Three new species of skink in the genus *Marmorosphax* Sadlier (Squamata: Scincidae) from New Caledonia

Ross A. SADLIER (1), Sarah A. SMITH (2, 4), Aaron M. BAUER (2) & Anthony H. WHITAKER (3)

(1) Section of Herpetology, Australian Museum, 6 College Street, Sydney 2000, New South Wales, Australia
rosss@austmus.gov.au
(2) Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA
(3) 270 Thorpe-Orinoco Road, Orinoco, RD 1, Motueka 7161, New Zealand
(4) current address: Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York 11794-5245, USA

ABSTRACT

Recent field studies have resulted in the discovery of three new species of skink in the genus *Marmorosphax* from closed forest on the ultramafic massifs of north-western New Caledonia. On these massifs closed forest is present only as small patches near the summits at around 900-1000 metres elevation. These new species vary mainly in subtleties of colouration, and to a lesser degree scalation. Genetic studies have played a crucial role in supporting the recognition of these species, and in identifying their relatively long evolutionary histories in New Caledonia.

RÉSUMÉ

Trois nouvelles espèces de Scincidae du genre *Marmorosphax* Sadlier (Squamata: Scincidae) de Nouvelle-Calédonie.

Des recherches récentes sur le terrain ont permis la découverte de trois nouvelles espèces de scinques du genre *Marmorosphax*. Elles proviennent de forêts fermées localisées sur les massifs ultramafiques du nord-ouest de la Nouvelle-Calédonie. Sur ces massifs, la forêt fermée n'est présente que sous la forme de petits fragments proches du sommet, à environ 900-1000 mètres d'altitude. Ces nouvelles espèces se distinguent principalement par de subtiles détails de coloration, et dans une moindre mesure par leur écaillure. Les analyses génétiques ont largement contribué à leur identification et à la mise en évidence de leur relativement longue histoire évolutive en Nouvelle-Calédonie.

SADLIER R. A., SMITH S. A., BAUER A. M. & WHITAKER A. H. 2009. — Three new species of skink in the genus *Marmorosphax* Sadlier (Squamata: Scincidae) from New Caledonia, *in* GRANDCOLAS P. (ed.), Zoologia Neocaledonica 7. Biodiversity studies in New Caledonia. *Mémoires du Muséum national d'Histoire naturelle* 198: 373-390. Paris ISBN: 978-2-85653-618-6.

INTRODUCTION

The island of New Caledonia is now widely recognised as one of the world's hotspots for endemic species, and thus a priority area for conservation action (Mittermeier *et al.* 1996; Myers *et al.* 2000; Lowry *et al.* 2004). Its recognition as such is based mainly on its rich and highly diverse flora (Lowry 1998), but similar patterns of diversity, richness, and endemism are seen in the invertebrate fauna (Chazeau 1993; Haase & Bouchet 1998). By contrast the vertebrate fauna was, with a few exceptions, formerly regarded as depauperate overall with low levels of diversity and endemism (Darlington 1969; Diamond 1984). Recent studies on the lizard fauna of the island challenge this perception. Our field research over the past 15 years has revealed the existence of an extremely rich lizard fauna, with a diversity of species on an area basis greater than any other island in Pacific region (Bauer & Sadlier 1993, 2000; Bauer 1999). Further, laboratory studies using both morphological and genetic analyses show this lizard fauna to be largely endemic and characterised by an exceptionally high degree of regional microendemism (Jackman *et al.* 2004; Smith *et al.* 2004).

Previous assessments of the distributions of lizards (Bauer & Sadlier 2000) had shown the existence of both narrow and broad range endemics, including a suite of species and genera apparently restricted to forest habitat on ultramafic soils in the south of the region. Among these were two species of skink, *Sigaloseps ruficauda* Sadlier & Bauer and *Marmorosphax montana* Sadlier & Bauer, both of which were only recently discovered and described from high elevation moist forests on the ultramafic ranges associated with the extensive Mt. Dzumac-Humboldt massif in the southern part of the island (Sadlier & Bauer 1999, 2000). Recent studies on the lizard faunas of the ultramafic ranges and peaks in the mid-west and north-west of the island have revealed similar patterns of endemism (Sadlier *et al.* 2004a, 2004b) in addition to that shown by the three new species of *Marmorosphax* described here.

Humid forests on ultramafic soils rarely form extensive stands, but rather are typically present as patches of various sizes at any one locality, with high elevation forests often present only as small patches on the summit or ridges surrounded by extensive areas of maquis shrubland (Jaffré 1974, 1980; Jaffré & Latham 1974). Studies on the distribution and relationships of the island's rich palm flora indicate that historically the moist forests of New Caledonia are considered to have undergone a series of old (Miocene) and more recent (Pleistocene) contraction events during periods of climate change (Pintaud *et al.* 2001). It is probable that the high elevation forests that occur on ultramafic ranges in the south and west of the island today represent, in part, natural remnants. Despite their small size, the ability of the peaks to trap moisture-laden cloud at around 1000 m elevation (the Massenerhebung effect; Flenley 1995), and of vegetation to comb moisture from the clouds (Rigg *et al.* 2002), allows forest patches on the summits of these ultramafic massifs to maintain the essential microhabitat components to support lizard species that are highly moisture dependant.

All species in the genus *Marmorosphax* are highly dependant on moist habitats. Even the widely distributed *M. tricolor* (Bavay) which occurs at many sites across the island at all elevations has, in most instances, been recorded primarily from moist forest habitat. Three species, *M. montana* and the species described here from Massif du Boulinda and Mt. Taom, appear to be high elevation, narrow-range endemics. Each is known only from a single massif and are known so far only from high elevation forest (and maquis shrubland with a thick fern understory on Mt. Toam). The other species described here from Mt. Kaala also appears to be a narrow range endemic, but occupies a broader altitudinal range, being recorded from both high and mid-elevation.

A phylogeny for the genus based on DNA sequence data places *M. montana* as the sister species to all remaining taxa, and the three new species as the sister clade to the widespread *M. tricolor*. The genetic distances between the three new species (and to *M. tricolor*) are large, indicating these taxa have long been on independent evolutionary trajectories. *Marmorosphax tricolor* shows some geographic sub-structuring across the species range as a whole, but the level of genetic distance between the various allopatric populations is low, even across great geographic distances, a pattern consistent with a species that has recently radiated and is undergoing a contraction of its specialised habitat.

MATERIALS AND METHODS

Abbreviations. Institutional abbreviations are as follows: Australian Museum, Sydney (AMS); California Academy of Sciences, San Francisco (CAS); Muséum national d'Histoire naturelle, Paris (MNHN).

The full suite of morphological characters listed below was scored for each specimen where possible.

Measurements. Snout to vent length (SVL), measured from tip of snout to caudal edge of anal scales; axilla to groin distance, measured from middle of base of forelimb to middle of base of hindlimb; forelimb to snout length, measured from tip of snout to middle of base of forelimb; hindlimb length, measured from middle of base of hindlimb to tip of fourth toe including nail; tail length, measured from caudal edge of anal scales to tip of tail, on complete original tails only. The body measurements (axilla to groin, forelimb to snout, hindlimb) are for all specimens and are expressed as percentages of snout to vent length in the taxon accounts, tail lengths were measured on complete tails only (as determined by X-rays) or in the absence of an original tail the length of the most completely original tail is given as a percentage of snout to vent length. Sexual maturity was determined by reproductive maturity (presence of enlarged yolked ovarian follicles or eggs in females, and presence of enlarged testes and distinctive colouration in males) and/or the largest class among obvious size classes.

Scalation. Midbody scale rows, number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scale rows, number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at dorsal level of vent opening; fourth finger and toe scales, number of dorsal scales on fourth digit of hand and foot, distal scale contains claw, basal scale broadly contacts adjacent basal scale of third finger or toe; fourth finger and toe lamellae, number of ventral scales on fourth digit of hand and foot, distal scale contains claw, basal scale is last largely undivided scale at, or proximal to, a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides and the mean value used. Values given are means and standard deviations from the mean.

Osteology. Specimens were radiographed using an Eresco AS2 X-ray machine to determine phalangeal formulae and the number of presacral vertebrae and postsacral vertebrae (complete original tails only) at exposures of 30 sec at 30 kV.

