discrete populations of *N. gracilis*, and by a complete lack of differentiation between regionally parapatric but morphologically distinguishable *N. gracilis* and *N. sleveni*. There was minimal support from the genetic study for monophyly of the ‘*mariei* group’ as defined by morphological criteria in earlier studies, despite all included taxa possessing an impressive and unique suite of morphological apomorphies. Recognition of individual taxa within the ‘*mariei* group’, all previously identified on morphological criteria, was strongly supported by the genetic data which also identified two previously unrecognized lineages. One of these was formerly included under *N. mariei*, and is here considered conspecific with *N. fuscus* Günther, previously regarded as a synonym of *Anotis mariei* Bavay. The

other lineage is from the Massif de Koniambo in the north-west region ultramafic ranges and represents a morphologically cryptic taxon similar to *N. hanchisteus*. The extent of genetic sub-structuring in *N. gracilis*, and to a more limited extent within *N. mariei* and *N. fuscus*, is indicative of a pattern of historically long-standing regional fragmentation of forests across the Grande Terre, which is also reflected in a number of other moisture-dependent New Caledonian skink species.

RÉSUMÉ

Spéciation cryptique dans le genre de lézard néo-calédonien *Nannoscincus* (Reptile: Scincidae) incluant la description d'une nouvelle espèce et la réinstallation de *Nannoscincus fuscus* Günther.

Nous présentons ici les relations intra-génériques des espèces du genre *Nannoscincus*, un genre comprenant de petits scinques fousseurs de Nouvelle-Calédonie (Pacifique sud-ouest), à partir des informations génétiques dérivées du gène mitochondrial ND2. L'analyse génétique supporte fortement la monophylie du genre et pour un groupe de trois taxons (*N. gracilis*, *N. sleveni* et *N. garrulus*), elle confirme les liens de parenté entre espèces établis auparavant à partir de caractères morphologiques et défini comme le 'groupe *gracilis*'. Cependant, la taxonomie des espèces incluses dans le 'groupe *gracilis*' est obscurcie par un niveau élevé de différenciation génétique, insoupçonné au préalable, entre les populations de *N. gracilis* localisées régionalement et chez *N. gracilis* et *N. sleveni*, par une absence totale de différenciation génétique entre populations parapatriques à l'échelle d'une région mais pourtant distinctes par leur morphologie. L'analyse génétique ne supporte que faiblement la monophylie du 'groupe *mariei*' tel qu'il a été défini par les critères morphologiques dans les études précédentes, malgré le fait que tous les taxons qu'il comprend possèdent une série impressionnante et unique d'apomorphies morphologiques. La distinction de taxons individuels au sein du 'groupe *mariei*', tous identifiés auparavant sur des bases morphologiques, est fortement soutenue par les données génétiques, mais ces dernières permettent en plus d'identifier deux lignées non reconnues auparavant. L'un d'elles, qui était autrefois confondue dans l'espèce *N. mariei*, est ici considérée comme conspécifique de *N. fuscus* Günther, un binôme autrefois considéré comme synonyme de *Anotis mariei* Bavay. L'autre lignée provient du Massif de Koniambo dans les massifs ultramafiques du region north-ouest et représente un taxon morphologique cryptique similaire à *N. hanchisteus*. La sous-structuration génétique encore active chez *N. gracilis*, et de façon plus limitée chez *N. mariei* et *N. fuscus*, est révélatrice d'un patron historique ancien de fragmentation forestière régionale de la Grande Terre, également reflété par le nombre d'espèces de scinques de Nouvelle-Calédonie tributaires de zones humides.

INTRODUCTION

Studies over the past 30 years have identified the existence of an exceptionally rich and highly diverse scincid lizard fauna in New Caledonia, one typified by regional and localised endemism at a level not indicated by earlier studies. The patterns of broad and finer-scale endemism revealed in the phylogenetic studies indicate a complex evolutionary history for the scincid lizard fauna, one which reflects the historical complexity of the island's environment, and provides a window into the likely processes that shaped the present day biota.

Recent investigations have also identified the ultramafic ranges in the far south and western Grande Terre as discrete biogeographic regions for skinks, with extensive and often highly localized endemism. These ultramafic substrates (peridotites and serpentines) now occur on the island as an extensive relatively unbroken block in the south, a series of ranges on the central-east coast, and an extensive chain of often isolated massifs along the central-west and north-west coast. Otherwise, the topography of Grande Terre is dominated by a chain of high mountains that runs along its entire length, with many massifs above 1,000 m in elevation and five summits that exceed 1,500 m. and in the far south by a mid elevation plateau around 250 with emergent ranges to 600 m.

Humid forests were considered to have once covered much of the island (Jaffré *et al.* 1998). However, its present distribution is characteristically fragmented to varying degrees. Over much of the central-east and north-east regions of the island areas of forest on metamorphic surfaces occur as a mosaic of small and large patches, while forests on ultramafic surfaces of the central-west and northwest regions are present as small isolated patches mostly near the summits of ultramafic massifs. On the extensive southern ultramafic surfaces forest is also highly fragmented and mostly often present as isolated patches of varying size. Some forest fragmentation, such as the high-elevation forests on the

ultramafic massifs, may be largely attributed to contraction during past regimes of climatic aridity, and as such are relictual. The impact of anthropogenic alteration of the landscape dating back nearly 3500 years has also resulted in extensive modification and loss of forest (Jaffré *et al.* 1998), particularly at mid to low elevation, making it difficult to assess the degree of historical connectivity of forest blocks prior to arrival of humans. Recent research has identified particularly high levels of microendemism among the endemic forest-dependant New Caledonian lizards (Bauer *et al.* 2000; Bauer & Sadlier 2000; Sadlier & Bauer 1999, 2000; Sadlier *et al.* 2002, 2004, 2006, 2009), among which have been several species of diminutive skinks in the genus *Nannoscincus* with distributions that identify them as regional or narrow-range endemics (see Sadlier *et al.* 2002, 2004, 2006).

The genus *Nannoscincus* is a radiation of skinks endemic to the region. Species in the genus are typically small, ranging from ~34 mm maximum snout to vent length for the smallest species (*N. manautei*) to 52.5 mm for the largest species (*N. garrulus*). All have elongate bodies, small limbs, and show some degree of loss of phalanges on the digits of the manus. They are fossorial in habit, generally being found beneath logs and rocks or in leaf litter piles. They are highly prone to desiccation and as such are usually found in moist environments. Most species have been recorded only from humid forest habitats, although *Nannoscincus hanchisteus* is known only from the seasonally dry sclerophyll (closed) forest of the northwest coast and in the far south of the Grande Terre, and *N. mariei* has also been recorded from canopied maquis on a broken lateritic.

With eleven described species *Nannoscincus* is one of the largest genera of New Caledonian skinks. Previous attempts to interpret relationships between the species of *Nannoscincus* were limited to an analysis of morphological characters at a time when the genus comprised only five species (Sadlier 1990). That study identified two monophyletic groups of species, one comprising *Nannoscincus sleveni* and *N. gracilis* (the ‘*gracilis* group’) and the other comprising *N. mariei*, *N. greeri* and *N. rankini* (the ‘*mariei* group’). Since then, four new species diagnosable as members of the ‘*mariei* group’ (*N. humectus*, *N. hanchisteus*, *N. exos* and *N. manautei*) and one (*N. garrulus*) as a member of the ‘*gracilis* group’ have been described (Sadlier *et al.* 2002, 2004, 2006). Here, we present a molecular phylogeny for all known taxa based on the mitochondrial NADH dehydrogenase 2 (ND2), recognize a cryptic species from the synonymy of *N. mariei*, and describe a new species endemic to the Massif de Koniombo in northern Grande Terre.

MATERIAL AND METHODS

SYSTEMATICS

Acronyms. AMS - Australian Museum, Sydney; BMNH - British Museum-Natural History; CAS - California Academy of Sciences; and MNHN - Muséum national d’Histoire naturelle, Paris.

Measurements. Body measurements follow Sadlier *et al.* (2002) for the new species described and are compared to data for other species of *Nannoscincus* as given in Sadlier *et al.* (2002, 2004), and are expressed as percentages of snout to vent length (SVL) in the taxon account.

Scalation. Head scalation follows Sadlier *et al.* (2002) and Sadlier (2010), and scalation of the body and limbs Sadlier *et al.* (2002).

Osteology. Phalangeal formula for the manus and pes and the number of presacral and postsacral vertebrae were determined from radiographs prepared using a Eresco AS2 X-ray machine at exposures of 30 sec at 30 kV.

GENETIC STUDIES

We obtained sequence data from a 514 bp fragment of the mitochondrial NADH dehydrogenase 2 (ND2) gene for all described species of *Nannoscincus*. Species assignable to the ‘*gracilis* group’ were represented by 20 specimens from 10 locations for *N. gracilis*, 4 specimens from 2 locations for *N. sleveni* and 2 specimens from the type locality for *N. garrulus*. Species assignable to the ‘*mariei* group’ were represented by 18 specimens from 6 locations for *N. mariei* *sensu lato*, 1 specimen of *N. rankini* from the type locality, 2 specimens of *N. greeri* from a single location, 1 specimen of *N. humectus* from the type locality, 2 specimens of *N. hanchisteus* from the type locality, 1 specimen of *N. exos* from 1

location, 2 specimens of *N. manauitei* from the type locality and 2 indeterminate samples from the Massif de Koniambo (Appendix 1). Outgroups were selected on the basis of a broader phylogenetic analysis of New Caledonian skinks by Smith *et al.* (2007) and sequences for these were obtained from GenBank (Appendix 1).

