

Massif Speciation Events in New Caledonian Lizards: Diversification in the Genus *Marmorosphax* (Scincidae) Tracks Isolation on the Island's Ultramafic Surfaces

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An extensive molecular phylogeny of the endemic New Caledonian scincid lizard *Marmorosphax* based on the mitochondrial ND2 gene retrieves four major lineages. The basal divergences within the phylogeny progressively split off lineages concordant with the boundaries of the island's major ultramafic regions, and are believed to be the product of vicariant events. Three of these lineages are restricted to ultramafic surfaces and are allopatric in distribution: one, comprising a single species, *M. montana*, occurs in high elevation habitat in the ranges of the southern ultramafic region; another, comprising the taxa *M. kaala*, *M. bouldina*, and *M. taom*, occupies ultramafic massifs in the central-west and northwest region; and the third, represented by the undescribed species *M. cf. tricolor*, is present in the central-east region ultramafic ranges. The fourth major lineage is represented by the widespread species *M. tricolor* which, by default of earlier vicariant events, evolved within the north-eastern/central-east metamorphic region, and its presence now on ultramafic surfaces is attributed to subsequent range expansion. Past periods of aridity and accompanying widespread loss of forest habitat at low to mid elevation are the likely historical processes initiating regional isolation of *Marmorosphax* populations on ultramafic surfaces, with the persistence of higher elevation forest and/or moister habitat providing refugia within which isolated populations in the ultramafic regions further diversified. While some of the newly sampled populations in this study potentially represent genetically distinct undescribed taxa, the samples to allow the complementary morphological comparisons required are insufficient. The *Marmorosphax* species restricted to particular ultramafic massifs are threatened primarily by activities of an expanding nickel mining industry, as are numerous other restricted range lizard species on these surfaces, and the described taxa have been assessed under International Union for the Conservation of Nature (IUCN) criteria as Endangered (*M. bouldina*, *M. montana*, and *M. taom*) to Critically Endangered (*M. kaala*).

KEYWORDS: New Caledonia, Scincidae, *Marmorosphax*, phylogeography, ultramafic.

INTRODUCTION

The scincid lizard fauna of New Caledonia is exceptionally rich and diverse with 63 recognized named species in 18 genera that are strictly endemic (or nearly so) to the territory. Molecular studies based on mitochondrial and nuclear DNA sequence data (Smith et al. 2007; Chapple et al. 2009) have identified the endemic skink genera of New Caledonia as part of a monophyletic ‘Tasmantis’ group that also includes the endemic New Zealand and Lord Howe Island taxa.

One of the most significant attributes of the New Caledonian lizard fauna to emerge in recent years is the presence of extensive narrow-range endemism throughout the main island, or Grande Terre. The exceptional diversity now documented likely reflects the historical interplay of geology, climate, and vegetation that has yielded numerous cladogenic events which have subdivided ancestral populations and promoted speciation within lineages. Underlying this exceptional diversity is the extent to which historical processes on the islands ultramafic surfaces have played in driving speciation in the endemic lizard fauna. The ultramafic surfaces in New Caledonia cover about 5,500 km² or about one third of its total land area (Jaffré et al. 1987), and are a dominant part of the landscape. They are derived from an overthrusting of oceanic lithosphere over continental lithosphere during the late Eocene to form the New Caledonian Peridotite Nappe. The timing at which emergent land was present in the region and the dating of the New Caledonian fauna and flora has been the focus of much debate (see Nattier et al. and Giribet and Baker 2019). The most recent assessment determined that emergent land has existed in the area occupied by the Grande Terre since 25Ma (Maurizot and Campbell 2020). Postobduction tectonic events and erosion have disrupted the Peridotite Nappe into units (massifs) of different sizes (Maurizot et al. 2020) seen today. Ongoing studies in the past two decades have identified both broad-scale and highly localized endemism on the islands ultramafic massifs, in particular those in the central-west/northwest regions (Bauer et al. 2006; Sadlier et al. 2004, 2009, 2014; Sadlier, Bauer et al. 2014a, 2014c), and on the ranges of the Chaîne Centrale in the southern region (Bauer et al. 2006, 2008; Sadlier et al. 2006, 2013, 2014 2018; Sadlier, Bauer et al. 2014b, 2014c). The presence of a number of endemic species on ultramafic surfaces in both areas has identified each region as a distinctive phylogeographic zone for lizards (Sadlier 2010) (see Fig. 1). For skinks the southern ultramafic ranges have an extensive suite of taxa restricted to the region which includes four endemic genera with nine constituent species and seven endemic species from within more widespread genera (in total ~40% of the scincid lizard fauna of southern New Caledonia). A similarly extensive suite of ten skink species is restricted to the central-west/northwest region ultramafic ranges, but no skink genera are endemic to the ultramafic surfaces of this region. By comparison, the extent of narrow-range endemism within the skink fauna on the island’s metamorphic surfaces is modest, with only a few species restricted to small areas, one on the summit area of Mt. Aoupinié in the central-east region (*Nannoscincus greeri*) and one in the ranges of the Roche des Ouaïème in the northeast (*Nannoscincus exos*). Rather, the tendency is towards broader scale regional endemism as typified by the various species of *Caledoniscincus* (Sadlier et al. 1999) and most *Nannoscincus* (Sadlier et al. 2002). Similarly, high levels of microendemism characterize other elements of the island’s fauna (Caesar et al. 2017), but none of these studies have sampled the ultramafic surfaces as extensively or documented the extent of microendemism seen in the New Caledonian lizard fauna on these surfaces.

While it is clear the endemic New Caledonian skink radiation is highly diverse with well-defined genera (Sadlier 2010; Sadlier et al. 2015), there are no clear and well supported relationships basally between groups of genera, other than for the diminutive *Nannoscincus* as the sister to a larger group containing most other New Caledonian taxa (see molecular phylogenies of Smith et

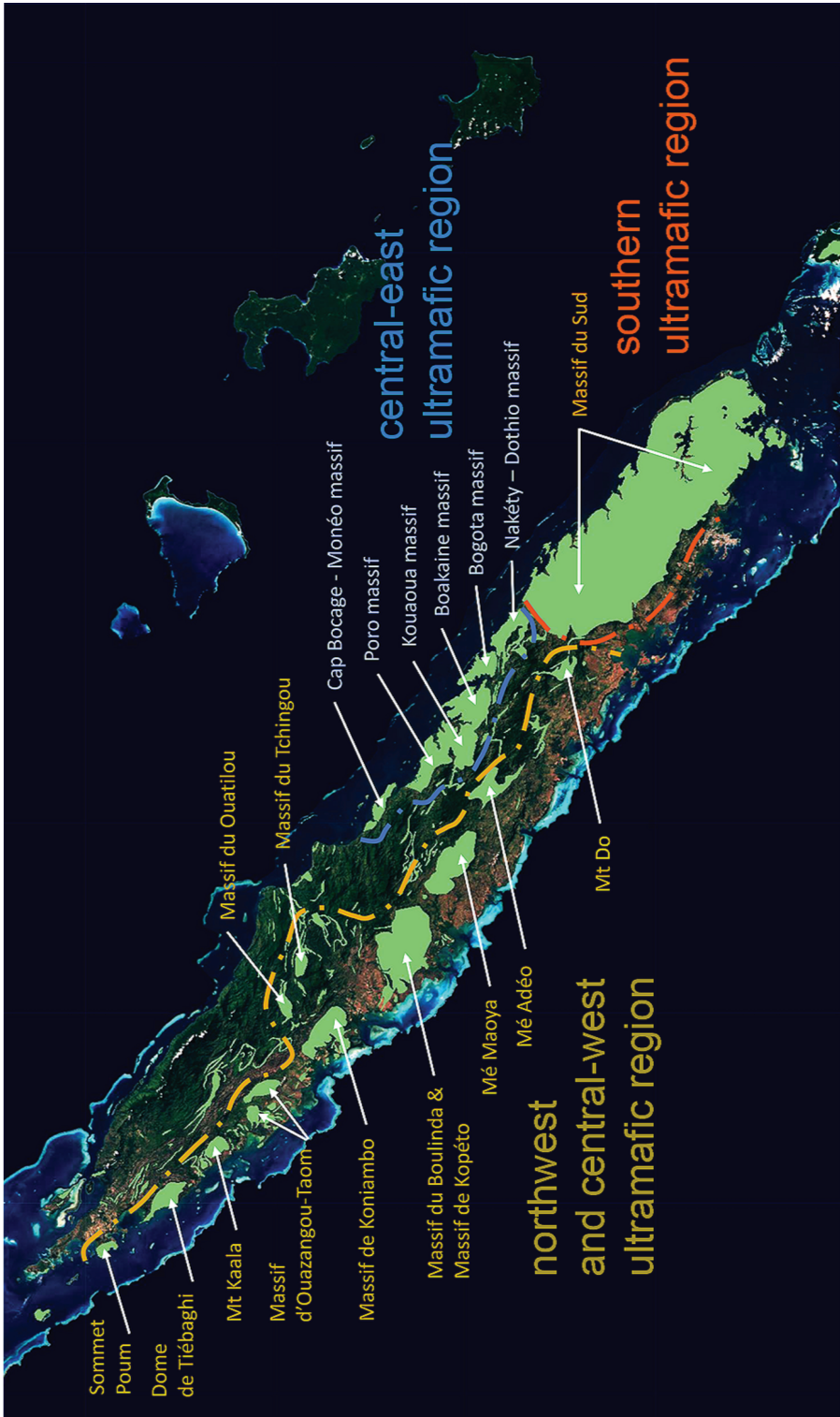


FIGURE 1. Distribution of ultramafic surfaces in New Caledonia: yellow = northwest and central-west ultramafic region; blue = central-east ultramafic region; orange = southern ultramafic region.

al. 2007 and Chappell et al. 2009). As such, no broad phylogeographic trends are apparent in the distribution of the supra-generic groups identified by molecular data, and the clearest (and sometimes repeated) phylogeographic patterns come from the distribution of taxa within genera.