Genetic studies. We obtained mitochondrial ND2 sequence data from all species (see Appendix 1), including *Marmorosphax tricolor* (n = 41) from 21 localities. Our sampling of *M. tricolor* included samples regionally sympatric with both *M. montana* (Mt. Ouin) and one of the taxa described herein (Massif du Boulinda). Representatives of four other endemic New Caledonian skink genera (*Caledoniscincus*, *Celatiscincus*, *Kanakysaurus* and *Nannoscincus*) were used as outgroups. ND2 was amplified and sequenced using primers L4437b (Macey *et al.* 1997) and ND2r102 (Sadlier *et al.* 2004a). Sequence data were analysed using parsimony and Bayesian approaches, with support assessed using the bootstrap and posterior probability respectively. Parsimony analysis was conducted using PAUP* (Swofford 2002) to implement a heuristic search with 1000 random addition-sequence replicates. Bootstrap analysis used 1000 pseudoreplicates each including 50 random addition-sequence replicates. Bayesian analysis was implemented using MrBayes v3 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). We used a mixed strategy to find the best combination of models and partitioning strategies, hierarchical likelihood-ratio tests (implemented in MrModeltest version 2.0; Nylander 2004) to choose reasonable models for separate genes, and comparison of Bayes factors (see Nylander *et al.* 2004) to select the best partitioning strategy (see Brandley *et al.* 2005; Wiens *et al.* 2005). Two independent analyses were run for 5 million generations with trees sampled each 1000 generations; stationary was determined by examining likelihood and parameter traces. Both runs reached stationarity by 45,000 generations; the final tree was obtained by summarising the combined post burn-in trees from two runs.

To verify our results from ND2 with an independently evolving locus, we sequenced the nuclear Rag-1 gene from a subset of the samples including representatives of each putative species and *M. tricolor* from localities throughout it's range, including the two localities where it occurs in sympatry with other species. Rag-1 primers were R13 from Groth & Barrowclough (1999) and an additional reverse primer G425 (primer sequence: 5'- AAA GCA AGG ATA GCG ACA AGA G -3'; Smith 2001). These sequences were added to the matrix of mitochondrial data and all analyses were repeated as above.

SYSTEMATIC ACCOUNT

The genus *Marmorosphax* when proposed (Sadlier 1986) included two species, *Lygosoma tricolor* Bavay, 1869 (type species) and *Lygosoma euryotis* Werner, 1909. *Marmorosphax montana* was later described from high elevation forests in the south of the island (Sadlier & Bauer 2000). New information on key features in osteology and reproductive biology led to a review of the content of the genus (Sadlier & Bauer 2000), ultimately resulting in the transfer of *Lygosoma euryotis* Werner to a newly erected genus, *Celatiscincus* (Sadlier *et al.* 2006).

The species of *Marmorosphax* are all medium-sized skinks with well developed limbs. They share a number of features of scalation that include: moderately large prefrontals that are moderately to widely separated; fused frontoparietals; a distinct interparietal; a single large upper secondary temporal and nuchal scale bordering each parietal; nasals well separated; two loreals, anterior of which is semilunar in shape and fails to contact the labials; supraciliaries usually 7; upper labials usually 7; a complete subocular row of scales between preocular and pretemporal scales; primary temporal single; lower secondary temporal single; tertiary temporals two; postlabials two; the lower eyelid with an obvious, centrally located semi-transparent disc; body scales with 3-5 carinations that break the posterior free edge of each dorsal scale. All species in the genus are sexually dimorphic in colouration.

All species are dependent on closed forest habitats and are generally associated with moist microhabitats such as logs and rocks. *Marmorosphax tricolor* is widespread in this habitat type throughout most regions of the island, whereas *Marmorosphax montana* is so far only known from Mt. Ouin, a high elevation peak in the south of the island where these two species are sympatric above 900 metres elevation. The three new species of *Marmorosphax* described here have allopatric distributions on isolated ultramafic peaks in the north-western part of New Caledonia.

Each of the new species described here is similar overall in morphology to one of the existing species and there is often overlap in mensurable characters, for this reason it is inappropriate to attempt to construct a dichotomous key to the species in the genus. Subtle differences in colouration, and in some cases to a limited extent scalation, serve to distinguish each of the new species, their recognition as distinct evolutionary species rests primarily on the deep divergences between taxa identified in the DNA sequence data, or when available evidence of sympatry between the taxa.

Marmorosphax kaala n. sp.

Figs 1, 2

TYPE MATERIAL. — New Caledonia, Province Nord. Holotype: MNHN 1987.1508 (Field tag "S6"), Mt. Kaala, (station 255), 20°38'48"S, 164°23'23"E, collected by J. Chazeau & S. Tillier, 27.VIII.1986. Paratypes: AMS R161091-92, Mt. Kaala, headwaters of Oué Injob, 20°37'03"S, 164°22'49"E, collected by A. H. & V. A. Whitaker, 3.VI.2002.

DIAGNOSIS. — *Marmorosphax kaala* n. sp. can be distinguished from other members of the genus by the following combination of characters: dorsal scale rows 69; fourth toe lamellae 31-35; dorsal surface with dark markings along the paravertebral axis at the joining edge of scale rows three and four (sometimes restricted to the nape); lateral surface with pale markings aligned to form a broken mid-lateral stripe; underside of head with bold dark blotches on the throat.

Marmorosphax kaala n. sp. most closely resembles *Marmorosphax tricolor* and *M. taom* n. sp. in colouration and scalation. The presence of dark markings along the paravertebral axis and the alignment of pale markings along the lateral surface to form a broken mid-lateral stripe distinguishes *Marmorosphax kaala* n. sp. from *Marmorosphax taom* n. sp. and *Marmorosphax tricolor*, both of which lack dark markings aligned along the dorsal surface and tend to have the pale markings on the side of the body scattered over the mid- to lower lateral surface. Scalation characters readily distinguish *Marmorosphax kaala* n. sp. from *Marmorosphax boulinda* n. sp. and *Marmorosphax montana*, both of which have more scales under the toes (see Table 1). The presence of pale markings aligned along the lateral surface to form a broken mid-lateral stripe further distinguishes *Marmorosphax kaala* n. sp. from *Marmorosphax boulinda* n. sp. and *Marmorosphax* *montana*, both of which have the pale markings on the lateral surface scattered or more transversely aligned.

ETYMOLOGY. – The epithet is a noun in apposition in reference to the type locality, Mt. Kaala.

DESCRIPTION. – Based on the type series of 3 specimens comprising one adult male (55.5 mm SVL), one subadult male (44.5 mm SVL), and one juvenile (33.5 mm SVL). Measurements are for the adult male and subadult female only.

Measurements: distance from axilla to groin 50.5-51.7% of SVL ($\bar{x}$ = 51.1, n = 2); distance from forelimb to snout 41.4-46.1% of SVL ($\bar{x}$ = 43.8, n = 2); hindlimb length 45.9-47.2% of SVL ($\bar{x}$ = 46.6, n = 2); tail length 168% of SVL for the specimen with the most nearly complete tail.

Scalation: midbody scale rows 38 (n = 3); paravertebral scales 69 (n = 2); scales on top of fourth finger 11 (n = 3); lamellae beneath fourth finger 17-18 ($\bar{x}$ = 17.2 ± 0.29, n = 3); scales on top of fourth toe 16-18 ($\bar{x}$ = 17 ± 1.0, n = 3); lamellae beneath fourth toe 31-35 ($\bar{x}$ = 32.7 ± 1.6, n = 3).

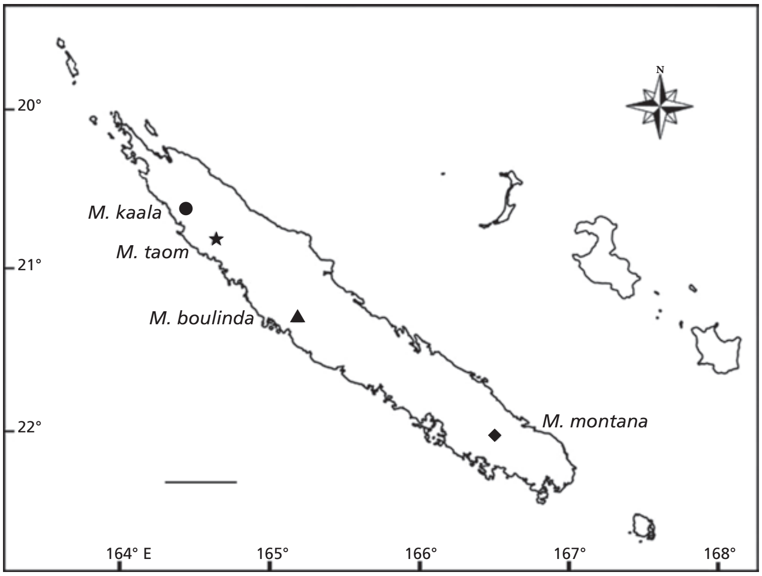

FIG. 1. Distribution of *M. kaala* (circle), *M. taom* (star), *M. boulinda* (triangle) and *M. montana* (diamond).