Total Genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). The target gene was amplified using a double-stranded Polymerase Chain Reaction (PCR). Included in the reaction were 2.5 µl genomic DNA, 2.5 µl light strand primer MET F6 L4437 5'-AAGCTTTCGGGCCCATACC-3' (Macey *et al.* 1997), 2.5 µl heavy strand primer TRP R3 H5540 5'-TTTAGGGCTTTGAAGGC-3' (Macey *et al.* 1997), 2.5 µl dinucleotide pairs, 2.5 µl 5x buffer, MgCl 10x buffer, 0.18 µl Taq polymerase, and 9.82 µl H₂O. All reactions were executed on an Eppendorf Mastercycler gradient thermocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 sec, annealing at 50-54°C for 35 sec, followed by a cycle extension at 72°C for 35 sec, for 31 cycles. PCR products were visualized on 1.5% agarose gel electrophoresis.

PCR products were purified using AMPure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) to remove any impurities in the PCR products. Purified PCR products were then sequenced using DYEnamic™ ET Dye Terminator kit (GE Healthcare, Piscataway, NJ, USA). Products were purified using a Cleanseq magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA). Purified sequence reactions were analyzed using an ABI 3730XL automated sequencer. Sequences were analyzed from both the 3' and the 5' ends independently. Both the contiguous and the complimentary strands were uploaded and edited in Genious™ version 5.4 (Drummond *et al.* 2011), ambiguous bases were corrected. After editing the sequences they were initially aligned by eye. MacClade v4.08 (Maddison & Maddison 2005) was used to check for premature stop codons and to ensure that the alignment was in the correct amino acid reading frame.

PHYLOGENETIC ANALYSES

Character state polarities for features of scalation and osteology follow Sadlier (2010).

For our phylogenetic analyses we applied a pluralistic approach using both model-based (Maximum Likelihood — ML and Bayesian Inference — BI) and character-based methods (Maximum Parsimony — MP). Maximum Parsimony was implemented in PAUP™ v4.0 (Swofford 2002). The heuristic search algorithm was used with a starting tree obtained by stepwise addition. One thousand random addition replicates were carried out with a TBR branch swapping algorithm. Branch lengths of zero were collapsed to yield polytomies and gaps were treated as missing data. Bootstrap support values (Felsenstein 1985) for nodes in MP trees were calculated using 1000 pseudo-replicates each including 50 random addition-sequence replicates.

The Akaike Information Criterion (AIC) as implemented in ModelTest v3.7 (Posada & Crandall 1998) was used to calculate the best-fit model of evolution for both ML and BI. For both model-based approaches we partitioned our data set by codon position. The General Time Reversal (GTR) plus (I) for proportional sites plus (Γ) for gamma distribution among site variation was applied for all codon positions.

ML analysis was performed using RAxML HPC v7.2.3 (Stamatakis *et al.* 2008). The analysis was performed using the above model of evolution. Gaps were treated as missing data and for clade confidence we applied 1000 bootstrap pseudoreplicates via the rapid hill-climbing algorithm (Stamatakis *et al.* 2008).

The BI analysis was carried out in MrBayes v3.1 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) using default priors. The GTR+I+Γ model was applied to each codon position. Two simultaneous parallel runs were performed with 4 chains per run, 3 hot and 1 cold following default settings. The analysis was run for 10,000,000 generations and sampled every 1000 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after 10,000,000 generations if the average standard deviation split frequency was below 0.01. The program, Are We There Yet? (AWTY) (Nylander *et al.* 2008) was used to plot the log likelihood scores against the number of generations to assess convergence and to determine the appropriate burnin. A consensus tree from the two runs was built using TreeAnnotator v1.6.1 (Drummond & Rambaut 2006). Nodes that had posterior probabilities above 0.95 were considered significantly supported.

In this study we employ a lineage-based species concept (Mayden 1997; De Queiroz 1998) taking a pluralistic approach to the evidence used to infer species boundaries. A variety of operational criteria for diagnosing species boundaries have been proposed (Sites and Marshall 2003, 2004). Although numerous studies have found congruence between character- and mtDNA tree-based approaches to this issue, significant discordance can occur (Wiens & Penkrot 2002). In some cases haplotype differentiation may evolve more rapidly than diagnostic morphological characters. In other instances, however, mitochondrial genes may fail to reveal species boundaries that are well-supported by both morphology and nuclear data (e.g., Bollmer *et al.* 2006; Ennen *et al.* 2010) due to phenomena such as incomplete lineage sorting or introgressive hybridization. We accept evidence from either of the types of data (morphology and mitochondrial DNA) we collected as evidence of lineage independence. Our hypotheses about species limits are testable with additional data (e.g., nuclear DNA) and will be the subject of future contributions to the systematics of the genus *Nannoscincus*.

RESULTS

The genetic analysis (Figure 1) strongly supports monophyly of the 11 taxa currently assigned to *Nannoscincus* as an endemic New Caledonian lineage, as suggested by previous morphological studies (Sadlier *et al.* 2006; Sadlier 2010) and genetic studies (Smith *et al.* 2007). Within *Nannoscincus* there was little resolution of basal relationships other than for an expanded ‘*gracilis* group’ (*N. gracilis* + *N. sleveni* + *N. garrulus* – 1.0/95/97 support), and monophyly of the taxa assigned to the expanded ‘*mariei* group’ (*N. mariei*, *N. greeri*, *N. rankini*, *N. humectus*, *N. hanchisteus*, *N. exos*, *N. manautei*, *N. fuscus* and *N. n. sp.*) received only a low level of support (0.59/10/-). The morphological data continues to support a monophyletic ‘*gracilis* group’ and an expanded monophyletic ‘*mariei* group’.

The low level of support for a monophyletic ‘*mariei* group’ is problematic given the close relationship between species in the group as defined by a convincing suite of derived character states that includes: loss of an anterior loreal, a reduction in the number of lower labial scales, and loss of the left oviduct (Sadlier 1990; Sadlier *et al.*, 2002). The genetic analyses identified all recognized (described) species within the ‘*mariei* group’ as highly differentiated units (Table 1), giving a high level of congruence between the terminal taxa identified by the genetic data and the species recognized in earlier morphological studies (Sadlier 1986, 1990; Sadlier *et al.* 2002, 2004) under a biological species concept where levels of

TABLE 1

Genetic distance (uncorrected p-distances) between species of *Nannoscincus*, between populations assigned to *N. fuscus*, and between morphologically-defined species within the *N. 'gracilis* group’ and populations currently assigned to *N. gracilis* on morphological criteria.

	<i>fuscus</i>	<i>greeri</i>	<i>manautae</i>	<i>humectus</i>	<i>hanchisteus</i>	<i>rankini</i>	<i>koniambo</i>	<i>mariei</i>	<i>garrulus</i>	<i>gracilis</i>	<i>exos</i>	<i>sleveni</i>
<i>N. fuscus</i>	-											
<i>N. greeri</i>	12.7-15.3%	-										
<i>N. manautei</i>	13.1-14.5%	12.5-12.9%	-									
<i>N. humectus</i>	12.7-14.7%	11.8%	12.8%	-								
<i>N. hanchisteus</i>	10.6-13.5%	11.0-11.4%	11.4-11.8%	8.9-9.3%	-							
<i>N. rankini</i>	10.8-13.0%	10.3-10.4%	11.8%	11.0%	10.8-10.9%	-						
<i>N. koniambo</i> n.sp.	12.3-15.8%	10.5-11.8%	12.8-14.4%	11.1-13.6%	11.7-12.8%	11.1-12.0%	-					
<i>N. mariei</i>	10.0-14.0%	12.1-14.3%	12.8-13.8%	12.2-14.3%	11.3-12.7%	10.3-11.5%	12.6-15.5%	-				
<i>N. garrulus</i>	12.3-13.8%	13.0-13.6%	14.7%	14.2%	11.2-11.4%	13.4%	13.4-15.7%	12.6-15.5%	-			
<i>N. gracilis</i>	9.4-16.1%	8.6-16.7%	13.8-17.5%	13.6-18.0%	11.4-14.7%	13.0-16.3%	11.6-16.1%	9.4-15.0%	4.8-10.5%	-		
<i>N. exos</i>	11.2-13.5%	10.6-11.0%	12.6%	12.2%	11.6-11.7%	12.0%	10.5-11.5%	11.6-13.2%	15.7%	11.3-15.1%	-	
<i>N. sleveni</i>	9.0-15.2%	10.8-15.7%	14.9-16.4%	15.6-16.3%	11.4-13.6%	14.3-15.1%	11.0-15.4%	9.4-14.2%	9.7-10.1%	0.7-11.2%	11.3-15.3%	-