The genus *Marmorosphax* is one of the more speciose New Caledonian skink genera, with five described species and one or more undescribed putatively distinctive taxa. An earlier genetic study using DNA sequence data (Sadlier et al. 2009) identified three distinct evolutionary lineages within the genus, the southern ultramafic region species *M. montana*, a group of several narrow range species from the central-west/northwest ultramafic ranges comprising *M. kaala*, *M. taom*, and *M. bouldinda*, and lastly, the widespread *M. tricolor*. Subsequent field studies have yielded additional genetically distinct massif-specific populations of *Marmorosphax* in the northwest ultramafic ranges, and a lineage restricted to the ultramafic surfaces of the central-east related to, but genetically distinct from, *M. tricolor*. These field studies have also greatly extended the range of genetic samples available for *M. tricolor*.

The species of *Marmorosphax* have a relatively specialized biology. Individuals of *M. tricolor* are active within the confines of their sheltering sites by day, but are secretive and rarely seen in the open, usually only appearing to venture beyond their sheltering sites in the late afternoon and evening, a behavioral trait that likely extends to other members of the genus. *Marmorosphax tricolor* has been recorded mainly from humid forest habitat on both metamorphic and ultramafic surfaces (Bauer and Sadlier 2000), but also extends into maquis habitats where the species niche requirements (a humid and cool microclimate) are met by the presence of a surface rock matrix that provides sheltering sites with the required niche attributes. On metamorphic surfaces the concordance between the distribution of *M. tricolor* to that of primary forest habitats is particularly strong, and it has not been recorded from other habitat types on this surface. Although less well known, the remaining species, all of which occur only on ultramafic surfaces, appear to have similar biological traits to *M. tricolor* and have been recorded mainly from mid to high elevation forest habitat but also occur in dense maquis habitat with a suitable surface rock matrix (*M. taom*, *M. montana* and *M. cf. tricolor*). Overall, the habits and habitat preferences of *Marmorosphax* spp. indicate they are 'moisture' dependent, that is they require a humid and cool environment, and their distribution across the landscape is tempered primarily by these factors.

Diversification within the genus is most pronounced on the massifs across the central-west/northwest ultramafic region. These massifs are mostly situated along or near the west coast in the rain-shadow of the eastern and interior ranges which form the extensive and continuous Chaîne Centrale, and typically experience much lower and marked seasonality in rainfall than eastern ranges. However, they are also subject to the 'Massenerhebung' effect which lowers the average altitude of formation of cloud masses, increasing atmospheric humidity until saturation and giving rise to significant "occult" or hidden precipitation at elevations between 600 and 1,500 m. (Fig. 2). This increased moisture in the form of fog and water droplets (Nasi et al. 2002) in turn supports peak and ridge-top forest formations. A number of lizard species are restricted to individual peaks and massifs of these central-west/northwest ultramafic ranges. Among the dipodactylid geckos five species of *Dierogekko* are each known only from a single massif (Bauer et al. 2006), as are several species of *Bavayia* in the *B. montana* complex and genus *Oedodera* (Bauer et al. unpublished research). A number of skinks are also known only from a single massif, most from forest habitat at or near the summit (*Nannoscincus koniambo* - Massif de Koniambo, *Nannoscincus manautei* - Massif de Kopéto, *Phaeoscincus taomensis* - Mt. Taom). Forest habitat on these massifs is now typically present as a mosaic of patches (Fig. 3a), usually on the summit area or in gullies on the slopes, with extensive areas of low open to dense maquis between. A feature of the summit areas is the presence of an exposed cuirasse rock cap that variably occurs on the tops of the



FIGURE 2. Persistent high elevation cloud formation on northwest Massif Katépahié (adjacent to the Massif de Koni-ambo) during the dry season.

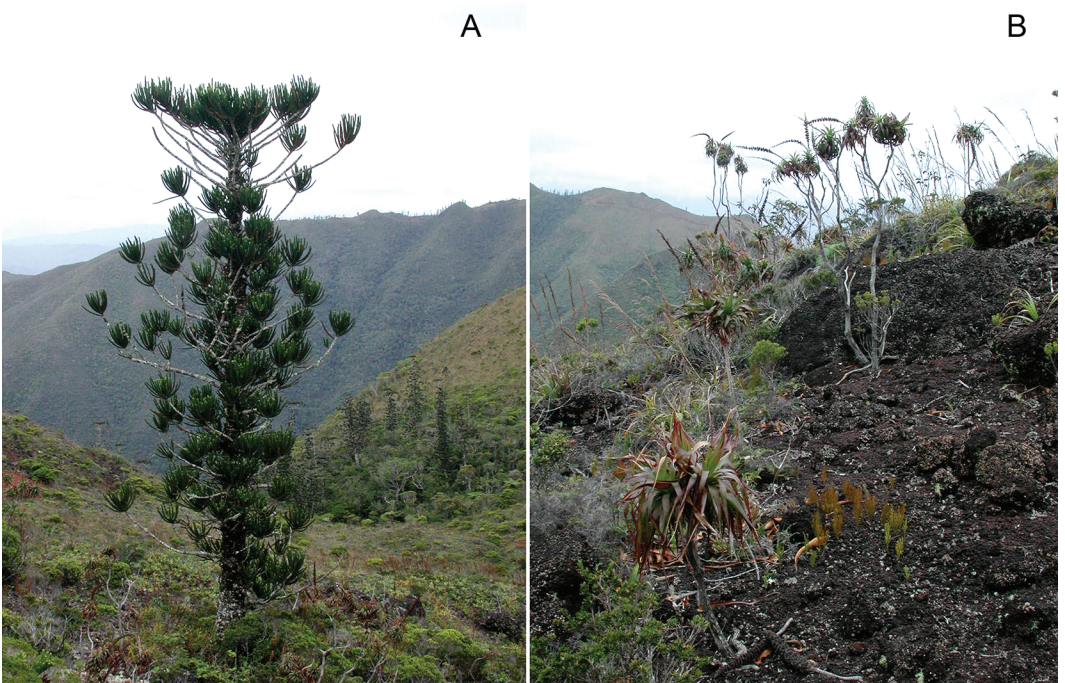


FIGURE 3. High elevation forest habitat on the Massif d'Ouazangou-Taom (A) and exposed cuirasse rock cap variably distributed across the summit area and ridges of massifs in the central-west and northwest ultramafic region (B).

massifs and associated ridges (Fig. 3b). This rock matrix provides important microhabitat for skinks in the form of both shelter and a cool and humid sub-surface environment in areas of both forest and dense maquis habitats. The southern ultramafic ranges also have a number of species restricted to higher elevation habitat, primarily forest. Of these several are localized in distribution (several narrow-range taxa in the genus *Sigaloseps* Sadlier, Bauer et al. 2014b, and *Phaeoscincus ouinensis* Sadlier, Bauer et al. 2014c), and *M. montana* shows substantial genetic sub-structuring of populations across peaks in the region.

The extent of micro-endemism seen on the islands ultramafic surfaces has most likely been driven by contraction and fragmentation of forest habitat in response to historically adverse climatic conditions, whereby preferred habitat is reduced to the upper altitudinal areas of massifs and ranges. Under such conditions populations of species that fail to adapt become isolated on the summit areas, a scenario consistent with the concept of niche conservatism as outlined by Wiens (2004). In this context, many of the narrow-range endemics on ultramafic surfaces represent the evolutionary end products of extreme cases of historical forest fragmentation and contraction, and their continued existence on these massifs and peaks not only identifies these areas as historical refugia, but also as potential refugia for taxa now more widely distributed under future climate warming.