TABLE 1. Comparison of key scalation characters between the species of *Marmorosphax*.

	kaala	*toam*	*boulinda*	*montana*	*tricolor Ouin-Dzumac*	*tricolor Aoupinié*
midbody scale rows						
range	38	38-40	40	36-40	38-44	36-42
mean ± sd.		38.8 ± 1.09		38.8 ± 1.40	40.5 ± 1.77	39.7 ± 1.20
N	3	5	2	9	8	32
vertebral scale rows						
range	69	65-71	75-76	71-78	66-69	65-74
mean ± sd.		68.4 ± 2.61		73.4 ± 2.61	67.25±1.28	69.0 ± 2.10
N	3	5	2	8	8	32
fourth finger scales						
range	11	11-12	11-12	12-14	11-12	9-12
mean ± sd.		11.3 ± 0.27	11.5 ± 0.7	12.6 ± 0.63	11.2 ± 0.26	10.9 ± 0.60
N	3	5	2	9	8	32
fourth finger lamellae						
range	17-18	16-21	19	19-22	17-21	15-19
mean ± sd.	17.2 ± 0.29	17.3 ± 1.86		20.9 ± 0.85	19.4 ± 1.18	17.0 ± 0.94
N	3	5	2	9	8	32
fourth toe scales						
range	16-18	17-19	18-20	19-21	15-18	13-18
mean ± sd.	17 ± 1.0	17.9 ± 0.55	19.2 ± 1.06	19.3 ± 0.5	16.8 ± 0.84	15.5 ± 0.96
N	3	5	2	9	7	32
fourth toe lamellae						
range	31-35	31-36	36-39	35-41	31-38	26-33
mean±sd.	32.7 ± 1.6	34.0 ± 1.87	37.75 ± 2.5	37.6 ± 1.81	34.5 ± 2.25	30.0 ± 1.44
N	3	5	2	9	8	32

FIG. 2. Paratype of *M. kaala* n. sp. (AMS R161091), adult male.

Osteology: presacral vertebrae 29 (n = 3); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Colouration: adult male (Fig. 2): dorsal surface mid-dark brown, with dark markings along the paravertebral axis of the nape (along the contact of scale rows three and four). Upper lateral surface of body dark brown to black, becoming paler towards the hind limbs, and without pale markings. Mid- to lower lateral surface of body mid-brown to grey lowermost and with numerous pale blotches, those uppermost forming a broken line and occasionally joining to give the overall effect of a broken pale mid-lateral stripe. Lateral surface of neck dark brown to black with a pattern of pale blotches similar to the side of the body. Side and top of head brown, subocular labial with a few dark markings and a pale spot below the eye and running behind the eye. Lower labials brown but with a pale area at the edge of each scale. Ventral surface of body white with a pale yellow flush in life, underside of neck and chin grey, with bold black blotches on the throat, neck, and lateral edges of the abdomen, orientated obliquely (chin) or transversely (neck and chest) across the body and continuous with the adjacent dark lateral colour.

Subadult male: body distinctly two-toned, dorsally mid-brown, with dark markings along the vertebral (along the contact of scale row one either side) and the paravertebral axis (along the contact of scale rows three and four) of the nape and body. Dorsal colour becoming noticeably lighter at the level of hindlimbs, giving the appearance of a pale hip-stripe to the dorsolateral area above the hindlimbs enclosed by the dark paravertebral markings above and the black upper lateral area below. Upper lateral surface of body black, without pale markings. Mid- to lower lateral surface of body mid-brown, becoming lighter lowermost and with numerous pale blotches, those uppermost forming a broken line and occasionally joining to give the overall effect of a broken pale mid-lateral stripe, emerging from behind hindlimbs and obvious for a short distance but then merging with the overall light brown tail colour. Lateral surface of neck similar to the side of the body. Side and top of head brown, with pale markings forming a broad stripe from the anterior edge of the ear to below the eye, broken only by some dark markings on the penultimate and subocular supralabial scales. Infralabials brown but with a pale area at the edge of each scale. Ventral surface pale with obscure grey blotches on the throat and neck, orientated obliquely (chin) or transversely (neck).

Juvenile: similar overall to subadult male but with the mid- to lower lateral surface of body black and with numerous pale blotches, becoming lighter below. Black transverse markings on the underside of the neck, and oblique markings in the chin black at the outside, becoming progressively lighter medially.

Reproduction: unknown.

DISTRIBUTION AND HABITAT. – The species is known only from forest habitats on Mt. Kaala, near Koumac in the far northwest of Grande Terre (Fig. 1). The two paratypes were collected beneath boulders on an old roadway at about the ecotone between maquis and closed forest with emergent *Araucaria* sp. The holotype was collected in mid-altitude (400-600 m) dry forest on the southern slope of the mountain.

Marmorosphax taom n. sp.

Figs 1, 3, 4

TYPE MATERIAL. — New Caledonia, Province Nord. Holotype: MNHN 2005.0318 (formerly AMS R161183), Massif Ouazangou-Taom, Mt. Taom summit, 20°47’05”S, 164°34’42”E, collected by A. H. & V. A. Whitaker, 12.VI.2002. Paratypes: AMS R164175-77, Massif Ouazangou-Taom, Mt. Taom summit, 20°46’52”S, 164°34’46”E, collected by R. A. Sadlier & G. M. Shea, 7.XII.2004; AMS R165973, Mt. Taom summit, 20°46’50”S, 164°35’00”E, collected by R. A. Sadlier, 23.I.2003.

DIAGNOSIS. — *Marmorosphax taom* n. sp. can be distinguished from other members of the genus by the following combination of characters: dorsal scale rows 65-71; fourth toe lamellae 31-36; dorsal surface with dark markings scattered randomly; lateral surface with pale markings present as light blotches either scattered or aligned transversely down the side of the body; underside of head of adult females with bold dark blotches on the throat.

Marmorosphax taom n. sp. most closely resembles *Marmorosphax tricolor* and *M. kaala* n. sp. in colouration and scalation. The random alignment of dark markings on the dorsal surface and the scattered or transverse alignment of pale markings along the lateral surface distinguishes *Marmorosphax taom* n. sp. from *Marmorosphax kaala* n. sp. which has a distinct row of dark markings along the paravertebral axis and pale markings on the side of the body aligned to form a broken mid-lateral stripe. *Marmorosphax taom* n. sp. was compared to the specimens of *Marmorosphax tricolor* from Mt. Aoupinié (85 km south) which represents the population from which the neotype for *Lygosoma tricolor* Bavay, 1869 was selected. No single feature of morphology readily distinguishes from *M. taom* n. sp. from *M. tricolor*, and its recognition as distinct evolutionary species rests primarily on the deep divergences between the two taxa as identified in the DNA sequence data. Scalation characters readily distinguish *Marmorosphax taom* n. sp. from *Marmorosphax boulinda* n. sp. and *Marmorosphax montana*, both of which have more vertebral scales on the body and usually more scales under the toes (see Table 1).

ETYMOLOGY. — The epithet is a noun in apposition in reference to the type locality, Mt. Taom.

DESCRIPTION. — Based on the type series of 5 specimens comprising two adult males (52.0-54.5 mm SVL), one adult female (54.0 mm SVL), one subadult female (46.0 mm SVL), and one juvenile (37.0 mm SVL). Measurements are for the adults and subadult only, and the tail measurement is for the juvenile, the only specimen with a complete tail.

Measurements: distance from axilla to groin 48.6-55.6% of SVL ($\bar{x} = 51.3$, n = 3); distance from forelimb to snout 40.7-45.0% of SVL ($\bar{x} = 43.1$, n = 3); hindlimb length 44.4-48.9% of SVL ($\bar{x} = 46.1$, n = 3); tail length 178.4% of SVL (n = 1).

Scalation: midbody scale rows 38-40 ($\bar{x} = 38.8 \pm 1.09$, n = 5); paravertebral scales 65-71 ($\bar{x} = 68.4 \pm 2.61$, n = 5); scales on top of fourth finger 11-12 ($\bar{x} = 11.3 \pm 0.27$, n = 5); lamellae beneath fourth finger 16-21 ($\bar{x} = 17.3 \pm 1.86$, n = 5); scales on top of fourth toe 17-19 ($\bar{x} = 17.9 \pm 0.55$, n = 5); lamellae beneath fourth toe 31-36 ($\bar{x} = 34.0 \pm 1.87$, n = 5).

Osteology: presacral vertebrae 29 (n = 5); postsacral vertebrae 53 (juvenile specimen with complete tail showing no evidence of regeneration); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Colouration: there is marked sexual dimorphism between the adult males and adult female, with the subadult and juvenile similar in colouration to the adult female.