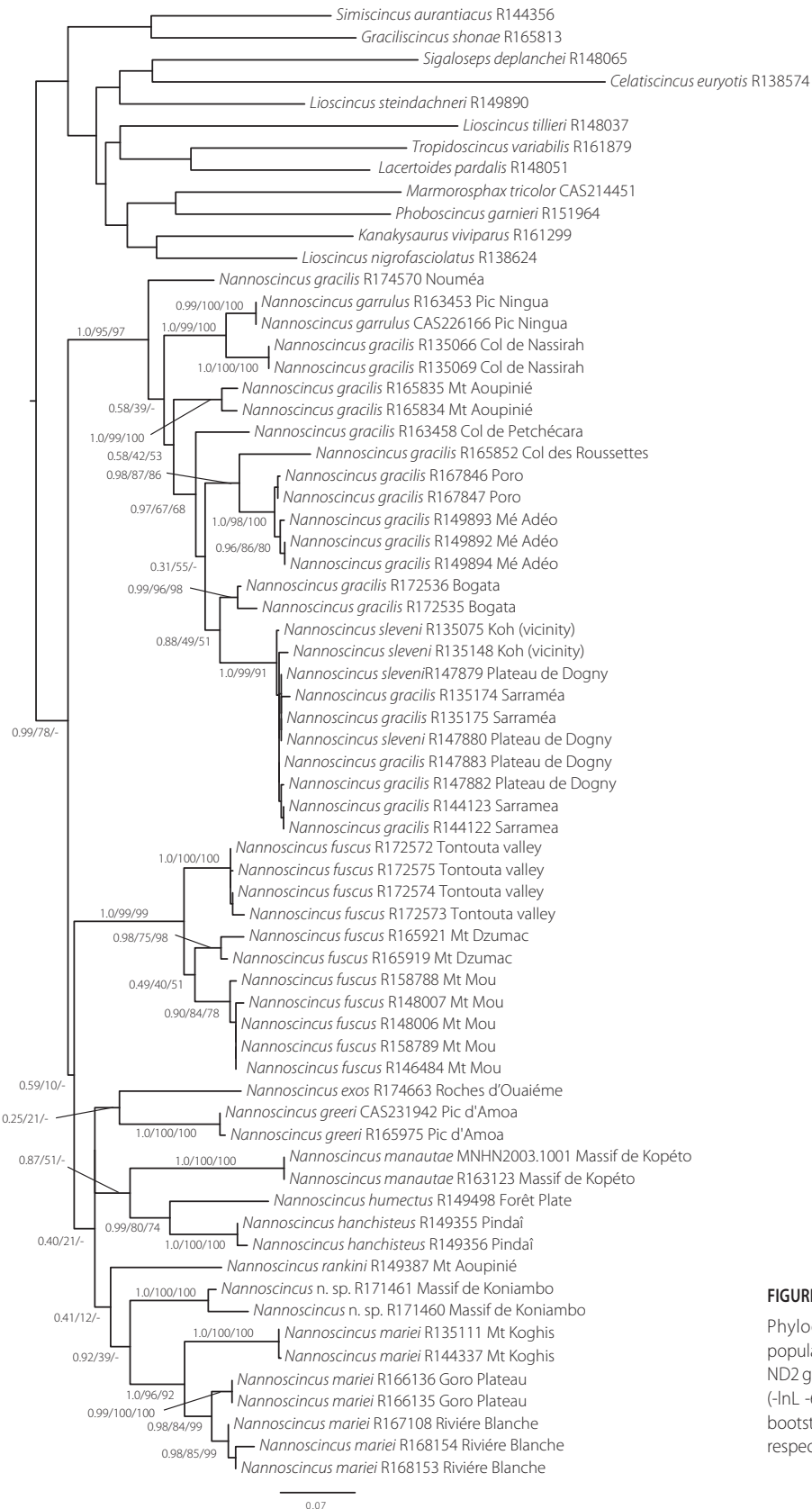


FIGURE 1

Phylogenetic relationships among species and populations of *Nannoscincus* based on mitochondrial ND2 gene sequences. Maximum Likelihood topology (-lnL -6066.503241) with posterior probabilities, ML bootstrap support, and MP bootstrap support shown respectively (BPP/ML/MP).

morphological variation were used as indicators of reproductive isolation between putative species. The genetic study also revealed the presence of two previously unrecognized highly-differentiated lineages, one within what has previously been regarded as a single species, *Nannoscincus mariei*, the other from the Massif de Koniambo in the north-west region and similar in morphology to *N. hanchisteus*. The morphological characters that diagnose a monophyletic 'mariei group' are shared by both lineages and argue strongly for their inclusion into a monophyletic 'mariei group'.

The presence of two clearly-differentiated lineages within *Nannoscincus mariei* was unexpected. Subsequent examination of specimens from localities matching those used in the genetics study identified a high degree of concordance between the two lineages and the modal difference of states for two morphological characters not previously investigated in detail. Comparison of this information with the types *Anotis mariei* Bavay and *Nannoscincus fuscus* Günther identifies the specimens in one lineage as best regarded as conspecific with the holotype of *N. mariei* sensu stricto (s.s.) and specimens in the other lineage as conspecific with the holotype of *N. fuscus*. These taxa share two morphological characters not seen in any other species of *Nannoscincus*, complete loss of an external ear opening and the presence of an extensive sheathing scale over extremely long terminal phalanges (claws) of the digits, which in combination with a suite of several other morphological apomorphies argues very strongly for a sister relationship between these putative species. The lack of support for a close relationship between these two lineages in the molecular phylogeny is problematic and symptomatic of the lack of basal relationships for, and within, the 'mariei group', other than for a group of three taxa (*manautei* + *humectus* + *hanchisteus* – 0.87/51/-) from the central-west and north-west regions.

Within *Nannoscincus mariei* s.s., the genetic distance between the Mt. Koghis population and that sampled from Rivière Bleue + Goro Plateau is moderately high (7.9%), indicating the potential for significant regional genetic sub-structuring within the species with further sampling across the species range. The *N. fuscus* lineage comprises three populations, one on the Mt. Ouin/Mt. Dzumac saddle (900 m), one on Mt. Mou (250 m and 1000 m), and one in the Tontouta Valley (500 m). These populations are each situated ~12km apart on a series of interconnecting ranges which rarely fall below 800 m elevation, but which now have few intervening patches of suitable moist forest habitat. There is a moderate level of genetic differentiation between each population (Table 2) indicative of long-term isolation. Earlier studies identified differences in size between high and low-elevation samples from Mt. Mou, the latter being up to 15% longer in the body (Sadlier *et al.* 2002), but there was no discernible genetic differentiation with elevation between the samples studied.

The genetic data clearly identifies a monophyletic 'gracilis group', but there was a high level of inconsistency between the genetic lineages retrieved and the taxa currently recognized on morphological criteria. Two species, *N. sleveni* and *N. garrulus*, unequivocally diagnosable on morphological criteria are nested within a polytypic *N. gracilis*. Specimens identified as *N. sleveni* on the basis of morphology show no genetic differentiation from regionally proximate *N. gracilis*, and *N. garrulus* is retrieved as the sister to the geographically most proximate population of *N. gracilis* at Col de Nassirah (with only a low level of genetic differentiation -4.8%).

The morphological data continues to support a monophyletic 'gracilis group' and recognition of the species *N. garrulus*, *N. sleveni* and *N. gracilis*. The recovery of a highly polytypic *N. gracilis* in the molecular phylogeny with relatively a high level of genetic differentiation between some of the lineages retrieved was however unexpected. Most geographically discrete samples of *N. gracilis* show relatively high levels of inter-population genetic differentiation (see Table 3) of similar magnitude. Within the 'gracilis group' the molecular phylogeny identified a well supported large regional group (0.97/67/68) in the central-east region comprising three sub-groups (as a polytomy) that includes Col de Petchécara as one sub-group, the regionally proximate samples from Sarraméa/Dogney (including populations of *N. sleveni* sampled in this region) and Presqu'Île Bogata (0.88/49/51) as another with a moderate level of differentiation between these areas (5.8-8.3%, Table 3), and the regionally proximate samples from Menazi and Mé Adeo (1.0/98/100) as part of a sub-group that also includes Col des Roussettes as another sub-group (0.98/87/86), again with a moderate level of differentiation between these areas (7.1-7.5%, Table 3). *Nannoscincus gracilis* as it is currently conceived covers a broad geographic area

TABLE 2

Genetic distance between populations of *N. fuscus*.

	1	2	3
1 Mt. Vulcain	0.2-1.1%	-	-
2 Mt. Dzumac	6.4-7.6%	0.0-2.5%	-
3 Mt. Mou	2.2-7.2%	4.7-6.6%	0.6-2.0%

TABLE 3

Genetic distance between species and populations in the *N. gracilis* group.

	1	2	3	4	5	6	7	8	9
1 <i>N. gracilis</i> Col de Nassirah	-								
2 <i>N. gracilis</i> Col de Petchécara	9.3%	-							
3 <i>N. gracilis</i> Bogota	9.3-9.6%	6.6-7.2%	-						
4 <i>N. gracilis</i> Menazi + Mé Adeo	10.7-11.4%	8.7-9.7%	7.3-9.2%	-					
5 <i>N. gracilis</i> Col des Roussettes	12.6%	9.3%	8.7-9.2%	7.1-7.5%	-				
6 <i>N. gracilis</i> Mt. Aoupinié	8.5-9.1%	8.9-9.1%	7.0-8.0%	9.5-10.3%	9.7-10.1%	-			
7 <i>N. gracilis</i> + <i>N. sleveni</i>	7.8-9.9%	7.0-8.7%	5.0-8.6%	5.8-8.3%	6.9-9.9%	8.3-9.9%	-		
8 <i>N. gracilis</i> Nouméa	10.5%	10.1%	9.7-10.1%	10.8-11.6%	12.2%	9.10%	9.1-11.2%	-	
9 <i>N. garrulus</i> Pic Ningua	4.86-4.87%	9.3%	10.1-10.4%	9.7-10.5%	11.80%	8.3-8.5%	8.3-9.9%	10.1%	-

and populations over that range are relatively stable for the morphological characters that presently diagnose the species. The populations of *N. gracilis* from Nouméa, Col de Nassirah and Mt. Aoupinié are highly divergent from each other and from the broad central-east regional group identified above, with a level of genetic differentiation (generally above 9%). These populations show subtle differences in morphology which reflect some of the highly genetically differentiated lineages retrieved. There is significantly more material available since the species was last reviewed (Sadlier 1987) and a more extensive morphological study could support recognition of the genetic lineages identified within *N. gracilis* as cryptic species. Such a review of the members of the '*gracilis* group' would be a separate study in its own right, and the data presented here on the members of this group is intended as a platform for future research.