The ultramafic surfaces of New Caledonia are rich in iron and magnesium and several heavy metals, most notably nickel, and as such, many are, or will be, under considerable pressure from mining activities (Pascal et al. 2008). Of all the landscapes in New Caledonia the ultramafic surfaces are of the highest conservation significance for lizards given their exceptionally high levels of regional and localized endemism. Almost half of the described endemic skinks ($n = 28$, ~45%) and geckos ($n = 17$, ~45%) are restricted to ultramafic surfaces, and the number of geckos restricted to central-west/northwest ultramafic ranges is expected to nearly double from 6 to 11 with the formal description of known new species. Further, the summit areas of a number of ultramafic peaks have either not, or only poorly, been investigated for lizards. As such, the current state of knowledge of species restricted to higher elevation habitats on ultramafic surfaces is likely to represent a substantial underestimation, as evidenced by the recent description of the two species of *Phaeoscincus*, each known from a single specimen, one (*P. toamensis*) from the summit of the massif of Mt. Taom in the northwest ultramafic region, and one (*P. ouinensis*) from the summit area of Mt. Ouin in the southern ultramafic region (Sadlier et al. 2014c).

Over half of the 25 (~55%) described lizard species restricted to ultramafic surfaces have been identified as Endangered or Critically Endangered on IUCN criteria, including three of five described species of *Marmorosphax*, with mining identified as the primary threat for 19 of these. The presence of such extensive narrow range endemism in areas actively or potentially under threat from intensive development clearly identifies the ultramafic ranges of New Caledonia as true 'hotspots' for conservation in the strictest sense of the term (Mittermeier et al. 1999). This situation is further exacerbated by many of these narrow range species being restricted to the summit areas of massifs, the area where remnant tracts of forest and/or exposed cuirasse rock cap habitat occurs, and where mining activity is often likely to be most intensive and destructive. Ironically, having survived millennia in an environment shaped by its geological heritage, the high elevation forests on New Caledonia's ultramafic surfaces and many of the lizard (and other) species peculiar to them, may be at the brink of extinction in the face of escalating development of the mineral resources they sit on (Fig. 4a and 4b).

The information presented here represents the result of extensive field work over a period of 20 years on the Grande Terre, and builds on the results of previous genetic work on *Marmorosphax* (Sadlier et al. 2009). Our primary purpose is to present the extent of diversity in the genus uncov-

ered in this study which identifies further narrow range lineage endemism in the central-west/north-west ultramafic ranges and southern ultramafic ranges, reinforcing the identity of these regions each as phylogeographic zones for fauna, and providing some insight into the processes likely driving speciation on ultramafic surfaces across the whole of New Caledonia. We have refrained from attempting to formally describe some of the novel lineages identified in this study until samples to adequately assess the extent of morphological and/or genetic variation between these lineages are available. In this context further field research is required to fully appreciate and document the extent of diversity on the islands' ultramafic surfaces.

MATERIAL AND METHODS

Acronyms: AMS - Australian Museum, Sydney; CAS - California Academy of Sciences; and MNHN - Muséum National d'Histoire Naturelle, Paris.

Genetic studies: The species phylogeny for *Marmorosphax* represents 162 individuals from 46 collecting sites distributed across the majority of large, extant humid forest blocks in New Caledonia.

We obtained sequence data from a 514 bp fragment of the mitochondrial NADH dehydrogenase subunit 2 gene (ND2) for all described species of *Marmorosphax* (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 ND2 was amplified using a double-stranded Polymerase Chain Reaction (PCR). Included in the reaction were 2.5 µl genomic DNA, 2.5 µl (concentration 10µM) light strand primer (METF6 L4437a 5'-AAGCTTTCGGGCCCATACC-3', Macey et al. 1997), 2.5 µl (concentration 10µM) heavy strand primer (TRPR3 H5540 5'-TTTAGGGCTTTGAAGGC-3', Macey et al. 1997), 2.5 µl dinucleotide pairs (1.5 µM), 2.5 µl 5x buffer (1.5 µM), MgCl 10x buffer (1.5 µM), 0.18 µl Taq polymerase (5u/µl), and 9.82 µl H₂O. All reactions were executed on an Eppendorf Mastercycler gradient

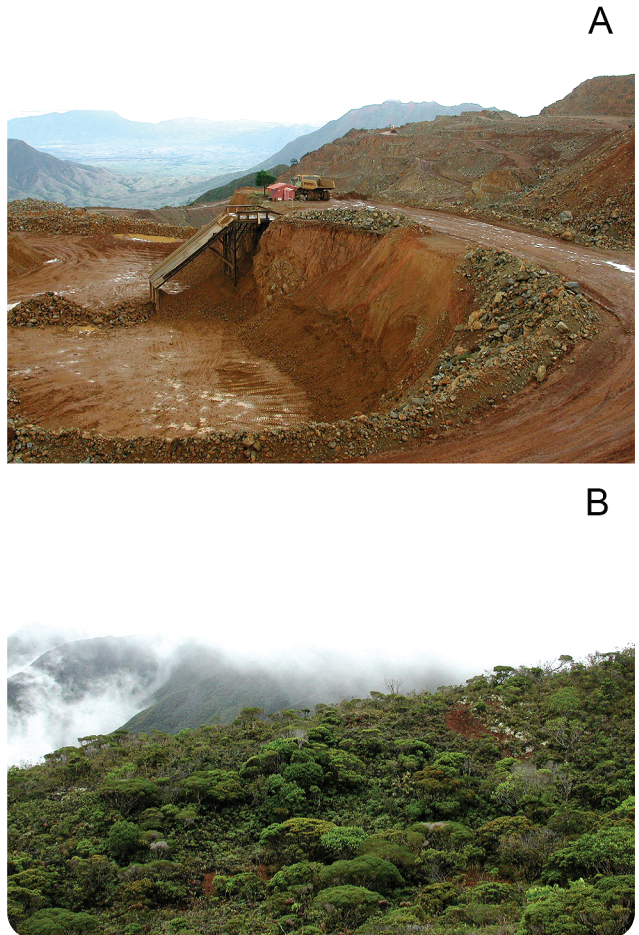


FIGURE 4. Mining on the Massif d'Ouazangou-Taom around 800 m. (A), only 200 m. in elevation below the summit area (B) which is home to the type population of *M. taom*, and only known location for the skinks *Phaeoscincus taomensis* and *Nannoscincus cf. manautei*, and the undescribed gecko *Bavayia cf. montana*.

thermocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 s, annealing at 50–54°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles. PCR products were visualized on 1.0% agarose gel electrophoresis.

PCR products were purified using AMPure magnetic bead solution (Agentcourt 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 (Agentcourt 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 manually. Mesquite v3.61 (Maddison and Maddison 2015) was used to check for premature stop codons and to ensure that the alignment was in the correct amino acid reading frame.

We conducted both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. We partitioned the data by codon partitions (three partitions in total) and estimated the best-fit models of molecular evolution for each partition in IQ-TREE (Nguyen et al. 2015) for the ML analysis using the Bayesian Information Criterion (BIC; Schwarz, 1978) implemented in ModelFinder (Kalyaanamoorthy et al. 2017). The ML analysis was performed using IQ-TREE v1.6.7 (Nguyen et al. 2015) with 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation (UFBoot) algorithm (Minh et al. 2013; Hoang et al. 2017). For the BI we used BEAST v2.6 (Bouckaert et al. 2014) and bModelTest (Bouckaert and Drummond 2017) to numerically integrate over uncertainty in models of substitution, while generating the phylogeny using a Markov chain Monte Carlo (MCMC). The MCMC chain was ran for 50 million generations while sampling every 5000 generation from the chain. To visualize if the effective sample sizes (ESS) were greater than 200 we used Tracer v1.7 (Rambaut et al. 2018) and if samples were, we assumed stationarity. Following confirmation that all ESS values reached stationarity we constructed a maximum clade credibility (MCC) tree using TreeAnnotator v2.6 (Bouckaert et al. 2014) with a 25% burnin and using mean node heights. We considered nodes strongly supported if ML UFboot were ≥ 95 and BPP were ≥ 0.95 (Huelsenbeck et al. 2001; Erixon et al. 2003; Huelsenbeck and Rannala 2004; Wilcox et al. 2002; Nguyen et al. 2015). Average pairwise sequence divergences (p -distances) for the major clades of *Marmorosphax* were calculated for between group distances and within groups using MEGA v7 (Kumar and Tamura, 2016) under the following conditions: substitutions included; transitions and transversions; uniform rates among sites and gaps were treated as missing data.