Adult males (Fig. 3 upper): MNHN 2005.0318 pale overall. Dorsal and upper lateral surface of neck, body, tail and limbs predominantly tan-light brown, dorsal surface with numerous scattered paler markings (usually a lighter coloured scale) along the length of the body and tail. Mid- to lateral surface of body light tan and with obscure scattered pale blotches (a cluster of several pale scales), grey on side of neck and scales behind the eye. Head similar in tone to body, but lacking dark markings above on snout and with a concentration of darker markings on the labials interrupted by several pale blotches along the subocular and postocular labial scale row. Ventral surface pale with no obvious dark

FIG. 3. Holotype of *M. taom* n. sp. (MNHN 2005.0318), adult male (upper) and paratype of *M. taom* n. sp. (AMS R164177), adult female (lower).

markings on the abdomen which is pale yellow in life. Throat and chin grey with a few darker blotches on the chest, throat, and edge of the chin. AMS R164175 darker in tone, dorsal and upper lateral surface predominantly mid-brown, dorsal surface with numerous scattered paler and dark markings. Mid- to lateral surface of body dark grey on neck and anterior half of body, lighter grey on posterior half, and with obscure scattered pale blotches (a cluster of several pale scales). Ventral surface pale with large obvious grey blotches on the throat, neck, and outer edges of the abdomen, generally orientated obliquely cranio-ventral on the ventrolateral surface of the body as an extension of the lower lateral colour.

Adult (Fig. 3 lower) and subadult females: body two-toned, dorsal surface of the body mid-brown with numerous scattered paler and dark markings (similar to adult males) along the length of the body and tail. Lateral surface of neck and upper lateral part of body black, contrasting markedly with the paler dorsal colour and containing a row of prominent white spots (a cluster of one to three scales) along the dorsolateral margin of the neck and anterior part of the body. Neck with a series of pale blotches running from behind the ear to above the forelimb (sometimes longitudinally elongate), with one or more white transverse bars running from the underside of the neck. Side of face black below and behind eye, with several pale blotches along the subocular and postocular upper labial scale row. Remainder of lateral surface of body grading from black above to grey below but dominated by clusters of large pale blotches, joined to form rough transverse bars in adult female. Lateral surface of tail with a broad pale stripe (1.5-2 scales wide) emerging from behind hindlimbs, obvious for a short distance but then becoming lost as the dorsal and lateral colors of the tail blend along the length of the tail. Ventral surface of adult female white and marked with bold black blotches on the throat, neck, and outer edges of the abdomen, orientated obliquely (chin) or transversely (neck, chest and abdomen) across the body and continuous with the adjacent dark lateral colour. Subadult with same general distribution of dark blotches but less profusely marked overall. In life with a pale yellow flush to the abdomen, remainder of underside of body and hind limbs white.

Juvenile: colour pattern typical of females but with a bold yellow flush to the pale lateral markings.

Reproduction: the adult female (AM R165801) collected in December 2004 had a developing early embryo in each oviduct, represented by an obvious fluid-filled amniotic sac dorsal to a large yolk mass. Although the embryo was not clearly visible within the translucent amniotic sac as viewed through the oviduct wall, there was no visible trace of an eggshell around the fetal mass, and hence it is clear that the species is viviparous.

DISTRIBUTION AND HABITAT. — The species is known only from Mt. Taom in the northwest of Grande Terre (Fig. 1).

It has been recorded from both closed forest and in maquis habitat near the summit (1100 m) of Mt. Taom. The closed forest sites are relatively small and comprise a narrow gully (Fig. 4) and a patch on the escarpment facing west. There are several other patches of forest in gullies along the range with apparently suitable habitat. The holotype was collected within a deep bank within closed forest with *Araucaria* sp.

The maquis site was a moderately dense but low maquis shrubland with a dense groundcover of *Gleichenia* sp. on a cuirasse outcrop. The presence of *M. toam* in the maquis more likely reflects the suitability of particular environmental parameters at the site rather than the vegetation type. At that elevation the massif summit is often under extensive cloud and mist, which in combination with the density of the groundcover provides a moist microhabitat while the cuirasse below the groundcover provides cool retreat sites.

FIG. 4. High elevation forest patch near the summit of Mt. Taom.

Marmorosphax boulinda n. sp.

Figs 1, 5

TYPE MATERIAL. — New Caledonia, Province Nord. Holotype: MNHN 2005.0319 (formerly AMS R163197), Massif du Boulinda, 2 km southwest Mt. Boulinda at headwaters of Oua Népoua, 21°16'34"S, 165°08'09"E, collected by A. H. & V. A. Whitaker, 20.X.2002. Paratype: AMS R163196 data as holotype.

DIAGNOSIS. — *Marmorosphax boulinda* n. sp. can be distinguished from other members of the genus by the following combination of characters: dorsal scale rows 75-76; fourth toe lamellae 36-40; dorsal surface with a pattern of alternating brown and white transverse rows (each one scale width); lateral surface lacking obvious pale markings (males) or with scattered pale blotches; underside of head with obscure grey blotches on the throat.

Marmorosphax boulinda n. sp. is most similar in colouration and scalation to *M. montana*. The presence of narrow alternating brown and white transverse rows on the dorsal surface will distinguish *Marmorosphax boulinda* n. sp. from *Marmorosphax montana* which has a pattern of roughly alternating broad brown (2-3 scales wide) and black (one scale wide) transverse rows on the dorsal surface. Scalation characters will readily distinguish *Marmorosphax boulinda* n. sp. from *Marmorosphax kaala* n. sp., *Marmorosphax taom* n. sp. and *Marmorosphax tricolor*, all of which have fewer scales under the toes (see Table 1).

ETYMOLOGY. — The epithet is a noun in apposition in reference to the type locality, the Boulinda Massif.

DESCRIPTION. — Based on the type series of 2 specimens, comprising one adult male (51 mm SVL) and one adult female (53 mm SVL).

Measurements: distance from axilla to groin 47.2-52.0% of SVL ($\bar{x}$ = 49.6); distance from forelimb to snout 42.2-44.3% of SVL ($\bar{x}$ = 43.2); hindlimb length 50.9-51.0% of SVL ($\bar{x}$ = 51.0); tail length 147% of SVL for the specimen with the most complete original tail (AMS R163196).

Scalation: midbody scale rows 40; paravertebral scales 75-76; scales on top of fourth finger 11-12 ($\bar{x}$ = 11.5); lamellae beneath fourth finger 19; scales on top of fourth toe 18-20 ($\bar{x}$ = 19.2); lamellae beneath fourth toe 36-39 ($\bar{x}$ = 37.8).

Osteology: presacral vertebrae 29 (n = 2); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Colouration: there is subtle and less pronounced sexual dimorphism between adult males and females.

Adult male (Fig. 5 upper): dorsal surface mid-brown with pale spots (usually a whole scale), arranged as roughly oblique, randomly oriented, transverse rows. Upper lateral surface of body mid-brown becoming gradually lighter over the rest of the lateral surface approaching the venter, and with obscure pale blotches. Lateral surface of neck predominantly grey with scattered paler coloured blotches. Head with pale spotting above except on snout. Subocular and postocular labials with faint darker markings to the centre of each scale. Fore- and hindlimbs with a dull orange flush above. Ventral surface of body posterior to forelimbs yellowish-orange in life, and orange at base of tail and underside of limbs, throat and chin with a mottling of obscure grey and creamy-grey blotches. In life the pale spots on the dorsal surface of the body and head and pale blotches of the body are yellowish in colour.

FIG. 5. Holotype of *M. boulinda* n. sp. (MNHN 2005.0319), adult male (upper) and paratype of *M. boulinda* n. sp. (AMS R165973), adult female (lower).

Adult female (Fig. 5 lower): dorsal surface dark brown to black with numerous pale spots (usually a whole scale) generally arranged as roughly oblique transverse rows. Head similar in tone to body, with pale spots above, except on the snout which is mid-brown above. Upper lateral surface black, becoming gradually lighter over the rest of the body approaching the venter and with scattered pale blotches (a cluster of several pale scales). Side of neck brownish below the dark upper lateral area, and with well defined pale blotches extending onto the posterior labial scales. Lateral surface of tail with a broad pale stripe (1.5-2 scales wide) emerging from behind hindlimbs for a short distance but then merging with the dorsal and lateral colours of the tail. Ventral surface predominately pale (cream in life) with obscure brownish-grey blotches on the outer margins of the throat and chin.

Reproduction: the adult female collected in October had two large yolked follicles, one in each ovary.

DISTRIBUTION AND HABITAT. — *Marmorosphax boulinda* n. sp. is known only from Massif du Boulinda, near Poya on the mid-west coast of Grande Terre (Fig. 1). The two specimens were collected beneath loose stones in *Araucaria* sp. forest at 980 m elevation. It is sympatric on the massif with *Marmorosphax tricolor*, which was recorded at 1040 m elsewhere on Massif du Boulinda.