Nannoscincus garrulus has a suite of distinctive morphological traits (seven vs six upper labials and seven vs six lower labials as seen in *N. gracilis* and *N. sleveni*; fragmented temporal and nuchal scales such that two vs one primary temporal scales and two small vs one elongate scale border the parietal either side as seen in *N. gracilis* and *N. sleveni*; five vs four digits on the manus as seen in *N. sleveni* and an increased number of phalanges on the manus (2.3.3.3.3 vs 2.3.3.3.2) to that seen in *N. gracilis*) that clearly indicate it is not conspecific with any of the lineages within the '*gracilis* group' and the relatively high level of genetic differentiation between *N. garrulus* and most of the 'populations' of *N. gracilis* and with *N. sleveni* is of similar magnitude (8.5-10.3%). As such, the strongly supported sister relationship of *N. garrulus* with the regionally adjacent population of *N. gracilis* from Col de Nassirah (straight line distance of 9 km), but low level of genetic differentiation between the two lineages, most likely reflects a recent shared ancestry.

Nannoscincus sleveni shows no discernible genetic differentiation from regionally parapatric *N. gracilis* in the central-east ranges. The species is differentiated from *N. gracilis* by a single but highly significant morphological trait, loss of the fifth digit of the manus, a condition unique not only within *Nannoscincus* but also within the entire *Eugongylus* group of skinks. This character state is consistent within samples from all populations examined, and is found only in populations within a discrete geographic region in the central ranges apart from of a single individual collected on ultramafic massif of Mé Maoya in the central-west ranges. There is no indication of geographic overlap in the morphological character that diagnoses these two species. This can be regarded as indication that *N. sleveni* is not conspecific with *N. gracilis* where diagnostic morphological characters are regarded as a probable signal of nuclear divergence. The lack of genetic differentiation between *N. sleveni* and the regionally adjacent population of *N. gracilis* could be interpreted as reflecting a relatively recent divergence between these two taxa accompanied by accelerated morphological differentiation (loss of the fifth digit of the manus - unique within *Eugongylus* group skinks, see Sadlier 1990), rather than conspecificity. Alternatively, the diagnostic morphological difference between the two species could be indicative of a deeper time of divergence for the morphological trait to become established with the lack of genetic differentiation indicative of recent introgression of mtDNA from one species to another.

SYSTEMATIC PART

Family SCINCIDAE Gray, 1825

Genus *Nannoscincus* Günther, 1872

Nannoscincus Günther, 1872: 472.

Type species. *Nannoscincus fuscus* Günther, 1872

Bavay (1869) published the first overview of the reptiles of New Caledonia in 1869, in which all of the skinks described were new. Included were two species of diminutive skink: one described as *Lygosoma gracilis*, the other as *Anotis mariei*, the generic name *Anotis* being proposed specifically for that species. Thereafter the generic name *Lygosoma* was used consistently, if only infrequently, for both *mariei* and *gracilis*, and later for the species *sleveni* described by Loveridge (1941). The allocation of these species to *Lygosoma* is puzzling given they did not have the disc in the lower eyelid that was one of the key diagnostic features of the genus. Greer (1974) resurrected *Anotis* to accommodate these species plus the two Australian species *Lygosoma maccoyi* Lucas and Frost and *Lygosoma graciloides* Lönnberg & Andersson. Czechura (1981) made a nomenclatural amendment and transferred these species to *Nannoscincus* on the suggestion that *Anotis* Bavay, 1869, was preoccupied by *Anotis* Rafinesque 1815. Sadlier (1986) further refined the intrageneric relationships of these species in removing *graciloides* from the genus, and later (Sadlier, 1990) in identifying the New Caledonia taxa as a monophyletic group with the Australian species *maccoyi* as its sister and for which the sub-generic name *Nannoseps* was proposed. Inclusion of *maccoyi* within a monophyletic *Nannoscincus* by Sadlier (1990) was based several morphological apomorphies, the most compelling of which was the shared pattern of phalanx loss between the included species which was unique within the *Eugongylus* group of skinks. However, other more distantly related taxa were subsequently described with this pattern of phalanx loss and the strength of the argument for a sister relationship with *maccoyi* diminished. As such, the species *maccoyi* was transferred to *Anepischetosis* (Sadlier *et al.* 2006), a name made available by priority of publication (over *Nannoseps*) despite having no workable diagnosis, and in doing so making *Nannoscincus* a strictly endemic New Caledonian genus of skinks.

Monophyly of Greer's (1979) *Eugongylus* group has been retrieved from independent molecular studies (Hutchinson *et al.* 1990; Honda *et al.* 2000 & 2003), as has a monophyletic Tasmantis lineage that includes the endemic New Zealand + New Caledonia + Lord Howe/Norfolk Island members of the group (Smith *et al.* 2007; Chappell *et al.* 2009), and a monophyletic New Caledonian *Nannoscincus* (Smith *et al.* 2007).

DIAGNOSIS — [*denotes apomorphic character states within the *Eugongylus* group as defined by Sadlier, 2010] The species of *Nannoscincus* are all small in size (maximum snout vent length range 34-52.5 mm) with an *elongate body, *short limbs and digits, and relatively *short tail (maximum tail length range 85-105% of SVL). The ear opening is *diminutive, or absent in some species.

Scalation. Frontonasal broader than long; *prefrontals diminutive and widely separated or absent; frontal short, almost as broad as long; supraoculars four; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; tertiary temporals two; postlabials two; nasals moderately separated; *anterior loreal reduced to a semilunar scale positioned on the anterodorsal margin of the nasal and failing to contact the labials, or absent; supraciliaries usually seven; *upper labials 6 with the fourth subocular and contacting the lower eyelid (division of the subocular labial scale gives 7 upper labials in *N. garrulus*); postmental contacting first and second lower labial; chinshields three, first pair in broad contact.

Osteology. All species are characterized by an *elevated number of presacral vertebrae of 29 or more, and by a *reduction of phalanges on the 4th digit of the manus in all species, and on the fifth digit of the pes in nearly all species (*N. greeri* has the primitive phalangeal number on the pes).

INCLUDED SPECIES — Taking into consideration both the morphological and genetic evidence which is currently available, thirteen species are recognized (presented chronologically), including one previously unrecognized species from the synonymy of *Nannoscincus mariei* to which the name *N. fuscus* Günther applies and one species new to science.

Nannoscincus mariei (Bavay, 1869)

Anotis mariei Bavay 1869: 29.

Type LOCALITY — New Caledonia.

DISTRIBUTION — Mt. Koghis in the southwestern ranges and the Goro Plateau (Figure 2).

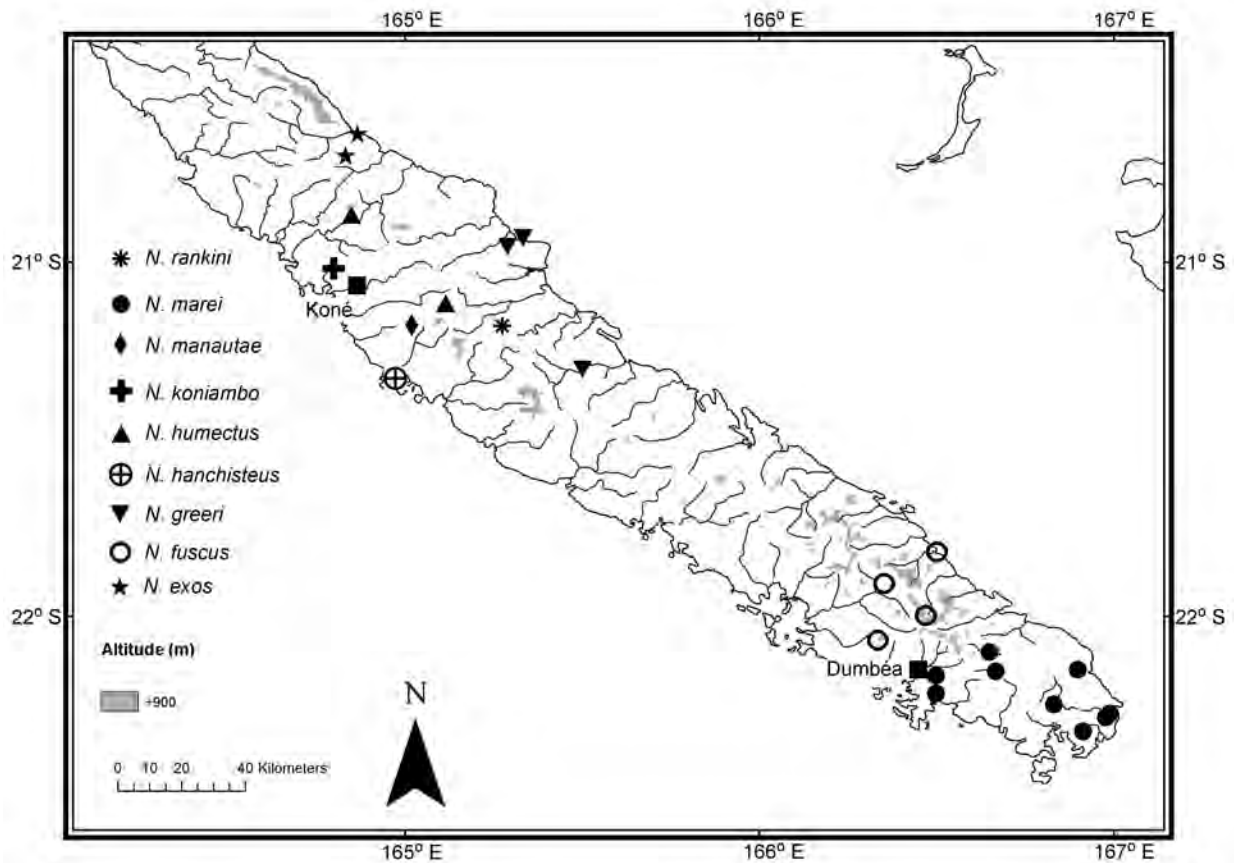


FIGURE 2
Distribution of the *N. 'mariei* group' in New Caledonia.