RESULTS

Phylogenetic relationships: The final sequence alignment of ND2 comprised 514 bp with 275 parsimony-informative sites based on ingroup and outgroup samples. The ML analysis selected K2P+G4, TN+F+G4, and TIM2+F+G4 for the models of molecular evolution for the 1st, 2nd, and 3rd codon positions respectively. Models selected from the bModelTest were 121134 (cumulative support = 19.5%), 123143 (cumulative support = 27.8%), and 121341 (cumulative support = 59.0%), for the 1st, 2nd, and 3rd codon positions respectively. The ML and the BI analyses produced highly concordant trees with only a few branches not recovered by both analyses.

The monophyly of *Marmorosphax* has been strongly supported in previous molecular studies (Smith et al. 2007; Sadlier et al. 2009). The mitochondrial ND2 gene dataset presented here

TABLE 1: Pairwise matrix of mean genetic distances between major groups (Groups 1–4, Fig. 5) within *Marmorosphax* (uncorrected p-distances) for the mtDNA ND2 gene. Values in bold represent within population mean uncorrected p-distances.

	1	2	3	4
1 – central-west/northwest ultramafic region endemics	6.60%			
2 – southern ultramafic region endemics (<i>M. montana</i>)	10.10%	3.10%		
3 – central-east ultramafic endemics (<i>M. cf. tricolor</i>)	10.80%	10.10%	4.20%	
4 – <i>M. tricolor</i>	9.80%	10.40%	10.10%	3.50%

TABLE 2: Pairwise matrix of mean genetic distances between nodes within the central-west/northwest ultramafic region endemic *Marmorosphax* (Group 1 clades 5–9; Fig. 5) (uncorrected p-distances) for the mtDNA ND2 gene. Values in bold represent within-population mean uncorrected p-distances.

	5	6	7	8	9
5 – <i>M. kaala</i> Mt. Kaala	n/a				
6 – <i>M. boulinda</i> Massif du Boulinda	7.30%	0.50%			
7 – <i>M. boulinda</i> Massif du Tchingou	7.70%	7.20%	1.60%		
8 – <i>M. taom</i> Mt. Taom	6.50%	8.60%	9.00%	1.20%	
9 – <i>M. taom</i> Dôme de Tiébaghi	8.00%	9.80%	10.00%	3.30%	0.20%

TABLE 3: Pairwise matrix of mean genetic distances between nodes within *Marmorosphax montana* populations (Group 2 clades 10–12; Fig. 5) for the mtDNA ND2 gene. Values in bold represent within population mean uncorrected p-distances.

	10	11	12
10 – <i>M. montana</i> Camp des Sapins	0.70%		
11 – <i>M. montana</i> Forêt de Saille	7.80%	0.00%	
12 – <i>M. montana</i> Mt. Ouin	6.90%	2.90%	0.00%

1, this study) as the sister species to all other species of *Marmorospax*. The present study also differs in the inclusion of additional populations in Group 1 and Group 2 clades, and of populations comprising a previously unknown lineage, Group 3 *M. cf. tricolor*. The extent of within-group genetic differentiation derived from this much-expanded sampling is discussed below in the context of the lineages recovered.

Group 1 *M. boulinda/taom/kaala*: the earlier study by Sadlier et al. (2009) retrieved a relatively high level of genetic differentiation between taxa on the Kaala, Ouazangou-Taom and Boulinda massifs, which was pivotal in assigning species status to the three taxa described given sample sizes from each massif were small ($n = 2, 5,$ and 2 respectively). A similarly high level of genetic differentiation is retrieved here between populations from these massifs (Table 2).

The expanded sampling for the central-west and northwest ultramafic regions now includes populations from the Massif du Tchingou and from Dome de Tiébaghi. The level of differentiation between the type population of *M. boulinda* from the Massif du Boulinda and the population from the Massif du Tchingou (uncorrected p mean 7.2% [Table 2]) is similar to that seen in pairwise comparisons between topotypic *M. boulinda*, *M. taom* and *M. kaala*. However, the type population of *M. boulinda* from Massif du Boulinda is known only from two individuals (an adult male and adult female) and the population from the Massif du Tchingou from eight specimens. Morpholog-

ical comparisons have proved of limited utility in assessing the status of these two geographically disjunct populations given the small sample size of the type population on the Massif du Boulinda ($n = 2$), particularly with regard to color and pattern.

The population from Dome de Tiébaghi is here retrieved as the sister to the type population of *M. taom* from the Massif d'Ouazangou-Taom. The level of differentiation between the two populations is markedly lower (uncorrected p mean 3.3%) than that seen in pairwise comparisons of populations on other massifs in the region, and there are no corresponding morphological markers to differentiate these two populations. Rather, adult females from both populations share a unique dark chevron-shaped marking on the throat, a morphological trait that supports the close relationship of these populations as a single species, and which also serves to diagnose the species from all other *Marmorosphax*.

Group 2 *M. montana*: two populations from the southern ultramafic region not represented in the earlier study by Sadlier et al. (2009) are here included, one from Forêt de Saille and one from Camp des Sapins, both from the north of the region and extending the species distribution the full length of the Massif du Sud. The level of differentiation between the populations (Table 3) from Forêt de Saille and Mt. Ouin is low (uncorrected p mean 2.9%), but significantly greater between these and the population from Camp des Sapins (uncorrected p mean 7.8% and 6.9% respectively).

Group 3 *M. cf. tricolor*: the Group 3 *M. cf. tricolor* lineage from the central-east region ultramafic region was retrieved as the well supported (UFboot = 99 and BPP = 1.0), but moderately divergent (uncorrected p mean 7.8%) sister to Group 4 *M. tricolor*. It comprises two well supported sub-lineages in the north of the central-east ultramafic ranges, one a single population from Njéré near Poro, and one represented by populations scattered across Mt. Menazi – the two sub-lineages are disjunct in distribution and separated by the valley of the Koua River. The identity of the Menazi sub-lineage is confounded by discordance between the genetic assignment of some individuals and the pattern of throat color in females, the morphological trait that otherwise diagnoses it from *M. tricolor* (males of either the Group 3 *M. cf. tricolor* lineage and Group 4 *M. tricolor* are morphologically indistinguishable from each other).

Group 4 *M. tricolor*: the numerous populations referable to Group 4 *M. tricolor* lineage form a well-supported lineage (UFboot 100 and BPP 1.0). The internal genetic structure from a broad range of samples across the Grande Terre shows some regional sub-structuring but with overall relatively low levels of divergence, even towards the base of the species phylogeny. Further, the internal genetic structure within this lineage is characterized by low support for most basal splits in the phylogeny and a generally low level of inter-population genetic divergence, although some of the broader groups received a moderate level of support and showed a level of genetic differentiation (uncorrected p intrapopulation mean 3.5%) approaching that seen between disjunct populations of the Group 2 *M. montana* lineage.

In summary the genetic data supports monophyly and distinctiveness of lineages representing the five currently recognised species in the genus, and several previously unrecognized and highly differentiated lineages which at this point are problematic to define and require further investigation.

DISCUSSION

The distribution of species Groups 1–3 and populations within are mostly consistent with geological boundaries of the island's ultramafic regions. The concordance between the distribution of the major genetic lineages and that of the islands ultramafic surfaces suggest vicariant events in the

history of the genus driven by factors that progressively isolated regional metapopulations (physically and/or biologically) in the major ultramafic blocks. Initially by isolation of populations in the western ultramafic region that gave rise to the Group 1 lineage species (*M. kaala*, *M. bouldina*, and *M. taom*), followed by isolation of populations in the southern ultramafic region the Group 2 lineage (*M. montana*), followed by isolation of populations in the central-east region ultramafic surfaces from populations in the adjacent metamorphic surfaces of the central-east and northeast regions giving rise to the Group 3 (*M. cf. tricolor*) and Group 4 lineage (*M. tricolor*) species respectively. The extent of intra-lineage differentiation seen within these major lineages on ultramafic surfaces indicate ensuing lineage splitting arising from more localized isolation of populations after primary divergence events.