Marmorosphax montana Sadlier & Bauer, 2000

Figs 1, 6

Marmorosphax montana as described by Sadlier & Bauer (2000) was based on four adult individuals. At that time it was known to be regionally sympatric with *Marmorosphax tricolor*, which had been recorded from two individuals from the contiguous block of forest at 900 m elevation on the adjacent Mt. Dzumac. Since its description the type locality has been visited several times and further samples of both *M. montana* and *M. tricolor* collected. This additional material has allowed us to revise and expand our original description, and provide additional information on the biology of the species that we report here.

MATERIAL EXAMINED. – AMS R148021, Province Sud, Mt. Ouin, south face, 22°00'51"S, 166°27'38"E; AMS R148025, R150732, R165800, R165922-23, CAS 229282, MNHN 1998.0466, Mt. Ouin, south face, 22°00'34"S, 166°27'26"E; AMS R165802, Mt. Ouin, track along northeast edge of Mt. Ouin range, 22°00'S, 166°27'E.

DIAGNOSIS. – *Marmorosphax montana* can be distinguished from other members of the genus by the following combination of characters: dorsal scale rows 71-78; fourth toe lamellae 35-41; dorsal surface with a pattern of light and dark markings in females forming roughly alternating brown (1-2 scale width) and black (1 scale width) rows across the body, males with a more muted pattern; lateral surface with scattered obscure pale blotches (males) or obvious pale markings (females); throat with overall light brown wash (males) or with small black blotches (females).

Scalation characters will readily distinguish *Marmorosphax montana* from *Marmorosphax kaala* n. sp., *Marmorosphax taom* n. sp. and *Marmorosphax tricolor* all of which have fewer scales under the toes (see Table 1). *Marmorosphax montana* can be further distinguished from sympatric *M. tricolor* in having more scales on the dorsal surface of the fourth finger and toe, and females in having obscure (*vs* bold) pale markings on the labials. *Marmorosphax montana* is most similar in overall appearance and scalation to *Marmorosphax boulinda* n. sp. It can be distinguished by its overall darker dorsal colouration (brown and black *vs* cream and brown) giving it an overall bolder appearance, and in females by having darker and more extensive throat markings. Recognition of *Marmorosphax montana* as an evolutionary species distinct from *Marmorosphax boulinda* n. sp. is supported by the deep divergences between the two taxa as identified in the DNA sequence data.

DESCRIPTION. – Based on three adult males (55-58 mm SVL), three adult females (51-67 mm SVL), one subadult male (46 mm SVL), and two juveniles (35-36.5 mm SVL). Measurements are for the adults only.

Measurements: distance from axilla to groin 50.9-53.4% of SVL ($\bar{x}$ = 52.0, n = 6); distance from forelimb to snout 40.3-43.6% of SVL ($\bar{x}$ = 41.8, n = 6); hindlimb length 44.0-50.9% of SVL ($\bar{x}$ = 47.4, n = 6); tail length 146.6% of SVL for the specimen with the most complete original tail.

Scalation: midbody scale rows 36-40 ($\bar{x}$ = 38.8 ± 1.40, n = 9); paravertebral scales 71-78 ($\bar{x}$ = 73.4 ± 2.61, n = 8); scales on top of fourth finger 12-14 ($\bar{x}$ = 12.6 ± 0.63, n = 9); lamellae beneath fourth finger 19-22 ($\bar{x}$ = 20.9 ± 0.85, n = 9); scales on top of fourth toe 19-21 ($\bar{x}$ = 19.3 ± 0.5, n = 9); lamellae beneath fourth toe 35-41 ($\bar{x}$ = 37.6 ± 1.81, n = 9).

Osteology: presacral vertebrae 28 (n = 1) to 29 (n = 6); postsacral vertebrae 53-56 (two juvenile specimens with tails showing no evidence of regeneration); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Colouration: there is marked sexual dimorphism between adult males and females, with subadults and juveniles similar in colouration to adult females.

Adult males: dorsal surface light or mid-brown, with darker markings variable in extent and definition forming a muted pattern of roughly alternating brown and black rows across the body. Lateral surface a continuation of light brown dorsal colour above and with scattered, obscure pale blotches along the body between fore- and hindlimbs; overall colour becoming progressively lighter approaching ventrolateral margin. Head dark (similar in tone to dark dorsal colouration of body), headshields along vertebral axis (frontonasal, prefrontal, frontal, frontoparietal, and interparietal)

FIG. 6. *M. montana* (AMS R165802), adult female.

with a marbling of both lighter and darker dorsal colours. Ventral surface between fore- and hindlimbs cream with a few scattered pale brown blotches near ventrolateral margin, throat and chest anterior of forelimbs with light brown markings to each scale giving an overall mid-brown colour to the chinshields, varying in intensity between individuals.

Adult females (Fig. 6): dorsal surface of body and tail mid-brown with an overall golden flush, and numerous dark markings which form a reticulate pattern of narrow, irregular, and merging black transverse bars; dorsal pattern extending onto upper lateral surface. Head brown, duller than dorsal colour and with dark markings over frontoparietal and interparietal scales. Lateral surface black above with pale markings intruding on upper and lower margins (or scattered over surface on one individual); remainder of lateral surface mottled with dark and pale blotches, dark markings merging to form broad, oblique, transverse bars between fore- and hindlimbs, and a marbled pattern between forelimbs and ear opening. Side of head similar in colour to dorsal surface of head and with only obscure pale markings, rim of eye cream. Ventral surface cream with scattered dark markings on the outer edge or medially between fore- and hindlimbs, chest and throat with dark markings variable in extent and intensity, ranging from predominant to scattered marbling, the dark markings tending to be continuous with dark transverse lateral markings.

Subadult and Juvenile: overall body colouration and pattern (including ventral surface) typical of adult females.

Reproduction: the adult female collected in December (AM R165802) contained two early embryos (unpigmented, unscaled) lying within fluid-filled amniotic sacs dorsal to large yolk masses, one in each oviduct.

DISTRIBUTION AND HABITAT. – The species is known only from Mt. Ouin in the southern high peaks (Fig. 1). It has been collected in and at the edge of primary closed forest habitat at 900-1000 m elevation. It appears to be broadly sympatric with *M. tricolor* at this elevation (see Appendix 1) but noticeably less common at the lower limit.

PHYLOGENETIC ANALYSIS

Analyses of the two genes combined included a total of 1392 nucleotides, 192 of which were parsimony informative (ND2 includes 580 bp and 170 parsimony informative characters, and Rag-1 includes 812bp and 24 parsimony informative characters for 21 OUTs). All analysis methods and genes recover a monophyletic *Marmorosphax*. Analysis of ND2 using Bayesian and parsimony analysis recovers *M. montana* as the sister group to all other species, and a clade made up of the northern restricted-distribution species (*M. boulinda* (*M. toam, M. kaala*)) as the sister group to *M. tricolor* (Fig. 7). Relationships within *M. tricolor* were consistent between parsimony and Bayesian analysis but overall were poorly supported by the data.

Reanalysis of the ND2 data supplemented by Rag-1 in some specimens (using both parsimony and Bayesian analysis) recovers slightly different relationships among the northern restricted-distribution species, with *M. kaala* as the sister species to *M. boulinda* rather than *M. toam* (Fig. 8). The remaining interspecific relationships are the same as those recovered by mitochondrial data alone.