Nannoscincus gracilis (Bavay, 1869)

Lygosoma gracilis Bavay, 1869: 24

Mocoo micropus Günther, 1872: 420

TypE LOCALITY — New Caledonia (Figure 3).

DISTRIBUTION — Poindimié in the north to Col de Nassirah in south, with isolated and apparently disjunct populations in the far north at Mt. Mandjéla and in the south at Nouméa.

Nannoscincus fuscus Günther, 1872

Nannoscincus fuscus Günther, 1872: 421.

TypE LOCALITY — ‘Feejee Islands’ – erroneous for New Caledonia.

DISTRIBUTION — Mt. Mou and Mt. Dzumac in the southern ranges (Figure 2).

Nannoscincus sleveni (Loveridge, 1941)

Lygosoma sleveni Loveridge 1941:193.

TypE LOCALITY — Canala.

DISTRIBUTION — Central ranges around Canala (including Sarraméa Col d’Amieu and Plateau de Dogny) (Figure 3).

Nannoscincus rankini Sadlier, 1986

Nannoscincus rankini Sadlier, 1986: 62.

TypE LOCALITY — Mt. Aoupinié.

DISTRIBUTION — Mt. Aoupinié (summit) in the central-east ranges (Figure 2).

Nannoscincus greeri Sadlier, 1986

Nannoscincus greeri Sadlier, 1986: 63.

TypE LOCALITY — Mt. Koyaboa, Poindimié.

DISTRIBUTION — Central-east region coast and ranges (Figure 2).

Nannoscincus humectus Sadlier, Bauer & Whitaker, 2002

Nannoscincus humectus Sadlier et al., 2002: 245

Type LOCALITY — Forêt Plate.

DISTRIBUTION — Central-west and north-west region ranges (Figure 2).

Nannoscincus hanchisteus Sadlier, Bauer & Whitaker, 2002

Nannoscincus hanchisteus Sadlier et al., 2002: 248

Type LOCALITY — Pindai.

DISTRIBUTION — North-west coast (Figure 2).

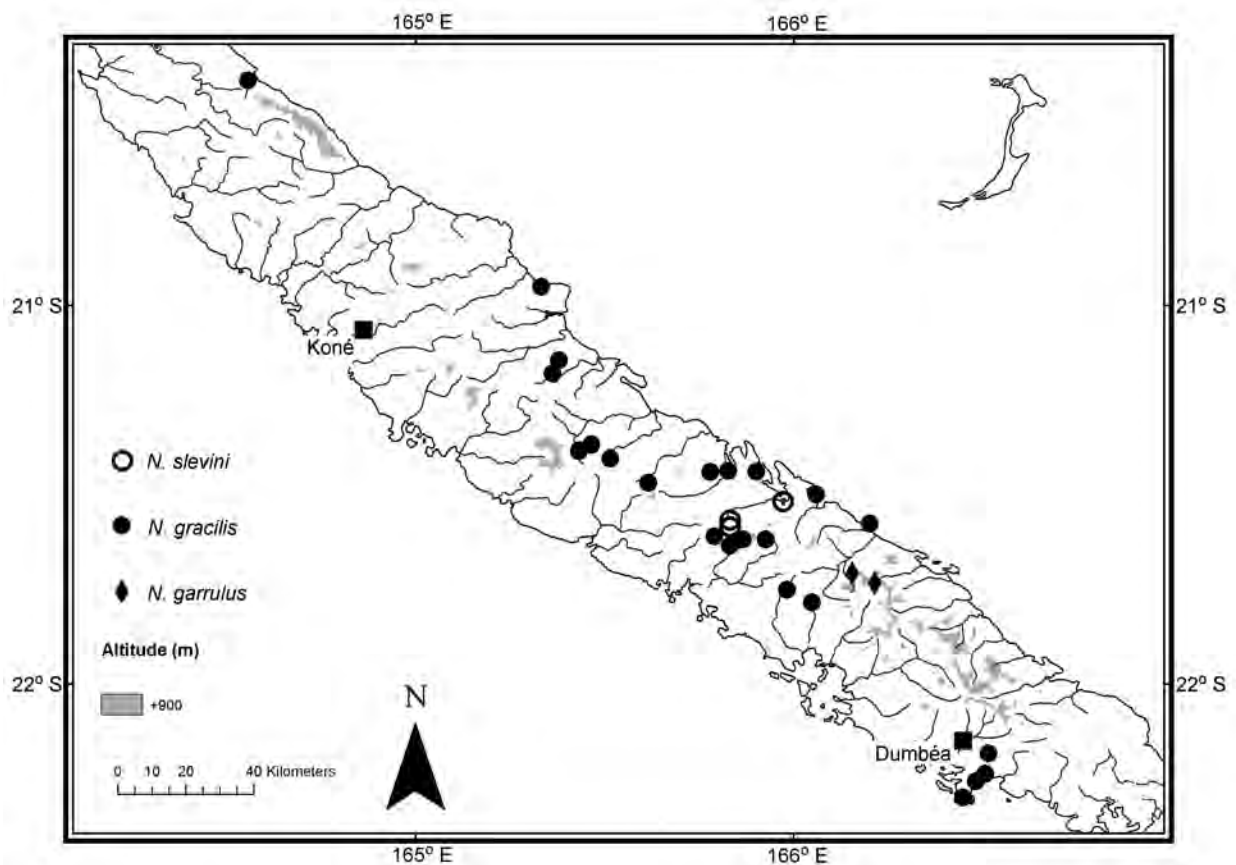


FIGURE 3
Distribution of the *N. 'gracilis' group* in New Caledonia.

Nannoscincus exos Sadlier, Bauer & Whitaker, 2002

Nannoscincus exos Sadlier et al., 2002: 248

Type LOCALITY — Roches de Ouiaème, 3 km west of Ouinguip.

DISTRIBUTION — North-east region coastal ranges bounded by the Hienghène River valley in the south and the Ouaième River valley in the north (Figure 2).

Nannoscincus manautei Sadlier, Bauer, Whitaker & Smith, 2004

Nannoscincus manautei Sadlier et al., 2004: 215

Type LOCALITY — Massif de Kopéto, Papainda.

DISTRIBUTION — Massif de Kopéto in the north-west ranges (Figure 2).

Nannoscincus garrulus Sadlier, Bauer & Smith, 2006

Nannoscincus garrulus Sadlier et al., 2006: 31

Type LOCALITY — Pic Ningua.

DISTRIBUTION — Pic Ningua, Koungouhaou Nord and Mont Çidoa in the southern region ranges (Figure 3).

Nannoscincus koniambo Sadlier, Bauer, Wood & Whitaker, n. sp.

Type LOCALITY — Massif de Koniambo.

DISTRIBUTION — Massif de Koniambo in the north-west ranges.

Nannoscincus koniambo Sadlier, Bauer, Whitaker & Wood, n. sp.

Figures 4, 5

Type MATERIAL — *Holotype*. New Caledonia, MNHN 2011.0283 (formerly AMS R.171460) Massif de Koniambo, headwaters of Rivière Pandanus 20°59'40"S 164°48'41"E, 720 m (19 Jan. 2009; R. Sadlier).

Paratype. AMS R.141461 Massif de Koniambo, headwaters of Creek Coco (south Branch) 20°58'32"S 164°47'50"E, 670 m (20 Jan. 2009; A. Whitaker).

ETYMOLOGY — The epithet is a noun in apposition in reference to the type locality, the Massif de Koniambo. The content and order of authors for the description of the new species reflects the individual contributions of those individuals to the discovery and recognition of that species.

DIAGNOSIS — *Nannoscincus koniambo* n. sp. can be distinguished from all other members of the genus by the following combination of characters: frontoparietals fused; loreal single; left oviduct lost in females; lower labials five; lower eyelid with a semi-translucent window; ear opening minute; body scales smooth; adult dorsal color two toned; ear opening positioned two scales posterior to lower secondary temporal; presacral vertebrae 32; phalangeal formula for manus 2.3.4.4.3.; phalangeal formula for pes 2.3.4.5.3.