Historical changes in climate have been proposed as a significant factor in the distribution of vegetation on New Caledonia, particularly with respect to size, shape and area of humid forest (Pintaud et al. 2001), and its extent as historical refugia under periods of glacial aridity (Pintaud et al. 2001; Poncet et al. 2013; Pouteau et al. 2015). Historical aridity and accompanying widespread loss of forest habitat at low to mid elevation may have been causal in initiating regional and intra-regional isolation of *Marmorosphax* populations on ultramafic surfaces. Under such conditions species-specific niche conservatism (Wiens, 2004) likely played a fundamental role, whereby populations once continuously distributed at lower elevations fail to adapt to new and adverse environmental conditions and are forced to stay within (and follow) the limits of their preferred niche, and move to higher elevations. By failing to adapt to new environmental conditions and maintaining ecological traits that prevent dispersal across a new ecological barrier at lower elevations, gene flow is prevented between populations, leading to differentiation over time in the face of extended periods of separation maintained by the persistence of unsuitable conditions. While this may have been a likely scenario to account for the persistent isolation of genetically distinct lineages within the Group 1, 2 and Group 3 lineages, it would appear not to apply to the Group 4 lineage species, *M. tricolor*. Earlier vicariant events within the genus suggest it was originally limited in distribution to metamorphic surfaces of central-east and northeast. The northeast of the Grande Terre has been identified as one of four areas that received sufficient moisture during periods of Pleistocene aridity to maintain lowland rainforest refugia for palms (Pintaud et al. 2001). Such refugia would likewise have sustained elements of the moisture-dependant fauna. Thus, populations of the Group 4 lineage species, *M. tricolor*, may not have been subject to the same environmental pressures historically as other lineages, and may have maintained traits that allowed expansion into the Grande Terre across a broad altitudinal range under more favorable conditions. In the case of *Marmorosphax* niche conservatism would appear to be accompanied by morphological conservatism between and within lineages. Although the genus as a whole is characterized by a number of morphological apomorphies, the individual species of *Marmorosphax* are all very similar in overall body form, coloration, and behavior. Here we discuss the geographic attributes of the major lineage-based groups identified in the molecular phylogeny for *Marmorosphax*, the possible processes leading to their differentiation, and the potential role of the interplay between historical climate change and species niche conservatism in the extent of intra-lineage diversification observed.

Massif specific differentiation - the Group 1 lineage taxa of the central-west and north-west region ultramafic ranges. — The terms northwest ultramafic region and central-west region are used here as arbitrary divisions of the ultramafic surfaces primarily located on the western side of Grande Terre (see Fig. 1). These surfaces extend as a chain of near coastal massifs and ranges from Sommet Poum in the north to Mé Maoya near Bourail in the south but also include several adjacent interior massifs including the Massif du Tchinguou and the Massif du Ouatilou. In the



FIGURE 6. The Mt. Kaala Massif in the distance from the summit of the Massif d'Ouazangou-Taom, separated by the low-lying Iouanga River valley.

northwest of the region to the north of the Pouembout Valley these massifs, Massif de Koniambo, Massif d'Ouazangou-Taom, Mt. Kaala and the Dôme de Tiébaghi, exist as isolated entities, separated from each other by low-lying (often broad) river valleys (Fig. 6). By contrast, the massifs in the central-west south of the Pouembout valley, Massif de Kopéto (including Paéoua), Massif du Boulinda, show some degree of connectivity via intervening mid-high elevation ranges, with the exception of the most southern, Mé Maoya, which is isolated from massifs to the north by the Poya River valley. The Massif du Tchingou is an isolated massif which lies inland of the Pouembout valley, and is treated here as part of the central-west region massifs.

The well-supported branching pattern within the Group 1 lineage suggests initial isolation of the sub-lineage on Mt. Kaala (*M. kaala*), but with only moderate support, followed closely by isolation and divergence of the other massif-specific sub-lineages. The extent of intra-regional massif-specific lineage splitting following primary divergence suggests an ongoing history of fragmentation and isolation of populations at a very localized scale within the ultramafic surfaces of central-west and northwest Grande Terre, equating to a scenario of multiple intra-regional vicariant events. Mount Kaala (*M. kaala*), the Massif du Boulinda (*M. boulinda s.s.*), the Massif du Tchingou (*M. boulinda*), Massif d'Ouazangou-Taom (*M. taom*), and Dôme de Tiébaghi (*M. taom*) all have genetically divergent massif-specific populations. The level of genetic differentiation between these massif-specific lineages is typically high (between 6.5% and 10.0% - Table 2), indicating a history of long-standing inter-massif divergence. The exception is between the populations of *M. taom* from Massif d'Ouazangou-Taom and Dôme de Tiébaghi, in which the extent of differentiation is markedly lower (uncorrected *p* mean 3.3%), suggesting a more recent loss of connectivity between these two massifs or a recent expansion event from one massif to the other. The latter of these scenarios appears unlikely given the two widely separated and a lack of evidence for between-massif migration historically in the lineage.

Several isolated massifs in central-west and northwest ultramafic regions appear to lack Group 1 lineage taxa. Sommet Poum (maximum elevation 413 m) and Massif de Koniambo (maximum

elevation ~950 m) in the northwest region have been well investigated, but there are no confirmed records of *Marmorosphax* from Sommet Poux, and only the Group 4 *M. tricolor* lineage has been recorded from the Massif de Koniambo. Similarly, the Massif de Kopéto (maximum elevation ~1050 m) in the central-west region has been well investigated, but only the Group 4 *M. tricolor* lineage has been recorded. Both the Koniambo and Kopéto-Paéoua massifs have areas of high elevation forest and maquis habitat at or above 900 m in elevation. Current habitat availability provides no explanation as to why Group 1 lineage taxa are absent from these massifs. Further, both massifs each have a suite of massif-specific endemic skinks and geckos, a number of which are restricted to high elevation habitat. The absence of any *Marmorosphax* on Sommet Poux, the most northern of the ultramafic massifs on the Grande Terre, is not entirely unexpected given its location in the dry far north of the island. This massif only rises to a plateau of 400 m in elevation and is separated from the nearest population of *Marmorosphax* to the south on Dôme de Tiébaghi (*M. taom*) by a straight-line distance of 25 km, and the nearest population to the east, on Mt. Mandjelia (*M. tricolor*), by 32 km.

Overall, the extent of intra-regional massif specific divergence and differentiation within the Group 1 lineage is interpreted as reflecting a history of progressive fragmentation and isolation of populations within the central-west and northwest regions early in its history, a pattern which in turn likely reflects an accompanying history of long-term and progressive isolation of forest habitat on the massifs via contraction to higher elevation in response to aridity, with post-isolation barriers to dispersal persisting.

High elevation endemism - the Group 2 lineage species *M. montana* of the Massif du Sud.

— The ultramafic surfaces of southern Grande Terre extend as a near continuous block of ranges south of the Thio Valley (see Fig. 1), dropping to a plateau of ~250 m on the Plaine des Lacs in the far south. The region has been identified as an area rich in endemic lizard species and representing a distinct bioregion for lizards (Sadlier 2010; Sadlier et al. 2019), but also as having extensive intra-regional microendemism. Its northern boundary for the most-part is defined by the Thio Valley, which extends from the east coast nearly two-thirds of the way across the island to the Col de Nasirah (~450 m) at its upper reaches in the west to Thio in the east, with an extension of ‘related’ surfaces north along the coast to near Cap Bocage. To date the Group 2 lineage *M. montana* has only been recorded from higher elevation sites on the southern ultramafic ranges, at Mt. Ouin in the south (900–1100 m), Bwa Bwi (~1100 m) in the central area, and Forêt de Saille (750–800 m), Camp des Sapins (600–800 m) and Kongouhaou Nord (900–1000 m) near the northern boundary of the region. The vegetation cover of high elevation ranges in much of the region is now predominately maquis shrubland, often open and degraded, but with areas of forest of varying size towards the top of the ranges (Fig. 7), although these become progressively smaller and more isolated in the central and northern parts of the region. The species has been recorded mostly from high elevation forest habitat, but also occurs in adjacent maquis shrubland.

The extent of genetic differentiation between the three populations available for analysis is anomalous in the context of their proximity to each other. The population from Forêt de Saille and Mt. Ouin are 40 km distant but form a well-supported sub-lineage with a relatively low level of differentiation (uncorrected p mean 2.9%), whereas the population from Camp des Sapins (including adjacent Kongouhaou Nord) is highly differentiated from both the Mt. Ouin (uncorrected p mean 6.9%) and Forêt de Saille (uncorrected p mean 7.8%) populations, despite only being ~15 km straight line distance the latter.

An additional population of *M. montana* from Bwa Bwi, which also sits on this ridge at around 1200 m has recently been reported, but there is no genetic data available for this population. This ridge also includes the Massif du Humboldt, but neither *M. montana* or *M. tricolor* have been



FIGURE 7. High elevation ranges of southern Grande Terre (from Pic Ningua), predominately maquis shrubland but with isolated forest at the top of the ranges.

recorded from high elevation forest habitat on the massif (Sadlier and Jourdan, 2011), despite the presence of extensive ‘moss forest’ (forêt moussé) along the ridges between 1000–1400 m in elevation, although *M. tricolor* has been recorded from nearby sites at lower elevation (low elevation forest of the Ni Valley and low-mid elevation forest on the western drainage of Mt. Vulcain).