Mitochondrial divergence within species varies between 0.12-3.71%, and between species varies from 7.88-12.03% (Table 2). A single ND2 haplotype was shared between populations of *M. tricolor* throughout the southern part of the

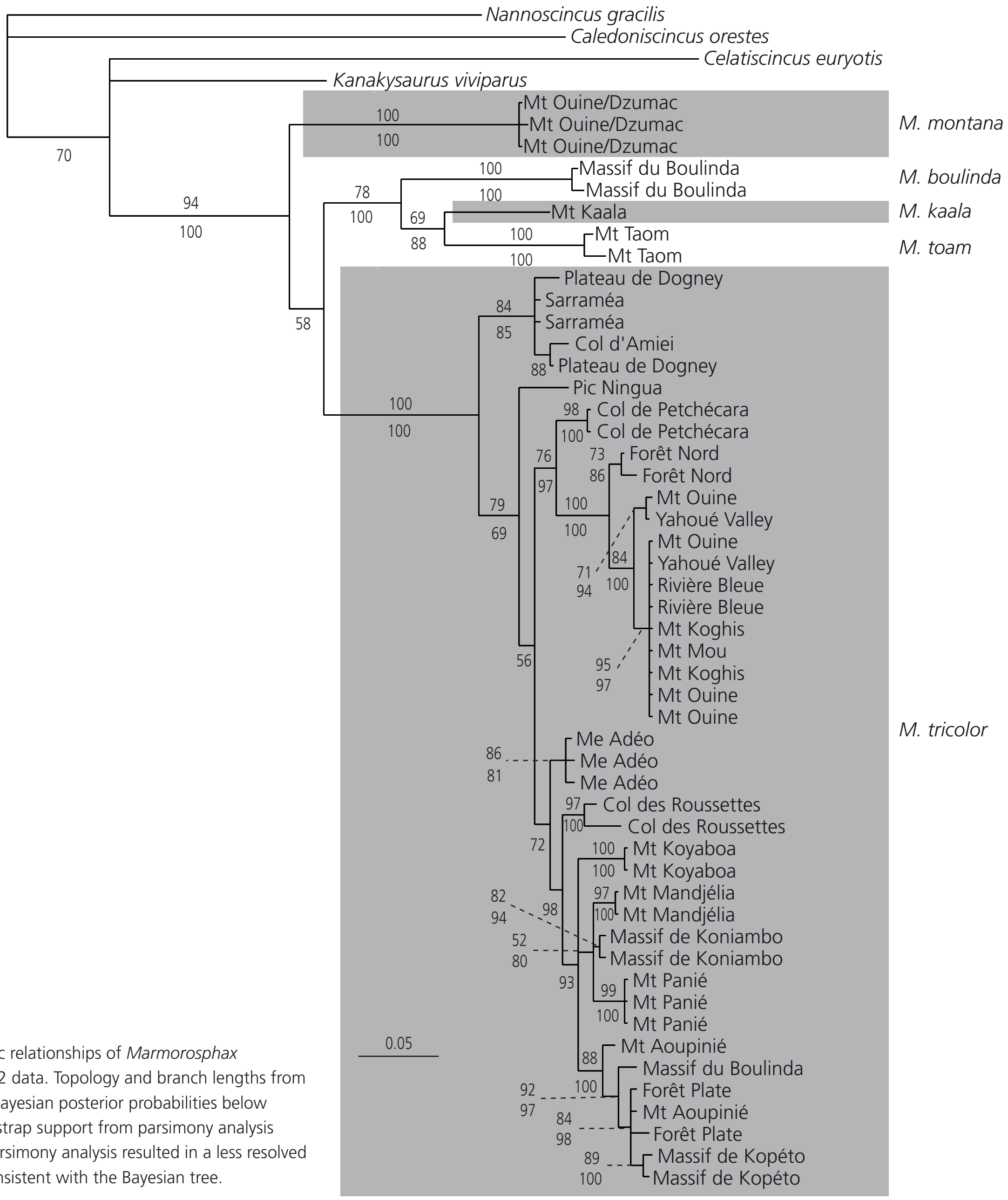

FIG. 7. Phylogenetic relationships of *Marmorosphax* estimated from ND2 data. Topology and branch lengths from Bayesian analysis. Bayesian posterior probabilities below branches and bootstrap support from parsimony analysis above branches. Parsimony analysis resulted in a less resolved topology that is consistent with the Bayesian tree.

TABLE 2. Pairwise ND2 divergence (% and s.e.) between species and within species (italics).

	M. kaala	***M. boulinda***	***M. toam***	***M. montana***	***M. tricolor***
M. kaala	--				
M. boulinda	9.18 (1.25)	0.39 (0.26)			
M. toam	7.88 (1.05)	9.10 (1.23)	1.03 (0.41)		
M. montana	10.86 (1.29)	11.48 (1.33)	11.38 (1.28)	0.12 (0.11)	
M. tricolor	10.40 (1.04)	11.72 (1.28)	11.59 (1.17)	12.03 (11.68)	3.71 (0.43)
kaala + toam	--	9.12 (1.11)	--	11.21 (1.17)	11.19 (1.03)

species range including Mt. Koghis, Mt. Mou, the Yahoué Valley, Rivière Bleue, and Mt. Ouin. Studies on interspecific relationships between some rainforest endemic vertebrates in the Wet Tropics of north-eastern Australia (Schneider *et al.* 1998; Schneider & Moritz 1999; Moritz *et al.* 2000), an area of similar size and relief to New Caledonia, show similar levels of sequence divergence. These deep phylogenetic splits between taxa have been attributed to late-Miocene or early-Pliocene events. Large scale global climate change resulting in disruption to rainforests has been proposed as the speciation mechanism for vicariant differentiation among populations of widespread taxa. Evidence from the Wet Tropics region of north-eastern Australia indicate that high elevation forests in that region persisted during periods

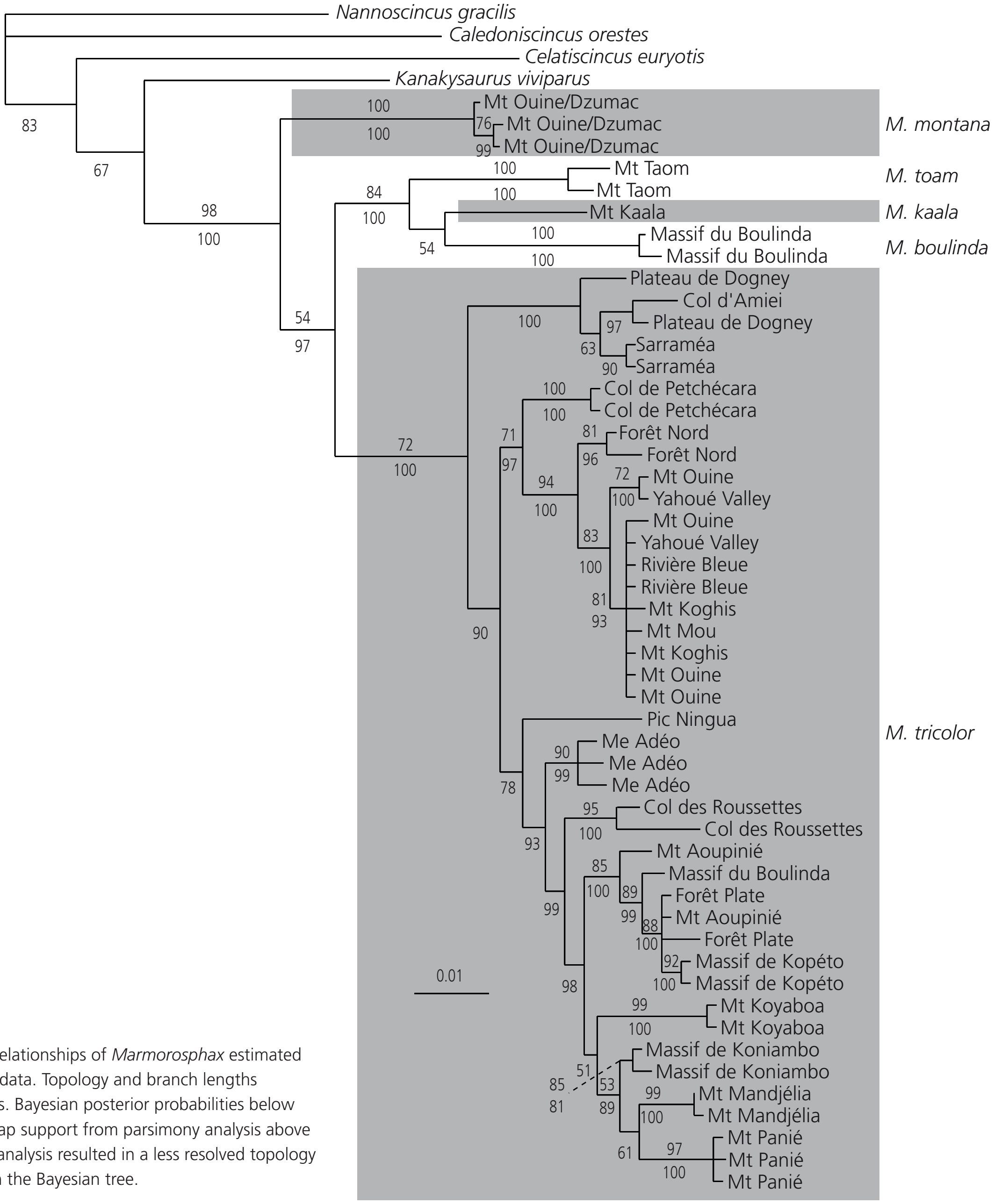

FIG. 8. Phylogenetic relationships of *Marmorosphax* estimated from ND2 and Rag-1 data. Topology and branch lengths from Bayesian analysis. Bayesian posterior probabilities below branches and bootstrap support from parsimony analysis above branches. Parsimony analysis resulted in a less resolved topology that is consistent with the Bayesian tree.

of dryness associated with the Pleistocene glacials and acted as refuges for moist forest dependant species. The deep branch lengths of the narrow range endemic *Marmorosphax* species are indicative of old speciation events, and the timing and climatic scenario could be analogous to those proposed to explain similar deep sequence divergences seen between sister taxa in the Australian Wet Tropics.