The first five characters readily distinguish *N. koniambo* n. sp. from *N. gracilis*, *N. sleveni*, and *N. garrulus*, all of which have divided frontoparietals, six lower labials, two loreals (the anterior semilunar and failing to contact the labials), a right and left oviduct, and a (secondarily) scaled lower eyelid.

Nannoscincus koniambo n. sp. shares the apomorphic character states of a single loreal, loss of the left oviduct, and reduction to five lower labials with eight other species (*N. mariei* s.s.; *N. fuscus*; *N. greeri*; *N. rankini*; *N. humectus*, *N. hanchisteus*, *N. exos* and *N. manautei*). The presence of a minute ear opening will distinguish *N. koniambo* n. sp. from *N. mariei* and *N. fuscus*, both of which have no obvious ear opening, and it can be further distinguished from these two species by the presence of a “windowed” (vs scaled) lower eyelid and fused (vs paired) frontoparietals. The smooth body scales of *N. koniambo* n. sp. will readily distinguish it from *N. greeri*, *N. mariei*, *N. fuscus* and *N. rankini* all of which have 3-4 fine striations on the body scales. Further, *N. koniambo* n. sp. has a two-toned adult color pattern, whereas the coloration of adult *N. rankini*, *N. manautei*, *N. mariei* and *N. fuscus* is predominately uniformly dark.

Nannoscincus koniambo n. sp. most closely resembles *N. humectus*, *N. hanchisteus*, and *N. exos* in having a two-toned adult color pattern and smooth body scales. It can readily be distinguished from *N. exos* by having an increased number of phalanges on the 4th digit of the pes (2.3.4.5.3 vs 2.3.4.4.3) and a lower number of midbody scale rows (20 vs 22). It can readily



FIGURE 4

Holotype of *Nannoscincus koniambo* n. sp. (MNHN 2011.0285) from Massif de Koniambo.

be distinguished from *N. humectus* by the positioning of the ear opening two (vs three) scales posterior to lower secondary temporal and in subtleties in coloration in which the dorsolateral edge defining the point of contact between the dark lateral and paler dorsal surfaces is clean and unbroken (vs rough edged). *Nannoscincus koniambo* n. sp. shares most of the traits of *N. hanchisteus*. The characteristics distinguishing the two taxa are subtle and include for *Nannoscincus koniambo* n. sp. a more gracile habitus, overall darker coloration of the lateral surfaces of the body and head (very dark brown vs light-mid brown) and extensive dark medial marking to the rostral scale (most of scale and extending onto frontonasal vs lower margin of the scale with a slight inflexion back medially), and marginally more lamellae beneath the 4th digit of the pes (15-16 vs 13-14).

The level of genetic differentiation between *Nannoscincus koniambo* n. sp. and its congeners in the 'mariei group' is of similar magnitude to that between all species in the group, all of which are also diagnosable as distinct species on morphological criteria. As such, this level of genetic differentiation provides strong support for recognition of *N. koniambo* n. sp. as an evolutionary lineage distinct from all other members of the genus. However, relationships between this species and other members of the 'mariei group' retrieved in the molecular phylogeny are problematic. *Nannoscincus koniambo* n. sp. is well supported as the sister taxon of *N. mariei* in the phylogeny and *N. fuscus* as a separate lineage, yet on morphological criteria *N. mariei* and *N. fuscus* share a unique and distinctive suite of apomorphies that clearly indicates these species are sister taxa.

DESCRIPTION (based on holotype and paratype) — **Measurements.** SVL 31-34 mm; distance from axilla to groin 60.3-60.6% of SVL (mean = 60.4); distance from forelimb to snout 30.0-33.9% of SVL (mean = 31.9); hindlimb length 21.2-24.5% of SVL (mean = 22.8); tail length 113.2% of SVL or more (estimated from individual with most complete tail).

Scalation. Nasals large and moderately separated; frontonasal broader than long; prefrontals very small and widely separated; supraciliaries seven, with the first supraciliary contacting frontal (thereby excluding contact between the prefrontal and first supraocular); frontal short almost as broad as long; supraoculars four; frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; upper labials six; lower labials five; primary temporal single; upper and lower secondary temporals single; tertiary temporals two; postlabials two; ear opening positioned two scales posterior to lower secondary temporal; postmental contacting first and second lower labial; chinshields three, first pair in broad contact; body scales smooth, midbody scale rows 20; paravertebral scales 50-54 (mean = 52); scales on top of fourth finger 4, scales at base of second, third, and fourth fingers variable, ranging from a single broad scale at the base of (and common to) each digit (holotype), to two scales of equal size or partially divided (paratype); lamellae beneath fourth finger 5; scales on top of fourth toe 6-7; lamellae beneath fourth toe 15-16 (mean = 15.3).

Osteology. Presacral vertebrae 32; phalangeal formula for manus and pes 2.3.4.4.3 and 2.3.4.5.3, respectively.

Coloration (in preservative). Dorsal color light to mid-brown, nape with a pattern of dark markings enclosing a (slightly) pale blotch. Lateral surface noticeably darker than dorsal, unmarked. Dorsal and lateral surfaces defined by a narrow black (darker than lateral color) dorsolateral stripe, pale-edged above and extending from back of eye (inflexed over tympanic region) to level of hindlimbs, breaking up and becoming poorly defined along tail. Head darker at sides than adjacent areas of body, dark coloring extending around lower edge of rostral scale and inflecting upwards to form a broad dark midrostral streak that extends medially to and past the rostral-frontonasal suture. Ventral surface with a concentration of pale brown markings on the tail and abdomen, scattered markings on the chest, and the throat relatively unmarked.

DISTRIBUTION AND BIOLOGY — *Nannoscincus koniambo* n. sp. is known from two high elevation sites on the Massif de Koniambo (Figure 2). Both sites are in closed humid forest (Figure 5). The holotype was collected inside a rotting log and the paratype in shallow leaf litter.

CONSERVATION STATUS — *Nannoscincus koniambo* n. sp. is known from two locations on the Massif de Koniambo at ~700 m elevation. The extent of high-elevation humid forest habitat on the extensive summit area of the massif has been greatly reduced by fire and there are numerous mining exploration tracks to and through the edges of the forest. The estimated distribution of forest habitat on the upper part of the massif is difficult to determine but both the area of occurrence

**FIGURE 5**

Humid forest habitat on the summit region of the Massif de Koniambo.

and area of occupancy based on the extent of this habitat type could be $<10 \text{ km}^2$. The greatest threat to *N. koniambo* n. sp. is further loss of habitat leading to a reduction in the area of occupancy, and a further decline in the quality of existing habitat. There is a history of repeated wildfires on the massif which has reduced the extent and quality of the forest edge, and introduced ungulates (deer and pigs) are present and threaten habitat quality, particularly by damaging the litter layer. The Massif de Koniambo is also the site of a large new nickel mine development that will result in large areas of the summit being mined, potentially resulting in further loss of forest habitat. Given the limited extent of humid forest on the massif and level of existing degradation to this habitat from previous fires and the presence of feral animals, and the threat from mining, the species could be categorized as Critically Endangered B1ab(i-iii,v) under IUCN criteria.

DISCUSSION

TAXONOMIC DISCUSSION

The genetic study revealed the presence of two clearly differentiated lineages within what has previously been regarded as a single species, *Nannoscincus mariei*. Although the geographic range of samples available for the genetics study is not as extensive as that represented by museum specimens it is, in combination with morphological data, sufficient to indicate that the samples represent two parapatric taxa: *Nannoscincus mariei* Bavay (Mt. Koghis south to the Goro Plateau, including Rivière Bleue), and *Nannoscincus fuscus* (the Chaîne Centrale at Mt. Mou, Mt. Dzumac and Mt. Vulcain).

Sadlier *et al.* (2002) had previously discussed geographic variation in scalation in *N. mariei* and had compared samples from low elevation at Mt. Mou (250 m) with mid-elevation samples from Mt. Koghis (500 m). Significant (but not wholly diagnostic) differences between the two samples were found in scalation (midbody scale rows and lamellae beneath the fourth toe) and osteological characters (number of presacral vertebrae). It was also noted that specimens from Mt. Koghis all had a broad transverse basal scale common to the 2nd, 3rd and 4th digits of the manus whereas most specimens from Mt. Mou (70%) had the broad transverse basal scale common only to the 3rd and 4th digits, the condition seen in most other *Nannoscincus*, although the only two specimens from Yahoué Valley at the base of Mt. Koghis had the character state more typical of the Mt. Mou sample. The species was also noted as being variable in the degree of contact between the 1st supraciliary and frontal in some populations, a character otherwise considered an apomorphy for the genus.

Specimens from localities matching those used in the genetics study were re-examined to assess for concordance in the distribution of character states for the scales at the base of the digits of the manus and the contact between the frontal and 1st supraciliary with the lineages identified in the genetic study. In addition, specimens from other localities were re-examined to assess the broader distribution of the scalation characters on the manus and thereby the putative identity of these specimens with regard to the two genetic lineages. Samples from Mt. Mou, Mt. Dzumac, and Mt. Vulcain usually (80% n= 32) had a broad transverse basal scale common to the 3rd and 4th digits only of the manus, and usually (68% n= 32) had the 1st supraciliary usually contacting the frontal scale. All specimens in the sample from Mt. Koghis (mid-elevation) had a single broad transverse basal scale common to the 2nd, 3rd and 4th digits of the manus and the 1st supraciliary failing to broadly contact the frontal scale. Specimens from Yaté and most from the (albeit small) samples from Goro Plateau and Rivière Bleue (all low elevation sites) also share these character states. Two individuals from Yahoué Valley at the base of the Koghis Range have a broad transverse basal scale common to the 3rd and 4th digits only of the manus and the 1st supraciliary contacting the frontal scale, the character states diagnostic for the Mt. Vulcain, Mt. Mou and Mt. Dzumac populations. These two scalation characters are not wholly diagnostic for all individuals of either species, and as such specimens from locations represented by small sample sizes of a few individuals cannot be unequivocally identified on morphology alone. The identity of the individuals from Yahoué Valley is a case in point, and the identity of this population is only likely to be resolved by additional sampling and genetic analyses.