The landscape over much of the southern ultramafic region appears to have been extensively modified since the arrival of humans, and it is difficult to envisage to what extent natural forest habitat might have existed historically (pre-human), particularly on its northern ranges. In this context, the extent of genetic differentiation observed between populations suggests greater continuity of habitat (forest at high elevation) historically along the ranges than currently seen, with past connectivity between populations on Forêt de Saille and Mt. Ouin, possibly via high elevation habitat between these sites along a near continuous ridge that runs down the Massif du Sud, despite much of the intervening area now being dominated by maquis shrubland. Conversely, the extent of differentiation of the Camp des Sapins/Kongouhaou population suggests early and persistent isolation of those ranges.

The Group 3 *M. cf. tricolor* lineage in the central-east ultramafic ranges. — Differentiation of the Group 3 *M. cf. tricolor* lineage on ultramafic surfaces of the central-east ultramafic ranges follows the pattern of cladogenesis consistent with vicariance and isolation of populations seen in early in the history of the genus. By default, the distribution of populations giving rise to its sister species, the Group 4 *M. tricolor* lineage, would have originally been limited to the adjacent central-east and northeast metamorphic surfaces.

The Group 3 *M. cf. tricolor* lineage comprises two populations on ultramafic massifs in the central-east ultramafic ranges, one at Njéjère on the Poro massif and one scattered over Mt. Menazi on the Kouaoua massif, each a well-supported sub-lineage (nodes 13 and 14 Fig. 5) and with a high level of interpopulation differentiation (uncorrected *p* mean 7.8%). These two populations are disjunct, being separated by the Koua River valley. On Mt. Menazi individuals genetically assign-

able to the Group 3 *M. cf. tricolor* lineage are locally sympatric with individuals genetically assignable to the Group 4 *M. tricolor* lineage. Throat color and pattern of juveniles, subadults and adult females is the sole morphological character that can otherwise diagnose the two taxa. The pattern of juveniles and subadults is carried over to adult females, whereas in adult males it becomes muted and adult males of the Group 3 *M. cf. tricolor* lineage and Group 4 *M. tricolor* lineage are not readily distinguished. All juveniles/subadults and adult females assigned to the Group 3 *M. cf. tricolor* genetic lineage had a muted marbled throat pattern. By comparison, juveniles/subadults and adult females assigned to the Group 4 *M. tricolor* lineage from elsewhere throughout the species range typically have a boldly marbled black and cream throat pattern.

Across Mt. Menazi the distribution of morphotypes and genotypes was complex. All juveniles/subadults and adult females on Mt. Menazi assigned to the Group 3 *M. cf. tricolor* genetic lineage had a muted marbled throat pattern. However, at one high elevation site where the two lineages occur in local sympatry, the *M. tricolor* genetic lineage contained adult females with a muted marbled throat pattern and juveniles/subadult individuals with the boldly marbled black and cream throat pattern. Further complicating this situation, seven adult females and two juveniles (and all males) from Bwa Méyu, 20 km to the southeast of Mt. Menazi and on the adjacent Boakaine massif, had the muted marbled throat pattern typical of the Group 3 *M. cf. tricolor* genetic lineage but were all uniformly assigned to the Group 4 *M. tricolor* genetic lineage. Aside from these discrepancies the Group 3 *M. cf. tricolor* genetic lineage is ringed by populations assigned to Group 4 *M. tricolor* on both ultramafic (Nakéty, Mé Adéo and Mé Maoya) and metamorphic (Plateau Dogny, Col d'Amieu and Col des Rousettes) substrates (Fig. 8), morphologically typical of that species.

The extent of genetic introgression between *M. tricolor* and *M. cf. tricolor* appears to be unidirectional, into the *M. cf. tricolor* lineage, and in some instances, such as at Bwa Méyu to the south, might have completely swamped that population. The pattern of genetic introgression between the Group 3 *M. cf. tricolor* genetic lineage and sympatric Group 4 *M. tricolor* genetic

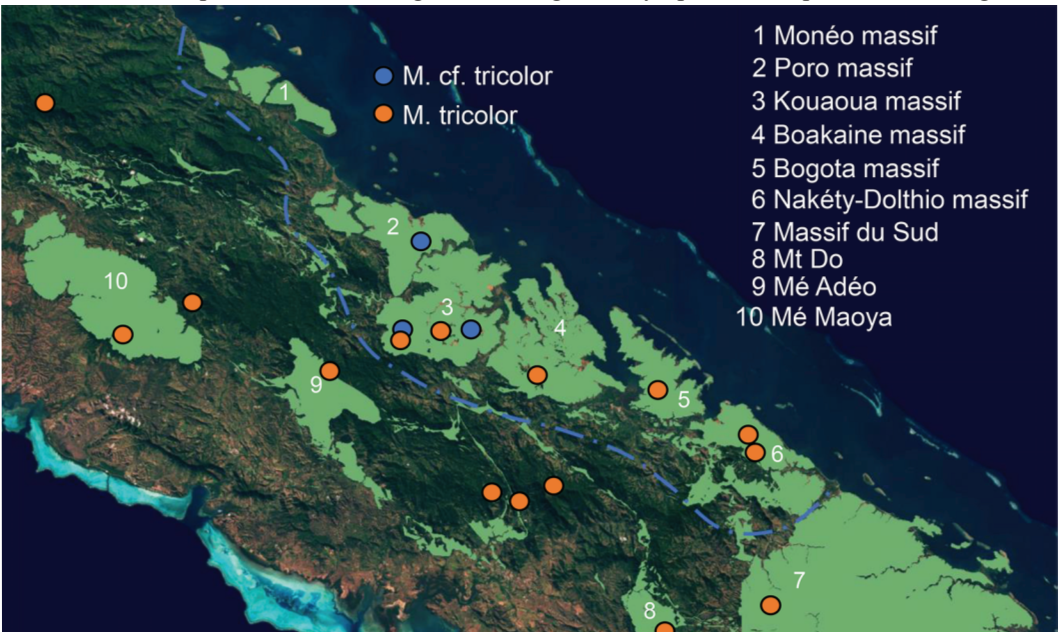


FIGURE 8. Distribution of ultramafic surfaces in the central-east region of Grande Terre showing location of populations in the Group 3 *M. cf. tricolor* lineage and regionally sympatric Group 4 *M. tricolor* lineage.

lineage on Mt. Menazi suggests secondary contact between the two lineages, probably via dispersal of *M. tricolor* from adjacent metamorphic surfaces to the east. In this regard the ‘purity’ of the population from Poro may be a legacy of isolation, being geographically disjunct from Mt. Menazi and from other Group 4 *M. tricolor* lineage populations in the region.

Distribution of the Group 4 *M. tricolor* lineage across Grande Terre - the case for range expansion onto the ultramafic surfaces. — Populations assigned to Group 4 *M. tricolor* lineage extend broadly across the main island, Grande Terre, but are absent from the Îles Belep and Île des Pins, extensions of mainland to the north and south respectively now separated by straits of ocean, and is found widely on both ultramafic and metamorphic surfaces. On ultramafic surfaces it has been recorded primarily from forest habitat, but also occurs in nearby maquis habitat in association with a surface rock matrix (see below). On metamorphic surfaces it is restricted to humid forest habitat and has not been recorded from secondarily (disturbed) habitat, or savannah woodland (naiouli).

Several intraspecific groups are retrieved in the phylogeny for the Group 4 *M. tricolor* genetic lineage, one a group including a cluster of populations on the central metamorphic ranges (Sarraméa, Plateau Dogny, Col d’Amieu) and central-east Bogota ultramafic massif (Bogota), one groups of populations on both metamorphic and ultramafic surfaces of the central and northern regions, and one a complimentary group of populations on the ultramafic and metamorphic surfaces to the south – but with no support for relationships between these groups. Within each of these ‘northern’ and ‘southern’ groups some sub-structuring concordant with broad geographic subregions was evident, and sometimes well supported, but with comparatively low levels of differentiation between these regionally discrete groups of populations. This pattern suggests the species distribution could, in part, be the product of a recent and rapid expansions in range, in some cases followed by post-expansion contraction, resulting in isolation and differentiation of regional groups of populations. In this context the genetic relationship of *M. tricolor* populations may provide insights into the distribution and natural disjunctions of forest across the landscape, which is now largely obscured by anthropogenic fragmentation and loss of forest habitat.