The presence of morphologically similar high elevation *Marmorosphax* species in relictual mountain top forests (*M. montana* and *M. boulinda*) is a classic example of phylogenetic niche conservatism where natural selection favours traits that keep individuals within the niche (Wiens 2004). Under this model populations of species fail to adapt to novel ecological conditions initiating a split into allopatric lineages. In the case of *M. montana* and *M. boulinda*, climate change caused the preferred habitats to move upwards in elevation and effectively isolated the once continuous populations onto separate peaks or ranges, with areas of unsuitable intervening habitat at lower elevations. The tendency for specialised species to stay within a preferred niche range during vicariance and therefore not be under selective pressure to evolve new traits could explain the conservatism in morphology observed between these high elevation *Marmorosphax* species.

The widespread *Marmorosphax tricolor* shows some structure and some populations (the geographically proximate Sarraméa and Plateau de Dogny) are relatively genetically distinctive, but there is little variation elsewhere throughout the range sampled, although northern and southern clades are geographically coherent and reciprocally monophyletic. The low level of divergence between populations is indicative of a very recent expansion over much its range. Similar patterns have been observed in intrapopulation studies of some reptiles and amphibians in the Wet Tropics (Schneider *et al.* 1998; Schneider & Moritz 1999) and are interpreted as being consistent with an initial large-scale population contraction to refugia during climate-induced rainforest contractions through the Pleistocene, followed by colonization of currently disjunct areas of rainforest during a cool wet phase of the mid-Holocene (c. 7500-6000 BP).

The level of morphological divergence between the species of *Marmorosphax* is relatively conservative given the apparent age of the evolutionary splits. Little or no ecomorphological variation was observed between disjunct populations of reptiles and amphibians in the Australian Wet Tropics, despite the presence of relatively high levels of genetic differentiation between some regions. Both scenarios indicate that isolation combined with population bottlenecks have minimal effect on driving morphological change in rainforest dependant species. One explanation for this is that species responded to rapid climate change by migration to structurally similar environments with morphology under stabilizing selection, rather than adaptive differentiation, somewhat akin to the phylogenetic niche conservatism model proposed by Wiens (2004). A very similar scenario has been proposed for the speciose, but morphologically conservative New Caledonian geckos of the genus *Bavayia* (Jackman *et al.* 2004).

CONSERVATION STATUS

Marmorosphax kaala, *Marmorosphax taom, Marmorosphax boulinda*, and *Marmorosphax montana* satisfy the criteria for inclusion into one of the threatened species categories under a modification of the IUCN classification system for New Caledonian conditions (see Sadlier & Bauer 2003). Each of these taxa is most likely restricted to a single massif, and primarily to high elevation forest on these mountains. The extent of potential area of occupancy on each massif is likely to be significantly less than 100 km^2, and the lizards occurring in the various disjunct patches of forest are part of a single fragmented population. The occurrence of *Marmorosphax taom* in high elevation maquis on cuirasse indicates that under the right conditions there may be some connectivity between the forest patches. What is known from the biology of members of the genus indicates remnant closed high elevation forest is likely to be the preferred habitat of all taxa. This habitat is highly fragmented, and is present as patches small in both individual size and combined area. These patches most likely represent natural relicts of a once more widespread vegetation type that has been both reduced in extent and fragmented by climate change. However, there is also likely to have been a decline in the extent of occurrence of this habitat as a result of the impact of human-induced burning of adjacent maquis shrubland in both historical and recent times.

Due to the fragmented nature of closed high elevation vegetation, the small size of individual patches, the deleterious effect of even infrequent firing on this habitat, the presence of invasive species, and the direct and indirect threats posed by the presence or potential for mining (Nasi *et al.* 2002), *M. kaala*, *M. taom,* and *M. boulinda* could be conservatively ranked as endangered under the modified IUCN classification system used for the New Caledonian lizard fauna (area of occupancy < 100 km^2, severely fragmented *i.e.* isolated sub-populations with a reduced probability of colonisation if once extinct; number of locations 1; continuing decline in area and extent of occurrence as indicated by a continuing decline in quality of habitat at some sites) (Sadlier & Bauer 2003). All taxa could be placed at a higher level of threat if continued declines in the area, extent and/or quality of habitat in the species' very narrow ranges persist.

ACKNOWLEDGMENTS

The authors thank the New Caledonian authorities, particularly M. Jean-Jérôme Cassan for issuing permits to collect and conduct research in Province Nord. The types of *Marmorosphax kaala* and *Marmorosphax taom* were collected under permit No.49/02/SFE (to A. Whitaker), No.01/03 COLL-SCE (to A. Bauer), No.60912-7273-2003/JJC (to R. Sadlier), and *Marmorosphax boulinda* under permit No.56/02/SCE issued by the Service Forêt-Bois et Environment of the Province Nord, New Caledonia. Funding for the genetic work was provided by grant DEB 0108108 from the National Science Foundation (U.S.A.). We are grateful to Robert Frouin and Christoph Montagnat for permission to visit Mt. Kaala, and to Philippe Faivre and Henri Italiano for permission to visit Mt. Taom. We also acknowledge the unfailing logistical support and encouragement that was provided by Jean Chazeau, formerly of the IRD Centre de Nouméa. Vivienne Whitaker and Glenn Shea assisted with fieldwork in obtaining specimens of the new taxa.

REFERENCES

BAUER A. M. 1999. — The terrestrial reptiles of New Caledonia: the origin and evolution of a highly endemic herpetofauna, *in* OTA H. (ed.), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. Elsevier Science B.V, Amsterdam: 3-25.

BAUER A. M. & SADLIER R. A. 1993. — Systematics, biogeography and conservation of the lizards of New Caledonia. *Biodiversity Letters* 1: 107-122.

BAUER A. M. & SADLIER R. A. 2000. — *The Herpetofauna of New Caledonia*. Society for the Study of Amphibians and Reptiles, Ithaca, NY, 310 p., 24 pls.

BRANDLEY M. C., SCHMITZ A. & REEDER T. W. 2005. — Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology* 54: 373-390.

CHAZEAU J. 1993. — Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiversity Letters* 1: 123-129.

DARLINGTON P. J. 1965. — *Biogeography of the Southern End of the World*. Harvard University Press, Cambridge Massachusetts, x + 236p.

DIAMOND J. 1984. — Biogeographic mosaics in the Pacific, *in* RADOVSKY F. J., RAVEN P. H. & SOHMER S. H. (eds), *Biogeography of the Tropical Pacific.* Bishop Museum Special Publication, Honolulu, 72: 1-14.

FLENLEY J. R. 1995. — Cloud Forest, the Massenerhebung Effect, and Ultraviolet Insolation, *in* HAMILTON L. S., JUVIK J. O. & Scatena F. N. (eds), *Tropical Montane Cloud Forests*. Springer-Verlag, Ecological Studies, vol. 110, New York: 94-96.

GROTH J. G. & BARROWCLOUGH G. F. 1999. — Basal divergence in birds, and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12: 115-123.

HAASE M. & BOUCHET P. 1998. — Radiation of crenobiontic gastropods on an ancient continental island: the *Hemistomia*-clade in New Caledonia (Gastropoda: Hydrobiidae). *Hydrobiologia* 367: 43-129.

HUELSENBECK J. P. & RONQUIST F. 2001. — MrBayes: Baysian inference of phylogeny. *Bioinformatics* 17: 754-755.

JACKMAN T. R., BAUER A. M. & KIEBISH M. 2004. — Molecular systematics of the New Caledonian forest geckos (Diplodactylidae: *Bavayia*). *New Zealand Journal of Zoology*. 31: 105.

JAFFRÉ T. 1974. — La végétation et la flore d'un massif de roches ultrabasiques de Nouvelle-Calédonie: le Koniambo. *Candollea* 29: 427-456, 3 pls.

JAFFRÉ T. 1980. — Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle-Calédonie. *Travaux et Documents de l'ORSTOM* 124: 1-274.

JAFFRÉ T. & LATHAM M. 1974. — Contribution à l'étude des relations sol-végétation sur un massif de roches ultrabasiques de la côte ouest de la Nouvelle-Calédonie: le Boulinda. *Adansonia, série* 2, 14: 311-336, 4 folding pls.