The types of *Anotis mariei* Bavay and *Nannoscincus fuscus* Günther (the latter previously considered a synonym of *Nannoscincus mariei* *sensu lato*) were examined for these key diagnostic characters. The description by Bavay of *Anotis mariei* in 1869 did not specify the number of specimens examined, but did allude to the species being observed at several sites, and hence the possibility of the existence of a syntype series, but no mention was made of where the specimens alluded to were lodged. Sadlier (1986) reviewed the species and nominated a lectotype for *Anotis mariei* Bavay from one of the two specimens in the BMNH listed as syntypes by Boulenger (1887), at that time considering no other Bavay specimens existed for this species. However, Brygoo (1985) in a catalogue of skink types held at the Museum national d'Histoire naturelle, Paris listed types of several Bavay taxa recently located at and listed by that institution, including specimens representing syntypes of *Anotis mariei*. Unfortunately the re-discovered type material of *Anotis mariei* in the MNHN is in poor condition. The provenance of the syntypes of *Anotis mariei* Bavay are unknown other than that they came from New Caledonia. Re-examination of the lectotype of *Anotis mariei* Bavay (BMNH 1946.8.17.79) for key morphological characters showed it to have a broad transverse basal scale common to the 2nd, 3rd and 4th digits of the left and right manus and the 1st supraciliary is in point contact with the frontal scale on both sides. The other syntype of *Anotis mariei* in the BMNH is in poor condition and was not re-examined. The condition of the 'syntype' material of *Anotis mariei* Bavay in the MNHP (four specimens all desiccated) does not allow the contact of the frontal scale and 1st supraciliary to be determined with any degree of confidence, and the distribution of character states for the basal toe scales of the manus is equivocal: one (MNHN 5398C) has a single broad transverse basal scale common to the 2nd, 3rd and 4th digits the manus of both forelimbs; two have this condition on the right manus only; and one a transverse basal scale common to the 3rd and 4th digits only of the manus of both forelimbs. The level of variation in these key characters among Bavay's syntypes of *Anotis mariei*

is problematic and highlights the difficulty in attempting to pin any individual specimen unequivocally to any of the populations examined in recent studies (Sadlier *et al.* 2002), remembering that the original description indicates the species was encountered at more than a single locality. The holotype of *N. fuscus* is less problematic in that it has a broad transverse basal scale common to the 3rd and 4th digits only of the manus, and the 1st supraciliary on both sides in broad contact the frontal scale, and is moderately large (SVL 35.5 mm), all features typical of populations on Mt. Mou and Mt. Dzumac.

Günther (1872) described *Nannoscincus fuscus* from specimens in the BMNH purportedly obtained from the 'Feejee Islands' during the voyage of the HMS Curaçoa. Sadlier (1986) in reviewing *Nannoscincus mariei* retained *Nannoscincus fuscus* Günther as a synonym of *mariei*, and formally identified the single type in the BMNH as holotype for *N. fuscus*. A later review of *Nannoscincus mariei* by Sadlier *et al.* (2002) similarly retained *fuscus* as a synonym of *mariei*. Aside from a short stop on the south coast of the island at "Good Cove" in "Praslin Bay" (= Bonne Anse, Baie de Prony), during its stay in New Caledonia (28 September to 8 October, 1865), the Curaçoa was anchored in Nouméa (Brenchley 1873). Thus, it appears likely that the holotype of *N. fuscus* was collected in the course of an outing from Nouméa. Of the known localities for the species Mt. Mou is the closest in proximity to Nouméa and given the likely extent of roads existing in the 19th century it is possible Bavays' types came from the vicinity of this massif.

The following designations are here proposed in recognizing two taxa based on the evolutionary lineages identified by the genetic data in combination with the distribution of the two key morphological characters states among the types and the populations sampled:

- *Nannoscincus mariei* (Bavay) for the species characterized by a broad transverse basal scale common to the 2nd, 3rd and 4th digits of the manus, and with the 1st supraciliary failing to contact the frontal scale. This species occurs in the far south of the island on the Koghis Range on the west coast and the Goro plateau (Foret Nord and Pic du Grand Kaori), and tentatively (in the absence of genetic data) the coast (Yaté) and valleys (Rivière Bleue) adjacent to the Goro plateau.
- *Nannoscincus fuscus* Günther for the species that is characterized by a broad transverse basal scale common to the 3rd and 4th digits only of the manus, and with the 1st supraciliary contacting the frontal scale. This species occurs on southernmost ranges of the Chaîne Central (Mt. Vulcain, Mt. Dzumac) and adjacent massifs on the west coast (Mt. Mou).

The sample collected by Roux and Sarasin in 1913 from "Ngoye" (= Ngoi) on the east coast adjacent to the Humboldt massif (3 specimens -all relatively small) all have the 1st supraciliary failing to contact the frontal scale, but the condition of the scales/scale at the base of the 2nd, 3rd and 4th digits the manus was not recorded at the time (1987) they were examined. Given the data are incomplete for the small sample of specimens from Ngoi, this population cannot be assigned to either species with any degree of confidence.

PHLOGEOGRAPHIC PATTERNS

A number of phylogenetic patterns have recently been identified within the New Caledonian skink fauna (Sadlier 2010). These include: deep and shallow splits between congeneric taxa in the southern region ultramafic ranges *vs* regions to the north, broad-scale and localized regional endemism in the ultramafic ranges of the southern and central-west/north-west regions, broad-scale regional endemism in the central and north region metamorphic ranges, and narrow-range high-elevation endemism. Among the secretive and primarily forest dependent species of skinks, localized endemism in the genus *Marmorosphax* appears to have resulted from multiple cladogenic events, most likely tracking historical, regional fragmentation of forest habitat on ultramafic surfaces across the entire Grande Terre and in *Sigaloseps*, historical fragmentation of forest habitat in the southern ultramafic region has given rise to an extensive suite of species over a relatively small area. By contrast the pattern of endemism in the central and northern regions on metamorphic substrates is mostly broad-scale, as seen in the broadly parapatric distributions of species in the genus *Caledoniscincus* in the north and east of Grande Terre.

The molecular phylogeny for *Nannoscincus* retrieved in this study for the mitochondrial ND2 gene gives no clear indication of basal relationships from which phylogeographic patterns early in the history of the genus can be inferred with confidence. However, it does retrieve some well supported regional groupings of populations within the ‘*gracilis* group’ and ‘*mariei* group’ of species. Within the ‘*gracilis* group’, a highly-supported group from the central-east region between Col de Petchécara and Col des Rousettes is retrieved comprising a polytomy of three regional sub-groups (Sarramea + Dogne + Koh + Bogata; Adeo + Menazi + Col des Rousettes; and Col de Petchécara) that includes populations on both metamorphic and ultramafic surfaces. This regional grouping also includes the morphological species *N. sleveni* which has a discrete distribution that includes the ranges incorporated in the drainage of the Négropo River near Canala and is closely parapatric with adjacent populations of *N. gracilis*. The molecular phylogeny also retrieves a highly supported group of three species in the ‘*mariei* group’ ((*N. humectus*, *N. hanchisteus*) (*N. manautei*)) from the central-west region between Pouembout and Poya on ultramafic, metamorphic and sedimentary surfaces. This relationship is also well supported in a combined mitochondrial (ND2) and nuclear (Rag1) gene phylogeny for the genus (unpublished) with a reduced overall sampling of taxa (*N. exos* and *N. koniambo* n. sp. were not available at the time). This combined mitochondrial and nuclear gene phylogeny also retrieved a broader sub-group of taxa that included *N. rankini* and *N. greeri* with a moderate level of support (as a polytomy), the overall range of which extends along the adjacent central-east region metamorphic ranges.

An early morphological phylogeny for *Nannoscincus* (Sadlier 1990) clearly identified a monophyletic ‘*gracilis* group’ and ‘*mariei* group’, with a basal split in the ‘*mariei* group’ between the southern region lineage *N. mariei* sensu lato as the sister lineage to the northern taxa *N. rankini* and *N. greeri* from the central-east region. This scheme of relationships within the ‘*mariei* group’ based on morphological evidence is unlikely to change with the inclusion of the five additional taxa in the group recognized here, and would yield a basal dichotomy between the two taxa endemic to the southern ultramafic block (*N. mariei* s.s. + *N. fuscus*) as the sister to a clade of seven species in the central and northern regions. Such a pattern was seen in the genetic phylogeny for *Marmorosphax* (Sadlier *et al.* 2009) which resulted in the southern region endemic *M. montana* as the sister to all other species in the genus, most of which were restricted to the central and northern regions.