The relationships between populations of *M. tricolor* on the western ultramafic massifs and those on adjacent metamorphic surfaces also provide some support for a recent expansion of the species onto these ultramafic surfaces. *Marmorosphax tricolor* has been recorded from four massifs, (N-S) Koniambo, Kopéto-Paéoua, Boulinda, and Mé Maoya, in the central-east and north-west regions. The present-day distribution of the species suggests environmental conditions at lower elevation on these western ultramafic massifs are sub-optimal. On the more mesic east coast is known to occur at low-mid elevation (northeast ranges 300–500 m, Sadlier 1986; central-east coast ranges ~50 m, Bauer and DeVaney 1987; southeast ranges, Sadlier and Delafenetre 2009), but on the Koniambo and Kopéto-Paéoua massifs it has only been recorded from mid-high elevation habitat at or >600 m. Populations on these western ultramafic massifs are more closely related to populations on the adjacent metamorphic ranges than they are to other populations ultramafic surfaces. Those on the Kopéto-Paéoua and Boulinda ultramafic massifs cluster with populations from Mt. Aoupinié and Forêt Plate on metamorphic ranges to the east, the population on the Koniambo ultramafic massif with those from the Panié Range and Mt. Koyaboa on non-ultrabasic ranges to the northeast, and the population from the Mé Maoya ultramafic massif to the population from Col des Rousettes on metamorphic ranges to the southeast. This pattern of multiple, independent events of historical connectivity between the western ultramafic massifs and metamorphic ranges to the east suggests the species presence on these ultramafic massifs is the result of expansion from the adjacent metamorphic ranges, likely via intervening mid-high elevation ranges (Fig. 9).

Marmorosphax tricolor has not been recorded from several massifs (Massif d'Ouazangou-Taom, Dôme de Tiébaghi, Sommet Poum) in the northwest ultramafic region, despite repeated survey work, indicating persistent region-wide isolation of these massifs from the metamorphic ranges to the east (Panié Range). Much of this intervening area is the white ranges of the Montagnes Blanches Nappe (Maurizot et al. 2020) which largely lacks suitable habitat (forest) today, and by inference historically. However, the recent discovery of a population of *M. tricolor* (no genetic data is yet available) on the Mt. Kaala massif indicates the distribution of this and other species of *Marmorosphax* in the region is more complex than anticipated.

Within the 'southern' group of *M. tricolor* there was strong support for a broad sub-group of populations within the southern ultramafic region of the Massif du Sud, but with little internal genetic differentiation or regional structure between these populations. The low level of genetic differentiation and lack of internal structure between populations in sub-group which extends from the Ni river to the southern tip of the island, suggests the species distribution in the southern ultramafic region to be the product of a recent expansion in range.

As such, aspects of the phylogeography of *M. tricolor* suggest its distribution on ultramafic surfaces of the central-west and northwest ultramafic regions, central-east region, and even southern ultramafic region, may stem from a number of independent historically recent expansion events into these regions.

SUMMARY

The scheme of relationships retrieved in the molecular phylogeny for *Marmorosphax* identified basal breaks in the ancestral species distribution concordant with the boundaries of the island's major ultramafic regions. The regional and intra-regional lineage diversification in the genus represents a pattern of historical fragmentation and contraction of populations, one which likely reflects a change in the distribution of preferred habitat. Given what is known of the biology of the species of *Marmorosphax*, loss of low elevation forest on ultramafic surfaces would appear to be a probable candidate in initiating isolation of ancestral populations that gave rise specific and intraspecific lineages. A scenario of historical fragmentation and contraction of preferred forest habitat in the face of changed climatic conditions, combined with the species reliant on that core habitat, is consistent with the dynamics of niche conservatism as outlined by Wiens (2004). While loss or marginalization of low elevation forest habitat on the ultramafic massifs in the face of adverse climatic conditions may have provided the mechanism to initiate speciation within *Marmorosphax*, it is likely the persistence of high elevation forest habitat on the ultramafic ranges, often limited to the summit areas, that provided the historical refugia for these lineages to differentiate in isolation over time.

The level of intraspecific genetic differentiation within *M. boullinda*, *M. montana* and *M. cf. tricolor* in some pairwise comparisons of populations was substantial and of a similar extent to that seen been recognized species within the genus. While these differences may be indicative of the existence of potentially undescribed taxa in these lineages, they either require further genetic analyses, and/or the samples available are insufficient for the complementary morphological comparisons required for their formal recognition, and further targeted field collections are required.

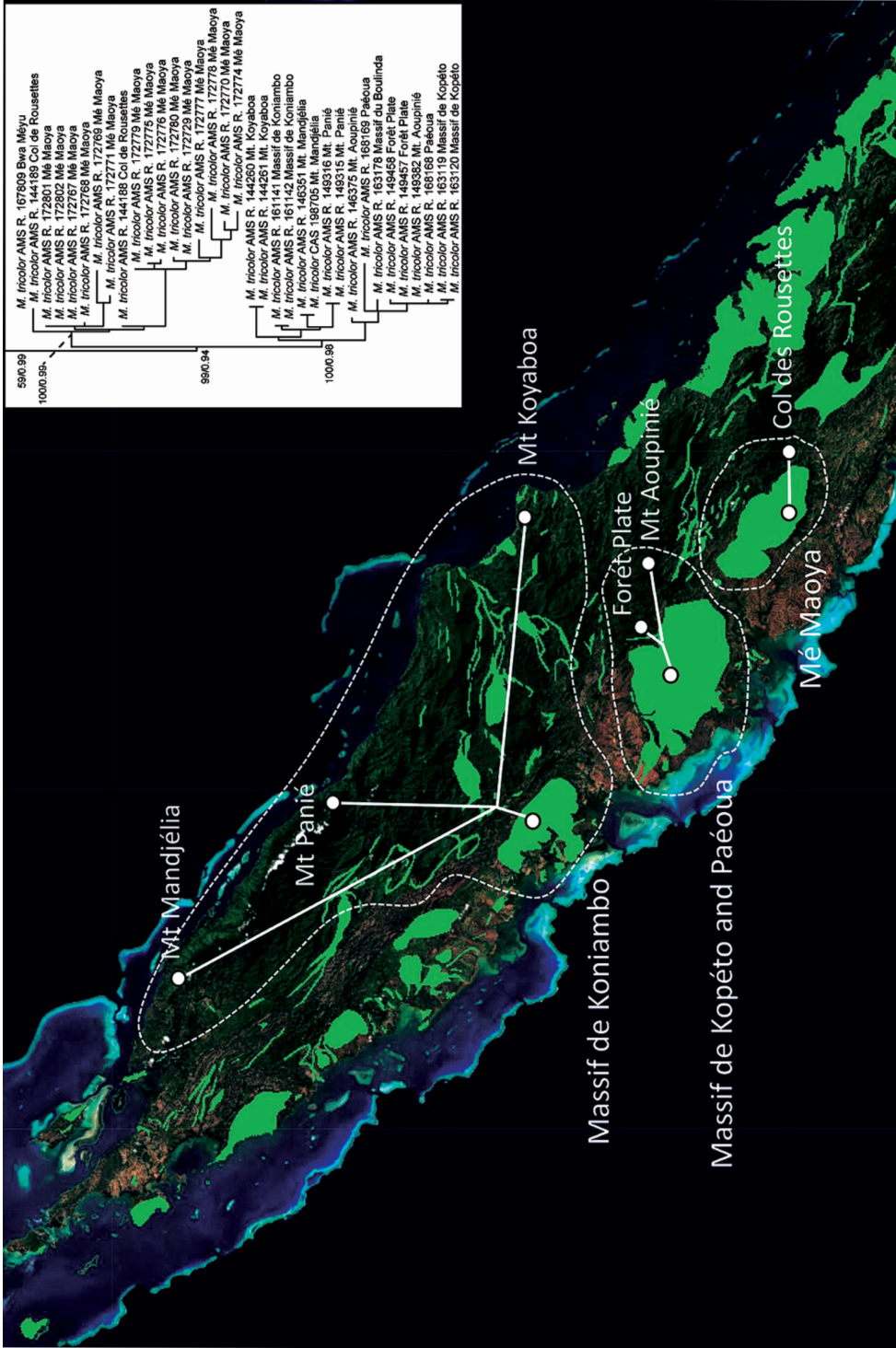


Figure 9. Approximate boundaries (dashed line) for related populations of *M. tricolor* in northern and central Grande Terre showing the affinities (solid line) of populations on the ultramafic massifs of the northwest and central west to populations on the metamorphic ranges to the east, rather than to each other. The relationships of these populations as retrieved in the ND2 phylogeny are shown in the inset.

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Appendix

Specimens used in the genetic study (for museum acronyms see Materials and Methods).