LOWRY II P. P. 1998. — Diversity, endemism, and extinction in the flora of New Caledonia: a review, *in* PENG C. I. & LOWRY P. P., II (eds), *Rare, Threatened, and Endangered Floras of Asia and the Pacific Rim.* Institute of Botany, Academia Sinica Monograph Series No. 16, Taipei: 181-206.

LOWRY II P. P. , MUNZINGER J., BOUCHET P., GÉRAUX H., BAUER A. M., LANGRAND O. & MITTERMEIER R. A. 2004. — New Caledonia. *in* MITTERMEIER R. A., GIL P. R., HOFFMANN M., PILGRIM J., Brooks T., MITTERMEIER C. G., LAMOREUX J. & DA FONSECA, G. A. B. (eds), *Hotspots Revisited*. CEMEX, Mexico City: 192-197.

MACEY J. R., LARSON A., ANANJEVA N. B. & PAPENFUSS T. J. 1997. — Evolutionary Shifts in Three Major Structural Features of the Mitochondrial Genome Among Iguanian Lizards. *Journal of Molecular Evolution* 44 (6): 660-674.

MITTERMEIER R. A., WERNER T. B. & LEES A. 1996. — New Caledonia – a conservation imperative for an ancient land. *Oryx* 30 (2): 104-112.

MORITZ C., PATTON J. L., SCHNEIDER C. J. & SMITH T. B. 2000. — Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* 31: 533-563.

MYERS N., MITTERMEIER R. A., MITTERMEIER C. G., DA FONSECA G. A. B. & KENT J. 2000. — Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

NASI R., JAFFRÉ T. & SARRAILH J. M. 2002. — Les forêts de montagne de la Nouvelle-Calédonie. *Bois et Forêts des Tropiques* No. 274 (4): 5-18.

NYLANDER J. A. A. 2004. — *MrModelTest*. 2.0th edition. Upsalla, Distributed by the author. Evolutionary Biology Centre, Uppsala University.

NYLANDER J. A. A., RONQUIST F., HUELSENBECK J. P. & NIEVES-ALDREY J. L. 2004. — Bayesian phylogenetic analysis of combined data. *Systematic Biology* 53: 47-67.

PINTAUD J. C., JAFFRÉ T. & PUIG H. 2001. — Chorology of New Caledonian palms and possible evidence of Pleistocene rain forest refugia. *C.R. Acad. Sci. Paris, Sciences de la vie / Life Sciences* 324: 453-463.

RIGG L. S., ENRIGHT N. J., PERRY G. L. W. & MILLER B. P. 2002. — The Role of Cloud Combing and Shading by Isolated Trees in the Succession from Maquis to Rain Forest in New Caledonia. *Biotropica* 34 (2): 199-210.

RONQUIST F. & HUELSENBECK J. P. 2003. — MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.

SADLIER R. A. 1986. — A review of the scincid lizards of New Caledonia. *Records of the Australian Museum* 39 (1): 1-66.

SADLIER R. A. & BAUER A. M. 1999. — The scincid lizard genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: description of a new species and review of the biology, distribution, and morphology of *Sigaloseps deplanchei* (Bavay). *Records of the Australian Museum* 51: 83-91.

SADLIER R. A. & BAUER A. M. 2000. — The scincid lizard genus *Marmorosphax* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: description of a new species restricted to high-altitude forest in the Province Sud. *Pacific Science* 54: 56-62.

SADLIER R. A. & BAUER A. M. 2003. — Conservation status of endemic New Caledonian lizards - an assessment of the distribution and threats to the species of lizard endemic to New Caledonia. URL: http://www.amonline.net.au/herpetology/research/lizards_conservation_intro.htm.

SADLIER R. A., BAUER A. M., WHITAKER A. H. & SMITH S. A. 2004a. — Two New Species of Scincid Lizards (Squamata) from the Massif de Kopéto, New Caledonia. *Proceedings of the California Academy of Sciences* 55: 208-221.

SADLIER R. A, SMITH S. A, BAUER A. M. & WHITAKER A. H. 2004b. — A new genus and species of live-bearing scincid lizard (Reptilia: Scincidae) from New Caledonia. *Journal of Herpetology* 38 (3): 320–330.

SADLIER R. A., SMITH S. A. & BAUER A. M. 2006. — A new genus for the New Caledonian scincid lizard *Lygosoma euryotis* Werner 1909, and the description of a new species. *Records of the Australian Museum* 58: 19-28.

SCHNEIDER C. J. & MORITZ C. 1999. — Rainforest refugia and evolution in Australia's Wet Tropics. *Proceedings of Royal Society of London B*. 266: 191-196.

SCHNEIDER C. J., CUNNINGHAM M. & MORITZ C. 1998. — Comparative phylogeography of and the history of endemic vertebrates in the Wet Tropics rainforests of Australia. *Molecular Ecology* 7 (4): 487-498.

SMITH S. A. 2001. — *A molecular phylogenetic study of the* Eugongylus *group of skinks*. Ph.D. dissertation, University of Adelaide, Adelaide, Australia.

SMITH S. A., SADLIER R. A. & BAUER A. M. 2004. — Molecular systematics of New Caledonia's endemic skinks. *New Zealand Journal of Zoology* 31: 109-110.

SWOFFORD D. L. 2002. — PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

WIENS J. J. 2004. — Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* 58 (1): 193-197.

WIENS J. J., FETZNER J. W., PARKINSON C. L. & REEDER T. W. 2005. — Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology* 54: 719-748.

APPENDIX 1. Collection localities and specimen numbers for *Marmorosphax* included in genetic analysis. Individuals marked [*] have both ND2 and Rag-1 sequences.

M. boulinda: Massif du Boulinda AMS R163196 (EBU15595*), MNHN 2005.0319 (EBU15596*).
M. kaala: Mt. Kaala AMS R161091 (EBU15216*).
M. montana: Mt. Ouin-Dzumac AMS R165802 (NR9951*), AMS R165922 (AMB7216*), CAS 229282 (AMB7217*).
M. taom: Mt. Taom AMS R165973 (AMB7803), MNHN 2005.0318 (EBU15307*).
M. tricolor: Massif du Boulinda AMS R163178 (EBU15577*); Col de Petchicara AMS R165938 (AMB7391), AMS R165939 (AMB7392); Forêt Plate AMS R149457 (NR4201), AMS R149458 (NR4202); Forêt Nord AMS R148052 (NR3649), AMS R148053 (NR3650); Col d'Amieu (vicinity) AMS R144362 (NR2572); Massif de Kopéto AMS R163119 (EBU15519*), AMS R163120 (EBU15520*); Mé Adéo AMS R149882 (NR4515), AMS R149883 (NR4516), AMS R149884 (NR4517); Mt. Aoupinié AMS R146375 (NR2873), AMS R149382 (NR4186); Mt. Koghis CAS 214451 (AMB6611*), AMS R144326 (NR2568); Massif de Koniambo AMS R161141 (EBU15265*), AMS R161142 (EBU15266*); Mt. Koyaboa AMS R144260 (NR2558), AMS R144261 (NR2559); Mt. Mandjélia AMS R146351 (NR2850), AMS R146351 (NR2851); Mt. Mou AMS R158784 (NR9760*); Mt. Ouin AMS R164924 (AMB7224), AMS R165925 (AMB7231*), AMS R165926 (AMB7232), CAS 229285 (AMB7250); Mt. Panié AMS R149314 (NR4119), AMS R149316 (NR4121), AMS R149317 (NR4122); Col Roussettes (vic.) AMS R144188 (NR2522), AMS R144189 (NR2523); Pic Ninga AMS R165940 (AMB7345); Plateau de Dogny AMS R147875 (NR3552), AMS R147876 (NR3553); Rivière Bleue AMS R147948 (R3620), AMS R147949 (NR3621); Sarraméa AMS R144097 (R2502), AMS R144098 (NR2503); Yahoué Valley AMS R135156 (NR194), AMS R135158 (NR196).
N. gracilis: Mt. Do Rd of Bouloupari-Thio Rd AMS R135066 (NR123).
C. orstes: Mt. Panié AMS R149983 (NR4596).
C. similis: Mt. Toam AMS R161184 (EBU15308).
K. viviparus: Dome de Tiebaghi AMS R161232 (EBU15112).

Collection localities and specimen numbers for *Marmorosphax tricolor* included in morphological comparisons (Table 2).
Mt. Aoupinié-neotype locality (several sites between 500-1000 m elevation): AMR R77612-13, R77615, R77617, R77622-23, R77625, R77628-30, R77679, R77696-99, R77701-05, R77748-49, R77751-52, R77754, R77764, R77766, R77768, R77790, R77797-99.
Mt. Ouin-Dzumac (several sites at 900 m elevation): AMS R165921, R165925-28, MCZ R184134 (AMB7271), MCZ R184135 (AMB 7272).