The presence of *N. fuscus* as a genetically divergent sibling species within *N. mariei* was unexpected. The geographic distance between populations of *N. fuscus* on Mt. Mou, Mt. Dzumac or Mt. Vulcain to the nearest population of *N. mariei* on Mt. Koghis is relatively small (~20 km). Humid forests over much of the southern ultramafic region are highly fragmented, occurring as patches of varying size near the summit of peaks and as small and widely scattered patches along the intervening ridgelines, otherwise much of the ranges are covered by maquis shrubland, and humid forests at lower elevations are mainly restricted to creek and gully lines. Historically, forest cover is thought to have been much more extensive. The level of fragmentation and discontinuity of forests seen today represents a combination of both historical contraction of forest over time through changes in climate (Pintaud 2001), over which is lain more recent human-induced changes, mainly through increased fire (Jaffré *et al.* 1998). However, the high level of genetic differentiation between the two taxa indicates they have been separated for a long time, and most likely reflects a major historical barrier to dispersal for forest dependent species, effectively maintaining separation of *N. mariei* and *N. fuscus* in the region. This barrier may reflect a long-term discontinuity in forest cover in the region, and by inference the historical persistence of extensive bands of maquis on the ranges, of even during periods when rainforest was otherwise more widespread.

The sampling for *N. mariei* s.s. is limited to several sites but the level of intraspecific genetic differentiation detected between the population on Mt. Koghis to those on the Goro Plateau and Rivière Bleue (7.8-8.3%) indicates the existence of significant regional sub-structuring within the species. Similarly, the genetic distance between the populations of *N. fuscus* on Mt. Mou, Mt. Dzumac or Mt. Vulcain (average 4.7-7.0) also indicates substantial, but more recent historical sub-structuring and isolation of the humid forest patches on the ranges in this region.

Nannoscincus gracilis occurs on both metamorphic and ultramafic surfaces in the central-east ranges between the Houailou valley and Thio valley, at a number of locations on adjacent metamorphic ranges of the Chaîne Centrale in the central-east region ranges between the Houailou and Amoa valleys, and as isolated populations in the north-east

and southern regions. However, no *N. 'gracilis group'* species have been recorded from the central-west and north-west ultramafic ranges. Like all species in the genus members of the '*gracilis group*' are highly dependent on moist, primarily humid forest habitats. The occurrence of taxa within the '*gracilis group*' in most of the large forest blocks of the Chaîne Centrale indicate an historically more continuous presence along these ranges, with the moderate to high levels of inter-taxon/population genetic differentiation the result of continued long-term isolation, most likely as a consequence of forest fragmentation in combination with a limited dispersal ability.

The absence of '*gracilis group*' species from the central-west and north-west region ultramafic ranges also lends further support for the existence of both long-term and persistent historical barriers to dispersal between this chain of ultramafic massifs and adjacent metamorphic ranges of the Chaîne Centrale for lizard species that are highly dependent on moist forest, or have limited dispersal ability. Support for the historical isolation of the west coast massifs has been demonstrated in the molecular phylogenies of moisture-dependant species in the genus *Marmorosphax* (Sadlier *et al.* 2009) which retrieves a well supported group of three (potentially five) putative narrow-range taxa restricted to this region. The species of *Marmorosphax* require habitat which provides a humid microclimate, that is, they are moisture dependent. Historical diversification within this western clade of *Marmorosphax* species appears to be 'massif driven', the level of genetic divergence between taxa indicating long-term isolation of these massifs. The persistence of barriers to dispersal between massifs is also evident in the inter-population relationships of the widespread *M. tricolor* in which populations on the central-west ultramafic massifs are genetically closer to those on the nearby metamorphic ranges than with the adjacent free-standing isolated massifs, clearly indicating greater potential for gene flow with populations on the adjacent metamorphic substrates for moisture dependant species, even in more recent historical times. However, despite the apparent ability of *M. tricolor* to bridge the barrier between the central-west massifs and the adjacent metamorphic ranges in recent times there is no evidence of any of the populations of *N. gracilis* extending west from the Chaîne Centrale onto the central-west ultramafic ranges, indicating the dispersal ability of this species is significantly more limited.

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AppENDIX 1

List of specimens used in this study. For museum acronyms see materials and methods.

GENUS	SPECIES	VOUCHER NUMBER	LOCALITY	GENBANK ACCESSION
OUTGROUP				ND2
<i>Celatiscincus</i>	<i>euryotis</i>	AMS R.138574	Île des Pins	DQ675204
<i>Graciliscincus</i>	<i>shonae</i>	AMS R. 165813	Mt. Ouin	DQ675207
<i>Kanakysaurus</i>	<i>viviparus</i>	AMS R.161299	Île Pott, îles Belep	DQ675209
<i>Lacertoides</i>	<i>pardalis</i>	AMS R.148051	Kwa Néie	DQ675211
<i>Lioscincus</i>	<i>nigrofasciolatus</i>	AMS R.138624	île des Pins	DQ675216
<i>Lioscincus</i>	<i>steindachneri</i>	AMS R.149890	Mé Adéo	DQ675218
<i>Lioscincus</i>	<i>tillieri</i>	AMS R.148037	Mt. Vulcain	DQ675220
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 214451	Mt. Koghis	DQ675227
<i>Phoboscincus</i>	<i>garnieri</i>	AMS R.151964	Mt. Dore	DQ675237
<i>Sigaloseps</i>	<i>deplanchei</i>	AMS R.148065	Plaine des Lacs	DQ675238
<i>Simiscincus</i>	<i>aurantiacus</i>	AMS R.144356	Mt. Koghis	DQ675250
<i>Tropidoscincus</i>	<i>variabilis</i>	AMS R.161879	Monts Kwa Né Mwa	DQ675242
INGROUP				
<i>Nannoscincus</i>	<i>exos</i>	AMS R.174663	Roches d'Ouaieme	JX015441
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.165919	Mt. Dzumac	JX015442
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.165921	Mt. Dzumac	JX015443
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.146484	Mt. Mou	DQ675232
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.148006	Mt. Mou	N/A
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.148007	Mt. Mou	N/A
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.158788	Mt. Mou	JX015444
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.158789	Mt. Mou	N/A
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.172572	Tontouta valley	JX015445
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.172573	Tontouta valley	JX015446
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.172574	Tontouta valley	JX015447
<i>Nannoscincus</i>	<i>fuscus</i>	AMS R.172575	Tontouta valley	JX015448
<i>Nannoscincus</i>	<i>garrulus</i>	AMS R.163453	Pic Ningua	DQ675261
<i>Nannoscincus</i>	<i>garrulus</i>	CAS 226166	Pic Ningua	DQ675262
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.135066	Col de Nassirah	JX015449
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.135069	Col de Nassirah	JX015450
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.165834	Mt. Aoupinié	JX015451
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.165835	Mt. Aoupinié	JX015452

GENUS	SPECIES	VOUCHER NUMBER	LOCALITY	GENBANK ACCESSION
INGROUP				
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.163458	Col de Petchécara	JX015453
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.172535	Bogata	JX015454
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.172536	Bogata	JX015455
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.165852	Col des Roussettes	JX015456
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.167846	Poro	JX015457
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.167847	Poro	JX015458
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.149892	Mé Adéo	DQ675233
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.149893	Mé Adéo	JX015459
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.149894	Mé Adéo	JX015460
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.147882	Plateau de Dogny	JX015461
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.147883	Plateau de Dogny	N/A
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.135174	Sarraméa	N/A
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.135175	Sarraméa	N/A
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.144122	Sarraméa	N/A
<i>Nannoscincus</i>	<i>gracilis</i>	AMS R.144123	Sarraméa	JX015462
<i>Nannoscincus</i>	<i>greeri</i>	AMS R.165975	Pic d'Amoa	JX015463
<i>Nannoscincus</i>	<i>greeri</i>	CAS 231942	Pic d'Amoa	DQ675230
<i>Nannoscincus</i>	<i>hanchisteus</i>	AMS R.149356	Pindai	JX015464
<i>Nannoscincus</i>	<i>hanchisteus</i>	AMS R.149355	Pindai	DQ675270
<i>Nannoscincus</i>	<i>humectus</i>	AMS R.149498	Forêt Plate	DQ675269
<i>Nannoscincus</i>	<i>manautae</i>	AMS R.163123	Massif de Kopéto	JX015465
<i>Nannoscincus</i>	<i>manautae</i>	MNHN 2003.1001	Massif de Kopéto	JX015466
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.135111	Mt. Koghis	DQ675231
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.144337	Mt. Koghis	JX015467
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.167108	Rivière Blanche	JX015468
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.168153	Rivière Blanche	JX015469
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.168154	Rivière Blanche	JX015470
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.166136	Goro Plateau	JX015471
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.166135	Goro Plateau	JX015472
<i>Nannoscincus</i>	<i>rankini</i>	AMS R.149387	Mt. Aoupinié	JX015473
<i>Nannoscincus</i>	<i>slevini</i>	AMS R.147879	Plateau de Dogny	DQ675256
<i>Nannoscincus</i>	<i>slevini</i>	AMS R.147880	Plateau de Dogny	N/A
<i>Nannoscincus</i>	<i>slevini</i>	AMS R.135075	Koh (vicinity)	JX015474
<i>Nannoscincus</i>	<i>slevini</i>	AMS R.135148	Koh (vicinity)	JX015475
<i>Nannoscincus</i>	<i>koniambo</i> n. sp.	MNHN 2011.0283	Massif de Koniambo	JX015476
<i>Nannoscincus</i>	<i>koniambo</i> n. sp.	AMS R.171461	Massif de Koniambo	JX015477