Genus	Species	Reg. No.	Location	Genbank ND2
Outgroup				
<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, Iles Belep	DQ675209
<i>Lacertoides</i>	<i>pardalis</i>	AMS R.148051	Kwa Néie	DQ675211
<i>Epibator</i>	<i>nigrofasciolatus</i>	AMS R.138624	Île des Pins	
<i>Lioscincus</i>	<i>steindachneri</i>	AMS R.149890	Mé Adéo	DQ675218
<i>Phasmasaurus</i>	<i>tillieri</i>	AMS R.148037	Mt. Vulcain	DQ675220
<i>Nannoscincus</i>	<i>mariei</i>	AMS R.146484	Mt. Mou	DQ675232
<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	Kwa Né Mwa	DQ675242
Ingroup				
<i>Marmorosphax</i>	<i>kaala</i>	AMS R.161091	Mt. Kaala	KF176382
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.163196	Massif du Boulinda	KF176383
<i>Marmorosphax</i>	<i>boulinda</i>	MNHN 2005.0319	Massif du Boulinda	KF176384
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.167263	Massif de Tchingou	KF176385
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.167264	Massif de Tchingou	KF176386
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.167274	Massif de Tchingou	KF176387
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.167275	Massif de Tchingou	KF176388
<i>Marmorosphax</i>	<i>boulinda</i>	AMS R.167277	Massif de Tchingou	KF176389
<i>Marmorosphax</i>	<i>taom</i>	AMS R.165973	Mt. Taom	KF176390
<i>Marmorosphax</i>	<i>taom</i>	MNHN 2005.0318	Mt. Taom	KF176391
<i>Marmorosphax</i>	<i>taom</i>	AMS R.168011	Dôme de Tiébaghi	KF176392
<i>Marmorosphax</i>	<i>taom</i>	AMS R.168012	Dôme de Tiébaghi	KF176393
<i>Marmorosphax</i>	<i>taom</i>	AMS R.168029	Dôme de Tiébaghi	KF176394
<i>Marmorosphax</i>	<i>taom</i>	AMS R.168030	Dôme de Tiébaghi	KF176395
<i>Marmorosphax</i>	<i>taom</i>	AMS R.168031	Dôme de Tiébaghi	KF176396
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174973	Koungouhaou Nord	KF176397
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174974	Çidoa - Pic Ningua	KF176398
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174943	Camp des Sapins	KF176399
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174946	Camp des Sapins	KF176400
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174947	Camp des Sapins	KF176401
<i>Marmorosphax</i>	<i>montana</i>	AMS R.174948	Camp des Sapins	KF176402
<i>Marmorosphax</i>	<i>montana</i>	AMS R.165922	Mt. Ouin	KF176403
<i>Marmorosphax</i>	<i>montana</i>	CAS 229282	Mt. Ouin	KF176404
<i>Marmorosphax</i>	<i>montana</i>	AMS R.165802	Mt. Ouin	KF176405
<i>Marmorosphax</i>	<i>montana</i>	AMS R.173002	Forêt de Saille	KF176406
<i>Marmorosphax</i>	<i>montana</i>	AMS R.173004	Forêt de Saille	KF176407
<i>Marmorosphax</i>	<i>montana</i>	AMS R.173005	Forêt de Saille	KF176408
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167158	Mt. Menazi	KF176409
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167163	Mt. Menazi	KF176410
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167160	Mt. Menazi	KF176411
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167831	Mt. Menazi	KF176412

<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167833	Mt. Menazi	KF176413
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167834	Mt. Menazi	KF176414
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167830	Paraméré	KF176415
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167842	Néwayéré	KF176416
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167843	Néwayéré	KF176417
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167844	Néwayéré	KF176418
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167849	Néjéré	KF176419
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167952	Néjéré	KF176420
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167957	Néjéré	KF176421
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167958	Néjéré	KF176422
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167959	Néjéré	KF176423
<i>Marmorosphax</i>	cf. <i>tricolor</i>	AMS R.167960	Néjéré	KF176424
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.148882	Mé Adéo	KF176425
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.148883	Mé Adéo	KF176426
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.148884	Mé Adéo	KF176427
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167152	Mt. Menazi	KF176428
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167153	Mt. Menazi	KF176429
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167159	Mt. Menazi	KF176430
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167162	Mt. Menazi	KF176431
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167164	Mt. Menazi	KF176432
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167165	Mt. Menazi	KF176433
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167168	Mt. Menazi	KF176434
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167169	Mt. Menazi	KF176435
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167835	Mt. Menazi	KF176436
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167836	Mé Mwa	KF176437
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167837	Mé Mwa	KF176438
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167838	Mé Mwa	KF176439
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167839	Mé Mwa	KF176440
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167840	Mé Mwa	KF176441
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167841	Mé Mwa	KF176442
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167478	Bwa Méyu	KF176443
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167479	Bwa Méyu	KF176444
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167480	Bwa Méyu	KF176445
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167482	Bwa Méyu	KF176446
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167483	Bwa Méyu	KF176447
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167484	Bwa Méyu	KF176448
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167485	Bwa Méyu	KF176449
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167486	Bwa Méyu	KF176450
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167496	Bwa Méyu	KF176451
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167497	Bwa Méyu	KF176452
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167499	Bwa Méyu	KF176453
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167795	Bwa Méyu	KF176454
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167796	Bwa Méyu	KF176455
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167809	Bwa Méyu	KF176456
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.167814	Bwa Méyu	KF176457
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172523	Bogota	KF176458
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172524	Bogota	KF176459
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172525	Bogota	KF176460
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172500	Nakéty	KF176461
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172501	Nakéty	KF176462
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165938	Col de Petchécar	KF176463
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165939	Col de Petchécar	KF176464

<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165940	Pic Ningua	KF176465
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168239	Pic Ningua	KF176466
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168240	Pic Ningua	KF176467
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.171393	Ni River	KF176468
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.171394	Ni River	KF176469
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.171419	Pourina River	KF176470
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.171420	Pourina River	KF176471
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.171421	Pourina River	KF176472
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172577	Tontouta Valley	KF176473
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165924	Mt. Ouin	KF176474
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165925	Mt. Ouin	KF176475
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.165926	Mt. Ouin	KF176476
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 229285	Mt. Ouin	KF176477
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.158785	Mt. Mou	KF176478
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.135156	Yahoué	KF176479
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.135158	Yahoué	KF176480
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 214451	Mt. Koghis	KF176481
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 214452	Mt. Koghis	KF176482
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144326	Mt. Koghis	KF176483
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.147948	Rivière Bleue	KF176484
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.147949	Rivière Bleue	KF176485
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172654	Chutes de la Madeleine	KF176486
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172663	Chutes de la Madeleine	KF176487
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172641	Yaté Barrage	KF176488
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172642	Yaté Barrage	KF176489
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172643	Yaté Barrage	KF176490
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172644	Yaté Barrage	KF176491
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172665	Yaté Barrage	KF176492
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172666	Yaté Barrage	KF176493
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172720	Yaté Barrage	KF176494
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172721	Yaté Barrage	KF176495
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172722	Yaté Barrage	KF176496
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168123	Rivière Ya	KF176497
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168124	Rivière Ya	KF176498
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.148052	Forêt Nord	KF176499
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.148053	Forêt Nord	KF176500
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172625	Ouitchambo	KF176501
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172626	Ouitchambo	KF176502
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172638	Ouitchambo	KF176503
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.147875	Plateau de Dogney	KF176504
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.147876	Plateau de Dogney	KF176505
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144097	Sarraméa	KF176506
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144098	Sarraméa	KF176507
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144362	Col d'Amieu	KF176508
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144188	Col des Roussettes	KF176509
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144189	Col des Roussettes	KF176510
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172729	Mé Maoya	KF176511
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172767	Mé Maoya	KF176512
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172768	Mé Maoya	KF176513
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172769	Mé Maoya	KF176514
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172770	Mé Maoya	KF176515
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172771	Mé Maoya	KF176516

<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172774	Mé Maoya	KF176517
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172775	Mé Maoya	KF176518
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172776	Mé Maoya	KF176519
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172777	Mé Maoya	KF176520
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172778	Mé Maoya	KF176521
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172779	Mé Maoya	KF176522
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172780	Mé Maoya	KF176523
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172801	Mé Maoya	KF176524
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172802	Mé Maoya	KF176525
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.172803	Mé Maoya	KF176526
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.163178	Massif du Boulinda	KF176527
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.149457	Forêt Plate	KF176528
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.149458	Forêt Plate	KF176529
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168168	Paéoua	KF176530
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.168169	Paéoua	KF176531
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.163119	Massif de Kopéto	KF176532
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.163120	Massif de Kopéto	KF176533
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.146375	Mt. Aoupinié	KF176534
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.149382	Mt. Aoupinié	KF176535
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144260	Mt. Koyaboa	KF176536
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.144261	Mt. Koyaboa	KF176537
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.161141	Massif de Koniambo	KF176538
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.161142	Massif de Koniambo	KF176539
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.149315	Mt. Panié	KF176540
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.149316	Mt. Panié	KF176541
<i>Marmorosphax</i>	<i>tricolor</i>	CAS 198705	Mt. Mandjélia	KF176542
<i>Marmorosphax</i>	<i>tricolor</i>	AMS R.146351	Mt. Mandjélia	KF176543

